CENTER for BIOLOGICAL DIVERSITY

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Sent via Electronic Mail

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Re: MRC HCP/NCCP/PTEIR/DEIS

Dear Agencies,

The Center for Biological Diversity ("Center") submits the following comments on the proposed Habitat Conservation Plan ("HCP"), Natural Communities Conservation Plan ("NCCP"), PTEIR, and EIS for the Mendocino Redwood Company ("MRC"). The Center is a non-profit conservation organization with more than 40,000 members dedicated to the protection of imperiled species and their habitats. The Center is concerned about the impacts to several endangered species, particularly the marbled murrelet, coho salmon, Chinook salmon, steelhead, California and northern red-legged frog, coastal tailed frog, northern spotted owl, Point Arena mountain beaver, and 31 rare plants.

We appreciate the significant time and effort that has gone into preparing the existing documents. However, given what is at stake – the well being of many threatened and endangered species – we believe it is necessary for the Agencies and MRC to clearly explain the baseline situation and data, clearly explain the quality of the existing habitat and how it will change over time, and to clearly explain how the silviculture and other actions proposed will maintain or improve the habitat over time. Only then can the public make a meaningful assessment of the Plans and what their impacts will be.

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In light of the following legal background and substantive issues, we recommend that the HCP/NCCP and its associated documents be re-circulated so that the public can understand what exactly is being proposed and what exactly MRC is agreeing to do, and likewise, so that the public can understand what data exists regarding the species that will be impacted so that there is a clear and explicit baseline to work from and assess the current and future conditions as well as cumulative impacts. Furthermore, while under the current documentation we recommend adoption of Alternative A, we believe that the existing data and alternatives offered do not provide the public with enough information to make a meaningful assessment of the alternatives, and therefore we urge that the Plans be re-circulated with at least one additional alternative as explained below.

I. THE FEDERAL ENDANGERED SPECIES ACT

A. Section 10 Exception to the ESA's Take Prohibition

Section 9 of the ESA and its implementing regulations prohibit any person from "taking" a threatened or endangered species. 16 U.S.C. § 1538(a)(1); 50 C.F.R. § 17.31. A "person" includes private parties as well as local, state, and federal agencies. 16 U.S.C. § 1532(13). "Take" is defined broadly under the ESA to include harming, harassing, trapping, capturing, wounding, or killing a protected species either directly or by degrading its habitat sufficiently to impair essential behavior patterns. 16 U.S.C. § 1532(19).

Congress created two "incidental take" exceptions to section 9's take prohibition. One of these exceptions is found in section 10 of the ESA. Section 10(a)(1)(B) authorizes the FWS to issue private parties and state and local governmental entities incidental take permits for "any taking otherwise prohibited by section 1538(a)(1)(B) [section 9] of this title if such taking is incidental to and not the purpose of the carrying out of any otherwise lawful activity." 16 U.S.C. § 1539(a)(1)(B).

B. Section 10(a)(2)(A) Requirements

A permit applicant must prepare and submit to NMFS and FWS a habitat conservation plan ("HCP"). 16 U.S.C. § 1539(a)(2)(A). As its name explicitly mandates, a <u>conservation</u> plan must contain specific measures to "conserve" (i.e. provide for the recovery of) the species and its habitat. *Id.* The ESA and its implementing regulations also require all HCPs to include the following: (1) a complete description of the activity sought to be authorized; (2) names of the species sought to be covered by the permit; (3) the impact which will likely result from such taking; (4) what steps the applicant will take to monitor, minimize, and mitigate those impacts; (5) the funding that will be available to implement such monitoring, minimization, and mitigation activities; (6) the procedures to be used to deal with unforeseen circumstances; and (7) what alternative actions to such taking the applicant considered and the reasons why such alternatives are not being utilized. 16 U.S.C. § 1539(a)(2)(A)(i)-(iv); 50 C.F.R. §§ 17.22, 17.32. NMFS and FWS cannot issue an incidental take permit if the HCP does not contain this information. 16 U.S.C. § 1539(a)(2)(A). Moreover, impacts to all threatened, endangered, candidate, proposed-listed, sensitive, rare, endemic, or otherwise at-risk or ecologically, socially,

or economically important plant and animal species should be assessed, regardless of whether those species are officially "covered" by the HCP.

C. Section 10(a)(2)(B) Findings

Upon reviewing an HCP and before permit issuance, the Services must find that (i) the taking will be incidental; (ii) the applicant will, to the maximum extent practicable, minimize and mitigate the impacts of such taking; (iii) the applicant will ensure that adequate funding for the plan will be provided; (iv) the taking will not appreciably reduce the likelihood of the survival and recovery of the species in the wild; and (v) any other measures NMFS or FWS requires will be met. 16 U.S.C. § 1539(a)(2)(B); 50 C.F.R. §§ 17.22, 17.32. Should FWS make positive findings under section 10, FWS must issue the applicant an incidental take permit. 16 U.S.C. § 1539(a)(2)(B). Failure to comply with the mandatory terms and conditions of an incidental take permit constitutes a violation of the section 9 "take" prohibition. 16 U.S.C. § 1539(a)(2)(C).

One of the Section 10 prerequisites to an ITP is that the proposed HCP minimize the harm to the species "to the maximum extent practicable." 16 U.S.C. § 1539(a)(2)(B)(ii). The ESA requires the applicant to disclose the range of actions considered as alternatives to the plan finally proposed and to explain why it rejected those alternatives. 16 U.S.C. § 1539(a)(2)(A)(iii). NMFS and FWS must make an independent determination of practicability and make a finding that the impacts of the taking will be minimized and mitigated "to the maximum extent practicable." 16 § 1539(a)(2)(B)(ii). The ESA requires NMFS and FWS FWS scrutinize, not just identify, alternative HCPs and HCP measures that involve greater conservation benefit. 16 U.S.C. § 1539(a)(2)(B)(ii).

D. Section 10(a)(2)(C) Permit Revocation

Under Section 10(a)(2)(C), NMFS and FWS must revoke any ITP issued if "the permittee is not complying with the terms and conditions of the permit." However, the availability of permit revocation does not remedy the flaws of an HCP relying on highly speculative conservation measures. Nor should permit revocation be the only enforcement tool available for ensuring implementation of the HCP.

E. ESA Section 2 and Section 7 Duties

1. Section 2(c) and 7(a)(1) Duty to Conserve

Federal agencies have an affirmative duty to promote the conservation (*i.e.*, recovery) of threatened and endangered species. Section 2(c) of the ESA provides that it is "...the policy of Congress that all Federal departments and agencies shall seek to conserve endangered species and threatened species and shall utilize their authorities in furtherance of the purposes of this Act." 16 U.S.C. §1531(c)(1). Section 7(a)(1) also establishes an affirmative duty to conserve. 16 U.S.C. § 1536(a)(1).

2. Section 7(a)(2) Duty to Avoid Jeopardy and Adverse Modification

In addition to section 10 "take permits," Congress also created incidental take statements ("ITS") to exempt federal agencies from section 9's take prohibition. 16 U.S.C. § 1536(a)(2). Upon concluding the section 7 consultation process on the HCP, the NMFS and FWS may issue a "take statement" after rendering a "no jeopardy" biological opinion. *Id.* at § 1536(b)(4)(A). An incidental take statement must (1) specify the impacts on the species, (2) specify the reasonable and prudent measures that NMFS and FWS considers necessary to minimize such impact, and (3) set forth terms and conditions that must be complied with by the federal agency to implement these reasonable and prudent measures. 16 U.S.C. § 1536(b)(4). Failure to comply with the mandatory terms and conditions of a take statement renders the agency's action in violation of the take prohibition.

Pursuant to Section 7(a)(2) of the ESA, before granting the application for an ITP, NMFS and FWS must "insure" that the HCP ITP "is not likely to jeopardize the continued existence of any endangered or threatened species or result in the destruction or adverse modification of habitat of such species . . . determined . . . to be critical . . ." 16 U.S.C. § 1536(a)(2). To fulfill this mandate, NMFS and FWS must engage in self-consultation on its action, which "may affect" listed species. 16 U.S.C. § 1536(a)(2); 50 C.F.R. § 402.14(a).

Consultation under Section 7(a)(2) on the HCP's covered activities will result in the preparation of a Biological Opinion ("BO") by NMFS and FWS that determines if the proposed action is likely to jeopardize the continued existence of a listed species or adversely modify a species' critical habitat. While NMFS and FWS have not yet issued the BO on the HCP, the BO must include a summary of the information on which it is based and must adequately detail and assess how the action affects listed species and their critical habitats. 16 U.S.C. § 1536(b)(3). Additionally, if the BO concludes that the agency action is not likely to jeopardize a listed species or adversely modify its critical habitat, it must include an Incidental Take Statement which specifies the impact of any incidental taking, provides reasonable and prudent measures necessary to minimize such impacts, and sets forth terms and conditions that must be followed. 16 U.S.C. § 1536(b)(4). If NMFS and FWS's action may affect a listed species, the absence of a valid BO means that the action agency has not fulfilled its duty to insure its actions will neither jeopardize a listed species nor adversely modify the species' critical habitat.

The BO must include an evaluation of the direct, indirect, and cumulative effects of the action on listed species. 16 U.S.C. § 1536(a)(2); 50 CFR §§ 402.02, 402.12, 402.14(d), 402.14(g)(3). In addition to effects of other federal actions, "cumulative effects" include "effects of future State or private activities, not involving Federal activities, that are reasonably certain to occur within the action area of the Federal action subject to consultation." 50 C.F.R. § 402.02.

Throughout its analysis, the BO must utilize the "best scientific and commercial data available." 16 U.S.C. § 1536(a)(2); 50 C.F.R. §402.14(d). NMFS and FWS must consider all the relevant factors and articulate a rational connection between the facts and its ultimate conclusion.

If an action's impact on a species' habitat threatens either the recovery or the survival of a species, the BO must conclude that the action adversely modifies critical habitat. The ESA

defines critical habitat as areas which are "essential to the conservation" of listed species. 16 U.S.C. § 1532(5)(A). The ESA's definition of "conservation" includes the recovery of species. *See* 16 U.S.C. § 1532(3).

II. THE NATIONAL ENVIRONMENTAL POLICY ACT

The purpose of NEPA is to "promote efforts which will prevent or eliminate damage to the environment." 42 U.S.C. § 4331. NEPA's fundamental purposes are to guarantee that: (1) agencies take a "hard look" at the environmental consequences of their actions before these actions occur by ensuring that the agency has, and carefully considers, "detailed information concerning significant environmental impacts," *Robertson v. Methow Valley Citizens Council*, 490 U.S. 332, 349 (1989); and (2) agencies make the relevant information available to the public so that it "may also play a role in both the decisionmaking process and the implementation of that decision." *Id.*

NEPA emphasizes "coherent and comprehensive up-front environmental analysis" to ensure an agency "will not act on incomplete information, only to regret its decision after it is too late to correct." *Blue Mountains Biodiversity Project v. Blackwood*, 161 F.3d 1208, 1216 (9th Cir. 1998), *cert. denied*, 527 U.S. 1003 (1999) *quoting Marsh v. Oregon Natural Resources Council*, 490 U.S. 360, 371 (1989); *see also Foundation on Economic Trends v. Heckler*, 756 F.2d 143, 157 (D.C. Cir. 1985) ("The NEPA duty is more than a technicality; it is an extremely important statutory requirement to serve the public and the agency *before* major federal actions occur.").

NEPA also requires federal agencies to analyze the direct, indirect, and cumulative impacts of the proposed action. 42 U.S.C. § 4332(C); 40 C.F.R. §§ 1508.7, 1508.8. Cumulative impacts include the "impact on the environment which results from the incremental impact of the action when added to other past, present, and reasonably foreseeable future significant actions." 40 C.F.R. § 1508.7. Direct effects are caused by the action and occur at the same time and place. *See id.* § 1508.8(a). Indirect effects are caused by the action and are later in time or farther removed in distance, but are still reasonably foreseeable. *See id.* § 1508.8(b). Both include "effects on natural resources and on the components, structures, and functioning of affected ecosystems," as well as "aesthetic, historic, cultural, economic, social, or health [effects]." *Id.* NEPA also requires an EIS to "inform decision-makers and the public of the reasonable alternatives which would avoid or minimize adverse impacts or enhance the quality of the human environment." 40 C.F.R. § 1502.1.

In addition to alternatives and impacts, NEPA requires agencies to consider mitigation measures to minimize the environmental impacts of the proposed action. 40 C.F.R. § 1502.14 (alternatives and mitigation measures); 40 C.F.R. § 1502.16 (environmental consequences and mitigation measures). Furthermore, throughout the EIS, the agency is required to "insure the professional integrity, including scientific integrity," of its discussions and analyses. *Id.* § 1502.24.

A. Environmental Baseline

NMFS and FWS are required to "describe the environment of the areas to be affected or created by the alternatives under consideration." 40 CFR § 1502.15. The establishment of the baseline

conditions of the affected environment is a practical requirement of the NEPA process. In *Half Moon Bay Fisherman's Marketing Ass'n v. Carlucci*, 857 F.2d 505, 510 (9th Cir. 1988), the Ninth Circuit states that "without establishing . . . baseline conditions . . . there is simply no way to determine what effect [an action] will have on the environment, and consequently, no way to comply with NEPA."

B. Analysis of Impacts

The Ninth Circuit has made clear that NEPA requires agencies to take a "hard look" at the effects of proposed actions; a cursory review of environmental impacts will not stand. *Idaho Sporting Congress v. Thomas*, 137 F.3d 1146, 1150-52, 1154 (9th Cir. 1998). In addition to analyzing the direct and indirect impacts of the HCP, NMFS and FWS are required to complete an analysis of the cumulative impacts of the HCP with other past, present and reasonably foreseeable projects. This requirement ensures that the combined effects of separate activities do not escape consideration. A cumulative impact is "the impact on the environment which results from the incremental impact of the action when added to other past, present, and reasonably foreseeable future actions regardless of what agency (Federal or non-Federal) or person undertakes such other actions. Cumulative impacts can result from individually minor but collectively significant actions taking place over a period of time." 40 C.F.R. § 1508.7.

The Ninth Circuit requires federal agencies to "catalogue" and provide useful analysis of past, present, and future projects. *City of Carmel-By-The-Sea v. U.S. Dept. of Transp.*, 123 F.3d 1142, 1160 (9th Cir. 1997); *Muckleshoot Indian Tribe v. U.S. Forest Service*, 177 F.3d 800, 809-810 (9th Cir. 1999). Furthermore, NEPA requires that the Forest Service's cumulative impacts analysis provide "some *quantified* or *detailed* information," because "[w]ithout such information, neither courts nor the public . . . can be assured that the Forest Service provided the hard look that it is required to provide." *Neighbors of Cuddy Mountain v. United States Forest Service*, 137 F.3d 1372, 1379 (9th Cir. 1988); *see also id.* ("very general" cumulative impacts information was not hard look required by NEPA). As the Ninth Circuit stated in *Neighbors*, it is not appropriate to "defer consideration of cumulative impacts to a future date. 'NEPA requires consideration of the potential impacts of an action *before* the action takes place.'" *Neighbors*, 137 F.3d at 1380 *quoting City of Tenakee Springs v. Clough*, 915 F.2d 1308, 1313 (9th Cir. 1990).

Furthermore, NEPA requires NMFS and FWS to ensure the scientific integrity and accuracy of the information used in its decision-making. 40 CFR § 1502.24. The regulations specify that the agency "must insure that environmental information is available to public officials and citizens before decisions are made and before actions are taken. The information must be of high quality. Accurate scientific analysis, expert agency comments, and public scrutiny are essential." 40 C.F.R. § 1500.1(b). Where complete data is unavailable, the EIS also must contain an analysis of the worst-case scenario resulting from the HCP. *Friends of Endangered Species v. Jantzen*, 760 F.3d 976, 988 (9th Cir. 1985) (NEPA requires a worst case analysis when information relevant to impacts is essential and not known and the costs of obtaining the information are exorbitant or the means of obtaining it are not known) *citing Save our Ecosystems v. Clark*, 747 F.2d 1240, 1243 (9th Cir. 1984); 40 C.F.R. § 1502.22.

C. Alternatives Analysis

NEPA requires that an EIS contain a discussion of the "alternatives to the proposed action." 42 U.S.C. §§ 4332(C)(iii),(E). The discussion of alternatives is at "the heart" of the NEPA process, and is intended to provide a "clear basis for choice among options by the decisionmaker and the public." 40 C.F.R. § 1502.14; *Idaho Sporting Congress*, 222 F.3d at 567 (compliance with NEPA's procedures "is not an end in itself . . . [but] it is through NEPA's action forcing procedures that the sweeping policy goals announced in § 101 of NEPA are realized.") (internal citations omitted). NEPA's regulations and Ninth Circuit caselaw require the agency to "rigorously explore" and objectively evaluate "all reasonable alternatives." 40 C.F.R. § 1502.14(a). The courts, in the Ninth Circuit as elsewhere, have consistently held that an agency's failure to consider a reasonable alternative is fatal to an agency's NEPA analysis. *See, e.g., Idaho Conserv. League v. Mumma*, 956 F.2d 1508, 1519-20 (9th Cir. 1992) ("The existence of a viable, but unexamined alternative renders an environmental impact statement inadequate.").

If NMFS or FWS reject an alternative for consideration, it must explain why a particular option is not feasible and was therefore eliminated from further consideration. 40 C.F.R. § 1502.14(a). The courts will scrutinize this explanation to ensure that the reasons given are adequately supported by the record. *See Muckleshoot Indian Tribe v. U.S. Forest Service*, 177 F.3d 800, 813-15 (9th Cir. 1999); *Idaho Conserv. League*, 956 F.2d at 1522 (while agencies can use criteria to determine which options to fully evaluate, those criteria are subject to judicial review); *Citizens for a Better Henderson*, 768 F.2d at 1057.

D. Mitigation Measures

"Implicit in NEPA's demand that an agency prepare a detailed statement on 'any adverse environmental effects which cannot be avoided should the proposal be implemented,' 42 U.S.C. § 4332(C)(ii), is an understanding that an EIS will discuss the extent to which adverse effects can be avoided." *Robertson*, 490 U.S. at 351-52. The DEIS must discuss mitigation in sufficient detail to ensure that environmental consequences have been fairly evaluated." *Robertson*, 490 U.S. at 352; *see also Idaho Sporting Congress*, 137 F.3d at 1151 ("[w]ithout analytical detail to support the proposed mitigation measures, we are not persuaded that they amount to anything more than a 'mere listing' of good management practices"). As the Supreme Court clarified in *Robertson*, 490 U.S. at 352, the "requirement that an EIS contain a detailed discussion of possible mitigation measures flows both from the language of [NEPA] and, more expressly, from CEQ's implementing regulations" and the "omission of a reasonably complete discussion of possible mitigation measures would undermine the 'action-forcing' function of NEPA."

E. Global Warming

Last, but certainly not least, the HCP and DEIS must address global warming impacts. The NMFS and FWS must evaluate this impact, disclose it to the public and analyze the impact in the context of the HCP and the ESA overall. The Ninth Circuit Court of Appeals has ruled that federal agencies must evaluate global warming in all federal actions. *Center for Biological Diversity v. National Highway Traffic Safety Administration*, 508 F.3d 508 (9th Cir. 2007).

III. NATURAL COMMUNITY CONSERVATION PLANS

California Code establishes that the "purpose of natural community conservation planning is to sustain and restore . . . species and their habitat," and consequently, the CDFW may "enter into an agreement . . . for the purpose of preparing a natural community conservation plan . . . to provide comprehensive management and conservation of multiple wildlife species . . . ." This NCCP must "provide for the protection of habitat, natural communities, and species diversity on a landscape or ecosystem level through the creation and long-term management of habitat reserves or other measures that provide equivalent conservation of covered species . . . ." A fundamental aspect of NCCPs is that they "maintain the ecological integrity of large habitat blocks, ecosystem function, and biological diversity," and "protect and maintain habitat areas that are large enough to support sustainable populations of covered species."

IV. CALIFORNIA ENDANGERED SPECIES ACT REQUIREMENTS

Under California state law, the "take" prohibition in CESA can be overcome via Fish and Game Code Section 2835, which allows CDFW to "authorize . . . the taking of any covered species . . . whose conservation and management is provided for in a natural community conservation plan approved by the department."

In addition to prohibiting the "take" of listed species, CESA requires that "state agencies should not approve projects as proposed which would . . . result in the destruction or adverse modification of habitat essential to the continued existence of [any endangered or threatened species] if there are reasonable and prudent alternatives available consistent with conserving the species or its habitat which would prevent jeopardy." Fish and Game Code § 2053. Section 2053 further states that "it is the policy of this state and the intent of the Legislature that reasonable and prudent alternatives shall be developed by the department, together with the project proponent and the state lead agency, consistent with conserving the species, while at the same time maintaining the project purpose to the greatest extent possible."

Section 2055 further declares that "all state agencies, boards, and commissions shall seek to conserve endangered species and threatened species and shall utilize their authority in furtherance of the purposes of this chapter." "Conserve . . . means to use, and the use of, all methods and procedures which are necessary to bring any endangered species or threatened species to the point at which the measures provided pursuant to this chapter are no longer necessary." Fish and Game Code § 2061.

V. CALIFORNIA FISH AND GAME CODE AND PUBLIC TRUST

Section 711.7(a) of the California Fish and Game Code declares that: "the fish and wildlife resources are held in trust for the people of the state by and through the [DFG]." Furthermore, section 1802 provides: "The [DFG] has jurisdiction over the conservation, protection, and management of fish, wildlife, native plants, and habitat necessary for biologically sustainable populations of those species." When acting as a trustee agency during the review of an NCCP, DFG must adhere to its public trust obligations.

California courts have held that title to the fish and wildlife resources of the state are held in trust by the state of California for the benefit of the people. *See e.g., Ex Parte Maier* (1894) 103 Cal. 476, 483; *People v. Harbor Hut Rest.* (1983) 148 Cal. App. 3d 1151, 1154. In maintaining this public trust, "[t]he state has the duty to preserve and protect wildlife." *Betchart v. California State Dept. of Fish and Game* (1984) 158 Cal. App. 3d 1104, 1106. This duty carries with it the "implied power to do everything necessary to the execution and administration of the trust." *People v. California Fish Co.* (1913) 166 Cal. 576, 597.

Further, through CESA, the Legislature has required all state agencies, including DFG, to "conserve, protect, restore and enhance" any endangered or threatened species and their habitat when undertaking any state action, such as issuance of a permit. Fish & Game Code §§ 2052, 2055; *Mountain Lion Foundation v. Fish & Game Com.* (1997) 16 Cal.4th 105, 125. DFG, therefore, has an affirmative statutory public trust duty to ensure the preservation, recovery and enhancement of threatened, endangered, and candidate species and their habitat.

An HCP may not prohibit DFG from requiring that the applicant take additional conservation measures beyond those in the HCP, thereby preventing DFG from carrying out its affirmative public trust duties. Such assurances and limitations would violate DFG's public trust obligation because the agency is obligated to use "all necessary methods and procedures" to conserve, protect, restore and enhance listed species and to protect biologically sustainable populations of other species. Fish & Game Code §§ 1802, 2052, 2055, 2061.

VI. MARBLED MURRELET STATUS IN CALIFORNIA AND HABITAT NEEDS

As stated in the Marbled Murrelet 5-Year Review, "at the Conservation Zone scale, murrelet at-sea density estimates from Conservation Zones 1-5 in 2008 ranged from 0.14 birds/km2 in Conservation Zone 5 to 4.14/km2 in Conservation Zone 4 (Table 3). At-sea densities followed the same general pattern as observed previously, with high densities in Oregon and northern California (Conservation Zones 3 and 4), and very low densities in Conservation Zone 5."[1] In short, in the Mendocino area [Conservation Zone 5], murrelets are at extremely low numbers.

Furthermore, the Marbled Murrelet Recovery Plan states the following:[2]

> The marbled murrelet was federally listed as a threatened species mainly due to the substantial loss of older forest nesting habitat. The low elevation, older forests close to the coast, which marbled murrelets require for nesting, have been heavily harvested throughout the bird's range and are severely degraded due to fragmentation.

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[1] U. S. Fish and Wildlife Service , Marbled Murrelet *(Brachyramphus marmoratus)* 5-Year Review (June 12, 2009)

[2] Recovery Plan For The Threatened Marbled Murrelet in Washington, Oregon, and California, U.S. Fish And Wildlife Service, 1997.

Loss of marbled murrelet nesting habitat is a major cause of the species' decline. Activities causing habitat loss are considered by the U.S. Fish and Wildlife Service to pose one of the highest risks of take based on our current understanding of the species' population trends. Habitat loss has negative effects that may last decades to centuries, depending on the extent of the habitat modification and its location on the landscape. Recruitment of juvenile marbled murrelets into the adult breeding population is believed to be occurring at extremely low rates. Therefore, maintenance of known and potential nesting habitat is a primary goal of this recovery plan.

The weight of evidence indicates that the major factors in marbled murrelet decline from historical levels in the early 1800's (or earlier) are (1) loss of nesting habitat and (2) poor reproductive success in the habitat that does remain, a phenomenon that appears due in large part to increased vulnerability of nests to predators in highly fragmented landscapes.

Logging proceeded in the forests of Sonoma and Mendocino counties throughout the 20th century, such that almost all old growth forest had been lost in this region by the mid to late 1900's.

Estimates for the amount of reduction of northern California's coastal old-growth redwood forests range from approximately 85 to 96 percent (Green 1985, Fox 1988, Larsen 1991). In addition, past and current forest management practices also have resulted in a forest age distribution skewed toward younger even-aged stands at a landscape scale (Hansen et al. 1991, McComb et al. 1993). Generally, older forests with large, old trees appear to be needed to develop the proper broad, horizontal branching structure in the forest canopy for the placement and visitation of nests.

The principal factor considered to affect the marbled murrelet throughout the southern portion of its range (from British Columbia south to California) is the loss of nesting habitat (older forests) (U.S. Fish and Wildlife Service 1992a), mainly from commercial timber harvest and forest management practices.

The geographical area of suitable marbled murrelet habitat was greatly reduced in Washington, Oregon, and California during the 1 800s and 1900s. Most suitable nesting habitat (old-growth and mature forests) on private lands within the range of the Washington, Oregon, and California population has been eliminated by timber harvest (Green 1985, Norse 1988, Thomas et al. 1990). Remaining tracts of potentially suitable habitat on private lands throughout the range are subject to continuing timber harvest operations. In most areas, second-growth forests have been or are planned to be harvested before they will attain the characteristics of older forests. Thus, this habitat loss is largely permanent, without considerable change in management actions over the next century.

Impacts due to timber harvest may include a complete loss of habitat (clear-cut), a degradation of habitat (some selective harvest), or harvest of unsuitable habitat adjacent to and contiguous with suitable habitat. Impacts from timber harvest can also occur in unsuitable habitat that is not contiguous with suitable habitat, but is in the vicinity (within 0.8 kilometers (0.5 miles)).

Take of marbled murrelets is not likely in suitable habitat that has been surveyed[3] to protocol with no occupancy detected (incidental take may still occur due to the potential for survey error). However, it is important to note that adverse effects to the species may still result from modification of suitable unoccupied habitat. As the population recovers, or as other occupied areas are lost to timber harvest or natural processes (e.g., wildfire), these areas may be used by dispersing or colonizing birds.

Maintenance of marbled murrelet populations on private lands is critical in arresting the decline of the species in the next 50—100 years. This is especially true where additional nesting habitat is not expected to be available on nearby Federal lands. While the Endangered Species Act section 9 prohibition against unauthorized incidental take provides some protection for the marbled murrelet, this may not be sufficient to protect and enhance habitat on non-Federal lands in the long term. This is because a continuing decline in populations would be expected to eventually result in unoccupied habitat where the prohibition against take may not apply. This unoccupied, but suitable, habitat might then be harvested, continuing the erosion of habitat that is needed to recover the species.

Much of the remaining marbled murrelet nesting habitat in [Zone5] is located on private lands. The maintenance of this population will require considerable cooperation between State, Federal and private management representatives. Recovery efforts in this Conservation Zone could enhance the probability of survival and recovery in adjacent Conservation Zones by minimizing the current gap in distribution. The population is so small that immediate recovery efforts may not be successful at maintaining this population over time and longer term recovery efforts (e.g., developing new suitable habitat) may be most important. However, if this small population can be maintained over the next 50 years, it will greatly speed recovery in this Conservation Zone.

The Mendocino Zone extends south from the southern boundary of Humboldt County, California, to the mouth fan Francisco Bay. It includes waters within 2

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[3] The limitations of surveys should also be noted:

> Because of their small body size, cryptic plumage, crepuscular activity, fast flight speed, solitary nesting behavior, and secretive behavior near nests located in densely forested habitat, the nests of the marbled murrelet have been extremely difficult to locate (Hamer and Nelson 1 995b). The first tree nest in North America was not located until 1974 (Binford et al. 1975), even though ornithologists had been searching for the nest site of the marbled murrelet in North America for many decades. (1997 Recovery Plan)

kilometers (1.2 miles) of the Pacific Ocean shoreline and extends inland a distance of up to 40 kilometers (25 miles) from the Pacific Ocean shoreline. The very small nesting and at-sea population of marbled murrelets along the coast of Mendocino, Sonoma and Main Counties is important to future reconnection of marbled murrelet populations in northern and central California, if they can survive over the short term. Almost all of the older forest has been removed from this area, although small pockets fold-growth forest occur in State parks and on private lands.

Stands should not be designated as unsuitable habitat because they have
(1) small patches of habitat or a few remnant old-growth trees;
(2) smaller limb sizes;
(3) little moss cover on tree branches;
(4) poor access conditions for birds; or
(5) particular aspects may cause suitable habitat to go unsurveyed. Field assessments prior to determining habitat suitability are of vital importance to the conservation and protection of marbled murrelet breeding sites.

Fragmentation of the remaining older forests may have resulted in increased populations of nest predators, and increased visibility and vulnerability of flying or nesting adults to potential predators. This change in turn has probably led to increased rates of predation on nests and possibly on adults. Rates of predation on marbled murrelet nests appear to be high, based on field observations, compared to most other seabirds and are due most often to predators whose populations have apparently increased as a result of forest fragmentation and related human activities.

Marbled murrelets use forests that primarily include typical old-growth forests (characterized by large trees, a multistoried stand, and moderate to high canopy closure), but also use mature forests with an old-growth component. Trees must have large branches or deformities for nest platforms, with the occurrence of suitable platforms being more important than tree size alone. The earliest possible recovery time for nesting habitat, once lost, is generally 100—200 years.

The effects of deforestation are chronic and can persist for 100-200 years until forests have regrown to achieve structure that permits marbled murrelet nesting. If forests were protected from cutting and were able to mature to old growth characteristics, the number of nesting marbled murrelets and their nesting success should increase slowly to levels typical of other alcids.

[W]e have concluded that the next 50 years will be the most critical period for marbled murrelet conservation efforts. Marbled murrelet populations in the Pacific Northwest are likely to continue to decline, certainly as a result of low reproduction due primarily to loss of nesting habitat.

Although some currently mature forest will become suitable nesting habitat during the next 50 years, most younger forest habitat will not become available for nesting marbled murrelets until after the year 2040 (U.S. Department of Agriculture et al. 1993). Until that time, immediate conservation efforts that minimize and mitigate the loss of actual and potential nest sites, as well as increase adult survivorship, will be necessary.

The most likely causes of poor reproduction appear to be due to the effects of deforestation, as discussed above. Deforestation has occurred on a large scale and in many areas may require a century or more of forest regrowth to reverse the trend (U.S. Department of Agriculture et al. 1993).

The three separate areas where marbled murrelets currently are found in California correspond to the three largest remaining blocks of old-growth coastal conifer forests (Carter and Erickson 1992). These populations are largely separated by areas of second-growth forest not used by marbled murrelets. A large break in the main breeding distribution is located at the southern portion of the range in California, where approximately 480 kilometers (300 miles) separate the southernmost breeding population in San Mateo and Santa Cruz counties (central California) from the next largest populations to the north in Humboldt and Del Norte counties (northern California). Most of this largely unpopulated section, especially in Mendocino County, probably contained significant numbers of marbled murrelets prior to extensive logging (Carter and Erickson 1988, Paton and Ralph 1988). Based on extrapolation from currently known population numbers in relation to remaining available nesting habitat, it was estimated that at least 60,000 marbled murrelets may have been found historically along the coast of California (Larsen 1991). The population size of marbled murrelets has been estimated for California over the past 20 years. Sowls et al. (1980) estimated the breeding population to be about 2,000 breeding birds. Carter and Erickson (1992) suggested that between 1,650 and 2,000 breeding birds might constitute the state's breeding population. Carter et al. (1992) derived a population estimate of 1,821 breeding birds. Ralph and Miller (1995) estimated a total state population of approximately 6,000 birds, including breeding and nonbreeding birds, from more intensive at-sea surveys specifically designed to estimate population size for marbled murrelets. Differences between estimates does not indicate that marbled murrelet numbers have increased over time between the censuses, because different methods and assumptions were used in estimating population numbers.

Long-term actions include increasing the amount, quality and distribution of suitable nesting habitat. Increasing the stand size of suitable habitat to provide more interior forest conditions and increasing the number of stands of suitable nesting habitat are considered key to long-term recovery. Within secured habitat areas, this means protecting currently unsuitable habitat to allow it to become suitable, reducing fragmentation, providing replacement habitat for current suitable nesting habitat lost to disturbance events and habitat lost to both timber

harvest and disturbance events in the past. In the long term, the distribution of nesting habitat should be improved.

The demographic bottleneck that the marbled murrelet population may experience during the next 50 to 100 years makes the maintenance of marbled murrelet populations not found within Federal lands (mainly on state and private lands) an important component of more guaranteed viability and eventual recovery over the coming decades and into the future.

Management recommendations for the marbled murrelet need to address two different biological time frames, which reflect
(1) aspects of the murrelet's life history and demographic trends, and
(2) the length of time required to develop the majority of new nesting habitat or improve current forest habitat conditions. Short-term actions must address the apparent rapid decline of current populations and the need for immediate stabilization. The ability of marbled murrelet populations to recover rapidly is low due to the low reproductive potential of the species. Long-term actions address the long time-frames required to cultivate or enhance mature forest habitat conditions or to improve marine habitat quality because of the nature and complexity of these ecosystems. Little additional older forest habitat will become available until after 2040.

Improving the distribution of nesting habitat helps to buffer existing populations against poor breeding success and catastrophic loss and probably facilitates gene flow among separated populations. Three major gaps in existing habitat are particularly apparent:
(1) from the southern Olympic Peninsula in Washington to Tillamook in northwestern Oregon;
(2) between Patrick's Point and southern Humboldt Bay in northern California (see Figure 1); and
(3) throughout most of the Mendocino Zone and the northern part of the Santa Cruz Mountains Zone (between southern Humboldt County and central San Mateo County).

These three geographic gaps represent probable partial barriers to gene flow across them. They include large areas of second-growth forests that originated after logging, from fire (parts of northwestern Oregon), or from natural discontinuities of nesting habitat (especially parts of northern and central California). Gap areas often have a high proportion of private lands and little or no Federal land. State lands cover significant portions of northwest Oregon (the Tillamook and Clatsop State Forests) and southwest Washington. Silvicultural techniques to create suitable habitat at both the stand and landscape level (discussed in task 3.2.1.3) may be particularly beneficial to marbled murrelet recovery in the long term if applied in these areas.

> The more contiguous the habitat distribution, the lower the likelihood of future large gaps in distribution of the species due to catastrophic events such as oil spills or large wildfires. Preventing further erosion of the already patchily-distributed nesting habitat is a key element in buffering the species against such catastrophic events. This is especially important in areas where gaps already occur. Furthermore, it is currently unknown how nesting success differs with distance from the coast, and far inland habitats may be as important to species survival as those nearer to shore. Therefore, it is important to maintain both north/south and east/west distribution of suitable habitat.
>
> Decrease fragmentation by increasing the size of suitable stands to provide a larger area of interior forest conditions. The majority of suitable nest stands currently exist as small islands within a matrix of younger forests.
>
> It also would be desirable to increase and block up suitable nesting habitat in the Mendocino and Santa Cruz Mountains Zones. Little habitat remains outside parks in these two zones, such that an increase in the short term does not appear feasible.

Other federal documents further explain:

> Forests with older residual trees remaining from previous forest stands may also develop into nesting habitat more quickly than those without residual trees. These remnant attributes can be products of fire, wind storms, or previous logging operations that did not remove all of the trees (Hansen *et al* 1991; McComb *et al.* 1993).[4]
>
> [N]esting habitat appears to be the most important factor affecting marbled murrelet distribution and numbers. (Nelson *et al.* 1992; Ralph *et al.* 1995b; Ralph and Miller 1995; Strong 1995; Varoujean *et al.* 1994).[5]
>
> [Timber harvest can] have the following effects on the primary constituent elements of murrelet critical habitat:
> (1) Removal or degradation of individual trees with potential nesting platforms, or the nest platforms themselves, that results in a significant decrease in the value of the trees for future nesting use. Moss may be an important component of nesting platforms in some areas.
> (2) Removal or degradation of trees adjacent to trees with potential nesting platforms that provide habitat elements essential to the suitability of the potential nest tree or platform, such as trees providing cover from weather or predators.
> (3) Removal or degradation of forested areas with a canopy height of at least one half the site-potential tree height and regardless of contiguity, within 0.8 km (0.5

[4] 61 Fed. Reg. 26255, 26264

[5] *Id.* at 26258

> mile) of individual trees containing potential nest platforms. This includes removal or degradation of trees currently unsuitable for nesting that contribute to the structure/integrity of the potential nest area (i.e., trees that contribute to the canopy of the forested area). These trees provide the canopy and stand conditions important for marbled murrelet nesting.[6]

Finally, there are two important aspects of murrelet habitat that must not be conflated. First, it is important to recognize that even very small patches of habitat of forest that contain potential nesting habitat should be acknowledged and accounted for in light of the fact that so little habitat exists for murrelets in the region. In other words, habitat that would otherwise be considered marginal may be the best that exists in some areas and therefore cannot be dismissed. Second, while small patches must be accounted for and addressed, the goal should be to maintain and expand all potential murrelet habitat given that higher quality habitat will be more likely to support murrelets. For example, as explained in the literature, murrelets are more likely to be found "in stands with higher dominant and codominant crown cover." In fact, "[t]he most important factor in indicating Occupied stands was density of the old-growth cover, that is, the percent of the area covered by the crowns of old-growth trees."

VII. THE HCP/NCCP/PTEIR/DEIS AS PROPOSED DO NOT APPROPRIATELY ADDRESS MURRELET CONSERVATION

The proposed HCP/NCCP would cover logging on MRC lands in the coastal redwood forest of Mendocino County. This area has been significantly logged in the past, but still contains remnant large, old trees and small stands of late-seral forest. Especially in light of the severe lack of nesting habitat for marbled murrelets in the Mendocino region, it is imperative to recognize, and to then address, the importance of even very small habitat areas for murrelets. Put another way, while certainly the best nesting habitat for marbled murrelets consists of large, intact, contiguous stands of old-growth – which should be the overall intent of the HCP/NCCP given their conservation mandates – the fact of the matter is that such habitat is extremely rare in the Mendocino region, and consequently, small stands are often all that there is for murrelets to survive upon in the area. As explained by the Pacific Seabird Group,[7] "because so much murrelet habitat has been lost or depleted in California, remaining suitable habitat is especially important, regardless of its size, if murrelets are to have a good chance of surviving over the next 100 years." The Pacific Seabird Group further explained that

> Suitable murrelet habitat includes stands of any size with at least one tree with limb diameters or platform structure >10 cm, or a residual/remnant tree with limb diameters or platform structure >10 cm. From research on Marbled Murrelet habitat use, it is clear that the species can utilize small patches of suitable habitat. Murrelets can also nest in large residual trees that often remain from past fire and management activities. These residual trees are often found at low densities, sometimes less than one tree/acre. Therefore, any assessment of habitat must

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[6] *Id.* at 26271

[7] March 24, 2010, Letter from PSG re "Impacts to the Marbled Murrelet from loss of suitable nesting habitat in California"

> include a walk-through of every acre of the area in question. Without this detailed assessment it is easy to miss small patches of habitat and residual trees.

Here, the HCP must acknowledge and account for the fact that the baseline situation in the region is such that murrelet nesting habitat is severely degraded, and this "reduction in suitable habitat could result in reduced population dispersal and create a 'genetic bottleneck.'"[8]

Moreover, it is essential –in order to meet their conservation mandates – that the HCP and NCCP ensure that the Plans do not result in the loss of suitable but unoccupied habitat. Such habitat is essential, especially in the Mendocino region, to ensuring that murrelets will survive in the coming decades, and is essential to any meaningful assessment of murrelet conservation in the Mendocino region. "Population modeling indicates that this population is declining and will be extinct in parts of Washington, Oregon and California within 100 years without changes in the amount and quality of nesting habitat and in demographic trends (McShane et al. 2004)."[9] As succinctly stated by the Pacific Seabird Group:

> (1) murrelet populations continue to decline due to habitat loss, low fecundity, high nest predation rates, and low adult survival; (2) most current recovery efforts rely on a system of reserves on federal land that is extremely limited in central and northern California, and, with the loss of occupied and unoccupied murrelet habitat continuing, State Lands and private lands with potential habitat play a crucial role in maintaining nesting habitat and ensuring future murrelet recovery; and (3) land use contrary to recovery objectives must be avoided within and adjacent to suitable habitats, especially ones significant to the stability and recovery of regional populations of imperiled species. Continued loss and fragmentation of habitat will increase the risk of extinction of this unique seabird in California. . . . It is unrealistic to expect that the species will recover before there is significant improvement in the amount and distribution of suitable nesting habitat (McShane et al. 2004: 6-34).[10]

The logging proposed in the HCP and NCCP does not ensure that nesting habitat (whether occupied or unoccupied) is protected and restored. For example, the HCP/NCCP states that timber operations need only be "100 ft away from potential habitat tree." (DEIS at 2-62). However, the "removal or degradation of forested areas with a canopy height of at least one half the site-potential tree height and regardless of contiguity, within 0.8 km (0.5 mile) of individual trees containing potential nest platforms" can cause harm and this standard "includes removal or degradation of trees currently unsuitable for nesting that contribute to the structure/integrity of the potential nest area (i.e., trees that contribute to the canopy of the forested area). These trees provide the canopy and stand conditions important for marbled murrelet nesting."[11] Moreover,

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[8] Id.

[9] Id.

[10] Id.

[11] 61 Fed. Reg. at 26271

the measures appear to only apply in the Lower Alder Creek area when they should apply to any tree that could act as a murrelet nesting tree.

Outside of the Lower Alder Creek area, 22 stands have been identified for which the HCP/NCCP proposes to "retain all primary murrelet trees and screen trees." However, this does not adequately describe or explain a) that all potential nest trees have in fact been identified, or b) what it means to retain screen trees. Therefore, the HCP/NCCP must do that – explain how all, not just some, potential nest trees will be addressed and conserved and how retention of screen trees will actually play out; as things stand, the phrase "retain screen trees" could mean many different things to different people and therefore it must be explained in detail so all interested persons can understand what in fact will occur.

To the extent that the HCP/NCCP does not contain data regarding potential nest trees on its acreage, MRC must either a) provide that data so it can be addressed, or b) commit to doing so when submitting any individual THP so that the issue will not be overlooked and subsumed under the HCP/NCCP. This is necessary both from a baseline information perspective as well as a data integrity perspective. In short, all potential nest trees must be indentified and accounted for at some point in the timber approval process and thus far the HCP/NCCP process has not done that – the current HCP/NCCP does not contain data regarding potential nest trees for murrelets for its entire acreage that would be covered by the approved HCP/NCCP.[12]

This baseline information regarding potential nesting habitat is also critical because such habitat may be the very lifeboat that prevents murrelets from going extinct in the coming decades. As discussed in Mazurek 2004:[13]

> Given the fragmented nature of mature forests in the redwood region, remnant patches of old-growth and individual legacy trees may function as 'mini-reserves' that promote species conservation and ecosystem function. Legacy structures increase structural complexity in harvested stands and, as a result, can provide the 'lifeboats' for species to re-establish in regenerating stands (Franklin et al., 2000). Although the lifeboat function may not be entirely fulfilled for vertebrates with large area needs, these habitat elements may make it possible for some species to: (1) breed in forest types where they may otherwise be unable, and (2) secure a greater number of important refuges from climatic extremes and predators. In addition, these functions may allow legacy trees to provide some measure of habitat connectivity ('stepping stones') to larger more contiguous tracts of old-growth forests (Tittler and Hannon, 2000; Noss et al., 2000). Because of their rarity in commercial forests, the first step in the management of legacy trees is to determine their locations and protect them from logging or from physical degradation of the site.

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[12] *See Sierra Club v. State Bd. of Forestry* (1994) 7 Cal.4th 1215, 1220-1221 ("Because the board approved the plans without having before it the data necessary to make an informed assessment of the environmental impact of the proposed timber harvest, that approval must be rescinded.")

[13] Mazurek, M. J. and W. J. Zielinski. 2004. Individual legacy trees influence vertebrate wildlife diversity in commercial forests. *Forest Ecololgy and Management* 193: 321-334.

> We expect that new silvicultural methods will be required to prescribe the process of identifying, culturing, and protecting residual legacy trees. Although we do not believe that any one tree will protect a species, we do believe that the cumulative effects of the retention, and recruitment, of legacy and residual trees in commercial forest lands will yield important benefits to vertebrate wildlife and other species of plants and animals that are associated with biological legacies. The results of our study beg us to consider habitat at a spatial scale that is smaller than that of habitat patches or remnant stands; we conclude that individual trees can have very important values to wildlife.

The failure to accurately describe the existing environmental setting also misleads the public by presenting the false impression that further logging in the plan area will have minor effects.[14] Here, the extreme rarity of murrelet nesting habitat in the Mendocino region means that any additional loss of potential habitat – even low quality habitat – is significant and to be avoided, and therefore, all potential nesting habitat must be assessed and accounted for so as to avoid its loss. Moreover, as the Fish and Wildlife Service found, critical factors for sustaining nest trees include not just protecting the tree itself or screen trees but also protecting surrounding structure:

> [Timber harvest can] have the following effects on the primary constituent elements of murrelet critical habitat: ....(2) Removal or degradation of trees adjacent to trees with potential nesting platforms that provide habitat elements essential to the suitability of the potential nest tree or platform, such as trees providing cover from weather or predators. (3) Removal or degradation of forested areas with a canopy height of at least one half the site-potential tree height and regardless of contiguity, within 0.8 km (0.5 mile) of individual trees containing potential nest platforms."[15]

The potential nesting habitat at stake – even though it may be currently unoccupied[16] – is of critical value to the future existence of the marbled murrelet. Indeed, the marbled murrelet's current status is largely due to the fact that so little old forest, upon which the species depends for its nesting habitat, is left in California. As succintly put by the U.S. Fish and Wildlife Service, while "[t]ake of marbled murrelets is not likely in suitable habitat that has been surveyed to protocol with no occupancy detected (incidental take may still occur due to the potential for survey error) . . . , it is important to note that adverse effects to the species may still result from modification of suitable unoccupied habitat. As the population recovers, or as other occupied areas are lost to timber harvest or natural processes (e.g., wildfire), these areas may be used by dispersing or colonizing birds."

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[14] *See, e.g., Joy Road Forest and Watershed Association v. California Department of Forestry and Fire Protection* (2006) 142 Cal.App.4th 656, 676 ("By approving a THP which contained an inadequate cumulative impact analysis regarding an admittedly important environmental issue, CDF failed to proceed in a manner required by law and prejudicially abused its discretion.")

[15] 61 Fed. Reg. at 26271.

[16] When murrelet surveys are conducted, however, they are not conclusive.

The U.S. FWS has further explained that marbled murrelets in California, especially those in Mendocino County, are at "very low densities"[17] and at a critical juncture in their ability to maintain their existence. "The weight of evidence indicates that the major factors in marbled murrelet decline from historical levels in the early 1800's (or earlier) are (1) loss of nesting habitat and (2) poor reproductive success in the habitat that does remain . . . ." Locally speaking, "[l]ogging proceeded in the forests of Sonoma and Mendocino counties throughout the 20th century, such that almost all old growth forest had been lost in this region by the mid to late 1900's." As a result of the devastating impacts of the past timber harvest, "[m]aintenance of marbled murrelet populations on private lands is critical in arresting the decline of the species in the next 50--100 years." "This is especially true where additional nesting habitat is not expected to be available on nearby Federal lands," such as in Mendocino County, where "[m]uch of the remaining marbled murrelet nesting habitat . . . is located on private lands." In fact, "[o]nly 2% remains of the original old-growth in Mendocino, Sonoma, and Marin Counties, where the largest grove, Montgomery Woods State Park, is only 160 ha." The FWS explained that "[t]he maintenance of this [Mendocino region] population will require considerable cooperation between State, Federal and private management representatives. Recovery efforts in [the Mendocino Region] could enhance the probability of survival and recovery in adjacent Conservation Zones by minimizing the current gap in distribution." In short, "[t]he very small nesting and at-sea population of marbled murrelets along the coast of Mendocino, Sonoma and Main Counties is important to future reconnection of marbled murrelet populations in northern and central California, if they can survive over the short term."

Unfortunately for murrelets, however, because "most younger forest habitat will not become available for nesting marbled murrelets until after the year 2040, . . . immediate conservation efforts that minimize and mitigate the loss of actual and potential nest sites, as well as increase adult survivorship, will be necessary." This means, as concluded by the FWS, that the "demographic bottleneck that the marbled murrelet population may experience during the next 50 to 100 years makes the maintenance of murrelet populations not found within Federal lands (mainly on state and private lands) an important component of more guaranteed viability and eventual recovery over the coming decades and into the future."

Because the coming decades represent a critical juncture in the murrelet's existence in this region, maintaining currently unoccupied habitat –even low quality habitat – in the Mendocino region as potential habitat for future use is necessary to meaningfully maintain the ability of murrelets to persist into the future. As stated by the FWS: "While the . . . prohibition against unauthorized incidental take provides some protection for the marbled murrelet, this may not be sufficient to protect and enhance habitat on non-Federal lands in the long term. This is because a continuing decline in populations would be expected to eventually result in unoccupied habitat where the prohibition against take may not apply. This unoccupied, but suitable, habitat might then be harvested, continuing the erosion of habitat that is needed to recover the species."

Timber harvest, and the resulting stand structure, directly dictates the ability of a forest to continue to function as murelet nesting habitat, and hence, the ability of the forest to contribute to the conservation of the species. Here, the timber harvest could cause a degradation or loss of

[17] U. S. FWS, Marbled Murrelet 5-Year Review (June 12, 2009)

habitat that is essential to the murrelet and such harvest (of potential nesting trees and any necessary associated structure to maintain the value of the nesting tree) must therefore be avoided. Consequently, all potential nesting habitat must be identified and accounted for and then analyzed so as to demonstrate that it will in fact be protected in a way that ensures the conservation of murrelets in the region.

Finally, CDFW has a public trust duty to take necessary action to protect wildlife resources affected by the HCP/NCCP.[18]

The Supreme Court has identified this substantive duty "to protect the people's common heritage," holding that an agency may surrender "that right of protection only in rare cases when the abandonment of that right is consistent with the purposes of the trust."[19] As a result, CDFW must "protect public trust uses whenever feasible."[20] Therefore, in this situation, CDFW must ensure that all potential murrelet nest trees are adequately addressed in order to comply with its public trust duties. This includes ensuring that all information necessary to make an informed decision about murrelet nest trees has been provided by MRC, which does not appear to be the case in light of the limited information available in the HCP/NCCP documents. CDFW must require MRC to account for all potential nesting habitat on the acreage covered by the HCP/NCCP, and to then adequately explain how it will be protected in order to ensure the conservation of murrelets.

Lack of information and explanation is also evidenced by the Navarro West situation. Because there were murrlet detections in the Navarro West area, potential murrelet trees there are to be treated as primary murrelet trees. However, the table at HCP 10-39 appears to show that habitat for owls will be reduced in Navarro West (and Albion and Southcoast) over the life of the plan, which is a contradiction—how will murrelets be protected but owls will not. There also exists a contradiction in that the Albion maps having to do with "potentially suitable murrelet habitat" (map atlas 7b) do not show any potential murrelet trees in the westernmost part of Albion and yet the EIS, Appendix F, map 14b on page f-41 shows that the area is potentially suitable. The contradictions must be addressed and accounted for and the Plans recirculated for comment.

VIII. HARDWOOD RETENTION IS NOT ADEQUATELY DEFINED

Class III hardwood stands are defined as "dominated by hardwoods only because of past management and are clearly suitable for conifer restoration." (DEIR at 2-55.) This definition is too subjective because it is not explained how it will be determined that the situation exists "only

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[18] *See* Fish & Game Cod, § 711.7, subd. (a) ["The fish and wildlife resources are held in trust for the people of the state by and through the department [of Fish and Game]]); *Environmental Protection & Information Center v. California Dept. of Forestry & Fire Protection, supra*, 44 Cal.4th at 515 (DFG has a public trust duty to protect wildlife, derived from statute); *Center for Biological Diversity v. FPL Group*, 166 Cal.App.4th at 1361 ("[I]t is clear that the public trust doctrine encompasses the protection of undomesticated birds and wildlife. They are natural resources of inestimable value to the community as a whole. Their protection and preservation is a public interest.")

[19] *Nat'l Audubon Soc'y v. Superior Court* (1983) 33 Cal. 3d 419, 441.

[20] *Id.* at 446.

because of past management," nor is it discussed how "clearly suitable" will be determined. This definition must therefore be rewritten to provide meaningful guidance.

IX. ADDITIONAL ALTERNATIVES ARE NECESSARY

The Alternatives as offered should be more encompassing. For example, to choose greater retention of habitat for marbled murrelets, one must also accept extensive clear-cutting. In addition to alternative B, therefore, there should exist alternatives that examine more modest reserves while not relying so extensively on clear-cutting. In other words, at least one alternative should be considered that is more protective than alternative A, but which is less protective than alternative B. Thus far, alternative B can be much more easily ignored than a more nuanced alternative (e.g., an alternative A.5 that extends more protections than A but less than B and contain less clearcutting than B).

X. THE HCP/NCCP AS PROPOSED LACKS BINDING MITIGATION

In order to be properly considered in the jeopardy analysis, mitigation measures must be "reasonably specific, certain to occur, and capable of implementation; they must be subject to deadlines or otherwise-enforceable obligations; and most important, they must address the threats to the species in a way that satisfies the jeopardy and adverse modification standards."[21] Section 10(a)(2)(B)(ii) requires the Secretary to make a finding that the "the applicant will, to the maximum extent practicable, minimize and mitigate the impacts of such taking."

Here, the mitigation measures as proposed to be undertain/voluntary, including, but not limited to, reliance on monitoring programs without adaptive management and on voluntary commitments. The HCP/NCCP must clearly explain how all mitigation is in fact binding.

XI. THE HCP/NCCP FAIL TO PROVIDE THE NECESSARY ASSURANCES THAT THE PLANS WILL BE IMPLEMENTED.

ESA Section 10(a)(2)(B) requires that the Secretaries of the Services must receive "such assurances as he may require that the plan will be implemented." The HCP/NCCP do not explain how they will ensure the ability to *implement* the plans. For example, monitoring, at least some of it, appears entirely voluntary, and funding is only assured in concluosry fashion without any evidence of such.

XII. CONCLUSION

We hope that these comments are helpful and will result in an HCP/NCCP that meets the requirements of all applicable law and promotes the conservation of the covered species as intended by the ESA, CESA, and California state law.

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[21] *Ctr. for Biological Diversity v. Rumsfeld*, 198 F.Supp.2d 1139, 1152 (D.Ariz.2002) (*citing Sierra Club v. Marsh*, 816 F.2d 1376 (9th Cir.1987)); *National Wildlife Federation v. National Marine Fisheries Service*, 524 F.3d 917, 935-936 (9th Cir. 2008) (requiring "more solid guarantees" and "specific and binding plans" in order for mitigation to be considered in a BiOp)

Thank you for your consideration of these comments. Please contact me if you have any questions.

Sincerely,

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DISTRIBUTION OF THE MARBLED MURRELET AT INLAND SITES IN CALIFORNIA

PETER W.C. PATON AND C. JOHN RALPH

ABSTRACT-We conducted transect surveys from the Oregon border to Monterey County in 1988 and 1989 to determine the distribution of marbled murrelets (*Brachyramphus marmoratus*) at inland sites in California. This seabird uses the coastal redwood (*Sequoia sempervirens*) forests of the northern half of California, but little is known of its distribution away from the ocean. We identified potential inland habitat from remote sensing data and then conducted systematic surveys of forest stands based on this inventory.

Murrelets were detected on 74 of 170 (44%) transects, with a patchy distribution concentrated in three regions in Del Norte, Humboldt, San Mateo, and Santa Cruz Counties: (1) east of Crescent City to Redwood Creek in Redwood National Park; (2) lands east of Humboldt Bay to Humboldt Redwoods State Park on the Eel River; and (3) state parks in southern San Mateo and northern Santa Cruz Counties. The primary habitat type where birds were detected was old-growth dominated forest, with 1.05 detections/station, compared to 0.02 detections/station on second-growth transects. Transects with high activity levels tended to be in or west of old-growth stands ≥250 ha. The farthest inland we observed murrelets was 39 km from the coast.

The marbled murrelet (*Brachyramphus marmoratus*) is unique among the alcids, as it is the only species which nests in trees. As of January, 1990, seven tree nests have been found, four in North America (Binford et al. 1975; Quinlan and Hughes 1990; Singer et al., 1990) and three in Asia (Kuzyakin 1963; Nechaev 1986; Labzyuk 1987). Research prior to 1984 focused primarily on their distribution and abundance at sea (Sowls et al. 1980; Sealy and Carter 1984; Carter 1984), breeding biology (Sealy 1974, 1975a; Simons 1980; Day et al. 1983; Hirsch et al. 1981), and feeding ecology (Sealy 1975b). At inland sites, murrelets are detected as they fly over and into forested stands. Censuses conducted in 1984-1986 by the U.S. Forest Service found murrelets at several inland localities in Oregon (K. Nelson, pers. comm.) and California (Paton et al., in press). Stationary counts in 1987 in northern California quantified their daily and seasonal activity patterns at several forested sites (H. Carter and T. Sander, pers. comm.).

In California, murrelets spend most of their time offshore, but occur inland throughout the year. Observations at inland forested areas peak from May to August, during the breeding season (Carter and Erickson 1988; Paton and Ralph 1988). Reasons for their use of inland sites during winter are not known; roosting or investigating nest sites are possibilities. Detection rates are highest near sunrise, with most observations between 30 min before and 30 min after sunrise (Paton and Ralph 1988). Both the male and female incubate, taking 24 hr shifts on the nest and switching in the morning (Naslund et al., 1990). Flock size of flying birds at inland sites is generally small, with single birds and pairs accounting for 85% of the observations (Paton and Ralph 1988). Marbled murrelets have a distinctive call that can be heard up to 300 m away. Birds tend to be vocal, with 30% of calling birds giving one to three notes, while 30% give >9 notes in succession. Birds flying silently are common, accounting for 40% of the detections at one of the most active stands in California (Paton and Ralph 1988). The flight characteristics and silhouette of silent birds are diagnostic if the observer has a clear view of the bird. The activity and behavioral patterns of this species make surveys possible to determine distributional patterns.

In California, the evidence points to this species nesting primarily in old-growth redwood (*Sequoia sempervirens*) dominated forests (Sowls et al. 1980; Carter and Sealy 1987; Carter and Erickson 1988; Paton and Ralph 1988). Less than 10% of the original 770,000 ha of old-growth redwood remain, a result of harvesting since the early 1800's (Fox 1989). The status and continued health of the California population may depend on these remnant forests (Marshall 1988). Despite the apparent loss of most of the potential murrelet nesting habitat in the state, only a few surveys had been conducted at inland sites prior to this study.

Our primary objectives were to: (1) determine the inland distribution of marbled murrelets in California, and (2) describe the habitat characteristics of the areas surveyed. This field work was designed to determine activity centers for further research to find nests.

STUDY AREA AND METHODS

The study area included state, federal, and private forested lands from the Oregon border south to Monterey County (Figs. la-c). We surveyed up to 40 km from the ocean, although murrelets are known to visit locations as far inland as 75 km in British Columbia (Carter and Sealy 1986). Our study area is varied topographically, but is primarily mountainous with scattered rivers, streams, and lagoons. The forests are dominated by redwoods, although Douglas-fir (*Pseudotsuga menziesii)* is the dominant species in certain locations.

In order to identify potential stands to survey, we collaborated with Dr. Lawrence Fox of Humboldt State University, who had mapped the distribution of the redwood forests in California using remote sensing techniques (Fox 1989). Maps were based on 2 April 1986 aerial photos taken from U2 flights at 19,800 m. Habitat types delineated included stands dominated by: (1) old-growth redwood; (2) old-growth redwood/Douglas-fir; (3) second-growth redwood; and (4) young/clearcut redwoods. We defined old-growth following Franklin et al. (1986) as stands having at least 20 trees/ha in excess of 80 cm diameter-at-breast-height (DBH) and containing a multi-layered canopy.

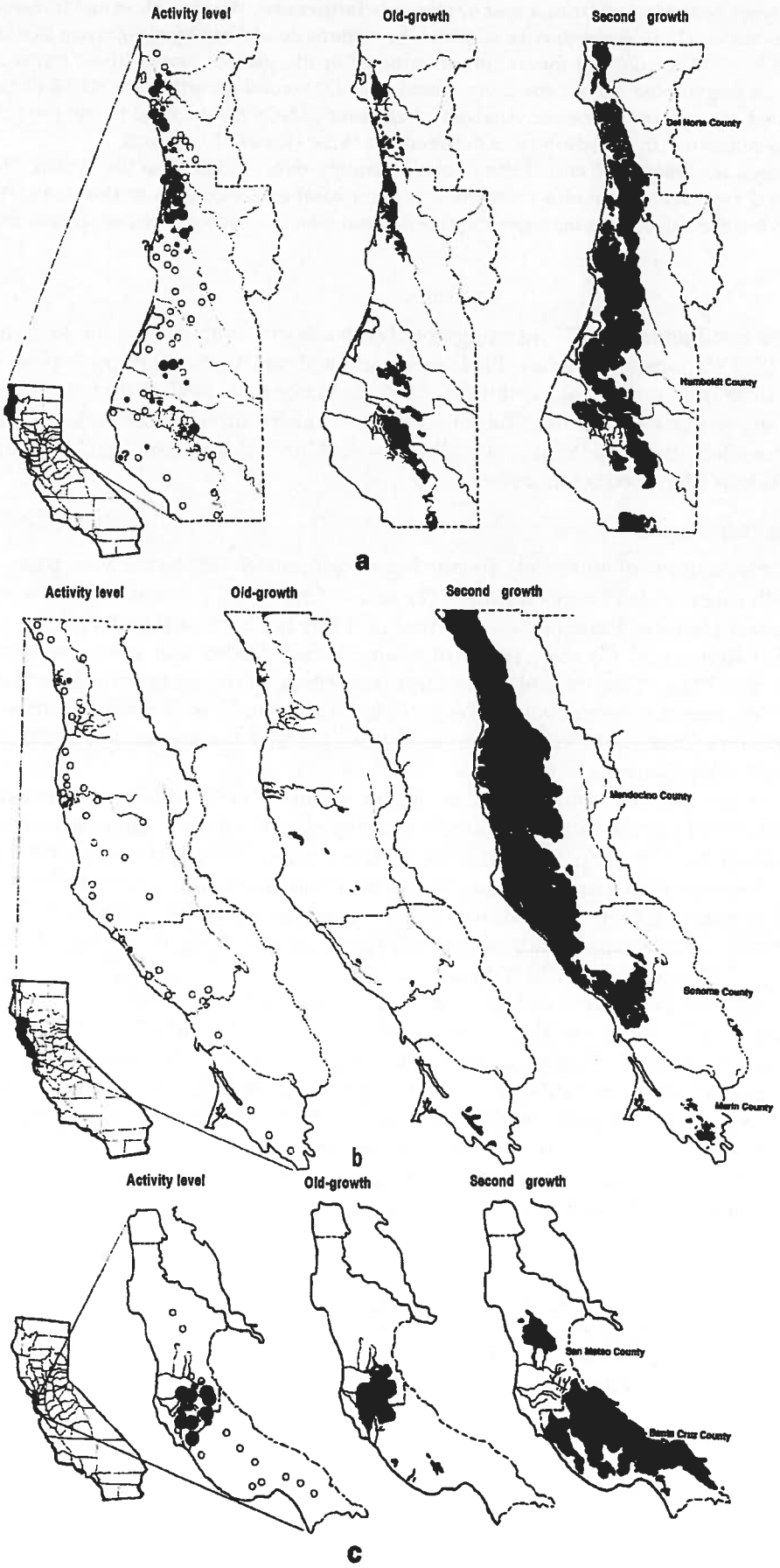
We surveyed 127 transects in 1988 and 43 other transects in 1989, attempting to census both old-growth and second-growth forests throughout the study area. The census period corresponded to the peak of murrelet activity at inland sites, 15 May to 15 August, and followed the protocol of Paton et al. (1990). We established 8 to 12 fixed stations along each transect. Depending upon conditions, spacing between stations was 250 m along trails, 500 m along rough roads, and 1 km on paved roads. Counts were conducted from 45 min before to 1.5 hr after official sunrise (Supplement to the American Ephemeris 1944). Each transect was visited at least twice, with the order of stations reversed. Stations were surveyed for 10 min on each visit, with observers standing silently in place, scanning the sky while listening for birds. No tape recordings were used to elicit calls from birds. We tried not to census transects at less than 2 wk intervals to minimize the effects of weather and monthly differences in detection rates. Observers were trained by taking them to inland sites with high murrelet activity to familiarize them with murrelet calls and flight characteristics. All observers were provided with a tape recording of various murrelet vocalizations.

The basis of the survey was the rate of "detection." A detection was defined as seeing or hearing a single bird or a group birds flying together in the same direction (Paton et al., 1990). We do not know the relationship between the number of detections and the number of birds using a stand. However, we feel that detections can be used as an index of murrelet activity levels to compare among stands at the same time of year.

Analyses

We divided the data into three categories to compare murrelet detection rates among transects: no, moderate, and high activity. Categories were based on the mean number of detections per station. We assumed transects with no detections had either no murrelets or very low murrelet activity levels, transects with a mean of <1 detection/station indicated moderate activity levels, and transects with a mean of ≥ 1 detection/station had relatively high activity levels.

To quantify the vegetation near stations, we used the Fox (1989) forest stand map. A 500 m radius circle was centered on each transect station. We then determined the amount of old-growth and second-growth in the east half of the circle. Each half-circle was assigned a habitat designation based on which age class accounted for $>50\%$ of the area. We assumed that murrelets observed at


Activity level
Old-growth
Second growth
Del Norte County
Humboldt County
a
Activity level
Old-growth
Second growth
Mendocino County
Sonoma County
Marin County
b
Activity level
Old-growth
Second growth
San Mateo County
Santa Cruz County
c

a census station were headed to, or from, a nest or roost site farther east. We then classified transects into one of three classes: (1) old-growth with ≥70% of the stations dominated by old-growth forests; (2) mixed age with >10% to <70% of the stations dominated by old-growth forests (these transects were generally on fragmented timber company lands); and (3) second-growth with <10% of the stations dominated by old-growth forests. Analysis of variance (ANOVA) was used to test the null hypothesis of no difference in detection rates between the three classes of transects.

We also measured the DBH (±10 cm) of the closest 10 canopy trees <50 m from the station. The trees we measured represented samples from the dominant basal area size class of the stand. We used ANOVA to test for differences between the size of trees near transects of low, moderate, and high use.

RESULTS

Surveys were conducted on 377 mornings on 170 transects, with a total of 3697 10-min counts at 1735 stations (Appendix). Birds were detected on 74 (43.5%) of the transects, with a mean detection rate of 0.56/station (2070 detections at 3497 stations). Three transects had single detections where the observer was not positive the bird heard (or seen) was a murrelet: Patrick's Point and Mill Creek in Humboldt County, and Russian Gulch State Park in Mendocino County.

Inland Murrelet Distribution

The inland distribution of murrelets in northern and central California was patchy (Figs. 1a-c), with three areas of concentration: (1) east of Crescent City south to Redwood Creek in Redwood National Park; (2) east of Humboldt Bay to Humboldt Redwoods State Park on the Eel River; and (3) state parks in southern San Mateo and northern Santa Cruz Counties. San Mateo County had the highest percentage of transects with detections, 10 of 15 (67%). We found progressively lower rates in Del Norte, 15 of 25 (60%); Humboldt, 40 of 78 (51%); Santa Cruz, 4 of 13 (31%); Sonoma, 1 of 9 (11%); Mendocino, 3 of 27 (11%); and Marin, 0 of 3 (0%), Counties.

Ownership of areas where murrelets were found included both public and private lands. The majority of stands used by murrelets occurred in California state parks and Redwood National Park. State parks had a mean detection rate of 0.99/station (1110 at 1121 stations), National Parks had 1.00/station (520 at 518 stations), U.S. Forest Service lands had 1.13/station (216 at 192 stations), private commercial timberlands had 0.22/station (144 at 646 stations), and lands of mixed private ownership had the lowest detection rate of 0.07/station (80 at 1220 stations).

Areas with high activity levels included: in Del Norte County-Jedediah Smith Redwoods State Park and Del Norte Redwoods State Park; in Humboldt County-Prairie Creek Redwoods State Park, Redwood National Park, Grizzly Creek Redwoods State Park, Pacific Lumber Company lands, and Humboldt Redwoods State Park; in San Mateo County-Butano State Park, Portola State Park, and San Mateo Memorial County Park; and in Santa Cruz County- Big Basin Redwoods State Park.

The only private commercial timberlands with high detection rates were stands owned by The Pacific Lumber Company southeast of Humboldt Bay. Moderate activity levels

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FIGURE 1a. Activity levels of marbled murrelets in Del Norte and Humboldt Counties. Open circles represent transects with no detections, small solid circles had moderate numbers of detections (<1 detection per 10 min census station), and large solid circles had high numbers of detections (≥1 detection per station). The distribution of old-growth and second-growth redwood dominated forests is also shown (Fox 1989).

FIGURE 1b. Activity levels of marbled murrelets and the distribution of old-growth and second-growth redwood dominated forests in Mendocino, Sonoma, and Marin Counties.

FIGURE 1c. Activity levels of marbled murrelets and the distribution of old-growth and second-growth redwood dominated forests in San Mateo and Santa Cruz Counties.

TABLE 1. Land area (ha) by forest classification summarized for three regions in northern California (Fox 1989). The Northern region includes Del Norte and Humboldt Counties, the Middle region includes Mendocino and Sonoma Counties, and the Southern region includes Marin, Napa, Alameda, San Mateo, Santa Cruz, Santa Clara, and Monterey Counties.

Region class	Forest classification			Total	Overall % by region
	Old-growth	Second-growth	Other habitat		
Northern					
Area (% by type)	58,078 (17)	262,744 (78)	16,360 (5)	337,181	38
% by region	69	36	30		
Middle					
Area (% by type)	7419 (2)	364,266 (92)	24,743 (6)	396,429	45
% by region	9	49	45		
Southern					
Area (% by type)	18,743 (13)	112,553 (78)	13,709 (9)	145,005	17
% by region	22	15	25		
Total area	84,240	739,564	54,811	878,615	100
Overall.					
% by type	10	84	6		

occurred on Simpson Timber Company lands north of the Klamath River in Del Norte County, especially along the Wilson Creek drainage. The other large tract of private timberland we surveyed was owned by Louisiana-Pacific. This area east of Trinidad had a few detections at stations west of old-growth stands in Redwood National Park.

We found no birds over extensive areas of Mendocino, Sonoma, and Marin Counties on 43 transects, with four exceptions (Stewart's Point, Usal Road, Hales Grove, and Russian Gulch State Park). The Hales Grove and Usal Road observations were near Westport State Park where three murrelets in breeding plumage were observed offshore on 22 July 1989 (D. Tobkin, pers. comm.). Murrelets have been seen inland near Russian Gulch State Park (Carter and Erickson 1988; Paton and Ralph 1988).

Habitat Relationships

The mean detection rate was greatest in forested areas dominated by old-growth, with 1.05/station (SE = 0.074, N = 1669 stations on 71 transects). Mixed age transects had 0.18/station (SE = 0.039, N = 693, 34 transects), while second-growth transects had the lowest detection rate of 0.02/station (SE = 0.006, N = 1335, 65 transects). There was a significant difference when comparing the detection rates among the three types of transects ($F = 103.56$, $p < 0.0001$).

The remaining old-growth redwood forest in California corresponds to where we found the highest concentrations of murrelets (Figs. 1a-c; Table 1; Fox 1989). Del Norte and Humboldt Counties had the largest stands of old-growth redwood in California, 58,078 ha or 69% of the state's 84,240 ha (Table 1; Fox 1989). The rest of the old-growth redwood exists primarily in San Mateo and Santa Cruz Counties (22%). Only 2% remains of the original old-growth in Mendocino, Sonoma, and Marin Counties, where the largest grove, Montgomery Woods State Park, is only 160 ha. In contrast, Del Norte and Humboldt Counties have four large parks: Jedediah Smith Redwoods (3543 ha); Prairie Creek Redwoods (4250 ha); Redwood National Park (8100 ha); and Humboldt Redwoods (8400 ha), all with high murrelet detection rates. Santa Cruz and San Mateo Counties also have relatively large parks with high activity levels: Butano (600 ha), Portola (570 ha) and Big Basin Redwoods (810 ha).

Transects with high activity levels tended to be in, or to the west of, stands of old-growth ≥250 ha (Fig. 2). Fifty-one percent of transects in or near stands ≥250 ha had

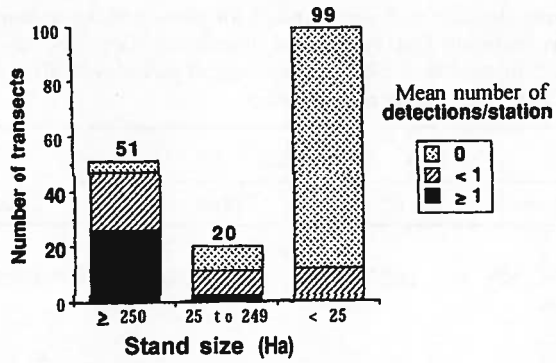

FIGURE 2. A comparison of the marbled murrelet detection rates in northern and central California to the size of the largest stand of old-growth ≤2 km east of the transect.

detection rates ≥ 1/station (N = 51). None of the transects near stands <25 ha had high activity levels, with most (87%, N = 99) having no detections. Over half of the transects near old-growth stands 25-249 ha in size (55%, N = 20) had detections, with 10% having high activity levels. However, murrelets were not recorded near all large stands of old-growth we surveyed. Stations near some stands at Humboldt Redwoods, the Northern California Coast Range Preserve (NCCRP, owned by the Nature Conservancy), and Whitehouse Creek west of Big Basin Redwoods State Park had no birds. Humboldt Redwoods is over 30 km from the ocean and murrelets appear to be concentrated at the north end of the park. The NCCRP is primarily Douglas-fir and located in Mendocino County where the birds may be extirpated. Murrelets were recorded in Whitehouse Creek in the past (G. Strachan, pers. comm.), but our lack of detections suggests this drainage is not a major flight corridor for birds travelling to Big Basin Redwoods.

We found a significant relationship between the size of canopy trees within 50 m of the survey station and the detection rate (F = 56.3, p < 0.001) (Table 2). Areas with high activity levels had a mean DBH of 86 cm, while areas with no activity averaged 48 cm DBH (Table 2).

The habitat type we surveyed most often had a redwood dominated canopy, with scattered Sitka spruce *(Picea sitchensis)*, western hemlock *(Tsuga heterophylla)*, and Douglas-fir. We detected murrelets in other habitat types, with birds heard along Myrtle Creek in the Six Rivers National Forest. The vegetation in this drainage was predominantly old-growth Douglas-fir and Port Orford cedar *(Chamaecyparis lawsoniana)*. We also heard birds in Monument Creek on Pacific Lumber Company lands, where grand fir *(Abies grandis)* and Douglas-fir were the dominant trees. We surveyed five Douglas-fir dominated

TABLE 2. Distance to the ocean and DBH of canopy trees of 170 marbled murrelet transects in northern and central California surveyed in 1988 and 1989, compared to three detection rates.

No. detections /station	$\bar{x}$	SD	Maximum	N
0				
Distance to ocean[1]	11.3	7.8	34	98
DBH of canopy trees[2]	44.7	34.1	190	
<1				
Distance to ocean	11.3	10.0	39	44
DBH of canopy trees	76.7	46.4	310	
≥1				
Distance to ocean	9.2	9.1	36	28
DBH of canopy trees	86.0	42.5	177	

[1] Shortest distance (km) from middle of transect to ocean.
[2] Mean DBH of canopy trees within a 50 m radius of the census point.

transects in the Kings Range in southern coastal Humboldt County and the North Coast Preserve, Mendocino County. We found no murrelets on these transects, even though the stands had old-growth characteristics similar in structure to stands having many detections, and were near the ocean.

Topographic Features

We found no significant effect of distance to ocean on number of detections. The mean distance from the ocean to the center of the transect was 9.2 km in high activity transects and 11.3 km in transects with moderate or low activity. This difference was not, however, significant ($F = 0.7$, $p > 0.05$) (Table 2). The ten most active transects were a mean distance of 6.5 km inland (SE = 1.4, max = 18 km). The farthest inland that birds were observed was 39 km, at Grizzly Creek Redwoods State Park.

Drainages with large tracts of old-growth near the ocean and in an east-west orientation tended to have high detection rates. The two most active areas were good examples: Godwood Creek in Prairie Creek State Park (8.7 detections/station) and along Redwood Creek in Redwood National Park (6.6 detections/station). It appeared that murrelets used drainages for flight corridors if they provided a relatively short route to the ocean and minimized the elevational gradient from the sea to the inland site. On the other hand, some murrelets used a low point in a ridge to minimize flight distances, rather than follow a meandering river. We observed this near Wheeler Creek on the Siskiyou National Forest in Oregon (Paton and Ralph 1988) and in the Kings Range over Panther Gap, an elevational gain of 840 m and a 35 km flight, rather than along the Eel River to the ocean, a 30 m elevation gain, but a 50 km flight.

DISCUSSION

In all probability, we did not find murrelets in some areas where they occurred, especially in areas with only one or two pairs. Little is known about the vocalizations of this species when comparing an isolated pair with a large concentration. Murrelets are best detected at an inland site by their calls. If isolated pairs tend to be quieter than larger groups, then finding solitary pairs would be more difficult.

The inland distribution pattern we found correlated well with that observed in the offshore surveys of Sowls et al. (1980) and H. Carter (pers. comm.), who found concentrations from the Oregon border to Eureka and from Half Moon Bay to Santa Cruz. Our records also corresponded with historical information compiled by Carter and Erickson (1988).

We documented use of several areas in California where murrelets had not been recorded previously. There were no records in the Myrtle Creek drainage, in Del Norte County, before our work on Six Rivers National Forest, and records from Simpson Timber Company lands along Wilson Creek were also new. However, birds had been recorded in an area adjacent to the Simpson lands, near Terwer Valley (Carter and Erickson 1988).

Probably the most significant discovery was finding the large concentration on Pacific Lumber Company lands, the largest tract of old-growth redwood owned by a private timber company. Prior to our study, there were only early historical records for this part of Humboldt County: Joseph Grinnell had observed murrelets in Carlotta in 1923 and 1929 (Grinnell and Miller 1944), 5-15 km southwest of Pacific Lumber Company lands.

There are no known historical records for Mendocino, Sonoma, or Marin Counties at inland localities, with the exception of one near Fort Bragg (Carter and Erickson 1988). In addition, a 1989 survey of offshore waters found no murrelets off Mendocino County (H. Carter, pers. comm.). However, we believe the redwood forests of these three counties provided suitable nesting habitat historically and that birds probably bred there. Redwood logging mills were operating in Monterey, Santa Cruz, Santa Clara, San Mateo, Alameda, Sonoma, and Marin Counties by the 1840's, with the eastern side of the Santa

Cruz mountains and the Oakland hills all logged by 1870 (Green 1985). Since much of the old-growth forest was gone by 1900, early ornithologists had no chance to describe their original avifauna. If one assumes that murrelets inhabited all old-growth redwood forests that once existed in California, and that only 10% of the old-growth is still standing (Green 1985; Fox 1989), then they have very likely experienced a dramatic population decline.

Areas with murrelet observations from the 1920's and 1930's that were subsequently logged now have few or no birds. The area east of Trinidad had many murrelets in 1916 (Dawson 1923) and was a collecting site for ornithologists in the 1920's (Anon. 1928). Yet we observed no birds near Trinidad in 1988, with one possible exception, a possible sighting at a station within 0.1 km of the coast at Patrick's Point State Park.

Areas with high activity levels were primarily old-growth forests in state and national parks protected from logging. Most of the high volume old-growth redwood in the state (36,200 ha) is found in parks, accounting for 63% of the state's standing old-growth redwood volume in 1983 (Green 1985).

Commercial timberlands tend to be located in drier, higher elevation sites than the parks, and the size of canopy trees tends to be smaller. Very few large contiguous tracts of old-growth redwood occur on private timberlands. However, at least one large concentration of birds occurs on private commercial timberlands, an area scheduled to be harvested in the next 20 years. The largest old growth stand, 1200 ha, is in the Salmon Creek drainage, where we found relatively high numbers of detections (3.4/station). The majority of private timberlands we surveyed had very fragmented landscapes, with most stands of old-growth less than 25 ha in size and with moderate detection rates at best.

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APPENDIX. Marbled murrelet transects surveyed in 1988 and 1989. The location refers to the center station on the transect. The total number of stations surveyed, total number of murrelet detections, shortest distance from the ocean to the center station, and the dominant age of the forest near the transect are given.

Study site	County[1]	Owner[2]	Legal description T	R	S	No. of stations	No. of detections	Distance inland (km)	Stand age[3]
Alder Camp	DeNo	NPS	13N	1E	8	22	10	1	OG
Boy Scout Trail	DeNo	SP	16N	1W	13	22	55	6	OG
Camp Klamath	DeNo	Misc	13N	1E	10	22	2	2	MG
Damnation Trail	DeNo	NPS	15N	1E	30	22	12	1	OG
H500/P500 Haul Rd.	DeNo	TimC	14N	2E	5	19	0	13	MG
Hiouchi	DeNo	Misc	17N	1E	3	22	7	16	OG
K-One Haul Road	DeNo	TimC	14N	2E	18	20	0	13	MG
Kermit Miller Exch.	DeNo	USFS	17N	1E	8	41	0	10	MG
Klamath	DeNo	NPS	13N	1E	33	22	5	1	MG
Klamath Mill area	DeNo	TimC	13N	1E	2	18	1	5	MG
Mill Cr. Campground	DeNo	SP	15N	2E	16	18	2	3	MG
Myrtle Creek	DeNo	USFS	16N	1E	4	30	11	14	MG
N. Redwood Ex. For.	DeNo	USFS	14N	1E	21	55	134	2	OG
Red Mountain	DeNo	USFS	13N	2E	14	22	0	16	SG
Requa	DeNo	NPS	14N	1E	29	22	3	0	OG
Rowdy Creek	DeNo	Misc	18N	1E	36	20	0	9	SG
S. of Crescent City	DeNo	Misc	15N	1W	12	20	5	1	SG
S. Redwood Ex. For.	DeNo	USFS	14N	1E	27	44	71	3	OG
S. Fork Smith River	DeNo	Misc	16N	1E	13	20	0	13	MG
Snavely Road	DeNo	Misc	18N	1E	16	20	0	12	SG
U-Ten Haul Road	DeNo	TimC	14N	2E	28	18	0	14	MG
Upper Corners	DeNo	TimC	14N	2E	30	20	0	11	MG
W-Ten Haul Road	DeNo	TimC	15N	1E	32	20	11	5	MG
Walker Road	DeNo	SP	17N	1W	31	20	29	9	OG
Wilson Creek	DeNo	TimC	14N	1E	17	16	14	3	MG
A-9 Road	Humb	NPS	10N	1E	35	27	14	5	OG
A-Line Haul Road	Humb	TimC	8N	1E	8	22	0	2	MG
Arcata City Forest	Humb	Misc	6N	1E	27	22	0	8	SG
B-900 Haul Road	Humb	TimC	12N	3E	17	22	0	18	MG
Bair Road	Humb	Misc	7N	3E	23	20	0	27	SG
Bald Hills Road	Humb	NPS	10N	1E	1	22	28	6	OG
Bear River Ridge	Humb	Misc	1N	1W	17	20	0	18	SG
Bear River Valley	Humb	TimC	1S	1W	11	22	0	19	SG
Big Tree	Humb	SP	1S	1E	25	18	5	26	OG
Bull Creek	Humb	SP	2S	1E	11	22	0	23	OG
Cal-Barrel Rd.	Humb	SP	11N	1E	1	17	39	4	OG

APPENDIX. Continued.

Study site	County[1]	Owner[2]	Legal description T	R	S	No. of stations	No. of detections	Distance in land (km)	Stand age[3]
Camp Snow Road	Humb	Misc	6N	3E	17	22	0	23	SG
Capetown	Humb	Misc	1N	3W	23	20	0	2	SG
Devil's Creek	Humb	NPS	9N	2E	16	22	1.2	17	OG
East C-line Road	Humb	NPS	10N	2E	31	33	8	10	OG
Elk River	Humb	Misc	4N	1W	22	20	2	10	SG
Elk's Head Spring	Humb	TimC	3N	1E	14	20	20	20	OG
Ferndale	Humb	Misc	2N	2W	22	20	1	8	SG
Fieldbrook	Humb	Misc	6N	1E	1	20	3	10	SG
Freshwater-Kneeland	Humb	TimC	4N	1E	1	29	0	19	SG
Geneva Road	Humb	NPS	11N	2E	19	22	5	9	MG
Gold Bluffs Beach	Humb	SP	12N	1E	33	20	34	0	OG
Greenlaw Creek	Humb	TimC	1N	1E	36	22	1	29	OG
Grizzly Creek	Humb	SP	1N	2E	10	75	61	36	OG
Hidden Spring	Humb	SP	2S	3E	7	11	0	28	OG
Honeydew	Humb	Misc	2S	1E	28	20	12	21	SG
Horse Trail	Humb	NPS	10N	1E	3	22	23	3	OG
Hwy 101-Prairie Cr.	Humb	SP	12N	1E	26	20	109	3	OG
Jacoby Creek	Humb	Misc	5N	1E	11	19	0	13	SG
James Irvine Trail	Humb	SP	11N	1E	2	17	148	4	OG
Kings Peak	Humb	Misc	4S	1E	9	22	0	4	SG
Lawrence Creek	Humb	TimC	3N	2E	8	9	5	23	MG
LB Johnson Grove	Humb	NPS	11N	1E	26	27	16	4	OG
Liscomb Hill Road	Humb	Misc	6N	2E	17	20	0	14	SG
Little River	Humb	TimC	7N	1E	7	20	0	4	SG
Long Ridge	Humb	TimC	1S	1W	16	18	0	14	SG
Look Prairie	Humb	SF	1S	2E	20	22	15	30	OG
Lost Man Creek	Humb	NPS	11N	1E	24	20	69	5	OG
Lower Freshwater Cr.	Humb	TimC	4N	1E	26	22	0	18	SG
Lower Mitchell Road	Humb	Misc	5N	1E	31	20	0	8	SG
Lower Redwood Cr.	Humb	NPS	11N	1E	2	33	218	4	OG
M-line, Redwood NP	Humb	NPS	9N	2E	8	22	0	14	OG
M-Line Haul Road	Humb	TimC	8N	2E	6	22	5	10	SG
Maple Creek	Humb	Misc	5N	2E	2	20	0	21	SG
Maple Creek-LP	Humb	TimC	8N	1E	12	21	0	9	SG
McCready Gulch	Humb	TimC	5N	1E	34	22	0	14	SG
Mill Creek	Humb	TimC	2S	2W	17	16	14	5	MG
Miranda	Humb	SP	2S	3E	34	22	0	27	MG
Miranda-Myers Flat	Humb	Misc	2S	3E	28	22	0	27	MG
Monument Creek	Humb	TimC	1N	1E	19	16	2	21	SG
Monument Ridge	Humb	Misc	1N	1W	24	20	0	20	SG
North 101 Bypass	Humb	NPS	12N	1E	13	22	0	5	SG
NW Ridge Trail	Humb	SP	12N	1E	10	20	43	2	OG
Owl Creek	Humb	TimC	2N	2E	15	22	7	32	OG
Patrick's Point SP	Humb	SP	9N	1W	26	18	14	0	SG
Pepperwood	Humb	Misc	1N	1E	32	22	4	31	OG
Piercy	Humb	SP	5S	3E	35	18	0	19	OG
R-Line Haul Road	Humb	TimC	8N	1E	25	22	0	8	MG
Redcrest	Humb	TimC	1S	2E	8	22	0	32	SC
Redcrest-Federation	Humb	SP	1S	2E	23	54	58	35	OG
Redway	Humb	SP	4S	3E	11	22	0	21	OG
Redwood Valley	Humb	Misc	7N	3E	17	22	0	23	SG
S. of Orick	Humb	NPS	10N	1E	4	33	11	2	OG
S. of Petrolia	Humb	Misc	2S	1W	33	20	0	9	SG
Salmon Creek	Humb	TimC	3N	1E	20	20	68	10	OG
Shaw Creek	Humb	TimC	3N	2E	20	22	0	28	OG
Skunk Cabbage Cr.	Humb	NPS	11N	1E	28	22	44	2	OG

APPENDIX. Continued.

Study site	County[1]	Owner[2]	Legal description T	R	S	No. of stations	No. of detections	Distance inland (km)	Stand age[3]
South 101 Bypass	Humb	NPS	12N	2E	31	20	0	6	SG
Big Tree/S. Fork	Humb	SP	1S	2E	29	20	7	32	OG
Stone Lagoon	Humb	Misc	10N	1E	29	22	0	1	MG
Stone-Big Lagoon	Humb	SP	10N	1E	16	23	1	1	MG
T-Line Haul Road	Humb	TimC	8N	1E	16	22	0	6	MG
Tall Trees Grove	Humb	NPS	9N	1E	1	21	41	8	OG
Ten Tappo Trail	Humb	SP	12N	1E	11	20	80	3	OG
West Ridge Trail	Humb	SP	11N	1E	2	19	67	5	OG
Westside Haul Rd.	Humb	NPS	10N	1E	8	33	1	2	OG
Wilder Ridge	Humb	Misc	3S	1E	20	20	0	10	SG
Yeager Creek	Humb	TimC	2N	1E	11	22	9	26	OG
Adm. Standley Grove	Mend	SP	21N	16W	26	22	0	17	OG
Bear Harbor	Mend	BLM	24N	19W	25	11	0	0	SG
Branscomb	Mend	Misc	21N	17w	26	20	0	4	SG
Caspar Creek	Mend	TimC	18N	17W	9	22	0	6	SG
Eureka Road	Mend	Misc	12N	16W	13	20	0	8	SG
Fish Rock	Mend	Misc	11N	15W	3	20	0	6	SG
Fort Bragg Sher. Rd.	Mend	Misc	18N	17W	2	20	0	8	SG
Four Corners	Mend	Misc	24N	19W	11	22	0	2	SG
Hales Grove	Mend	Misc	23N	17W	17	22	1	6	SG
Hendy Grove	Mend	SP	14N	15W		22	0	19	OG
Hwy 20-Middle	Mend	Misc	17N	15W	8	22	0	22	SG
Hwy 20-West	Mend	Misc	8N	16W	31	22	0	10	SG
Jackson SF	Mend	SF	18N	17W	2	22	0	5	SG
Maillard Redwoods	Mend	SP	12N	13W	8	22	0	21	OG
Mendocino Woodlands	Mend	SP	17N	17W	24	20	0	8	OG
Montgomery Woods	Mend	SP	16N	14W	23	20	0	34	OG
Mountain View	Mend	Misc	13N	16W	25	22	0	12	SG
Navarro River	Mend	Misc	15N	16W	16	22	0	6	SG
No. Coast Preserve	Mend	Misc	22N	16W	28	22	0	15	OG
Philo-Greenwood	Mend	SP	14N	14W	19	11	0	11	OG
Rockport	Mend	Misc	22N	18W	23	22	0	1	MG
Russian G/Van Damme	Mend	SP	16N	17W	4	30	24	4	OG
Sanctuary Forest	Mend	TimC	5S	2E	34	22	0	5	MG
Standish Hickey	Mend	SP	23N	17W	3	22	0	11	OG
Ten Mile Road	Mend	Misc	19N	17W	4	20	0	2	SG
Ukiah-Mendocino Rd.	Mend	Misc	16N	16W	4	20	0	12	SG
Usal Road	Mend	Misc	23N	18W	27	22	1	1	SG
Annopolis Road	Son0	Misc	10N	14W	15	22	0	3	SG
Armstrong Redwoods	Son0	SP	8N	10W	7	20	0	14	OG
Cazedero Hwy	Son0	Misc	8N	11W	18	22	0	5	SC
Fort Ross	Son0	TimC	8N	12W		16	0	1	SG
Joy Road	Son0	Misc	6N	10W	1	20	0	10	SG
Kruse Rhododendron	Son0	SP	9N	13W	28	22	0	1	OG
Russian River	Son0	Misc	7N	10W	6	22	0	11	SG
Stewart's Point	Son0	Misc	9N	13W	6	22	1	3	SG
Tin Barn Road	Son0	Misc	9N	13W	15	22	0	6	SG
Kent Lake	Mari	SP	IN	8W		20	0	6	MC
Muir Woods NP	Mari	NPS	1N	7W		18	0	3	OG
SP Taylor	Mari	SP	2N	8W		20	0	8	MG
Alpine Road	SaMa	Misc	7S	2W	30	20	0	15	MG
Butano Creek	SaMa	Misc	8S	4W	17	10	8	8	OG
Butano SP	SaMa	SP	8S	4W	29	8	1	5	OG
Filoli	SaMa	Misc	5S	4W	31	20	0	10	SG
Gazos Creek	SaMa	SP	8S	4W	28	18	27	6	OG
Goat Hill	SaMa	SP	8S	4W	27	26	16	5	OG

APPENDIX. Continued.

Study site	County[1]	Owner[2]	Legal description T	R	S	No. of stations	No. of detections	Distance inland (km)	Stand age[3]
Heritage-Alpine	SaMa	Misc	8S	4W	1	16	6	13	MG
Iverson Trail	SaMa	SP	8S	3W	8	36	107	18	OG
Memorial Park	SaMa	SP	7S	4W	34	12	7	10	OG
Pescadero-Haul Rd.	SaMa	Misc	8S	4W	1	19	28	14	MG
Pilarcitos Lake	SaMa	Misc	4S	5W	32	14	0	15	SG
Portola SP	SaMa	SP	8S	3W	8	20	27	18	OG
Ridge Trail	SaMa	SP	8S	1W	22	16	5	10	OG
San Gregoria-Hwy 84	SaMa	Misc	7S	4W	14	20	0	11	MG
Whitehouse Creek	SaMa	SP	8S	5W		12	0	4	OG
Aptos-Nisene Marks	SaCr	SP	10S	1E		36	0	7	MG
Bear Creek Road	SaCr	Misc	9S	2W	16	22	0	19	SG
Big Basin Hdqtrs.	SaCr	SP	8S	3W	33	36	64	12	OG
Brown's Vallev Road	SaCr	Misc	10S	1E	31	20	0	9	SG
Hecker Pass	SaCr	Misc	11S	3E		22	0	14	SG
Henry Cowell	SaCr	SP	10S	2W	26	30	0	8	OG
Hwy 9	SaCr	Misc	10S	2W	29	20	0	8	OG
Lodge Road	SaCr	SP	9S	3W	4	48	28	11	OG
San Lorenzo River	SaCr	Misc	9S	3W	1	22	0	14	SG
Sunset Trail	SaCr	SP	9S	4W	2	10	12	8	OG
Swanton Road	SaCr	Misc	10S	3W	2	12	0	1	OG
Waddell Creek	SaCr	SP	9S	4W	23	22	61	4	MG
Zayante Creek	SaCr	Misc	9S	1W	30	22	0	9	SG

[1]Counties: DeNo = Del Norte, Humb = Humboldt, Mend = Mendocino, Sono = Sonoma, Mari = Marin, SaMa = San Mateo, SaCr = Santa Cruz.

[2]Owners: BLM = Bureau of Land Management, Misc = miscellaneous private owners, NPS = National Park Service, SF = California State Forest, SP = California State Park, TimC = Timber Company, USFS = US Forest Service.

[3]Stand age (dominant age of forest near the transect): MG = Mixed ages, fragmented landscape of patches of old-growth, second-growth, and clearcuts; SG = Second growth, the dominant trees are less than 200 years old; OG = the dominant trees in the overstory are over 200 years old.

[4]Observer was not positive of identification.

Chapter 6

Characteristics of Marbled Murrelet Nest Trees and Nesting Stands

Thomas E. Hamer[1] **S. Kim Nelson**[2]

Abstract: We summarize the characteristics of 61 tree nests and nesting stands of the Marbled Murrelet (*Brachyramphus marmoratus*) located from 1974 to 1993 in Alaska, British Columbia, Washington, Oregon, and California. Evidence of breeding 30-60 km inland was common in California, Oregon, and Washington. Nesting greater distances from the coast may have evolved to avoid nest predation by corvids and gulls which are more abundant in coastal areas. In California, Oregon, Washington, and British Columbia, murrelets nested in low elevation old-growth and mature coniferous forests, with multi-layered canopies (>2), a high composition of low elevation conifer trees ($\bar{x}$ = 91 percent) and, on the lower two-thirds of forested slopes, with moderate gradients ($\bar{x}$ = 23 percent slope). Stand canopy closure was often low ($\bar{x}$ = 50 percent), suggesting use of canopy openings for access to nest platforms. Nests in the Pacific Northwest were typically in the largest diameter old-growth trees available in a stand ($\bar{x}$ = 211 cm); many nest trees were in declining conditions and had multiple defects. It is likely that western hemlock and Sitka spruce constitute the most important nest trees, with Douglas-fir important south of British Columbia. Many processes contributed to creating the nest platforms observed. Mistletoe blooms, unusual limb deformations, decadence, and tree damage, commonly observed in old-growth and mature stands, all appear to create nest platforms. Therefore, the stand structure and the processes within a stand may be more important than tree size alone in producing nesting platforms and suitable habitat. Moss cover was also an important indicator of suitable nesting habitat.

We summarize the characteristics of 61 tree nests and nesting stands of the Marbled Murrelet (*Brachyramphus marmoratus*) located from 1974 to 1993 in Alaska, British Columbia, Washington, Oregon, and California (*table 1*). The majority of the nest site information was unpublished and obtained directly from field biologists who were conducting inland studies on the murrelet. The preponderance of unpublished nest information is due to the recent discovery of most nest sites. The only other summary was completed by Day and others (1983), based on two tree nests and five ground nests of the Marbled Murrelet.

Because of the murrelet's small body size, dense forested nesting habitat, cryptic plumage, crepuscular activity, fast flight speed, and secretive behavior near nests, its nests have been extremely difficult to locate. The first tree nest was located only in 1974 (Binford and others 1975), despite decades of searching by ornithologists in North America. Although a significant amount of nesting habitat information has been collected over the past four years, the efficiency of locating active nests is still low. Experiences gained from nest search efforts have led to the development and refinement of methodologies for locating new nests (Naslund and Hamer 1994).

Fortunately, an increased understanding of murrelet nesting ecology has allowed biologists to locate nests that have not been used for several months or, in some cases, several years. This involves searching for old nest cup depressions, worn spots or "landing pads" created on moss-covered branches by visiting adults, old fecal rings, and habitat features commonly associated with suitable nesting platforms. In addition, biologists learned that eggshells could be located in the duff and litter of nest platforms unused for a year or more.

Intensive search efforts by biologists across the Pacific Northwest have led to the discovery of 65 tree nests since 1974, with 63 (95 percent) located since 1990. Although this is still a relatively small sample size considering the large geographic area these nests represent, the sample does allow a characterization of the tree nests and nesting stands.

The two species of murrelets in the genus *Brachyramphus* (Kittlitz's and Marbled) display a complete dichotomy in their choice of nesting habitat. The Kittlitz's (*B. brevirostris*) murrelet nests up to 30 km inland on the ground on exposed rocky scree slopes, often at higher elevations. The Marbled Murrelet is unique among Alcids in selecting almost exclusively to nest on large limbs of dominant trees, which can be located long distances from the marine environment.

Long considered a subspecies of the Marbled Murrelet, the Asian race of the Marbled Murrelet (*B.m. perdix* Pallas) is distributed from the Kamchatka Peninsula south to Japan. New genetic evidence (Friesen and others 1994a) indicates the it is most likely a distinct species from the Marbled Murrelet. From the little evidence collected to date, it may be an obligate tree nesting seabird (Konyukhov and Kitaysky, this volume), with its range coinciding closely with the coastal coniferous forests of Russia and Japan (Kuzyakin 1963).

At a few sites in Alaska and Russia, at or beyond the margin of Pacific Coastal coniferous forests, the Marbled Murrelet nests on the ground. From an examination of the summer distribution of the species, approximately 3 percent of the Alaskan murrelet population may nest on the ground (Piatt and Ford 1993). These nests have been found at

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Table 1—Records of nest trees and nest stands of the Marbled Murrelet found in North America from 1974 to 1993

State/province Record no.	Location	Date found	Sources
California			
1	Big Basin Redwood State Park	7 Aug. 1974	Binford and others 1975
2	Big Basin Redwood State Park	3 Jun. 1989	S.W. Singer (pers. comm.)
3	Big Basin Redwood State Park	28 Jun. 1989	S.W. Singer (pers. comm.)
4	Big Basin Redwood State Park	5 May 1991	S.W. Singer (pers. comm.)
5	Big Basin Redwood State Park	24 May 1992	S.W. Singer (pers. comm.)
6	Jedediah Smith State Park	9 Aug. 1993	Hamer (pers. obs.)
7	Prairie Creek State Park	23 Jul. 1993	Hamer (pers. obs.)
8	Bell-Lawrence	14 Oct. 1993	Chinnici (pers. comm.)
9	Elk Head Springs	16 Sep. 1992	Chinnici (pers. comm.)
10	Shaw Creek	30 Sep. 1992	Chinnici (pers. comm.)
Oregon			
11	Boulder and Warnicke Creeks	17 Jun. 1992	Nelson (pers. obs.)
12	Cape Creek	23 May 1991	Nelson (pers. obs.)
13	Iron Mountain	30 May 1992	Nelson (pers. obs.)
14	Five Mile Flume Creek	28 Sep. 1993	Nelson (pers. obs.)
15	Five Rivers	19 May 1990	Nelson (pers. obs.)
16	Five Rivers	14 Jun. 1991	Nelson (pers. obs.)
17	Five Rivers	23 Sep. 1993	Nelson (pers. obs.)
18	Green Mountain	17 Jun. 1993	Nelson (pers. obs.)
19	Green Mountain	22 Sep. 1993	Nelson (pers. obs.)
20	Siuslaw River	13 Aug. 1991	Nelson (pers. obs.)
21	Siuslaw River	30 Aug. 1991	Nelson (pers. obs.)
22	Valley of the Giants	29 Jun. 1993	Nelson (pers. obs.)
23	Valley of the Giants	29 Jun. 1993	Nelson (pers. obs.)
24	Valley of the Giants	24 Aug. 1993	Nelson (pers. obs.)
25	Valley of the Giants	24 Aug. 1993	Nelson (pers. obs.)
26	Valley of the Giants	24 Aug. 1993	Nelson (pers. obs.)
27	Valley of the Giants	21 Sep. 1993	Nelson (pers. obs.)
28	Valley of the Giants	25 Aug. 1993	Nelson (pers. obs.)
29	Valley of the Giants	21 Sep. 1993	Nelson (pers. obs.)
30	Valley of the Giants	12 Jul. 1990	Nelson (pers. obs.)
31	Valley of the Giants	14 May 1991	Nelson (pers. obs.)
32	Valley of the Giants	14 Jul. 1992	Nelson (pers. obs.)
Washington			
33	Nemah River	7 May 1993	Ritchie (pers. comm.)
34	Lake 22 Creek	9 Jul. 1990	Hamer (pers. obs.)
35	Lake 22 Creek	2 Aug. 1990	Hamer (pers. obs.)
36	Dungeness River	10 Sep. 1990	Holtrop (pers. comm.)
37	Heart of the Hills Trail	26 Jul. 1991	Hamer (pers. obs.)
38	Jimmey Come Lately Creek	24 Jul. 1991	Holtrop (pers. comm.)

continues

Table 1—continued

State/province Record no.	Location	Date found	Sources
British Columbia			
39	August Creek, Vancouver Is.	12 Sep. 1993	Burger (pers. comm)
40	Carmanah Creek, Vancouver Is.	2 Oct. 1992	Jordan and Hughes (in press)
41	Walbran Creek, Vancouver Is.	12 Oct. 1992	Jordan and Hughes (in press)
42	Walbran Creek, Vancouver Is.	3 Aug. 1990	Manley and Kelson (in press)
43	Walbran Creek, Vancouver Is.	24 Aug. 1991	Manley and Kelson (in press)
44	Walbran Creek, Vancouver Is.	25 Aug. 1992	Jordan and Hughes (in press)
45	Caren Range	1 Aug. 1993	P. Jones (pers. comm)
46	Clayoquot River	1993	Kelson (pers. comm.)
47	Megin River	1993	Manley (pers. comm.)
Alaska			
48	Afognac Is., Alaska Peninsula	26 Jul. 1992	Naslund and others (in press)
49	Afognac Is., Alaska Peninsula	6 Aug. 1992	Naslund and others (in press)
50	Kodiak Is., Alaska Peninsula	17 Aug. 1992	Naslund and others (in press)
51	Kodiak Is., Alaska Peninsula	17 Aug. 1992	Naslund and others (in press)
52	Naked Is., Prince William Sound	13 Jun. 1991	Naslund and others (in press)
53	Naked Is., Prince William Sound	25 Jun. 1991	Naslund and others (in press)
54	Naked Is., Prince William Sound	6 Jul. 1991	Naslund and others (in press)
55	Naked Is., Prince William Sound	26 Jul. 1991	Naslund and others (in press)
56	Naked Is., Prince William Sound	1 Jul. 1991	Naslund and others (in press)
57	Naked Is., Prince William Sound	25 May 1992	Naslund and others (in press)
58	Naked Is., Prince William Sound	20 Jul. 1992	Naslund and others (in press)
59	Naked Is., Prince William Sound	5 Aug. 1992	Naslund and others (in press)
60	Naked Is., Prince William Sound	6 Aug. 1992	Naslund and others (in press)
61	Naked Is., Prince William Sound	9 Jun. 1991	Naslund and others (in press)

Augustine Island (Cook Inlet), Kodiak Island, the Barren Islands, and the Kenai Peninsula (Day and others 1983, Mendenhall 1992, Simons 1980). All of these nests were located in areas of talus where surrounding rocks formed a protected area for the nests, or in areas dominated by alder. The egg was laid on existing mat vegetation or bare soil. Whereas most of these sites were above the local tree line and had only low-lying mat vegetation, the Kenai site had a forested area on a nearby slope. An additional ground nest found on Prince of Wales Island in southeastern Alaska in 1993 was located on a platform of moss covering three intertwined roots of a western hemlock (*Tsuga heterophylla*) tree at the top of an 11-meter high cliff (Ford and Brown 1994). The nest had many of the characteristics of a tree nest when approached from downslope, but was similar to a ground nest when approached from up slope.

Methods

We compiled information from 61 nest stands and nest trees throughout the geographic range of the Marbled Murrelet in North America using published and unpublished information. Information from three additional tree nests in Alaska were not obtained for this review. We did not include data from ground nests in this summary. We summarized tree and stand characteristics from 14 tree nests in Alaska (Naslund and others, in press), nine nests in British Columbia (Burger, pers. comm.; P. Jones, pers. comm.; Jordan and others in press; Kelson, pers. comm.; Manley, pers. comm.; Manley and Kelson, in press), six nests in Washington (Hamer, unpubl. data; Holtrop, pers. comm.; Ritchie, pers. comm.), 22 nests in Oregon (Nelson, unpubl. data), and 10 nests in California (Binford and others, 1975; Chinnici, pers. comm.; Folliard, pers. comm.; Hamer, unpubl. data; S.W. Singer, pers. comm.; Singer and others, 1991) (*table 1*).

The sample size for each nest characteristic varied because some variables were not measured at some nest sites, or the information was not available to us. A protocol that outlined a methodology for measuring the structure of nests was not available until 1993 (Hamer 1993), so some characteristics of earlier nests were not measured. Stands were delineated and stand sizes calculated generally by defining stands as a contiguous group of trees with no gaps larger than 100 m. Stand ages were derived from stand information data bases of the landowners or by aging individual trees in the stand using increment bores. Limb diameters were generally reported with the moss cover on the limb included in the measurement. Nest platform lengths were measured as the length of the nest branch until it was judged to be too narrow to support a nest (<10 cm).

We calculated the range, mean, and standard deviation for each nest and stand characteristic for each state or province. In addition, we pooled the sample of nests for what we term the "Pacific Northwest", using data from nests located in California, Oregon, Washington, and British Columbia (*tables 2* and *3*). Nests located in Alaska were treated as a separate sample (*tables 2* and *3*).

We chose to segregate the data using state or provincial boundaries because different forest types generally occur within these boundaries. Forest types in California within the murrelet's breeding range were predominately coastal redwood (*Sequoia sempervirens*). Oregon had fire regenerated stands dominated by Douglas-fir (*Pseudotsuga menziesii*), and in Washington, mixed forests of western red cedar (*Thuja plicata*), western hemlock, Douglas-fir, and Sitka spruce (*Picea sitchensis*), created by the combined forces of fire and wind, covered the majority of the landscape. British Columbia was similar to Washington, with the addition of yellow cedar (*Chamaecyparis nootkatensis*), found in stands at higher elevations. Forest types in Alaska were very distinct, with many stands dominated by mountain hemlock (*Tsuga mertensiana*) which were small in stature and diameter.

Results

Landscape Characteristics

Distance to Salt Water

A sample of 45 nests in the Pacific Northwest were located a mean distance of 16.8 km inland (*table 2, fig. 1*). Nests in California were found a mean distance of 13 km from salt water; the farthest inland nest in California was located 28.9 km inland (*table 2*). The farthest inland nest in Oregon was located 40 km from the sea. This coincides with a historical record of a downy young found on the ground 40 km inland on the South Fork of the Coos River in Coos County (Nelson and others 1992). In Washington, nests were located a mean distance of 16 km inland. Other information from Washington indicated nesting at stands further inland than known nest sites. A small downy chick was located by the senior author on the ground along a trail on the east shore of Baker Lake in 1991, 63 km from the ocean. Another downy chick was located 45 km inland in Helena Creek, in Snohomish County (Reed and Wood 1991). Six additional records of eggs, downy young, and fledglings found 29-55 km inland in Washington were compiled by Leschner and Cummins (1992a), and Carter and Sealy (1987b).

In British Columbia, nest trees were located a mean distance of 11.5 km from the Pacific. In addition, there was a record of a fledgling found on the ground near Hope, British Columbia, 101 km from salt water (Rodway and others 1991). This is the farthest inland distance recorded for Marbled Murrelets in North America. Nest trees in Alaska were typically located close to the coast, with a mean distance of 0.5 km (*table 2*), corresponding to the closer inland distribution of suitable nesting habitat.

Elevation

The mean elevation of nest trees from a sample of 45 murrelet nests in the Pacific Northwest was 332 m (*table 2*). In Alaska nest trees were low in elevation with a mean of 96 m and a maximum of 260 m (*table 2*).

Aspect

Nest stands in the Pacific Northwest occur on a variety of aspects. Twenty-six percent of the stands had northeast aspects, 12 percent southeast, 28 percent southwest, 12 percent northwest, and 21 percent were on flat topography with no aspect (*table 2*). In Alaska, 93 percent of the nest stands had westerly aspects (NW, W, or SW), with the majority (50 percent) facing northwest.

Slope

Nests in the Pacific Northwest were located on slopes with moderate gradients, with a mean of 23 percent. Slope gradients for nests in Alaska were higher than nests for the Pacific Northwest with a mean slope of 69 percent.

The majority of nests in the Pacific Northwest (80 percent) were located on the lower one-third or middle one-third of the slope. Nest stands in Alaska were located low in elevation, but were usually located on the top one-third of the slope, unlike nests in the southern part of the range. Nest stands in Alaska have been described as being located on gradual or moderate slopes (Naslund and others, in press).

Forest Characteristics

Age

For a sample of 16 nests in the Pacific Northwest the mean stand age was 522 years with the youngest stand age reported as 180 years old (*table 2*). The oldest stand was 1,824 years old located on the mainland coast of British Columbia, and was dated using nearby stumps from a recent clear-cut. To date, all 61 tree nests found in North America have been found in stands described as old-growth or mature forests.

Tree Size

The mean d.b.h. of trees in nest stands was not reported for many sites. Nest stands in Washington and Oregon were characterized by large diameter trees ($\bar{x}$ = 47.7 cm), a mean density of large trees (>46 cm d.b.h.) of 93.8/ha, an average

Table 2—The mean, standard deviation, range, and sample size for the forest stand characteristics of Marbled Murrelet tree nests located in North America. The Pacific Northwest data include nests located in California, Oregon, Washington, and British Columbia. For some characteristics, either no data were available for that state or province, or the sample size was too small to calculate the mean and range. Sample sizes for each variable are shown in parenthesis

Characteristics	California $n = 10$	Oregon $n = 20$	Washington $n = 6$	British Columbia $n = 9$	Pacific Northwest $n = 45$	Alaska $n = 14$
Aspect (°)	210±122	147±63	180±121	—	166±92	267±66
	45-352	48-253	39-331	—	35-39	270-360
	(7)	(19)	(5)		(33)	(14)
Elevation (m)	286±125	379±152	348±176	321±310	332±206	96±50
	45-46	61-646	15-610	14-1097	14-1097	30-260
	(10)	(10)	(6)	(9)	(35)	(14)
Slope (pct)	18±14	41±27	21±13	3±4	23±23	69±16
	0-41	10-87	0-39	0-11	0-87	47-100
	(7)	(10)	(6)	(7)	(30)	(10)
Slope position[1]	1±0	2.1±0.9	1.3±0.5	1.3±0.7	1.5±0.8	—
	1-1	1-3	1-2	1-3	1-3	—
	(7)	(10)	(6)	(7)	(30)	
Stand size (ha)	352±432	80±49	354±401	—	206±351	31±26
	100-1100	3-149	5-990	—	3-1100	4-63
	(4)	(9)	(5)		(16)	(10)
Pct. composition low elevation trees[2]	100±0	100±0	90±9	64±29	91±19	64±14
	100-100	100-100	78-100	20-100	20-100	39-91
	(10)	(10)	(5)	(6)	(31)	(8)
Total tree density (number/ha)	235±178	120±72	136±28	297±136	182±132	575±240
	92-504	48-282	84-162	148-530	48-530	295-978
	(5)	(10)	(5)	(5)	(25)	(8)
Canopy height (m)	88±0	59±8	54±5	—	64±16	23±4
	88-88	48-75	44-59	—	38-88	16-30
	(5)	(9)	(5)		(20)	(14)
Canopy layers (number)	—	2.2±0.4	3.4±0.5	—	2.5±0.7	—
	—	2-3	3-4	—	2-4	—
		(10)	(4)		(20)	
Canopy closure (pct)	39±6	43±27	69±18	—	49±23	62±15
	25-48	12-99	36-88	—	12-99	40-85
	(7)	(8)	(5)		(21)	(12)
Distance to coast (km)	13.1±8.3	25.8±9.7	15.9±13	11.5±3.7	16.8±10.6	0.5±0.3
	4.9-28.9	1.6-40.0	4.1-34.2	3.2-17.3	1.6-40	0.1-1.2
	(10)	(10)	(6)	(9)	(35)	(14)
Distance to stream (m)	108±67	280±312	70±69	100±165	159±224	109±108
	30-215	8-1000	14-200	5-500	5-1000	2-325
	(7)	(10)	(5)	(7)	(29)	(9)
Distance to nearest opening (m)	—	67±70	65±33	—	92±131	—
	—	15-300	18-120	—	15-700	—
		(20)	(5)		(30)	
Stand age (yrs)	—	209±48	879±606	—	522±570	—
	—	180-350	450-1736	—	180-1824	—
		(10)	(3)		(16)	

[1]Slope position codes: (1) lower 1/3, (2) middle 1/3, and (3) upper 1/3.
[2]Measure of the percent of western hemlock, Douglas-fir, western red cedar, Sitka spruce, and coastal redwood in a stand.

Table 3—The mean, standard deviation, range, and sample size for platform and tree characteristics of Marbled Murrelet tree nests (n = 61) located in North America. The Pacific Northwest data include nests located in California, Oregon, Washington, and British Columbia. For some characteristics, either no data were available for that state or province, or the sample size was too small to calculate the mean and range. Calculations were rounded to the nearest cm for all measurements except nest substrate depth. Sample sizes for each variable are shown in parenthesis.

Characteristics	California *n* = 10	Oregon *n* = 22	Washington *n* = 6	British Columbia *n* = 9	Pacific Northwest *n* = 47	Alaska *n* = 14
Tree species						
Sitka spruce		1		6	7	5
Douglas-fir	4	20	3		27	
Western hemlock	1	1	2	2	6	
Western red cedar			1		1	
Alaska yellow cedar				1	1	
Coastal redwood	5				5	
Mountain hemlock						7
Tree diameter (cm)	278±136 139-533 (10)	192±47 127-279 (22)	152±45 88-220 (5)	212±84 90-370 (9)	211±91 88-533 (46)	63±18 30-104 (14)
Tree height (m)	73±8 61-86 (10)	67±11 36-86 (22)	57±7 45-65 (5)	58±15 30-80 (9)	66±13 30-86 (46)	23±4 16-30 (14)
Tree diameter at nest height (cm)	106±48 70-199 (5)	81±23 36-122 (15)	72±21 40-97 (5)	110±60 50-209 (5)	88±39 36-209 (30)	— —
Branch height (m)	47±11 33-68 (10)	51±12 18-73 (21)	37±11 23-53 (5)	33±8 18-44 (9)	45±13 18-73 (45)	13±2 10-17 (14)
Branch diameter at trunk (cm)	35±13 21-61 (8)	31±11 14-56 (19)	36±12 14-49 (5)	32±9 18-43 (9)	32±11 14-61 (41)	15±5 9-27 (12)
Branch diameter at nest (cm)	34±13 16-61 (10)	34±18 10-81 (20)	29±13 11-46 (4)	27±9 15-38 (7)	32±16 10-81 (41)	19±5 12-28 (11)
Branch crown position (pct)	64±13 50-91 (10)	74±12 50-92 (21)	63±15 41-81 (5)	58±11 40-74 (9)	68±14 40-92 (45)	59±12 44-79 (14)
Branch orientation (°)	203±103 45-360 (10)	173±87 20-360 (20)	233±109 110-342 (4)	187±90 18-341 (9)	189±96 18-360 (43)	— —
Distance trunk to nest (cm)	47±61 0-184 (10)	101±160 1-762 (21)	26±26 0-57 (4)	134±122 0-340 (9)	89±132 0-762 (44)	62±66 0-224 (13)
Nest platform length (cm)	20±10 8-40 (10)	41±17 12-71 (21)	29±16 10-57 (5)	21±13 12-50 (6)	32±18 8-71 (42)	— —
Nest platform width (cm)	15±7 6-23 (10)	28±12 7-51 (21)	24±11 10-39 (5)	12±3 9-19 (6)	22±12 7-51 (42)	— —
Nest platform moss depth (cm)	2.9±2.7 0.8-8.1 (5)	5.1±2.5 0.6-12 (17)	2.7±0.7 2.0-3.5 (2)	4.8±1.4 2.7-7.0 (9)	4.5±2.4 0.6-12 (33)	3.9±1.3 2.0-6.0 (12)
Nest platform duff and litter depth (cm)	7.4±7.3 2.5-20.0 (4)	3.4±0.4 3.0-3.8 (2)	2.9±0.7 2.0-3.8 (3)	— —	5.0±5.2 2.0-20.0 (9)	— —
Cover above nest (pct)	90±28 5-100 (10)	79±14 40-100 (18)	90±10 70-100 (5)	100±0 100-100 (2)	85±20 5-100 (35)	89±05 81-95 (8)

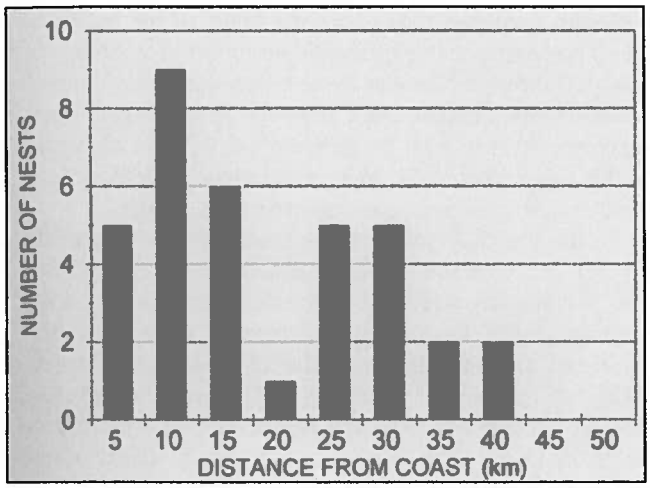

Figure 1—Distances from the Marbled Murrelet nest trees (n = 35) to the nearest salt water for nests found in the Pacific Northwest. The number of nests was listed in 5-km increments beginning with nests found 0-5 km inland.

total tree density (>10 cm d.b.h.) of 324/ha, multiple canopy layers (2-3), and the presence of snags (>10 cm d.b.h.) (mean density = 71/ha) (Nelson and others, in press). In Alaska, most nest trees were located in forests with significantly larger tree size classes (≥23 cm d.b.h.) and higher volume classes (1883-5649 m^3/ha) than other forest types (Kuletz and others, in press).

Tree Species Composition and Stem Density

Conifer species that typically grow at higher elevations in the Pacific Northwest include mountain hemlock, silver fir (*Abies amabilis*), and yellow cedar. Conifer species most abundant at lower elevations include Douglas-fir, western red cedar, Sitka spruce, western hemlock, and coastal redwood. Nest stands in the Pacific Northwest were composed primarily of low elevation conifer species ($\bar{x}$ = 91 percent) (*table 2*). In Alaska, the composition of low elevation trees was much lower, with a mean of 64 percent. The total mean tree density for nest stands in the Pacific Northwest was 182 trees/ha; total density was about three times greater in Alaska (*table 2*).

All nest trees in the Pacific Northwest were recorded in stands characterized as old-growth and mature forest. These stands were dominated by either Douglas-fir, coast redwood, western hemlock, western red cedar, or Sitka spruce. The one exception was a higher elevation nest stand found in the Caren Range of British Columbia which was dominated by old-growth mountain hemlock (60 percent) with smaller percentages of yellow cedar (20 percent) and silver fir (20 percent). In California, nest stands were dominated by coast redwood and Douglas-fir, with a component of western hemlock and Sitka spruce in some nest stands. In both central and northern California, all nest sites had a higher percentage of redwood trees than Douglas-fir. Nest stands in Oregon were dominated by Douglas-fir and western hemlock, with one site dominated by Sitka spruce. Forest types in Washington included stands dominated by western hemlock, Douglas-fir, and Sitka spruce. These stands commonly had a large component of western red cedar. Silver fir made up a smaller component of some of the nest stands in Washington.

In British Columbia, six nest stands were dominated primarily by Sitka spruce and western hemlock, with four stands also having a component of silver fir, and one stand with western red cedar. One nest stand in the Caren Range was dominated by mountain hemlock. For a sample of eight nests located in Alaska, mountain hemlock was the dominant tree species at five nests, and western hemlock was the dominant species at three nest stands (Naslund and others, in press). Sitka spruce were reported as an important component at most of these nest sites.

Canopy Characteristics

Nest stands in the Pacific Northwest had a mean canopy height of 64 m with the redwood zone included in this sample (*table 2*). The mean canopy height for stands located in Oregon, Washington, and British Columbia was 61 m. The canopy height of Alaska nest stands were lower ($\bar{x}$ = 23 m), reflecting the small stature of the trees in this geographic area.

For nest stands in the Pacific Northwest, the mean canopy closure was 49 percent, and all nest stands were reported to have 2-4 tree canopy layers where this variable was recorded (*table 2*). Canopy closures below 40 percent were reported for 40 percent of the nest stands (*fig. 2*). Mean canopy closures were especially low in California and Oregon. Canopy closures for a typical old-growth stand in Washington generally average 80 percent. Canopy closures reported from Alaska were similar to nest stands in the Pacific Northwest (*table 2*) with a mean of 62 percent.

The presence of dwarf mistletoe (*Arceuthobium*) in the nest stands or within the canopy of nest trees was not reported consistently enough to determine its importance to murrelets. Mistletoe was reported at 13 of 20 nest stands, where its occurrence was evaluated.

Stand Size

Mean nest stand size for the Pacific Northwest was 206 ha. Several nest stands were only 3, 5, and 15 ha in size. In Alaska, stands were naturally fragmented in many cases, and averaged 31 ha. Stand sizes were generally smaller in Alaska because of the naturally fragmented nature of the coastal forests in this region.

Distance to Openings

Distance of nest trees to streams for nests in the Pacific Northwest was variable, with a mean of 159 m. Nest trees were located a mean distance of 92 m from natural or man-made openings (*table 2*). A combined analysis indicated that the mean distance to an opening or stream was 123 m (n = 68, $s.d.$ = 177). Sixty-six percent of the nest trees were ≤100 m from an opening (*fig. 3*).

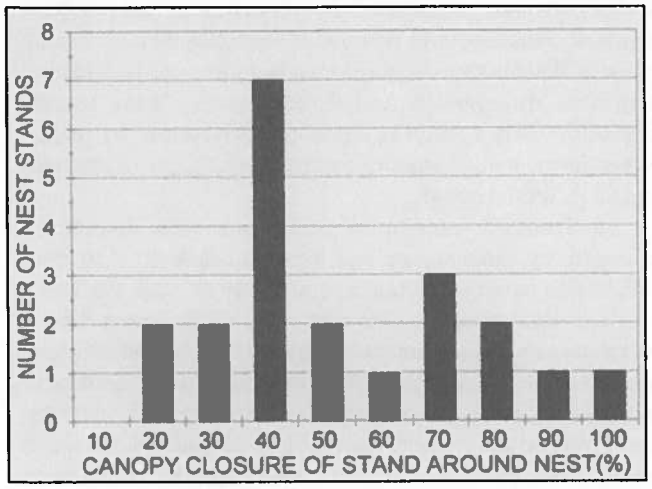

Figure 2—Canopy closure of the stand surrounding the nest tree for 34 Marbled Murrelet nests found in North America. The number of nests was listed in 10-percent increments beginning with nests with 0-10 percent canopy closure.

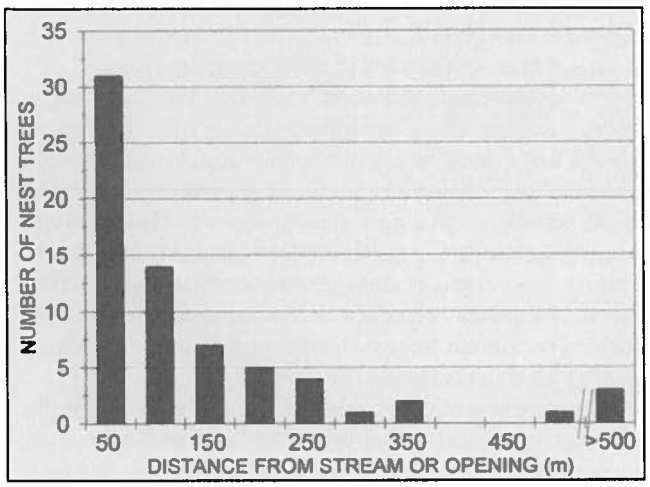

Figure 3—Distances from the Marbled Murrelet nest trees (n = 68) to the nearest stream, creek, or opening for nests found in North America. Some nests had two measurements, one to the nearest opening and one to the nearest stream.

Tree Characteristics

Nest trees used by murrelets in the Pacific Northwest included Douglas-fir (57 percent), Sitka spruce (15 percent), western hemlock (13 percent), coast redwood (11 percent), and western red cedar (2 percent) (*table 3*). In one exception, a nest in British Columbia was found in a yellow cedar (2 percent). Western hemlock was the only nest tree species reported used by Marbled Murrelets throughout their geographic range. Although Sitka spruce was only reported from Alaska, British Columbia, and Oregon, it is likely this species is also used throughout the range of the murrelet since it is common in coastal coniferous forests of Washington through California. Douglas-fir nest trees were only located in Washington, Oregon, and California. Nests in cedar trees were reported only from Washington and British Columbia, but this was probably due to a small sample size. Mountain hemlock nest trees were only reported from Alaska.

In the Pacific Northwest, the mean nest tree diameter was 211 cm, with the smallest diameter nest tree reported from Washington, which was a western hemlock 88 cm in diameter (*table 3*). Nest tree diameters were normally distributed with a maximum number of trees found between 140 and 160 cm, and 85 percent of the trees ranging between 120 and 280 cm (*fig. 4*). Nest tree diameters were much smaller in Alaska ($\bar{x}$ = 63 cm) due to the small stature of the trees in this region.

Mean nest tree heights were highest in California and Oregon where the majority of nest trees were in redwood and Douglas-fir trees which can grow to great heights. Mean tree heights were similar between Washington and British Columbia where more of the nest trees were in cedar, spruce, and hemlock. Mean tree heights in the Pacific Northwest were 66 m (*table 3*). Nest tree heights in Alaska were low, with a mean of 23 m, with one nest tree measured at 16 m.

The mean diameter of the tree trunk at nest height was 88 cm in the Pacific Northwest, with minimum trunk diameters of 36 cm and 40 cm reported for Oregon and Washington respectively. Trunk diameters at the nest height were not reported for nests in Alaska (*table 3*).

The condition of nest trees in the Pacific Northwest varied, with 64 percent recorded as alive/healthy and 36 percent as declining (n = 44). No nests were reported in snags. Nest trees with declining tops (8 percent), broken tops (37 percent) and dead tops (8 percent) were commonly reported, with only 47 percent of the nest tree tops recorded as alive/healthy. In Alaska (n = 14), 57 percent of the nest trees were reported as declining, and one nest tree was recorded as dead.

In the Pacific Northwest, mean nest branch height was 45 m (*table 3*). Mean nest branch height was highest in California and Oregon, where the mean tree height was also the highest. Mean nest branch height was lowest in Alaska (13 m), with one nest located only 10 m above the ground.

The mean diameter of nest branches measured at the tree trunk and at the nest varied little between each state or Province for the Pacific Northwest (*table 3*). Mean nest branch diameters at the nest for each state or province ranged from 27-34 cm with a mean diameter of 32 cm for the Pacific Northwest. The distribution of limb diameters at the nest in the Pacific Northwest were normally distributed, with a maximum number (22 percent) of nests located on limbs 35-40 cm in diameter (*fig. 5*). In Alaska, the smallest branch diameters at the nest were 12, 14, and 16 cm, with a mean diameter of only 19 cm. The length of the nest branches in the Pacific Northwest ranged from 1 m to 14 m, with a mean length of 5.3 m (n = 42).

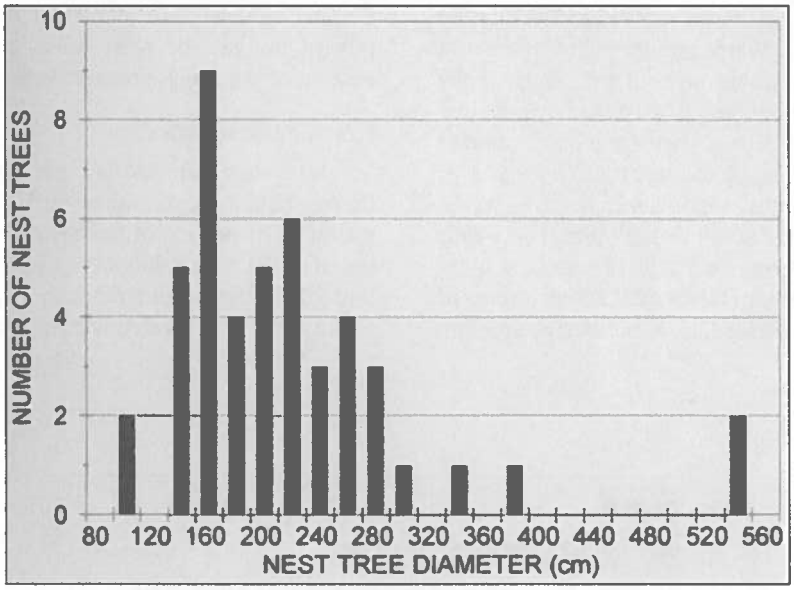

Figure 4—The diameter at breast height for 46 nest trees of the Marbled Murrelet found in California, Oregon, Washington, and British Columbia. The number of nest trees was listed in 20-cm increments beginning with trees 70-80 cm in diameter.

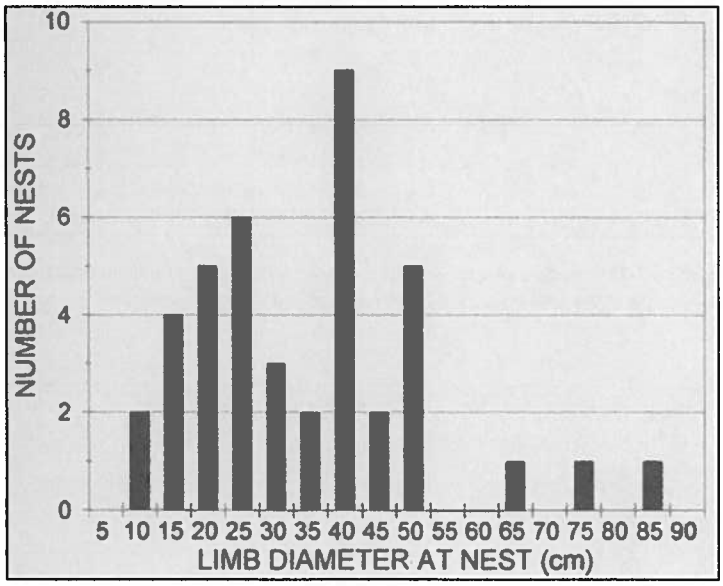

Figure 5—The diameter of the tree limbs under or next to 41 nests of the Marbled Murrelet found in California, Oregon, Washington, and British Columbia. The number of nests was listed in 5-cm increments beginning with limbs 0-5 cm in diameter.

The condition of the nest branches for nests in the Pacific Northwest varied from healthy limbs (70 percent) to those reported as declining (27 percent) or dead (3 percent) ($n = 37$). Nest limbs with broken ends were reported in 16 percent of the records ($n = 37$). In Alaska, 50 percent of the nest branches were recorded as declining, 7 percent were reported with broken ends, with 1 nest located on a dead branch ($n = 14$).

The position of the nest on the tree bole was calculated by dividing the nest height by the total tree height. Nests in the Pacific Northwest were located an average of 68 percent up the bole of the nest tree (*table 3*). Fifty-nine percent of the nests were located in the top one-third of the tree bole, and 87 percent of the nests were located in the top one-half of the tree. No nests were located lower than 40 percent of the total

tree bole height. Nests in Alaska were also located high up the tree bole with a mean of 59 percent. Positions of the nest on the tree bole for all nests throughout the range of the Marbled Murrelet showed that the top 10 percent of the tree was not utilized to any great degree, with a maximum number of nests located 70-80 percent up the tree bole (*fig. 6*).

The majority of nest limbs in the Pacific Northwest (n = 44) were oriented toward the south or the north. Forty-four percent of the limbs faced a southerly direction ranging between 136 and 225 degrees (*table 3*). Another group of nests (26 percent) were oriented in a northerly direction ranging between 316 and 45 degrees. Nest limbs oriented toward the east or west consisted of 14 percent and 16 percent of the sample respectively.

Nest Characteristics

Nest cups were located a mean distance of 89 cm from the tree bole for nests in the Pacific Northwest (*table 3*). Here, a total of 71 percent of the nests were located within 1 m of the tree bole. This relationship was also true for nests located throughout the North American range (*fig. 7*), as 51 percent of the nests were located within 40 cm of the tree trunk.

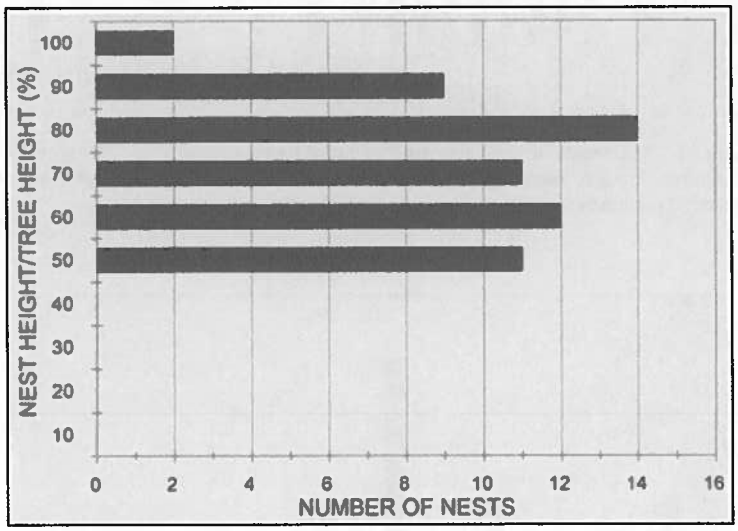

Figure 6—The relative vertical positions of Marbled Murrelet nests in relation to the heights of the tree bole for 59 tree nests found in North America.

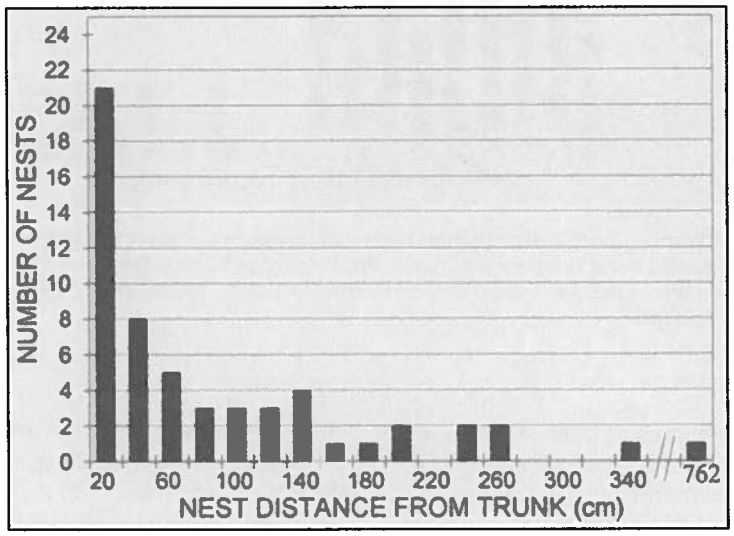

Figure 7—Nest distances from the tree trunk for 57 Marbled Murrelet nests found in North America. The number of nests was listed in 20-cm increments beginning with nests found 0-20 cm from the tree trunk

Nest platforms in the Pacific Northwest had a mean length of 32 cm and a mean width of 22 cm. The mean total platform area was 842 square cm (*table 3*). In the Pacific Northwest, moss (*Isothecium*) formed the major proportion of the substrate for 67 percent of the nests. Litter, such as bark pieces, conifer needles, small twigs, and duff, was substrate in 33 percent of the nests. For nests found throughout North America, moss formed 49 percent of the substrate, moss mixed with lichen or litter formed 30 percent of the nests, and litter 21 percent (n = 37). All nests found in Alaska had moss as a component of the nest substrate.

Mean moss depth at, or directly adjacent to, the nest cup was 4.5 cm (*table 3*). Mean litter depth was 5 cm for nests in the Pacific Northwest. Mean moss depths in Alaska were 3.9 cm. The majority (86 percent) of nests in North America (n = 52) had substrates that were >2 cm in depth with a large number of nests (n = 16) having substrate depths between 3.1 and 4.0 cm (*fig. 8*).

Nest platforms in the Pacific Northwest (n = 44) were created by large primary branches in 32 percent of the cases. In addition, 23 percent of the nests were located on tree limbs where they became larger in diameter when a main limb forked into two secondary limbs, or a secondary limb branched off a main limb. In many instances, branches were also larger in diameter where they were attached to the tree bole. Locations where a limb formed a wider area where it grew from the trunk of a tree formed 18 percent of the nest platforms. Cases of dwarf mistletoe infected limbs (witches' broom) (9 percent), large secondary limbs (7 percent), natural depressions on a large limb (7 percent), limb damage (2 percent), and an old stick nest (2 percent) were also recorded as forming platforms. Multiple overlapping branches at the point where they exited the trunk of a tree were sometimes used as a nest platform. Many of the tree limbs creating nest platforms had grooves or deformations forming natural depressions on the surfaces of the limb.

Cover directly above the nest was high in almost all cases in the Pacific Northwest, with a mean of 85 percent. Eighty-seven percent of all nests had >74 percent overhead cover. Cover above the nest platforms in Alaska was similar to that in the Pacific Northwest (*table 3*).

Discussion

Marbled Murrelets have a limit on their inland breeding distribution because of the energetic requirements of flying inland to incubate eggs and feed young. They forage at sea, carrying single prey items to the nest and feed their young several times per day during the late stages of nesting. To some extent, the inland distance information presented here is biased towards lower values, because nest search and survey efforts have been more intensive closer to the coast in all regions, where higher murrelet detection rates make locating nests an easier task. Even with the potential problems of energetic expenditure, murrelets displayed a great tolerance for using nesting stands located long distances from the ocean. Evidence of breeding was common in California, Oregon, and Washington, in areas located 30-60 km inland. Unlike many other alcids, the Marbled Murrelet forages in near-coastal shallow water environments. The use of tree limbs as a nesting substrate may have developed because older-aged forests were the only habitats that were abundant and commonly available close to the foraging grounds of this seabird. Areas of brush-free open ground or rocky talus

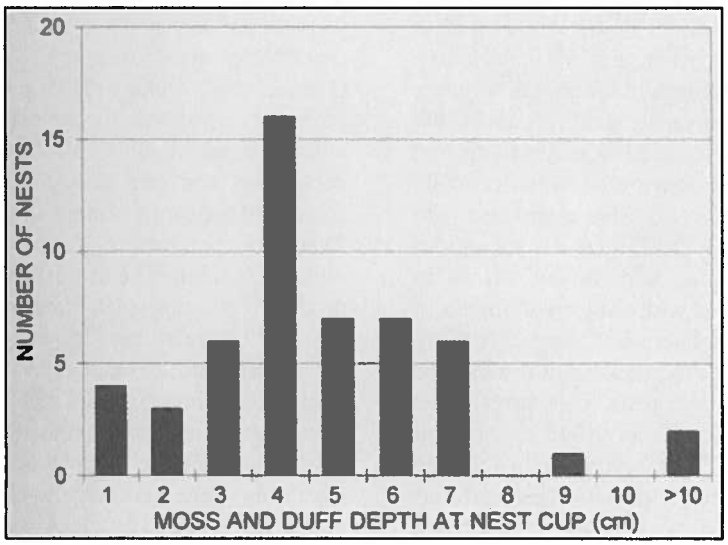

Figure 8—The depth of moss and litter under or directly adjacent to the nest cup for 52 nests of the Marbled Murrelet in North America.

slopes that are commonly used by other alcids as nesting habitat, are not commonly available along the forested coasts of the Pacific Northwest. Old-growth and mature forests also provided large nesting platforms on which to raise young. Nesting greater distances from the coast may have developed over time to avoid higher nest predation by corvids and gulls whose population numbers may be much higher in food-rich coastal areas. In addition, much of the near-coastal nesting habitat has been eliminated in the Pacific Northwest which may cause birds to nest further inland. Nest search efforts and surveys for the presence of murrelets should be conducted in areas farther inland in order to refine the abundance and distribution of this seabird away from the coast. We currently have no information to determine what proportion of the population nests in these inland areas, or any data to compare the reproductive success of far versus near-coastal nesting pairs.

In Washington, inland detection rates of Marbled Murrelets did not show declines until inland distances were >63 km from salt water (Hamer, this volume). In Oregon, most detections occurred within 40 km of the ocean (Nelson, pers. obs.). In British Columbia, murrelet detection rates in Carmanah Creek on Vancouver Island decreased with increasing distance from the ocean (Manley and others 1992). Savard and Lemon (1992) found a significant negative correlation between detection frequency and distance to saltwater on Vancouver Island in only 1 of 3 months tested during the breeding season. Inland distances for all nests in Alaska were low because rock and icefields dominate the landscape a few kilometers from the coast in most regions.

We found that all nest trees throughout the geographic range were located in stands defined by the observers as old-growth and mature stands or stands with old-growth characteristics. The youngest age reported for a nesting stand was 180 years. Marbled Murrelet occupancy of stands, and the overall abundance of the species has been related to the proportion of old-growth forest available from studies conducted in California, Washington, and Alaska (Hamer, this volume; Kuletz, in press; Miller and Ralph, this volume; Raphael and others, this volume). Carter and Erickson (1988) reported that all records of grounded downy young and fledglings (young that have fallen from a nest or unsuccessfully fledged) (n = 17) that they compiled were associated with stands of old-growth forests in California. All records of nests, eggs, eggshell fragments, and downy chicks in Washington have been associated with old-growth forests (n = 17) (Hamer, this volume; Leschner and Cummins 1992a).

Marbled Murrelets consistently nested in low elevation (<945 m) old-growth and mature forests. Tree species that are most abundant at lower elevations (<945 m) such as Douglas-fir, western hemlock, Sitka spruce, redwood, and cedar, may have a higher abundance of potential nest platforms than the higher elevation conifers such as silver fir and mountain hemlock.

Marbled Murrelets were found nesting in stands of very small size in some instances, although the reproductive success of these nests compared to stands of larger sizes was not known (but see Nelson and Hamer, this volume b). A wide range of canopy closures were reported for nest stands and around nest sites. A study conducted in Washington and Oregon compared random plots within a stand to plots surrounding the nest tree (Nelson and others, in press). They found that canopy closures were significantly lower around nest trees in Oregon compared to random plots adjacent to the nest tree, but the relationship was not significant in Washington. It is unknown how stand size and canopy closure affect nest success, but stands with lower canopy closures might have less visual screening to conceal adult visits to the nest tree (see Nelson and Hamer, this volume b). Therefore, it is possible that low canopy closures within a stand will make locating nests easier for visual predators such as corvids. In addition, smaller stands will have fewer nesting and hiding opportunities for Marbled Murrelets. They may be choosing lower canopy closures immediately around the nest to improve flight access, but select nest platforms with dense overhead cover for protection from predation, as indicated by the extremely high cover values found directly over the nest.

The majority of nests in the Pacific Northwest were located within 100 m of water, but a few nest sites were found at much longer distances (*fig. 3*). Small streams and creeks commonly bisect stands in the Pacific Northwest, creating larger openings and long travel corridors. Murrelets are often observed using these features to travel through a stand. This may be one reason nest sites were often in close proximity to streams. Many nests were also located near openings such as roads or clear-cuts, but there may be an observer bias to finding nests located in areas with better access and viewing conditions.

A variety of processes contributed to producing potential nest platforms within the forest including deformations and damage sustained by trees. This is probably why a measure of potential nest platforms, and not tree size, was the best predictor of stand occupancy by murrelets in Washington (Hamer, this volume), as larger diameter trees alone were often not responsible for the majority of available platforms within a stand. Mistletoe blooms, unusual limb deformations, decadence, and tree damage commonly observed in nest stands, all appear to create a large number of nest platforms. Therefore, the structure of a stand and the processes occurring within a stand may be more important than tree size alone in producing nesting platforms and suitable habitat for the Marbled Murrelet (see Grenier and Nelson, this volume).

It would still be desirable to know when trees, in general, begin producing potential nest platforms. In Washington, Hamer (this volume) measured potential nest platform abundance using a sample of 2,035 conifers, and found platforms were generally available when tree diameters exceeded 76 cm. The mean number of platforms/tree was found to increase rapidly with an increase in tree diameter

from 50-200 cm. No increase in the mean number of platforms was evident for larger trees that ranged from 220-300 cm in diameter. These results explain why all the nest trees found in the Pacific Northwest were ≥88 cm in diameter, although mistletoe brooms on smaller trees may also provide habitat. In southcentral Alaska, the minimum d.b.h. associated with a tree having at least one platform ranged from 29-37 cm (Naslund and others, in press).

In a study completed in 1993, nest tree and stand characteristics in Washington and Oregon were compared between 15 murrelet nests and randomly located dominant trees and plots within the same nest stand (Nelson and others in press). Nest sites were similar to the forest stands in which they were located, except that a significantly higher number of potential nest platforms were recorded at nest trees, than at random trees. They also found that Marbled Murrelets selected trees at nest sites that had ≥4 potential nest platforms, and trees with ≤3 platforms were avoided. In Alaska (Naslund and others, in press), one study compared nest tree characteristics (n = 14) to a sample of random trees surrounding each nest tree, and found nest trees were larger in diameter, had more potential nest platforms, and had greater epiphyte cover. This study also concluded that Sitka spruce appeared to be the most suitable tree for nesting when compared to western hemlock and mountain hemlock, because of its high number of platforms and greater epiphyte cover. They also found that nest and landing trees tended to be larger in diameter than surrounding trees, and nest trees were more likely to contain at least one potential nest platform with moderate to heavy epiphyte cover when compared to nearby trees. Stands with high potential nest platform densities may reduce competition for nest branches and provide a high diversity of nest site choices.

Nests located high in the canopy may provide better access by adults to the nest site in dense, old-growth stands. Nesting as high in the canopy as possible may also help in avoiding predation. Although positioning the nest as high off the ground as possible would likely reduce the incidence of mammalian predators, we have also observed that the Steller's Jays (*Cyanocitta stelleri*), predators of nestlings and eggs, often forage in the lower portions of the canopy. Better horizontal and vertical cover is available in the top portions of the tree crown which may help reduce predation. Data needs to be collected on the positioning of nests within the live crown of the tree, not just the tree bole, to determine if murrelets prefer certain areas of the tree crown foliage for nesting.

Murrelets may choose to place nests near the trunk of the tree for a variety of reasons. First, overhead and horizontal cover is higher around the nest cup due to the position of the tree crown directly overhead. Second, the tree trunk itself provides a large amount of cover and visual screening and branches are typically larger in diameter near the tree bole. Also, more duff and litter, which often form the nest substrate, is trapped near the tree bole, and the percent cover of moss on the limbs of trees is higher, often forms a more complete coverage, and forms a deeper layer near the tree bole. Some conifer species typically have little or no moss available on their limbs, so that platforms created by accumulations of duff and debris are the only nest choices available for murrelets in these forest types.

Murrelets nest on large limbs. The smallest limb used at the nest cup throughout the range of the murrelet was 10 cm in diameter, which is likely the smallest diameter branch that could support a successful nest. Nests located on smaller limbs would probably have a higher likelihood of losing chicks or eggs from accidental falls, an occurrence that is well documented (Hamer and Nelson, this volume a). Nests located on limbs <16 cm diameter all had moss as a nest substrate, except in one instances where a 13 cm nest branch had litter and lichen as a substrate. Small limb diameters without a moss covering may be avoided by nesting birds because the hazards of raising eggs and young are increased without the moss to help stabilize and insulate the egg on the limb, increase the diameter of the nest limb/platform, and provide a substrate on which to create a nest cup (depression). In addition, moss and litter may help insulate eggs and chicks during cold weather and may help drain water from eggs and chicks helping thermoregulation (Naslund and others, in press). An abundance of mosses creates a multitude of nest platform choices by providing substrate on many locations throughout a single limb. In addition, the presence of dwarf mistletoe in stands can increase the number of nesting opportunities for murrelets and may be important in providing nest platforms in areas with low moss abundance and dryer conditions.

The nest site selection of the Marbled Murrelet may have evolved primarily to reduce predation. Selection of nest sites away from the coast, in dense old-growth and mature forests with multi-layered canopies, high in the forest canopy, on limbs with high overhead and horizontal cover, and near the tree bole where the tree bole itself provides a large degree of cover, may help reduce nest predation. Results from studies of murrelet habitat use to date have been derived from comparisons of stands occupied by murrelets to unoccupied stands, comparisons of stands receiving high use versus low use, or comparisons of nest trees and nest plots to random trees and plots. Although these can provide extremely useful descriptions and definitions of suitable habitat, they do not provide information on the habitat characteristics associated with successful nests. Information on the landscape and within-stand habitat characteristics that influence reproductive success is needed to fully understand murrelet nesting ecology and to model optimum habitat suitability for this species. Such studies may find that stand size analyzed in conjunction with the number of nesting and hiding opportunities within the stand (habitat quality), may greatly influence reproductive success because of predation pressures at the nest site. Habitat factors that could influence reproductive success may include stand fragmentation, stand canopy closure, and the amount of overhead and horizontal cover surrounding the nest.

Acknowledgments

We would like to acknowledge the contributions of unpublished information made available to us by researchers and wildlife biologists throughout the range of the Marbled Murrelet. Their generous contributions of nest information made this summary possible. For the California data, we are extremely grateful to Steve Singer for the information he has collected over the last two decades. Additional information was kindly provided by Sal Chinnici of the Pacific Lumber Company in association with Dave Fortna and Steve Kerns. Lee Folliard of Arcata Redwood Company provided information from an additional 2 nests. We would like to thank Karen Holtrop for her efforts and successes in locating nests in Washington and her contributions of nest data. Stephanie Hughes, Kevin Jordan, Irene Manley, John Kelson, Paul Jones, and Alan Burger provided valuable nest information from British Columbia. We are also grateful to Nancy Naslund and Kathy Kuletz for contributing the majority of nest site information from Alaska. We thank Alan Burger, Martin Raphael, Nancy Naslund, Evelyn Bull, Kimberly Titus, and C. John Ralph for reviewing earlier drafts of this paper.

Chapter 20

Relationship of Marbled Murrelets with Habitat Characteristics at Inland Sites in California

Sherri L. Miller **C. John Ralph**[1]

Abstract: We examined the range and the relationships of Marbled Murrelet (*Brachyramphus marmoratus*) behavior with habitat and landscape characteristics in isolated old-growth and residual forest stands from 2 to 400 ha in California. In large contiguous stands of old-growth forest in parks, we examined relationships of murrelet detections with elevation and topography. In isolated stands we found higher murrelet detection levels in stands with higher dominant and codominant crown cover and >50 percent coast redwood (*Sequoia sempervirens*). Surveys also were more likely to detect occupied behaviors at stands with higher crown cover and a greater proportion of redwoods. Density of old-growth cover and species composition may be the strongest predictors of murrelet presence and occupancy in California. Contrary to previous studies, we did not find that larger stands were more likely to have murrelets present. In the large park stands, we found that mean detection levels and the number of occupied stations were highest in the major drainages and at lower elevations. Major ridges tended to have lower detection levels and fewer occupied behavior stations.

In recent years, much has been learned about the occurrence of Marbled Murrelets (*Brachyramphus marmoratus*) at inland forest sites. Throughout most of its range, the murrelet nests in old-growth forests within 50-75 miles of the coast (Carter and Morrison 1992). In California, Paton and Ralph (1990) conducted general surveys (Paton, this volume) to determine the distribution of murrelets in coastal old-growth and mature second-growth forests. Concentrations were found in regions containing large, contiguous, unharvested stands of old-growth redwood, mostly within state and federal parks, with the highest detection numbers in stands >250 ha. In excess of 200 detections for single-survey mornings have been recorded at some survey stations in remaining unharvested stands within parks in California, including Redwood National Park and Prairie Creek State Park in Humboldt County (Ralph and others 1990); and Big Basin State Park in San Mateo County (Suddjian, pers. comm.).

Federal listing of the Marbled Murrelet as threatened (U.S. Fish and Wildlife Service 1992) has created a need for information about the role of habitat and landscape features for the murrelet.

We conducted two studies to examine the relationships of the murrelet to habitat and landscape characteristics within old-growth forests, as defined by Franklin and others (1986). In isolated stands in fragmented landscapes (the Stand Study), we compared murrelet detections with stand size, structure, and landscape characteristics. In large contiguous stands of old-growth in state and federal parks (the Park Study), we examined murrelet detections with landscape features, such as elevation and topography. We confined our study to old-growth forests, because previous studies indicate murrelets nest only in forests with these characteristics.

Methods

The survey methods followed the intensive survey protocol of Ralph and others (1993). To maximize the number of visual detections, we selected station positions at the edges of the isolated stands or at interior locations with openings in the canopy whenever possible. Observers could move within a 50-m radius of the station.

We estimate that, for an individual forest stand, four surveys are needed to determine with a 95 percent probability that murrelets are present (*appendix A*). If below canopy behaviors were observed, we categorized the stand as Occupied (see below) for analyses. During 1992 and 1993 for the Stand Study, we attempted to survey each isolated stand at least four times between 15 April and 7 August. Surveys at each stand were distributed throughout the survey period whenever possible. However, due to difficult access for some stands, surveys in some areas were temporally aggregated. To eliminate potential effects from aggregated surveys, detection levels were standardized for seasonal variation (see Analyses below).

For the 1993 Park Study, within the boundaries of the large stands of old-growth forests in national and state parks (*fig. 1*), stations were placed in a matrix over the landscape, as illustrated in *figure 2*. We surveyed all sections of park stands with adequate accessibility. We placed stations 400 meters apart on roads and trails, and 400 meters out perpendicular to trails, creating a matrix. Ralph and others (1993) found that observers detect few birds at distances >200 m, therefore, we assumed each station covered a 200-m radius circle, approximately 12.5 ha. Due to safety considerations for observers hiking to stations in pre-dawn hours, we limited stations to within 400 meters of a trail or road. Stations were surveyed once during the survey season. We attempted to avoid surveys at adjacent stations on the same morning.

The species' range in northern California was determined by examining the results of inland surveys conducted from 1988 through 1992 by government agencies and private landowners. Murrelet use for each stand or station was determined by the number and type of detections. All survey stations were digitized into a Geographic Information System

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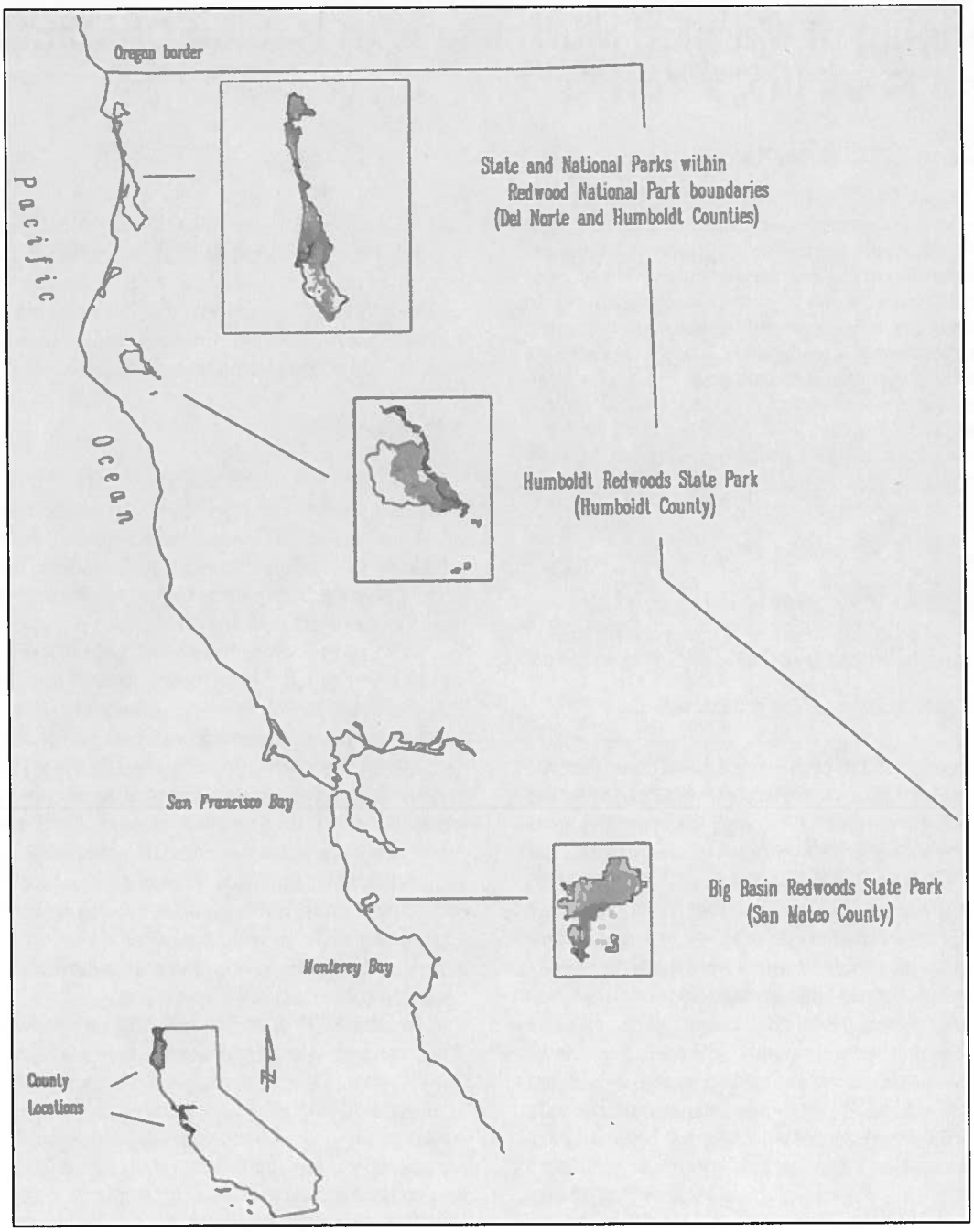

Figure 1—Location of state and national parks surveyed during the summer of 1993. Shaded areas represent distribution of old-growth forests within the parks.

(GIS) database (ARC/INFO 6.1.1) and grouped by distances from the ocean by 10-km bands from 0 to 60 km (*fig. 3*).

Definition and Selection of Isolated Study Stands

Isolated stands were located by examining habitat maps of private lands, state and federal parks, and national forests. The maps were drawn from interpretation of aerial photographs. For the stand selection process, stand size was estimated from measurements on the maps. Stands were randomly selected from size categories of 2 to 20 ha, 21 to 40 ha, 41 to 100 ha, and greater than 100 ha. If the stand was accessible, it was visited and visually inspected. If the stand was old-growth or residual forest, the stand was surveyed, if not, then another stand was selected. Upon completion of field work, station locations and stand perimeters were adjusted on maps according to ground-truthing, then digitized into a GIS database.

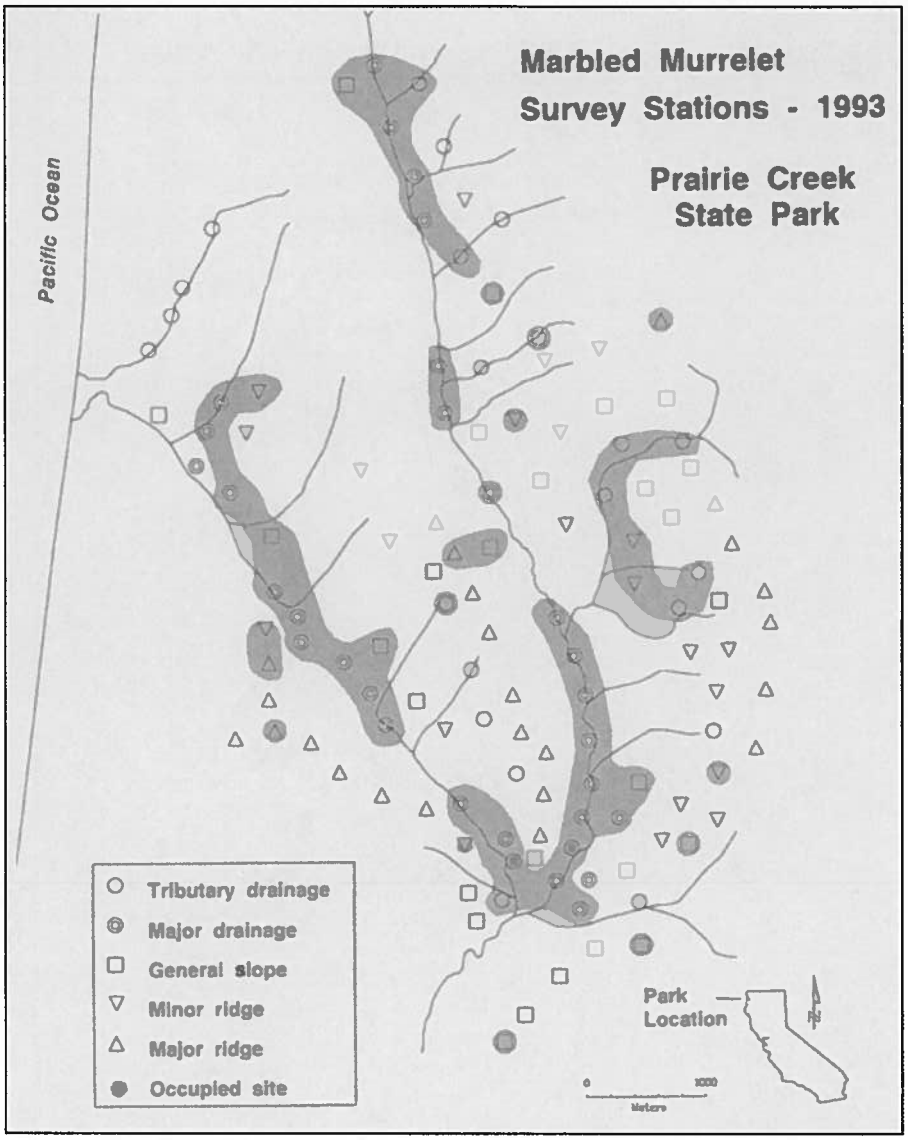

Figure 2—Spatial and topographical distribution of a subset of Marbled Murrelet stations surveyed at Prairie Creek Redwoods State Park during the summer of 1993. Occupied sites are shaded in groups to illustrate possible associations with topographical features.

Stand area, perimeter length, and distance from salt water were derived from the GIS database. For stands with inclusions of non-forested area within the stand, we added the length of the lines around the stand and around the inclusions for the total perimeter measurements. Perimeter, therefore, is a measure of the amount of forest edge in and around the stand.

Stand type was characterized as residual or old-growth. This variable is a measure of harvest history for the stand, but is not a direct measure of years since the last disturbance. Old-growth stands contained trees greater than 90 cm diameter at breast height (d.b.h.) with no history of timber harvest and some evidence of decadence in the canopy. Residual stands had some history of partial removal of large trees with the remaining dominant trees greater than 90 cm d.b.h.. Some stands with contiguous areas of old-growth and residual were classified as mixed.

Stands also were classified by density as determined by interpretation of aerial photographs. Density was defined as the percent of the old-growth canopy cover (dominant and codominant trees): sparse, <25 percent; low, 25-50 percent; moderate, 51-75 percent; and dense, >75 percent. Species of dominant trees (>50 percent) was determined from aerial photography and verified by vegetation information after visiting the stand. For the purpose of this study, a stand was a single, isolated group of old-growth trees surrounded by

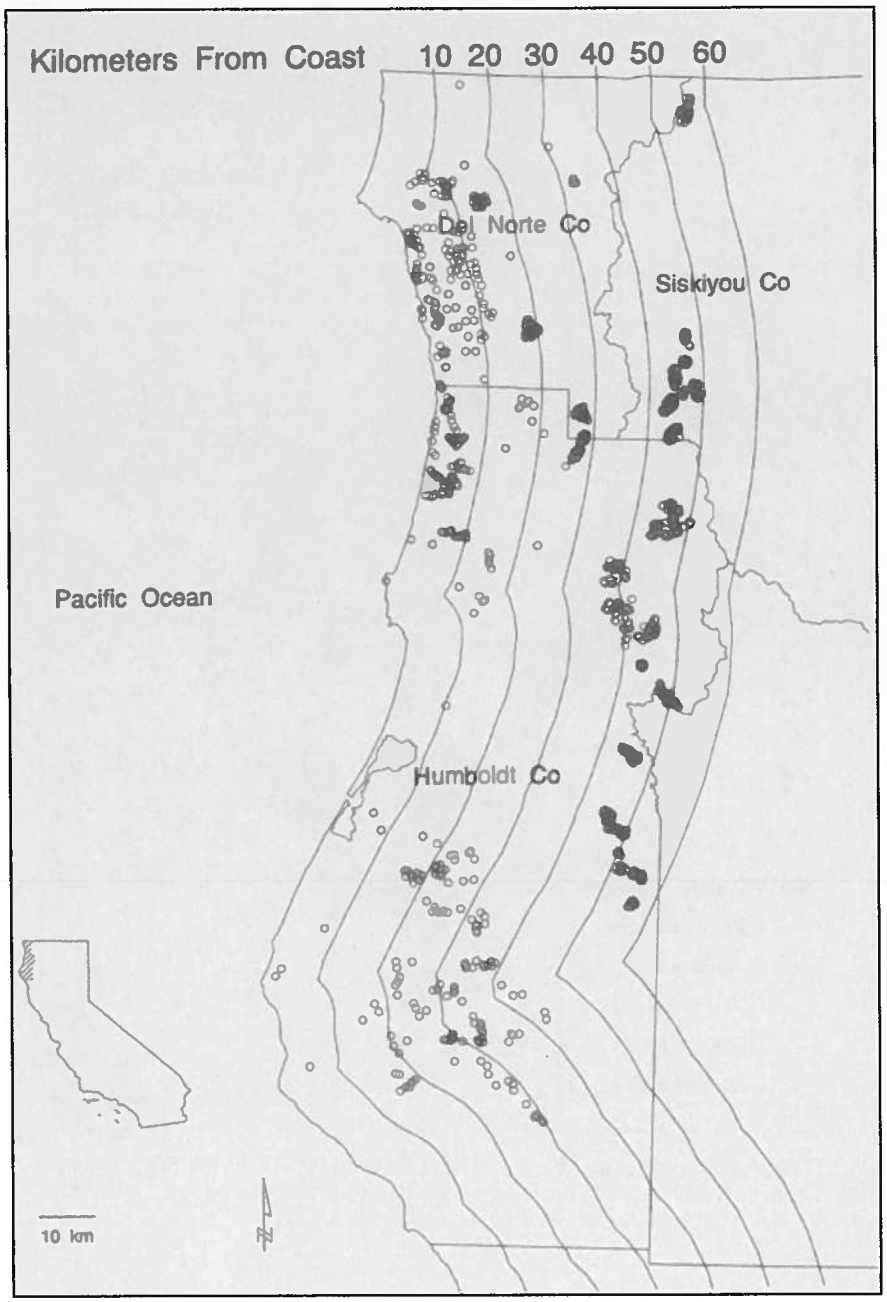

Figure 3—Distribution of Marbled Murrelet survey stations in northern California. Stations are located on private and public lands and surveys were conducted one or more seasons from 1988 to 1994. Open circles represent one survey station or a group of stations in one isolated stand. In areas with high concentrations of stations, open circles appear filled in or shaded.

non-forested or harvested habitat. If groups of trees were less than 160 meters apart they were considered one stand.

Stands that met all of the following criteria were included in the group of potential survey sites: old-growth or residual stands with dominant and codominant trees that comprised at least 20 percent canopy cover; size between 2 ha and 400 ha; distance from coast less than 40 km (25 miles); dominant vegetation type of coast redwood (*Sequoia sempervirens*) or Douglas-fir (*Pseudotsuga menziesii*) at elevations of less than 1,000 m; and safely accessible by road or well-defined trail.

Analyses

Standardization for Seasonal Variation

Various factors may influence the numbers of detections of murrelets at inland locations, including environmental conditions, time of year (O'Donnell and Naslund, this

volume), and observer (O'Donnell, this volume). To help eliminate the effects of observer bias, all stands were surveyed by two or more observers. The influence of weather on numbers of detections appears to be highly variable (Naslund and O'Donnell, this volume). The effect of weather is probably stochastic with respect to survey days, and we assumed it did not have an overall impact at a site because surveys were distributed throughout the breeding season. The seasonal variation in detection levels, however, has been well documented and quantified at several sites in California (O'Donnell and Naslund, this volume). To identify differences in murrelet use (detection levels) of stands in our study, we first accounted for the effect of season on detection levels.

Morning surveys were conducted throughout the breeding season in multiple years at three sites in Humboldt County. The sites at Lost Man Creek (Redwood National Park) and James Irvine Trail (Prairie Creek Redwoods State Park) were surveyed from 1989-1993. The Experimental Forest site was surveyed in 1989, 1990, 1992, and 1993. We attempted to monitor each site weekly. Data from these three sites was used to calculate standardization factors.

Standardization

The following method was used to calculate a factor to standardize the number of detections for seasonal differences.

1. We examined the distribution of detections (*fig. 4*) over all years for the three sites and used a Kruskal-Wallis test to determine that the distributions by season were similar for the three sites ($P < 0.0001$). Surveys from all sites and years then were pooled.
2. We calculated the mean number of detections per survey for the period 15 April to 12 August, that we refer to as the summer mean.
3. We then calculated the mean numbers of detections per survey for each 10-day interval, the interval mean. Detection levels for periods longer than 10 days began to show the effects of seasonal variation.
4. The ratio of each of the 12 interval means and the summer mean was calculated (interval mean/summer mean = standardization factor).

The 10-day intervals and corresponding standardization factors calculated for the data from the three sites are presented in *table 1*.

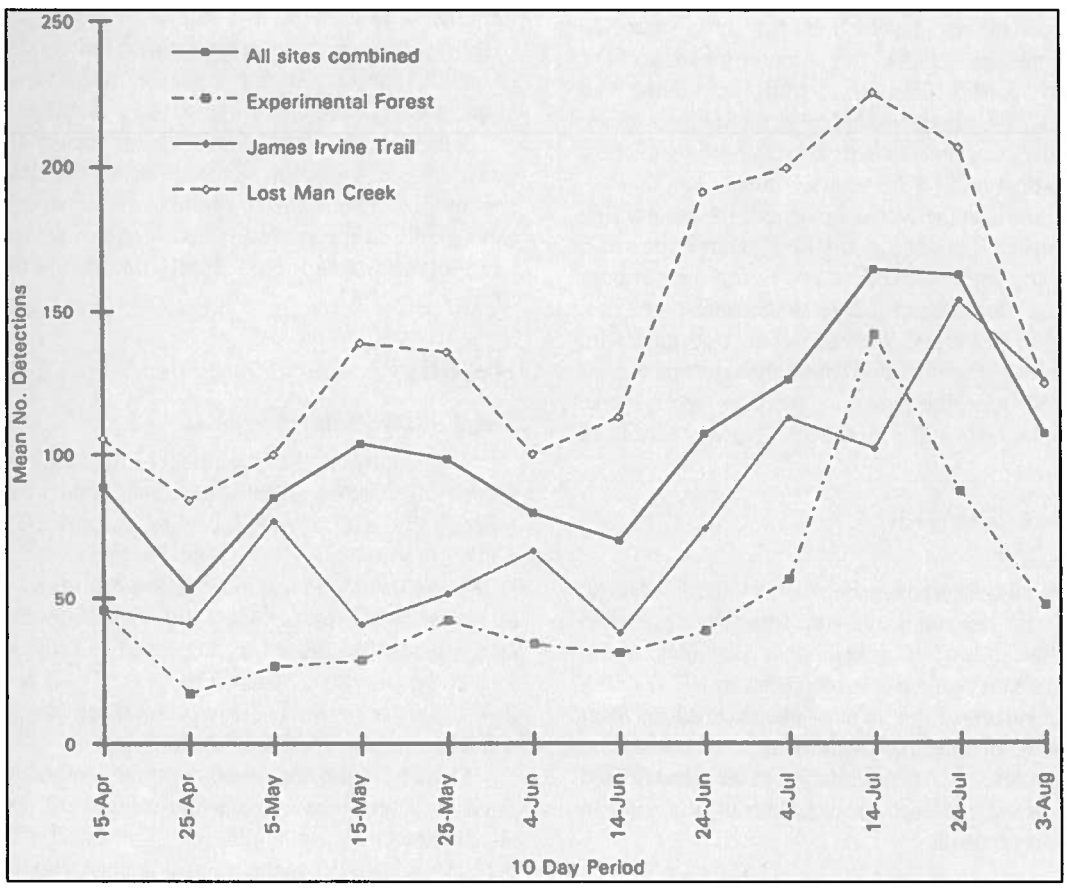

Figure 4—Mean Marbled Murrelet detections from forest surveys at three sites in northern California: James Irvine Trail, Prairie Creek Redwoods State Park; Lost Man Creek, Redwood National Park; and the USDA Forest Service Experimental Forest, Klamath. Means for the three sites combined by 10 day intervals also are presented. Surveys were conducted 3–4 times per month most years from 1989–1993 and points represent the means for 10-day intervals.

Table 1—Ten-day intervals and corresponding standardization factors for seasonal variation of mean Marbled Murrelet levels at three sites in northern California

Interval	Standardization factor
April 15 to April 24	0.86
April 25 to May 4	0.51
May 5 to May 14	0.82
May 15 to May 24	1.01
May 25 to June 3	0.95
June 4 to June 13	0.77
June 14 to June 23	0.68
June 24 to July 3	1.04
July 4 to July 13	1.22
July 14 to July 23	1.59
July 24 to August 2	1.04
August 3 to August 12	1.03

Thus for surveys conducted at the three sites from 14 July to 23 July, numbers of detections per survey were on average 1.59 times greater than the summer mean; surveys conducted from 15 May through 24 May had numbers of detections which were about equivalent to the summer mean; and numbers of detections for surveys from 25 April to 4 May averaged about half of the summer mean.

In applying the standardization, we made the assumption that the relationship between detections at any site on a given day and the mean detection levels for the summer period at that site would be the same as the relationship we found at the three test sites. We have compared data with one site with very low activity and found the seasonal curves were similar. Standardized mean detection levels were calculated for all stands and stations and this measure used for all analyses.

Stand Study: Isolated Stands

Multiple Regression

We examined the relationship between standardized mean detection levels for the stand, referred to as the dependent variable, and the following independent variables: stand size, Patton's index of perimeter to area (Patton 1975) which was used as a measure of the edge or shape, distance from salt water, density of old-growth trees, type of stand, and dominant tree species. As a transformation of the standardized mean detection level, we used the square root of the mean for the multiple regression.

Logistic Regression

For each stand we summarized the detections and behaviors for all surveys conducted during the study to determine the status of the stand. If no murrelets were detected during any of the surveys, then the status was "Undetected." Stands with murrelet detections were assigned a status of "Present" or, if occupied behaviors (Paton, this volume; Ralph and others 1993) were observed, a status of "Occupied."

Using logistic regression (SAS Institute, Inc. 1991) with maximum likelihood analysis of variance, we examined the relationship between a selection of independent variables, and status. We compared response variables Present (including Occupied stands) and Undetected, and response variables Occupied and Unoccupied (all stands with a status of Undetected or Present). For the stands with murrelets present we compared Occupied stands, with stands with a status of Present.

Park Study: Large Contiguous Stands

Elevation and position on the landscape were estimated from topographic maps to give a measure of topography for each station. Landscape position was described as one of five categories: (1) in the bottom of a major drainage, a drainage covering a large length of the landscape and isolated by parallel ridges; (2) in the bottom of a tributary (or minor) drainage, a drainage flowing into a major drainage, or a short, steep drainage flowing directly into the ocean; (3) on top of a major ridge, a ridge running parallel to a major drainage; (4) on top of a minor ridge, a ridge line that originated from the major ridge and was generally perpendicular to a major drainage; and (5) on a general slope, a station not on a ridge nor in a drainage.

When stations were located on slopes or ridges, it was possible to detect murrelets calling in the drainages. The topography within 100 m of the stations was similar to the topography at the station itself. To help isolate the effects of topography, we included only detections within 100 m of the observer.

Results

Stand Study: Isolated Stands

We identified 286 potential study stands in Del Norte, Humboldt, Trinity, San Mateo, and Santa Cruz counties meeting the criteria in the four size categories 2 to 20 ha (n = 184); 21 to 40 ha (n = 39); 41 to 100 ha (n = 35); >100 ha (n = 28). We located few stands >21 ha, therefore, we surveyed all accessible stands in those categories. From these potential study stands we selected and surveyed 152 stands as follows: 2 to 20 ha (n = 86); 21 to 40 ha (n = 22); 41 to 100 ha (n = 23); >100 ha (n = 21). Due to weather conditions, three stands were surveyed only three times.

Density of the combined dominant and codominant tree cover and presence of redwood trees were positively and significantly ($F_{0.05}$ = 2.428, df_{model} = 10, P = 0.0105, R^2 = 0.1625) related to mean murrelet detection levels in the multiple regression model. Because only 16 percent of the variation in the system was explained by the model, the predictive ability was limited. Other variables examined were not related to mean detection levels.

The logistic regression model included density of old-growth (dominant and co-dominant) tree cover, tree species, and stand size as variables explaining the differences between sites with no detections and those with murrelets present (*table 2*). Stands with higher density classifications, and with redwood as the dominant tree species, were more likely to have murrelets present. Results also indicated a very minor effect of smaller stands increasing the likelihood of murrelet presence. We found, however, no significant effect of stand size on the status of murrelets in the stands (Undetected, Present, or Occupied), when tested by Chi-square contingency table ($df = 6$, $\chi^2 = 3.294$, $P = 0.7721$) (*table 4*). Using these variables accounts for virtually all of the variability in the model.

For stands with a status of Occupied ($n = 37$), compared with all Unoccupied stands ($n = 115$), old-growth tree density and tree species were significant variables (*table 3*) for predicting observations of occupied behaviors. Stands in higher density classes with redwood as the dominant species were more likely to be classified as Occupied.

Among stands with murrelet detections ($n = 62$), we found no differences in habitat variables between stands with a status of Occupied ($n = 37$) and Present ($n = 25$).

Park Study: Large Contiguous Stands

Central California

Big Basin Redwoods State Park was surveyed in a matrix of 37 survey stations. The elevation ranged from 240-500 m and we divided stations into four equal categories (*table 5*). We found the mean detection levels and the number of Occupied stations higher for stations in lower elevation categories. The proportion of Occupied stations was not significantly different ($P > 0.05$) among topography categories (*table 5*). Occupied behaviors were observed in all topography categories, and the only station with a status of Undetected was on a major ridge.

Table 2—Results of logistic regression analysis for stands in California (n = 152) with a status of murrelets Present (Present and Occupied) (n = 62) and Undetected (n = 90). Only variables with significant contribution to the model are presented

Variable	Regression coefficient	Chi-square	Chi-square probability
Tree species[1]	1.8101	9.43	0.0021
Cover density[2]	0.8755	5.76	0.0164
Stand size	-0.0206	5.45	0.0195

[1]Coast redwood (*Sequoia sempervirens*) or Douglas-fir (*Pseudotsuga menziesii*) >50 percent of stand.
[2]Percent dominant and codominant tree cover.

Table 3—Results of logistic regression analysis for stands in California (n = 152) with status of Occupied (n = 37) and stands with murrelets Present or Undetected (Unoccupied)(n = 115). Only variables with significant contribution to the model are presented

Variable	Regression coefficient	Chi-square	Chi-square probability
Tree species[1]	1.9243	5.86	0.0155
Cover density[2]	1.0831	6.64	0.0100

[1]Coast redwood (*Sequoia sempervirens*) or Douglas-fir (*Psuedotsuga menziesii*) >50% of stand.
[2]Percent dominant and codominant tree cover.

Northern California

We surveyed 352 stations in the 8 stands within northern California parks. We found that topography had a major influence on murrelet use ($P < 0.0001$). The mean detection levels were three times higher in major drainages (*table 6*) than on the major ridges.

Table 4—Percent of stands by murrelet use or status in each size category of stands surveyed in California for the Stand Study. Stands with a designation of Present had murrelet detections, but no observations of below canopy, or Occupied behaviors

		Percent of stands by murrelet use (status)					
		Not detected		Present		Occupied	
Stand size (ha)	*n*	*n*	Percent	*n*	Percent	*n*	Percent
2- 20	86	55	63.9	14	16.3	17	19.8
21- 40	22	12	54.6	3	13.6	7	19.8
41-100	23	12	52.2	5	21.7	6	26.1
>100	21	11	52.4	3	14.3	7	33.3
Totals	152	90	59.2	25	16.4	37	24.3

Table 5—For central California: Summary of detections[1] and status for Marbled Murrelet stations surveyed in old-growth forests within state and national parks during the summer, 1993

Landscape variable	Mean number of detections[2]	*s.d.*	Range	Number of stations (*n*)			
				Occupied	Present	Absent	Total
Topography							
Tributary drainage	55	42	30-104	3	0	0	3
Major drainage	74	53	1-177	10	3	0	13
General slope	58	31	1-97	7	1	0	8
Minor ridge	34	31	1-83	5	2	0	7
Major ridge	11	14	0-37	3	2	1	6
Elevation							
240-305 m	70	53	1-177	10	2	0	12
306-360 m	64	36	13-122	10	1	0	11
361-420 m	35	31	1-946	4	0	10	10
421-500 m	4	6	0-122	1	1	4	4

[1]Includes only detections within 100 meters of observer
[2]Standardized detections

Table 6—For northern California: Summary of detections[1] and status of Marbled Murrelet stations surveyed in old-growth forests within the state and national parks during the summer, 1993

Landscape variable	Mean number of detections[2]	*s.d.*	Range	Number of stations (*n*)			
				Occupied	Present	Absent	Total
Topography							
Tributary drainage	22	33	0-134	18	19	54	91
Major drainage	30	28	0-160	67	25	17	109
General slope	14	17	0-83	40	67	22	129
Minor ridge	16	19	0-107	19	29	18	66
Major ridge	10	13	0-51	14	27	6	47
Elevation							
21-100 m	28	30	0-160	83	53	27	163
101-200 m	16	18	0-83	46	66	36	148
201-300 m	12	13	0-56	19	37	19	75
301-500 m	4	6	0-22	10	11	18	39

[1]Includes only detections within 100 meters of observer
[2]Standardized detections

The proportion of Occupied stations was significantly higher at stations of less than 100-m elevation than at stations >200 m ($P < 0.0001$) (*table 6*). The proportion of stations with no detections was significantly higher in the >300 m category and significantly lower in the <100 m category.

Inland Range

We found highest frequencies of presence (89.05 percent) and occupancy (21.91 percent) at stands and stations within 10 km of the coast (*table 7*). The proportion of Occupied sites decreased in the 10- to 20-km band. The number of stations with detections declined by more than 99 percent from the 30- to 40-km to the 40- to 50-km band, although four times the number of stations were surveyed in the 40- to 50-km band. The proportion of Occupied stations declined rapidly beyond 30 km from the coast.

Discussion

Stand Study

The most important factor in indicating Occupied stands was density of the old-growth cover, that is, the percent of the area covered by the crowns of old-growth trees. Occupied stands had a higher percentage of old-growth cover than stands with murrelets only present, or in stands with no detections. These relationships are consistent with those

Table 7—Marbled Murrelet use of forest stands in northern California. Numbers represent individual stands for isolated stands surveyed surveyed four times during the Stand Study or stations for surveys conducted in each 12.5 ha of a large contiguous stand for the Park Study or in preparation for timber harvest

Distance band km from coast	Number of stations surveyed	Number of stations by use			
		Detected[1]	Percent	Occupied	Percent
0-10	283	252	89.05	62	21.91
10-20	133	38	28.57	6	4.51
20-30	144	52	36.11	24	16.67
30-40	100	36	36.00	6	6.00
40-50	428	1	0.23	1	0.23
50-60	95	2	2.11	0	0.00
Totals	1183	379	32.04	98	8.28

[1]All stations or stands with murrelet detections, including occupied behaviors

found in Oregon (Grenier and Nelson, this volume) and Washington (Hamer, this volume).

We found the presence of redwood as the dominant tree species to be a factor for predicting higher mean detection levels and stand occupancy. In Washington, Hamer and others (1993) also found tree species composition to be an important factor for murrelet occupancy. Within the range of our study, stands dominated by Douglas-fir often were in drier areas with higher summer temperatures. Sites very close to the coast are usually dominated by Douglas-fir and Sitka spruce (*Picea sitchensis*) and, for unknown reasons, also lack murrelets.

Contrary to previous studies we did not find larger stands more likely to have murrelets present or to be occupied. Other factors, such as, stand history and juxtaposition to other old-growth stands may mask the effects, if any, of stand size on murrelet presence and use.

Although in the Stand Study we did not find a significant relationship between distance from the ocean and murrelet detections or behaviors, this possibly was related to the limited range of distances for stands surveyed. Our examination of all surveys from 1988 through 1992, however, indicates a strong pattern of declining murrelet presence with distance from the coast (*table 7*). The number of stations more than 40 km inland with murrelet detections was only about 2 percent. One factor which may have biased the bands >40 km inland was the selection of the survey sites. Many of these sites were located in forest habitat selected for timber planning and not considered optimal for murrelets. A lack of murrelet detections would then allow timber harvesting on some of these lands. Further studies inland in California at sites selected by unbiased methods would provide needed information on the murrelet's distribution in these areas.

It is unlikely that one factor alone will best describe murrelet habitat. Density of old-growth cover and species composition are included as important factors in more than one analysis. These variables may be the strongest predictors of murrelet presence in California.

Large Contiguous Stands

Within the large stands of old-growth in the parks, most stations with observations of occupied behaviors occurred in the major drainages and, correspondingly, at low elevations. Occupied behaviors were observed at 69 (73 percent) of the 95 stations in the major drainages. Trees in these drainages tend to be larger, and experience less limb breakage from wind (Tangen, pers. comm.). Both of these factors could contribute to larger diameter branches and more potential nest platforms.

Acknowledgments

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Appendix A

Designing a study to examine the relationship of Marbled Murrelets with forest habitats requires first determining if the birds are present or absent from individual forest stands. Here, we outline the methods used to determine the appropriate number of surveys required when the objective is to determine murrelet presence or absence.

For our study, we wished to know how many survey mornings were necessary to determine presence in a stand of murrelets with a 95 percent probability of being correct. We, therefore, set the level of probability of a false negative at 5

percent. That is, murrelets are present, but we accept a 5 percent probability that they are not detected. Data from previous surveys have been used in the discussion below (*table 1*). From the data provided by Rob Hewlett, Steve Kerns, Kim Nelson, and our studies, we determined the number of survey mornings needed to meet this level of confidence at sites having various levels of detection rates.

In the following example, we assumed murrelets are present in the relatively homogeneous stand of old-growth timber to be surveyed. Each survey consists of one person observing from a station for one morning.

The method for examining our data was:

$$P = 1 - (1 - p)^n$$

where—

P is the probability of at least one detection,

p is the proportion of surveys with at least one detection, that is, the number of surveys with at least one detection, divided by the number of surveys, and

n is the number of surveys required to detect at least one bird.

To determine the number of surveys needed if we want to be 95 percent certain ($P = 0.95$) we are not missing birds which are present, we solve for n:

$$n \geq \frac{\ln(1-P)}{\ln(1-p)}$$

where—

ln is the natural log.

Table 1—Detection rate at stations with low rates, and the percent of surveys with detections

Station name	Number of surveys	Mean detection rate	Percent of surveys with detections
Site F	8	0.4	13
ALCR 6	8	1.0	75
FRNO	7	1.3	57
Site E	8	2.1	25
ALCR 3	8	2.5	75
ALCR 9	8	2.6	63
ALCR 4	8	3.0	88
ALCR 1	8	3.1	75
FRSO	11	4.7	91
PATM	8	5.0	88
ALCR 10	8	5.1	75
ALCR 12	8	5.1	88
ALCR 13	8	5.6	88
KLMO	11	6.2	65
SFYA	13	6.5	77
EHSP 10	8	7.5	75
ALCR 11	8	9.4	75
ALCR 8	8	13.0	88
CUPE	13	16.6	92

We tested our survey sample size from 19 sites (*table 1*) with relatively low average detection rates and a minimum of seven survey mornings. The mean detection rate per morning was divided into four categories, 0.4 to 2.5, 2.6 to 5.0, 5.1 to 7.5, and 9.4 to 16.6 detections. We used the average percent of surveys with detections within each category to estimate p.

In the 0.4 to 2.5 category, the percent of survey mornings with detections varied from 13 percent to 75 percent, with an average of 48 percent of the mornings with detections. The calculation is as follows:

$$n \geq \frac{\ln(1-0.95)}{\ln(1-0.48)} = 4.58, \text{ or 5 surveys.}$$

In the 2.6 to 5.0 detection range, the percent of surveys with detections varied over a smaller range, from 63 percent to 91 percent, an average of 81 percent. Using the average number, the calculation is:

$$n \geq \frac{\ln(1-0.95)}{\ln(1-0.81)} = 1.80, \text{ or 2 surveys.}$$

In the 5.1 to 7.5 detection range, the percent of surveys with detections varied from 65 percent to 88 percent, an average of 78 percent. The calculation as above was 1.98 or a minimum of 2 surveys.

The highest detection range used for this calculation was 9.4 to 16.6 birds per morning, an average of 85 percent of survey mornings with at least 1 detection. The calculation resulted in 1.75, or 2 surveys.

From these data we can conclude that in areas with mean detection rates as low as 0.4 to 2.5 per survey (and presumably low occupancy rates as well), a minimum of five survey mornings will detect birds if they are present, with a 95 percent probability. In areas of detection rates from 9.4 to 16.6, the number of surveys necessary to prevent a false negative is about two. Using this formula, 4 surveys would be required to detect birds in areas with a mean of 1.0 to 2.5 detections per survey. We can then conclude that a suggested survey rate of four surveys per stand, will detect birds in excess of 95 percent of the time, and will likely detect all but the smallest populations 99 percent of the time.

Assumptions

There are several assumptions we have made in using these methods. We list them below and discuss each.

We assume that the amount of canopy cover at a station will have no effect on detection probability (P).

In most forests, the majority of detections are audio and are not affected by canopy cover. Though the number of visual detections decreases with increased canopy cover, there should be a compensating effect as we have found higher numbers of total detections (e.g., Paton and Ralph 1990) as forest age and canopy cover increase.

In calculating P, *the probability of at least one detection in a stand, we assume that murrelets are present in the stand when the survey is conducted.*

The effects of this assumption are discussed in detail in Azuma and others (1990), and the situation with the murrelet is similar. Since there is some probability that murrelets will be present in a stand and not be detected, the result would be an underestimate of the number of stands with murrelets present. Following data collection, bias adjustments presented in Azuma and others (1990) could be used to estimate the number of stands with murrelets in each stand category.

We assume that P *is constant and independent of stand size and habitat type.*

It is possible that as stand size increases and habitat matures, the number of birds in a stand will increase. Increased numbers will likely increase *P* as individuals may call in response to other birds as a result of social facilitation. Therefore, stands with few birds will have fewer detections than stands with many birds. We will be examining this assumption, and it forms the basis of the null hypothesis that stand size and habitat type have no effect on detection rate.

Frequency of surveys

If the habitat is homogeneous and we assume that the birds are distributed essentially evenly throughout the stand, the stations can be positioned throughout the stand and all stands, regardless of size, would be surveyed four survey mornings.

PART IV

The Marine Environment

United States
Department of
Agriculture

Forest Service

**Pacific Southwest
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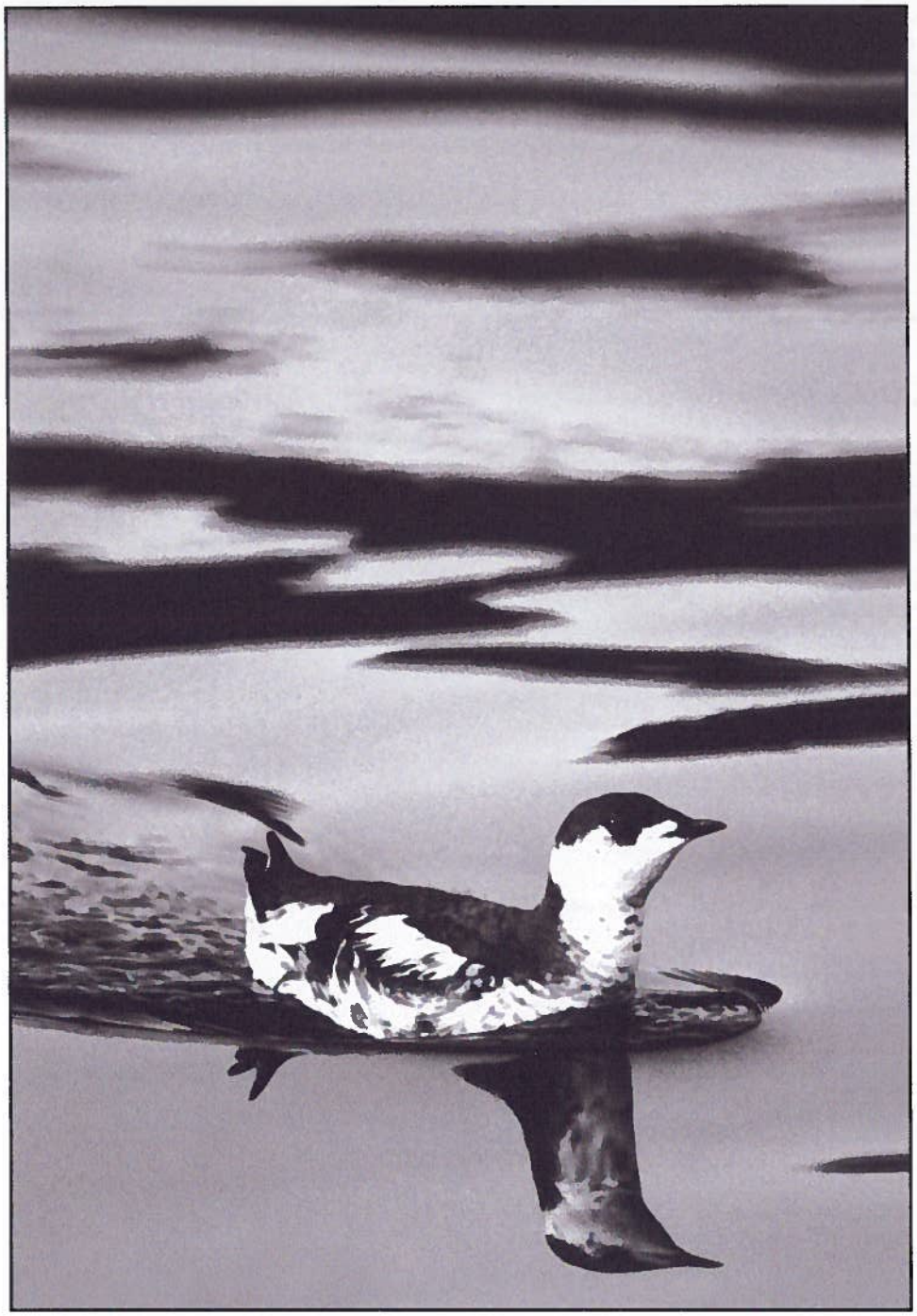
General Technical
Report PSW-GTR-152

State of the Science

Ecology and Conservation of the Marbled Murrelet



Abstract:

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This report on the Marbled Murrelet (*Brachyramphus marmoratus*) was compiled and editied by the interagency Marbled Murrelet Conservation Assessment Core Team. The 37 chapters cover both original studies and literature reviews of many aspects of the species' biology, ecology, and conservation needs. It includes new information on the forest habitat used for nesting, marine distribution, and demographic analyses; and describes past and potential effects of humans on the species' habitats. Future research needs and possible management strategies for both marine and forest habitats are suggested.

Retrieval Terms: Brachyramphus marmoratus, Marbled Murrelet, old-growth forests, habitat use, marine distribution, seabird.

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The Forest Service, U.S. Department of Agriculture, is responsible for Federal leadership in forestry. It carries out this role through four main activities:

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United States
Department of
Agriculture

Forest Service

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Research Station**

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C. John Ralph **George L. Hunt, Jr.** **Martin G. Raphael** **John F. Piatt**

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Preface

The Marbled Murrelet (*Brachyramphus marmoratus*) has long been regarded as a bird of mystery in the Pacific Northwest because its nesting habits have remained largely unknown to ornithologists, and its nearshore feeding habits made it difficult to survey. This small, dove-sized seabird inhabits coastal areas of North America from Alaska to central California. Throughout most of its range it nests in forests within about 25 to 50 miles of the coast, and feeds in nearshore marine waters on small fish and invertebrates. In contrast to most alcids, which nest colonially on rocky cliffs or relatively barren islands, the Marbled Murrelet nests inland throughout most of its range in solitary pairs (or perhaps loose associations), on the wide, upper branches of old, coniferous trees. This retiring habit delayed the discovery of its nest in North America until 1974, when one was found in central California (Binford and others 1975). Since then, despite many thousands of person-days of effort over the past decade, fewer than 60 nests have been located through the 1993 breeding season (Nelson and Hamer, this volume a).

In the 1980s, field biologists discovered evidence suggesting that many, if not most, individuals nest in unharvested coniferous old-growth forests. Further research, much of it presented for the first time in this volume, has provided additional information on habitat use, on their relatively low reproductive rates, and on the high predation they experience at the nest.

In at least some areas, evidence also began to accumulate that the Marbled Murrelet population has declined in recent years. This decline has been attributed to reduction and fragmentation of old-growth forests, increased predation, pollution (especially oil spills), and mortality from fishing nets. This potential decline heightened management sensitivity to assure the maintenance of healthy interacting populations throughout its range. At present, the murrelet is classified as threatened or endangered by the U.S. Fish and Wildlife Service in Washington, Oregon, and California, as well as by the State of California and the Province of British Columbia. For most land management agencies, these listings require inventories and analyses of potential impacts of proposed projects on the species. If adverse impact on murrelet habitat is found, it may result in mitigation measures, project modification, delays, and possible cancellation.

Issues

Several issues faced land management agencies in the United States and Canada in 1992 when the effort on this volume began.

Timber harvest—The legal status of the species was beginning to prevent or delay timber harvest activities throughout most of its range on the Pacific Coast of North America. No forest management standards and guidelines to maintain murrelet habitats existed, because documentation of the full range of the species' habitat was unknown.

Survey and monitoring efforts—Surveys to determine the species' presence or absence in forest stands throughout its range required substantial financial and personnel resources. Due to a lack of knowledge of its distribution and abundance, costly efforts often included surveys in areas that were unsuitable or of marginal value to the species.

Other resources—It seemed probable that the species occupied habitats containing large amounts of economically valuable timber.

These stands also functioned as reservoirs of biological diversity, and had great values as watersheds and as sources of a variety of wildlife and fishery resources. While at sea, the bird coexisted with large numbers of commercially important fish, especially salmon, the harvesting of which may result in significant murrelet mortality.

Consolidation of information—It was apparent that a need existed to consolidate available information, and to synthesize knowledge of population trends, distribution, habitat associations, and potential management alternatives. The U.S. Fish and Wildlife Service appointed a Marbled Murrelet Recovery Team early in 1993 to determine the status and mode of recovery of the species. They needed a rapid production of scientific background material for their deliberations.

Goals of the Assessment

To meet these issues, the USDA Forest Service began a "Marbled Murrelet Conservation Assessment" in late 1992 with the following mandate. The Assessment would consolidate the available information concerning Marbled Murrelet ecology and evaluate current habitat conditions to determine the likelihood of long-term persistence of healthy populations throughout its current range. The Assessment would include monitoring and research recommendations, be a primary source of information for the Recovery Team, and provide information that would enable agencies to make management plans.

This work would be accomplished by the following methods:

1. Identify patterns of habitat use in the forests and marine environments occupied by the murrelet, and develop an understanding of the spatial and temporal dynamics of these habitats and murrelet populations, by using a compilation of existing survey data.

2. Summarize and synthesize existing information from throughout the range about the life history, status, and trends of the murrelet and its utilized habitats, and provide the information gathered to all interested parties.

3. Identify additional inventory needs and methodology to facilitate statistically meaningful long term monitoring of both the species and its habitats, thus providing the information needed to develop sound strategies to provide for their maintenance and management.

4. Identify additional research needs to fill information gaps preventing a full understanding of Marbled Murrelet ecology.

5. Provide suggestions to improve the compatibility of data bases maintained by various entities.

Organization

The Assessment effort was organized into a set of working groups as follows:

• Interagency Conservation Assessment Coordinating Group—The intent of this group was to coordinate and provide support to Conservation Assessment activities among the state, provincial, and federal agencies with Marbled Murrelet management responsibilities. These agencies and organizations were invited to participate by the two Group Leaders: Garland N. Mason, Pacific Southwest Research Station, Albany, California; and Hugh Black, Pacific Northwest Region, Portland, Oregon—both with the USDA Forest Service.

• Conservation Assessment Core Team—The Core Team was headed by a Team Leader (C.J. Ralph), provided by the Pacific Southwest Station, and three senior scientists with established expertise in various aspects of ecology who, drawing on the knowledge provided by the Technical Working Group, provided the scientific expertise to formulate the Conservation Assessment. The Team Leader provided the overall technical and administrative leadership for assessment development and ensured good communication between the Coordinating Group, the Core Team, and the Technical Working Group. The scientists in the Core Team became the technical editors of the final volume.

• Conservation Assessment Technical Working Group—This group was open to all persons with knowledge or abilities that could contribute to the formulation of the Conservation Assessment (see *Appendix A* in this volume), and provided the following functions:

- Collected and provided technical information required by the Working Group.
- Wrote chapters of the Assessment, as appropriate.
- Provided assistance, advice, and input to other members of the Working Group as requested.
- Informed respective agencies, organizations, or regions as to progress and findings of the Conservation Assessment.
- Provided expertise to formulate inter-regional assessments.
- Identified and overcame obstacles to gathering information for the Assessment.

Members of the Working Group included:

- Marbled Murrelet specialists from universities, agencies, private industry, and conservation organizations.
- Regional representatives from USDA Forest Service Regions in Alaska, Washington, Oregon, and California.
- Agency Representatives from three U.S. Department of the Interior agencies— Fish and Wildlife Service, National Biological Service, National Park Service— and Canadian Wildlife Service, among others.
- Representatives from state and provincial fish and wildlife agencies not represented above.
- Specialists from various disciplines useful to the process of the Assessment.
- Line officers.

Financial assistance was provided by various agencies and organizations, acknowledged in each chapter, and also by the Assessment itself that provided certain members of the Technical Working Group with funds to enable them to analyze their data in a more timely manner than would have been possible in the normal course of events.

Working Environment

Working sessions of the Core Team and the Working Group were open to all persons interested in the proceedings, with the Team Leader acting as chair.

Working Group members participated fully with the Core Team and participated in all decisions. The Core Team provided direction and strived for consensus among the Team and Group members. Minority reports were possible and encouraged. Wildlife Society standards for authorship were used. In the final stages of compilation of the volume, the technical editors met and reviewed chapters which were then sent to authors for final approval of all contents.

Products

The primary product of the Assessment is this volume. Each chapter in the volume was reviewed by numerous researchers and biologists in appropriate fields, as well as by the Core Team. In addition, the entire document was reviewed by four persons appointed by the Presidents of learned societies: The Wildlife Society (David Marshall), American Ornithologists Union (Peter Conners), Ecological Society of America (Frank A. Pitelka), and the Cooper Ornithological Society (Douglas Bell).

The report is organized into chapters addressing the various aspects of Marbled Murrelet biology and provide data and analyses. Some general management considerations are offered in the overview chapter, and are intended to

supplement those offered by the Recovery Team, appointed by the USDI Fish and Wildlife Service.

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We hope that this effort will serve well the bird and the people charged with its management. Most importantly we dedicate this volume to the biologists who have spent so many cold, lonely, but exhilarating hours in pursuit of this sprightly, energetic bird, both on the ocean and in the forest, where it turns into a hurtling, small, dark shadow, as it enters the primeval forest in pursuit of its largely still mysterious habits.

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Chapter 7

Breeding and Natal Dispersal, Nest Habitat Loss and Implications for Marbled Murrelet Populations

George J. Divoky[1] **Michael Horton[2]**

Abstract: Evidence of breeding and natal dispersal in alcids is typically provided by the resightings of banded birds, the establishment of new colonies, and/or evidence of immigration to established colonies. The difficulties in banding, observing, and censusing Marbled Murrelets at nesting areas preclude using any of these methods for this species. Based on the limited number of nests observed in consecutive breeding seasons, breeding site fidelity (birds breeding in the same nest as the previous year) may be lower than most other alcids. This is likely due to low breeding success associated with high levels of nest predation. By contrast, annual use of nest stands suggests fidelity to a nesting area may be high. Natal dispersal, the breeding at locations away from their fledging site, is likely similar to that of other alcids. Loss or degradation of previously occupied nesting habitat will result in the displaced breeders prospecting for new nest sites. In areas with no unoccupied available habitat, this could result in birds being prevented from breeding, attempting breeding in suboptimal habitat, or increasing the distance dispersed from the previous breeding sites. Each of these is likely to result in a decrease in reproductive output. Dispersal patterns need to be considered when assessing the importance of stands and the status of populations. The small population size and fragmented nature of the remaining breeding habitat could increase the time required for prospecting birds to locate recently matured old-growth forest, resulting in underestimating the importance of a stand. Additionally, birds could be dispersing from regions of high production of young to areas with low production but where recruitment opportunities are higher, partially hiding the low reproduction of the latter population.

The ability of Marbled Murrelets to disperse from natal sites, and their fidelity to breeding sites or stands, has important implications for the potential of the species to respond to habitat loss and colonize or reestablish breeding areas when habitat has been altered. With knowledge of these factors, we could more accurately assess the effects of habitat destruction on the viability of populations throughout the species' range. In the discussion below, we examine what is known about dispersal in other alcid species and the possible implications for the Marbled Murrelet.

Dispersal of birds can occur both by established breeders changing breeding sites (breeding dispersal) and by birds nesting away from their natal nesting area (natal dispersal) (Greenwood and Harvey 1982). The degree of nest-site fidelity by established breeders can be expected to be related to previous breeding success and the frequency of change in availability of suitable nest sites and prey resources. Nest site availability can be decreased both through the destruction of nest sites and through chronic predation. An increased rate of natal dispersal should be related to the potential to be more successful in finding mates or nest sites away from the natal nest site or colony.

Breeding Dispersal

Breeding site fidelity in a long-lived species, which the Marbled Murrelet is presumed to be (Beissinger, this volume), can provide benefits in increased breeding success and lifetime fitness. Site fidelity can reduce potential reproductive effort by (1) increasing the chances of breeding with the previous year's mate, (2) eliminating or reducing the need to locate a suitable nest site, and (3) allowing the development of familiarity with the marine and terrestrial environment.

The rate of breeding dispersal is low for most alcid species that have been studied. Rates of nest-site fidelity of previously breeding alcids are: 91.5 percent Razorbills (*Alca torda*) (Lloyd 1976); 96 percent Common Murres (*Uria aalge*) (Birkhead 1977); 93.2 percent Atlantic Puffins (*Fratercula arctica*) (Ashcroft 1979), 57-95 percent Black Guillemots (*Cepphus grylle*) (Divoky, unpubl. data; Petersen 1981); 86 percent Pigeon Guillemots (*C. columba*) (Drent 1965); 78 percent Ancient Murrelet (*Synthliboramphus antiquus*) (Gaston 1992).

The degree of breeding dispersal displayed by an alcid should be related to the rate that nesting habitat is created and destroyed, the level of mortality of breeding birds, and the availability of nest sites. Species with a high probability of returning to a nest site destroyed over the winter would have fewer reasons to have evolved site tenacity. Harris and Birkhead (1985) suggested that the Thick-billed Murre (*Uria lomvia*) might show less site tenacity than other Atlantic alcids because rockfalls destroy or create nest sites in their colonies more frequently than for other species. Burrow nesting alcids could be expected to show higher rates of breeding dispersal than talus nesters due to the higher frequency of collapse of burrows.

Annual overwinter mortality could be expected to influence breeding site fidelity. High overwinter mortality would decrease the chances of a surviving bird being able to breed with the previous year's mate and, by creating more vacancies at established nest sites, increase the opportunities for dispersal for species that are nest site limited.

For those alcid species in which breeding site fidelity has been examined, and for birds in general (Greenwood and Harvey 1982), changes in nest site are more frequent after a breeding failure. For Black Guillemots, nest-site fidelity was 92 percent for successful pairs and 48 percent for failed

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pairs (Petersen 1981). For Ancient Murrelets, reoccupancy rates of burrows that supported successful breeding the preceding year was 80 percent, and only about 50 percent for unsuccessful burrows (Gaston 1992). Nest changes caused by simple breeding failure typically result in small scale movements (usually tens of meters) to nearby sites (Divoky, unpubl. data; Petersen 1981).

Chronic disturbance at the nest site can cause established breeders to move to a new breeding location thousands of meters away. A Pigeon Guillemot that experienced persistent disturbance at its nest site was found breeding on an island 7.7 km away 3 years later (Drent 1965). At a Black Guillemot colony where any movement of established breeders is typically to an adjacent nest site (<10 m), one bird moved approximately 1 km and another over 5 km, after Horned Puffins (*Fratercula corniculata*) using the same nest site had repeatedly disrupted nesting (Divoky 1982 and unpubl. data).

Essentially all information on breeding dispersal in alcids has been obtained through the banding and resighting of individuals. The difficulty of capturing and observing Marbled Murrelets at the nest site has prevented the collection of similar information for this species. The old-growth nesting habitat of the Marbled Murrelet is relatively stable. Natural destruction of old growth forests through fire or wind storms is rare enough, and the degradation of nest trees is slow enough, that high site fidelity could have evolved.

Observations of murrelets engaging in "occupied behavior," strongly suggesting nesting (Ralph and others 1993), indicate that Marbled Murrelets, as a species, exhibit high fidelity to a nesting area. Marbled Murrelets have been recorded in the same forest stands for a minimum of 20 years in northern California (Strachan, pers. comm.; Miller, pers. comm.), 18 years in central California (S.W. Singer, pers. comm.), 7 years in Oregon (Nelson, pers. comm.), and 3 years in Washington (Hamer, pers. comm.). These results are in part a function of the duration of survey effort. While these observations indicate that the species exhibits high fidelity to forest stands, no direct information is available on stand or nest-site fidelity of individual birds.

For species having high annual survival and site fidelity, the occupation of the same nest site in consecutive years is strongly suggestive of individual nest-site fidelity. Reoccupation of the same nest site has occurred only once in the 13 instances where Marbled Murrelet nests have been examined in the breeding season following a year of known occupancy (P. Jones, pers. comm.) and nesting occurred in the same tree four times (P. Jones, pers. comm.; Naslund, pers. comm.; Nelson, pers. comm.; Singer, in press). Additional evidence of fidelity to a nest tree is provided by Nelson's (pers. comm.) finding of three nest cups on three platforms in a single tree, although we do not know if it was the same individuals. While the sample size is small, the observed fidelity to the same nest depression in consecutive years appears to be lower than for other alcids. This could be related to the high rate of predation recorded for murrelet nests (Nelson and Hamer, this volume b). It also indicates that while breeding habitat for this species is reduced (Perry, this volume), and may be limiting, the number of nest platforms apparently is not. If the high predation rate is a recent phenomenon, nest-site fidelity may have been higher in the past. As previously mentioned, breeding dispersal increases with increased rates of nesting failure (Greenwood and Harvey 1982). The high rates of observed nest failure (Nelson and Hamer, this volume b) may explain murrelets not reoccupying a nest site in subsequent years.

Natal Dispersal

The primary benefit that a bird derives from breeding at its natal colony may be that the natal area is a known location where conspecifics of a similar genetic background successfully bred in the past (Ashmole 1962). However if a breeding location is near those of related individuals, there is the possibility of kin selection occurring and a moderate level of inbreeding (Shields 1983).

Philopatry (chicks returning to their natal colony or nesting location to breed) is more difficult to study than the fidelity of breeders to a nest site. It had been assumed that the majority of alcids surviving to breeding are recruited into their natal nesting area (Hudson 1985). More recent information, however, shows that prospecting by prebreeders at non-natal colonies is a regular occurrence in Common Murres (Halley and Harris 1993) and Atlantic Puffins (Harris 1983, Kress and Nettleship 1988). Until recently, the instances of banded birds initiating breeding at a non-natal colony were limited (Asbirk 1979, Lloyd and Perrins 1977). However, recent information indicates that, at least in the Atlantic Puffin, half the chicks that survive to breeding emigrate to a new colony (Harris and Wanless 1991).

Other evidence of natal dispersal is provided by the establishment of new colonies and growth rate of existing colonies that could only be explained by immigration (Divoky, unpubl. data; Gaston 1992; Petersen 1981). The frequency with which new alcid colonies have formed on the west coast of North America in the short period that systematic censusing has been conducted (*table 1*) proves that natal dispersal is common in the alcidae.

The distance that birds will breed from their natal site can be great. Banding returns show that the distance dispersed can be as great as 420 km (by sea) for the Common Murre (Halley and Harris 1993) and over 450 km for the Atlantic Puffin (Harris and Wanless 1991). The rate of increase of some breeding populations, and the establishment of new colonies, indicates that Ancient Murrelets are being recruited into breeding populations at least 30 km from their natal site (Gaston 1992), Black Guillemots from over 500 km, and Horned Puffins from over 200 km (Divoky, unpubl. data).

Because of the difficulties of marking and subsequently resighting Marbled Murrelets, any direct evidence of natal dispersal would have to come from observations of range expansion, occupation of previously unoccupied breeding

Table 1—Alcid species that have recently formed new colonies in western North America

Species	Alaska	British Columbia	Washington	Oregon	California
Common Murre		Campbell and others 1975	Speich and Wahl 1989	USFWS[1], unpubl. data Newport, OR	Sowls and others 1980 Carter and others 1992
Thick-billed Murre	Sowls and others 1982	Vallee and Cannings 1983			
Pigeon Guillemot	Sowls and others 1978 USFWS unpubl. data, Anchorage, AK	Campbell 1977	Speich and Wahl 1989	USFWS, unpubl. data Newport, OR	Sowls and others 1980 Carter and others 1992
Black Guillemot	Divoky and others 1974				
Cassin's Auklet					Carter and others 1992
Rhinoceros Auklet		Campbell and others 1975	Speich and Wahl 1989	USFWS, unpubl. data Newport, OR Scott and others 1974	Sowls and others 1980 Carter and others 1992
Tufted Puffin	Byrd and others 1980			USFWS, unpubl. data Newport, OR	Sowls and others 1980
Horned Puffin	Divoky 1982 Divoky, unpubl. data				

[1] USFWS — U.S. Fish and Wildlife Service

areas, or growth of local populations that could only be accounted for by immigration. The nesting habits of the species makes the detection of any of these difficult, as does the short period that the species has been the focus of research. In addition, the high rate of habitat destruction recently experienced (Perry, this volume) adds to these difficulties.

Natal dispersal can be expected to be high in Marbled Murrelets compared with other alcids for several reasons. The winter distribution is extensive, with the species wintering in the nearshore waters of the breeding range, as well as in areas where breeding does not occur. The distance that individual birds disperse from either their breeding or natal area can be great, as murrelets are regularly found in southern California some 300 km south of the closest known breeding area (Briggs and others 1987). Because murrelets attend inland breeding areas during the winter (Naslund 1993b), information on breeding areas is provided to prospecting nonbreeders at all times of the year. The prebreeding period for this species is probably between 2 and 5 years (Beissinger, this volume), allowing sufficient time to prospect for a suitable nesting area. Additionally, the area where Marbled Murrelets might discover suitable nesting habitat is a 60-km band adjacent to the coast. This extensive area of potential breeding habitat may have selected for more extensive prospecting behavior than in other alcids where potential breeding sites are largely linearly distributed in a narrow shoreline band.

Methods of Dispersal

The manner in which alcids coalesce into breeding pairs can have implications for the level of breeding and natal dispersal. The vast majority of breeding dispersal in alcids consists of birds moving to sites either immediately adjacent, or close to, the previously occupied nest site (Divoky, unpubl. data). This occurs even when an established breeder initiates a new pair bond with another established breeder (Divoky, unpubl. data), indicating that pairing for most, if not all, alcids occurs near the breeding site. If pairing occurs on the water when birds are staging near the breeding location, one would expect to see almost random movement of the established breeders that lose or change mates. Additionally, if established breeders paired on the water, the pair would have affinities to two sites.

Because ownership of a quality nest site or territory is an important prerequisite for breeding, pairing at the nest site allows a bird to find out whether a prospective mate owns a site and to determine the quality of that site. Pairing

with a bird that owns a nest site increases the chances that a bird will pair with an experienced breeder.

Nonbreeding birds, with no previous experience, also probably form pairs near the nest site. Observations of Black Guillemots in northern Alaska (Divoky, unpubl. data) show that nonbreeders are present at the colony throughout the breeding season, and many display a high level of mate and site fidelity. Although nonbreeders form pairs with each other, when one member of an established nest site owning pair dies, the vacancy is typically filled by a nonbreeder of the appropriate sex. Nonbreeding pairs can be recruited as a unit should a new site be created or should two vacancies occur at an established site. However, the low annual mortality rates of breeding alcids indicates that most recruitment occurs through a single vacancy in an established pair. With recruitment occurring at or near the nest site, the established breeder and the individual being recruited, can pair with a familiar bird. Recruitment in murrelets could occur in the same manner. Those birds prospecting new nesting areas could pair on the water before prospecting potential nest sites.

Implications of Habitat Loss and Fragmentation of Populations

The final rule listing Marbled Murrelets as threatened (U.S. Fish and Wildlife Service 1992) regards loss of older forests and associated nest sites as the main cause of decline in murrelet populations. When nest sites are limiting, the loss of nesting habitat has both immediate and long term impacts on the reproductive potential of a murrelet population. While alcid populations have been shown to recover in a relatively short period from episodic anthropogenic mortality events, such as gill net and oil spill mortality (Piatt and others 1991; Carter and others 1992), loss of nesting habitat directly affects the long term reproductive potential of a population. This is especially true for tree-nesting Marbled Murrelet populations where the creation of nesting habitat is extremely time-consuming, perhaps 200 years.

Fragmentation of old-growth also has the potential of reducing murrelet breeding success by increasing the densities of predator populations. Corvids are "edge species" that have been found to increase in numbers with increased forest fragmentation (Andren and others 1985, Wilcove 1985, Small and Hunter 1988). Similar findings have been reported in central Oregon regarding Great Horned Owls (Johnson 1992). In addition, corvid predation on small bird nests has been found to increase with increased forest fragmentation, decreased distance of nests from a forest edge or both (Gates and Gysel 1978, Andren and others 1985, Small and Hunter 1988, Yahner and Scott 1988). Factors that increase fragmentation, such as a wildfire or timber harvest, could reduce murrelet breeding success both through the reduction of cover and the increase in predator densities. This reduced breeding success could be expected to increase the rate, and possibly the distance, of breeding dispersal. The distances moved would probably relate to the level of disturbance and the threat that the predators pose to adult birds. The reduction and fragmentation of habitat would also act to increase the distance prospecting prebreeders would have to travel to find a suitable nest site.

Habitat loss could be expected to result in the displacement of breeding birds, while fragmentation could lead to both displacement and decreased breeding success. In cases where stands used for nesting are destroyed, the birds previously breeding in the stand would have to locate a new nesting area. If all available nest sites in adjacent habitats are occupied, the displaced birds could attempt to breed in suboptimal sites with a decreased chance of successful reproduction, prospect more distant areas, or not breed at all. There are no conclusive indications of higher densities of murrelet nesting in stands remaining after timber harvests (Ralph and others, this volume). The ease and rapidity with which displaced murrelets seek out new breeding areas could be expected to be related to how frequently murrelets normally change sites. If the level of individual nest-site fidelity is as low as observations indicate, then murrelets may be able to readily move at least short distances to new nest sites. The fidelity birds show to a previously used breeding area or site that no longer can support breeding, should be related to the rate and magnitude of habitat destruction. There is evidence of murrelets visiting remnants of newly harvested stands before disappearing from the area (Folliard, pers. comm.), thus indicating that murrelets might not immediately abandon the unsuitable nest stand. This is consistent with observations in other alcid species. Pairs have shown fidelity to previously occupied, and recently destroyed, nest sites for two years in the Black Guillemot (Divoky, unpubl. data), and a minimum of two years in the Least Auklet (*Aethia pusilla*) (I. Jones, pers. comm.). This type of nest loss would be similar to the loss of a previously used murrelet nest platform branch and not the removal of a nesting stand.

Management Implications of Dispersal

High levels and extensive distances of natal dispersal could result in source areas with high productivity producing young that will be incorporated into sink regions with low productivity, or high adult mortality, or both. This could result in populations in sink areas showing little change in numbers. Without monitoring breeding success, the inability of the sink population to produce enough young to balance adult mortality would not be evident. The maintenance of such a population would be dependent on the continued production of a surplus of young by the source population. The true reproductive status of the sink population would be masked until immigration declines. Such immigration could explain the ability of the central California murrelet population to lose an estimated 150 to 300 birds in the early 1980s (Carter and Erickson 1988) and not show any signs of decline (Carter and others 1992).

The secretive nature of murrelet nesting has precluded the determination of breeding areas solely by the discovery of nests, eggs or chicks. Biologists and managers have had to identify breeding areas based on the birds engaged in activities included in "occupied behavior" as strongly indicative of nesting (Ralph and others 1994). Relying on instances of occupied behavior as an indication of the importance of a stand to Marbled Murrelets has a number of potential weaknesses.

First, recently matured forests that are able to support nesting could not be expected to be immediately discovered and occupied by prospecting murrelets. The ability of alcids to occupy areas where suitable breeding habitat is made available is evident from the rapid colonization of islands in the Aleutian Islands where fox have been eliminated (Bailey and Kaiser 1993). The occupation of newly available suitable habitat by Marbled Murrelets in Washington, Oregon, and California may be delayed by the small stand size, high fragmentation and disjunct distribution of the old growth forest. The small size and apparently low breeding success (Nelson and Hamer, this volume b) of the population can be expected to further slow occupation of newly available habitats. Because almost all prospecting of currently unoccupied suitable habitat would occur through natal dispersal, low productivity would reduce the potential of a population to disperse. This would result in a lack of detections in stands that have the potential of supporting murrelet breeding, but have not yet been discovered by murrelets. The importance of this apparently suitable but currently unoccupied habitat to the future of the species needs to be recognized.

In regions where a large nonbreeding population is prevented from breeding by lack of nest sites, prospecting birds might investigate areas and habitats that do not support breeding. This could result in "occupied" behavior being recorded in areas where nesting is not occurring. Prospecting alcids can be present in apparently suitable habitat (Divoky 1982, unpubl. data; Kress and Nettleship 1988; Carter and others 1992), although no breeding is occurring. If loss of old-growth habitat has both increased the level of dispersal and limited potential nest sites, substantial numbers of murrelets could be displaying "occupied behavior" in habitats where breeding is not currently being attempted or where successful breeding could not occur. Such could be the case in central California where Carter and Erickson (1988) believed that all remaining nesting habitat is occupied and because the population is nest site limited, nonbreeding birds may be present over land and sea in a greater percentage than elsewhere. While this may result in overestimating the use of stands, it is unlikely that murrelets would be repeatedly encountered in stands that do not have some present or future potential for supporting successful breeding.

Discussion

The coastal old-growth forest utilized for breeding by Marbled Murrelets would have selected for relatively high rates of breeding and natal dispersal. Based on the behavior and cryptic coloration of the breeding adults and chicks, and the high rate of nest predation for observed nests (Nelson and Hamer, this volume b), the risk of nest predation appears to be higher than for other alcids. The assumed high rate of nest predation would have selected for frequent short distance movements, while the extensive time required for old growth stands to be destroyed or degraded under natural conditions would have selected for individual fidelity to a nesting stand. There is no indication that the distance that breeding murrelets typically disperse would be any greater than the conservative movements (usually <1 km) that have been observed for other alcids.

Most dispersal in alcids is probably due to natal dispersal, and Marbled Murrelets appear to have the capacity for extensive natal dispersal given the extent of the breeding range, the overlap between the wintering and breeding areas, and the distance individuals are known to move from breeding areas in winter. It would not be unreasonable to assume the percentage of birds that initiate breeding at a non-natal locality (natal dispersal) is as high or higher than has been reported for other alcids (approximately 50 percent) (Harris and Wanless 1991). The ability to prospect for breeding localities should be well developed in Marbled Murrelets. Unlike the potential breeding area of most alcids, which is linearly distributed in a narrow band on the shoreline, murrelet nesting habitat is found in a wide (as much as 60 km) band adjacent to the coast.

Breeding habitat fragmentation and loss can be expected to have affected the rate and extent of murrelet dispersal. In Washington, Oregon, and California, high predation rates apparently associated with fragmentation would select for increasing the rate and extent of breeding dispersal. However, the small size and highly fragmented and disjunct nature of the old-growth remaining in this area can be assumed to have decreased the potential distance for breeding dispersal (at least in areas where stand size is small). Natal dispersal rates and extent may have been increased as habitat in the natal locality was reduced and the distance to the location of suitable habitat is increased. These changes in dispersal may have the overall effect of depressing reproductive output.

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Chapter 36

Status of Forest Habitat of the Marbled Murrelet

David A. Perry[1]

Abstract: Marbled Murrelets (*Brachyramphus marmoratus*) have been shown to be dependant upon old-growth forests for nesting habitat. These forests have declined over the last century as they are cut for human use. This paper reviews the current status of old-growth forests along the west coast, in both the United States and Canada.

Marbled Murrelets (*Brachyramphus marmoratus*) are dependant upon forests for nesting habitat, particularly old-growth forests, as seen in several studies of murrelets along the west coasts of Washington, Oregon, and California (Grenier and Nelson, this volume; Hamer, this volume; Raphael and others, this volume; Miller and Ralph, this volume). Over the last century, the acreage of old-growth forests has declined as they are cut for human use. The impact of the loss of this habitat is discussed elsewhere in this volume (Divoky and Horton, this volume). In this paper, I gathered together the most current information on the acreage of old-growth forests remaining along the west coast of North America from various sources to indicate the current status of the nesting grounds of the Marbled Murrelet.

Washington, Oregon, California

Presently, the best information on area and distribution of forests that might provide suitable murrelet habitat in these states is provided by two sources: the Final Supplemental Environmental Impact Statement (FSEIS, USDA and USDI 1994) that updates the report of the Forest Ecosystem Assessment Management Team (FEMAT) (Thomas and Raphael 1993), which covers Federal lands in the three states; and unpublished data of Fox (pers. comm.), which covers the coastal redwood zone in California. Both studies used remote imagery to classify forests.

FEMAT, as updated in the FSEIS, documented the following amounts of murrelet nesting habitat on Federal lands, within the range of the species:

Physiographic Province	*Hectares*
Washington	
Olympic Peninsula:	246,260
Western lowlands:	0
Western Cascades:	146,945
Eastern Cascades:	2,670
Washington total:	**395,875**

Of the Washington total, 97 percent is in Late Successional Reserves, Adaptive Management Areas (AMA's), and Riparian Reserves.

Physiographic Province	*Hectares*
Oregon	
Coast Range:	16,600
Klamath:	211,530
Western Cascades:	450
Willamette Valley:	240
Oregon total:	**228,820**

Of the Oregon total, 88 percent is in Late Successional Reserves, AMA's, and Riparian Reserves.

Physiographic Province	*Hectares*
California	
FEMAT amounts	
Klamath:	238,800
Cascades:	0
Coast Range: (included in Fox's estimates below)	
California Coast Range (Fox, pers. comm.)	
Redwood National Park:	7,930
State Parks (within the boundaries of Redwood NP):	10,100
Other Ownerships:	74,940
Total:	92,970
California total:	**331,770**

Of the habitat in the Klamath province, 89 percent is in Late Successional Reserves, AMA's, and Riparian Reserves. Fox's unpublished data (pers. comm.) include both public and private lands. He classified old-growth as areas with at least 10 percent cover of trees greater than 24 in. (60 cm) d.b.h. This comprised 10.6 percent of total forest cover within Fox's study area. Of the area recorded by Fox, 18,030 ha are located in Redwood NP and State Parks (Hofstra, pers. comm.).

Three State Total	
Federal Lands:	1,036,625
State Parks in California Coast Range:	10,120
Private Lands in California Coast Range:	74,920

If Alternative 9 is implemented as described in the Final Supplemental EIS (USDA and others 1994), about 89 percent of current murrelet habitat on federal lands will be protected within Late Successional Reserves, Riparian Reserves, and Congressionally Reserved Areas. Of the remaining habitat

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with the matrix and AMA's (116,100 hectares), all suitable habitat contiguous with occupied sites will be protected from timber cutting, at least until final recommendations of the Marbled Murrelet Recovery Plan are in place. The FSEIS shows the extent of protection within each physiographic province in these three states.

At least two caveats go with these estimates. First, estimates are largely based on interpretations of satellite imagery that have not been thoroughly ground-truthed. Second, the estimates refer to quantity of habitat, not quality. Depending on proximity to the coast, landscape context, and size, a given stand may or may not provide quality murrelet habitat ("quality" habitat, as defined here, meets basic nesting requirements, provides refuge from predators, and is relatively stable against catastrophic disturbances). At this time, it is not possible to estimate the proportion of remaining habitat that could be considered of high enough quality to allow long-term nesting success.

FEMAT documents only Marbled Murrelet habitat on Federal lands. Very little murrelet habitat remains on private lands in Washington and Oregon. Some habitat exists on State lands, particularly on the Tillamook and Elliot State Forests in Oregon, which comprise areas burned over by wildfires in the early part of the century (see Raphael and others [this volume] for estimates of habitat on state lands in Washington). Murrelets are using these areas to some degree, however it is not possible at present to quantify amounts of suitable murrelet habitat on Oregon State Forest lands. The greatest value of these lands for murrelet conservation may be in providing habitat over the next several decades, while the large areas of young forests within Late Successional Old-Growth reserves delineated in Alternative 9 of the U.S. Administration plan for Spotted Owl habitat are maturing.

Significant amounts of habitat remain on private lands along the California coast. Unlike FEMAT estimates, however, Fox's estimates for the California Coast Range include all land ownerships.

Historic Habitat

The area of potential murrelet habitat has been significantly reduced in Washington, Oregon, and California during the 20th century. The first comprehensive survey of forests in western Oregon and Washington was conducted in the mid-1930s (Andrews and Cowlin 1940). At that time, old-growth Douglas-fir (*Pseudotsuga menziesii*), Sitka spruce (*Picea sitchensis*), and western hemlock (*Tsuga heterophylla*) covered 459,700 hectares in the Oregon Coast Range, and 1,314,650 hectares on the Olympic Peninsula and the Puget Sound region of Washington (generally within 60 miles [about 100 km] of Puget Sound). Old-growth Douglas-fir had been heavily logged prior to that inventory, especially in western Washington. Andrews and Cowlin (1940) report that "Puget Sound...was formerly surrounded by magnificent forests of old-growth Douglas-fir and western red cedar (*Thuja plicata*). Ease of logging and transportation attracted lumbermen to lands bordering the sound as early as the middle of the nineteenth century. Grays Harbor and Willapa Bay, on the coast of western Washington, offered almost equally attractive opportunities for forest exploitation. Practically all the old-growth Douglas-fir forests of western Washington were within 30 to 40 miles (50–65 km) of navigable waterways. Now western Washington, particularly in the vicinity of Puget Sound and Grays Harbor, is characterized by vast expanses of cut-over land largely barren of conifer growth".

Old-growth harvest continued at a high rate following the 1930s survey, especially on private lands, but increasingly on public lands as well. In 1958, a period of relatively low production, 2 billion board feet (International 1/4 in. rule) (4.7 million m^3) were harvested from private lands in western Washington, two-thirds of which was old-growth (Wall 1972). By 1970, annual harvest from private lands had nearly doubled to 3.8 billion board feet (9.0 million m^3), 80 percent of which was old-growth. At the same time, harvest from public lands in western Washington was accelerating, increasing from about 0.5 billion board feet (1.2 million m^3) in 1949 to 2 billion board feet (4.7 million m^3) in 1970. Most or all of this was probably old-growth, although I do not have data to give exact figures.

While the situation in Oregon was somewhat different than in Washington, the basic results were the same—the amount of old-growth has been reduced. Large wildfires burned in the Oregon Coast Range in the mid-1800s and early 1900s; consequently historic old-growth in that region was less extensive than in western Washington. Teensma and others (1991) estimate that 200-year and older stands comprised from 40 to 50 percent of Coast Range forests between 1850 and 1920, and declined to 20 percent in 1940, following large fires in the Tillamook area. If we include stands between 100 and 200 years old, some of which are likely to provide suitable murrelet habitat, stands that are potential murrelet habitat increases the proportion to between 50 percent (1940) and 70 percent (1920) of total forest area in the Oregon Coast Range. The 1930s survey documented 581,950 hectares of old-growth Douglas-fir, western hemlock and Sitka spruce in the Coast Range, and an additional 307,550 hectares of "large second growth"—90- to 160-year-old stands growing on old burns, with trees approaching the size of old-growth. At the time of the 1930s survey between 228,600 and 364,000 hectares had been cut over in the Oregon Coast Range, most or all from old-growth. These values indicate that, prior to logging, 1 to 1.5 million hectares of suitable murrelet habitat existed in the Oregon Coast Range. This may be compared to the current 178,500 hectares identified by FEMAT and the FSEIS on Federal lands in the Coast Range. Except for uncertain amounts of habitat on the two State forests mentioned above, virtually all remaining habitat in the Oregon Coast Range is on Federal lands.

In California, a large proportion of forests within nesting radius of the coast are privately owned. Once dominated by old-growth redwood, these forests have been heavily cut over.

Alaska

Approximately 50–60 percent of forests suitable for murrelet nesting occurs on two National Forests (Tongass and Chugach), with the balance on State lands and lands held by various Native Corporations (Iverson, pers. comm.). At this time I have data only for the National Forests.

Tongass National Forest

It is estimated that on the Tongass National Forest the original old-growth, classified as "productive" stands (i.e., stands with volumes estimated to be greater than 8,000 board feet per acre), was approximately 5,600,000 acres. These stands were composed primarily of western hemlock, Sitka spruce, and mountain hemlock (USDA Forest Service, Alaska Region, 1991). A subset of the productive stands has been classified as "highly productive", with volumes greater than 30,000 board feet per acre. On the Tongass National Forest, the original acreage of this subset consisted of about 933,000 acres. These stands have larger diameter trees, and thus probably more and larger lateral branches. More of these attributes would provide proportionally more high-quality murrelet nesting sites (Hamer and Nelson, this volume b). However, very few data are available on murrelet abundances and nesting habitat characteristics in southeast Alaska. At this time there is no direct evidence that highly productive stands are used to greater degree than those classified as productive in southeast Alaska. The results of Kuletz and others (in press, this volume) in Prince William Sound, Alaska, and Burger (this volume) in British Columbia do, however, indicate that high-density old-growth has characteristics associated with high murrelet use.

Since large scale commercial timber harvest began in the mid-1950's, harvest has largely occurred within the highly productive component. Approximately 350,000 acres of old-growth forest have been harvested through 1990 (USDA Forest Service, Alaska Region, 1991). Additional harvest from 1990 through 1994 has totaled 41,800 acres (M. Wilson, pers. comm.). Thus, an estimated 93 percent of the productive old-growth forests on the Tongass National Forest remains. However, only an estimated 58 percent of the highly productive forest remains. Indications are that forests in southeast Alaska held by Native corporations have and will continue to be extensively logged (C. Iverson, pers. comm.).

Chugach National Forest

Although a high proportion of productive forest lands on the Chugach National Forest is probably suitable nesting habitat (classed as mature and overmature timber), this represents a total area of only 101,200 hectares (USFS undated).

British Columbia

Data for British Columbia is being compiled and is not yet available. According to Beebe (1990), "preliminary estimates are that only 17 of the 124 coastal temperate rainforests of more than 20,000 hectares remain unlogged. On Vancouver Island, just six of 89 coastal watersheds of more than 5000 hectares remain unlogged." Though illustrative, these estimates are minimally useful as they give no information on watershed size or the extent of logging within logged watersheds. Beebe (1990) goes on to estimate that "perhaps 30 percent" of the original coastal forest remains in British Columbia.

Land and Seascape Patterns Associated with Marbled Murrelet Abundance Offshore

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Abstract. —We measured offshore Marbled Murrelet (*Brachyramphus marmoratus*) abundance from April through October between 1989 and 1998, in northern California and southern Oregon and investigated its relationships with marine and terrestrial habitats. We found that higher murrelet abundance offshore was strongly related to the presence of large, clustered and unfragmented old-growth forests on nearby inland areas. Murrelets were most abundant offshore of contiguous old-growth forest adjacent to relatively abundant medium-sized, second-growth coniferous forests. Compared to the forest habitat, marine habitat was relatively unimportant in determining murrelet abundance offshore; high marine primary productivity and nutrients were not associated with high murrelet numbers. Tidal flat shorelines were weakly associated with more murrelets, independent of inland habitat. Our findings suggest management efforts to conserve the Marbled Murrelet should focus on protecting or creating large, contiguous blocks of old-growth habitat, features which currently are rare in the study area.

Key words.—*Brachyramphus marmoratus*, fragmentation, landscape, Marbled Murrelet, marine habitat, offshore habitat, seascape.

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The Marbled Murrelet (*Brachyramphus marmoratus*) is a seabird that forages in the northeastern Pacific Ocean from Alaska to central California, and breeds inland from April through September, mostly on large branch platforms in old-growth forests, and in second-growth forests that have residual large trees (Hamer and Nelson 1995). The species' decline and listing as a threatened species in the southern part of its range is believed to be primarily due to loss and fragmentation of its nesting habitat (Miller *et al.* 1997; Meyer and Miller in press; Meyer 1999). In southern Oregon and California, we have found murrelets are most likely to nest in unfragmented old-growth forests in a matrix of forests with mature second-growth (Meyer *et al.* in press). These forests were located relatively close to river mouths, fine sandy beaches, and marine waters with high chlorophyll concentrations, an indicator of high primary productivity (Joint and Groom 2000; Robinson 1990). Proximity to submarine canyons and bays were also important. Nesting is generally restricted to areas with frequent fog, such as the Coast Redwood zone in California and the Western Hemlock zone in southern Oregon (Meyer 1999). Although these features are associated with inland habitat, it is still unknown what broad-scale land- and sea-scape patterns affect murrelet abundance offshore in their marine habitat. Marine habitat characteristics that relate to offshore murrelet densities have not been well-defined. One objective of our research was to determine which marine characteristics and inland spatial patterns, measured in broad-scale regions of southern Oregon and California, were correlated with offshore murrelet numbers during the breeding season. A second objective was to determine which was more limiting to offshore abundance, the marine habitat or the inland nesting habitat. In particular, we wished to determine if the same characteristics that predicted inland nesting habitat use were important to predicting marine habitat use.

We predicted that regions with the highest offshore murrelet densities would have both high quality inland and offshore habitats. Specifically, we expected offshore murrelet densities to be positively correlated

with inland regions that contained closely-spaced, large blocks of old-growth forests and a high percentage of land with medium-sized trees (61-90 cm diameter at breast height). After taking into account the effect of inland habitat, we expected murrelet densities to be highest in regions with abundant sandy shorelines, tidal flats, river mouths, submarine canyons, and high spring and summer marine chlorophyll concentrations, as proximity to such characteristics are important in predicting nesting habitat (Meyer *et al.* in press). Murrelets should also be more abundant in marine waters with high nutrient levels, as such waters are indicative of coastal upwelling, a process which increases nutrient availability and prey density (Ainley and Boekelheide 1990).

Murrelets appear to show a delayed response to recent fragmentation and continue to use small forest fragments for several years before abandoning the area (Meyer *et al* in press). In our study area, large amounts of old-growth forest have been harvested in the last 20 years. The lowered reproductive success expected as a result of loss and fragmentation of inland nesting habitat would not strongly affect the offshore abundance until enough time had passed for substantial numbers of the adults to die and not be replaced. Therefore, offshore murrelet abundance, estimated from surveys in the 1990s, is expected to be more strongly related to vegetation conditions in the mid- to late 1980s than conditions in the 1990s. We addressed this potential lag in response to habitat changes by quantifying inland habitat during the mid-1980s. Unfortunately, we could not verify whether this mid-1980s map was more predictive than a map from the 1990s because habitat maps in the 1990s were not available at the same resolution and consistency across the study area. Nevertheless, we obtained very good results using the 1980s map.

STUDY AREA

The study area extends from Coos Bay, Oregon to Point Lobos at the southern end of Monterey Bay in California, 1,088 km of coastline (Fig. 1). The adjacent inland habitat is the southern extent of the known nesting range of the Marbled Murrelet (Ralph *et al.* 1995). Nesting habitat for the murrelet was generally restricted to within 40 km of the coast and to the inland fog zone (Meyer *et al.* in press). Old-growth forests adjacent to the coast in areas without fog were not occupied by murrelets. Within the murrelet nesting area, the vegetation was predominantly in the Western Hemlock zone in southern Oregon and the Coast Redwood zone in California (Franklin and Dyrness 1973, Agee 1993). The marine habitat in the study area comprises a 6-km wide strip along the coastline, where most murrelets forage (Ralph and Miller 1995; Strong *et al.* 1995).

METHODS

The study area was divided into nine regions, which ranged from 2,121 to 6,504 km^2 and extended 40 km inland (Fig. 1), a distance which contained all known occupied nesting areas (Meyer *et al.* in press). Regions were centered on major clusters of old-growth forest, and the boundaries were selected to minimize high rates of bird movement between regions, assuming birds do not frequently travel much more than 20 km north and south of their nesting habitat (F. Cooke, unpublished data in British Columbia, Canada; Kuletz

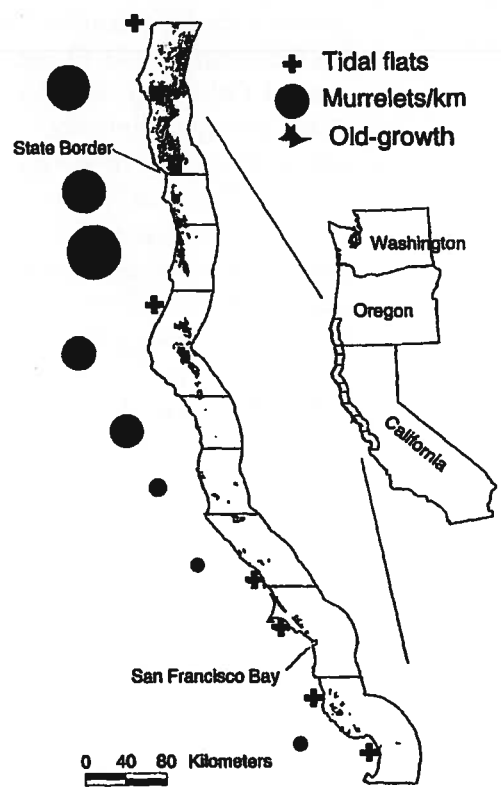

Figure 1. Study area divided into nine regions in southern Oregon and northern California. Potential old-growth nesting habitat for the murrelet is shown. Tidal flat locations and murrelet densities (proportional to areas of circles) are also shown.

et al. 1995; E. Burkett, unpublished data in central California). Within regions, the 6-km strip of marine habitat ranged from 366 to 1230 km^2 (Fig. 1).

We compiled available Geographic Information System (GIS) databases of marine features, marine water quality, old-growth forest and other land cover types within the nine regions. Using ARC/INFO (Environmental Systems Research Institute, Inc., Redlands, California, USA, v. 7.1), we calculated marine and terrestrial habitat variables including old-growth fragmentation patterns within each region and searched for relationships between habitat variables and offshore murrelet densities. Below we describe in more detail how we obtained our datasets.

Estimates of Murrelet Regional Numbers

We used methods detailed in Ralph and Miller (1995) to estimate the numbers of murrelets offshore for eight regions in California (883 km). Sections of the coast, 20 to 30 km in length, were surveyed and counts recorded for each 2-km segment of line transect. We estimated a 200-m effective survey width using line transect methods (Buckland *et al.* 1993). Estimates of the number of murrelets in each region were based on 5,739 two-km segments surveyed during April through October, from 1989 to 1998. The entire coastline was surveyed repeatedly using line transects parallel to the coastline at 800 m and 1,400 m from the shore. In addition, to determine the murrelet distribution at right angles to the shoreline, 25% of the coastline in the three northern regions of California and one location south of San Francisco Bay were intensively surveyed at increasing distances (400 m, 800 m, 1.4 km, 2 km, 3 km and 5 km) from the shore, in coastal sections 6 to 8 km long. Based on the intensive surveys, a linear regression was developed to estimate the number of murrelets in each of the eight regions. The independent variables were the average murrelet counts per 2-km segment at 800 m and 1,400 m transect distances for all intensive survey locations and the response variable was the extrapolated number of murrelets in a 6 km wide x 2 km coastal segment. The resulting regression equation and the mean counts at 800 m and 1,400 m were then used to estimate the total number of murrelets for each coastal section in California:

$$\text{Estimate of numbers in section} = 6.417 + 4.189 \cdot \bar{x}_{800m} + 5.190 \cdot \bar{x}_{1400m}$$

We summed the section numbers within each region to estimate the number of murrelets in the region (Table 1).

We obtained an estimate of numbers for the southern Oregon region by averaging those reported by Strong (1996). Strong's density estimates for southern Oregon were based on 343 transects, each 2 km long and with an effective survey width (Buckland *et al.* 1993) of 0.2 km. Surveys parallel to the coastline were conducted during June and July in 1992, 1993, and 1995 from boats at 300 to 750 m from the shore (Strong *et al.* 1995; Strong 1996). Additional surveys were conducted in 1995 at right angles to the shoreline in two 4-km long intensive survey areas to determine the proportion of murrelets offshore compared to the inshore (300-750 m) transect. Murrelet density was calculated in each transect by adding the proportion estimated to be farther offshore to the inshore counts. Densities were

Table 1. Murrelet offshore region population numbers and survey effort from April to October 1989 to 1998 for regions in California and southern Oregon.

Region name	Coastline length (km)	No. 2-km segments surveyed 800 m from shore	No. 2-km segments surveyed 1,400 m from shore	Total estimated birds	SE	Total birds per km coastline
South Oregon	205	343[1]	5	3495	243	17.0
Klamath	61	823	764	1178	42	19.2
Trinidad	72	534	576	1904	79	26.6
Humboldt Bay	127	1302	1257	1406	33	11.0
Kings Range	61	23	44	275	16	4.5
Point Arena	73	44	25	199	—[2]	2.7
Russian River	98	43	42	180	—[2]	1.8
San Francisco	233	35	33	0	0	0
Santa Cruz	158	109	85	717	93	4.5
Total	1088	3256	2831	9354	134	8.6

[1]These surveys were conducted between 300 and 750 m from shore in Oregon. Total surveyed lengths exceed coastline length because coastlines were repeatedly surveyed.
[2]Standard errors were not calculated for these regions because errors are based on number of pairs of 800 m and 1,400 m counts (Ralph and Miller 1995), but no 2-km segments were ever surveyed at both 800 m and 1,400 m distances from the shore for these areas.

extrapolated to the area surveyed in the region to obtain an estimate of numbers. For California and Oregon, we divided the estimate of total birds by the length of coastline in each region to obtain numbers of murrelets per km of coastline (Table 1).

Vegetation Databases

To map murrelet habitat, we created GIS maps from several sources. For California, we used an old-growth 1985-86 vegetation map developed from aerial photographs (Redwood Mapping Project, Larry Fox, Humboldt State University, 16 ha minimum mapping unit). For Oregon, we used two 1988 databases (Congalton *et al.* 1993 and BLM Western Oregon Digital Image Project, 1.2 to 6 ha minimum mapping unit) based on LANDSAT TM imagery. The final GIS maps for both states included old-growth only, defined as having >40% canopy cover and ≥10% cover in old, large trees present before Europeans arrived (typically >91 cm diameter at breast height in California). We used a third LANDSAT TM-based GIS map (CTTF 1993) to calculate percentage of land with medium-sized trees (61-90 cm diameter at breast height) in California.

Variables Sampled

Within each entire region, we quantified the major old-growth fragmentation and marine habitat variables that we found were important in Meyer *et al.* (in press) using FRAGSTATS (raster version, McGarigal and Marks 1995; Table 2). Because the area outside the Coast Redwood and Western Hemlock zones had very low murrelet use, we calculated old-growth variables only after eliminating any old-growth forest in the region that fell outside those zones (Fig. 1). We also included annual marine nitrate concentration, sampled at the surface of the ocean in 1 degree blocks along the coastline (NOAA 1994), as a variable because of its importance as an indicator of potential year round marine productivity (Granéli *et al.* 1990; Maranon *et al.* 2000) Nitrate concentrations during just the murrelet breeding season (spring and summer) were not available from NOAA for our entire study area. Latitude of the center of the region was included as an index of north to south changes in climate, which might affect murrelet abundance.

Data Analyses

Because the map resolution and methods used to calculate regional numbers were different in Oregon than California, we analyzed the data using California alone, and then with southern Oregon included. First, we calculated simple Pearson correlation coefficients between each variable and murrelets per km of coastline (Neter *et al.* 1989). Then we used best subsets linear regression to determine two-variable functions that best predicted murrelets per km. Best subsets regression calculates all possible subsets of the candidate variables. The adjusted R^2 and Mallows' C_P (C_P estimates bias and random error to assess fit) were the criteria used to select the best subset of variables (following Neter *et al.* 1989). Because we had only nine data points (regions), we needed to limit the number of candidate variables. Therefore, the inland variables included as candidates in the two-variable regressions were only those that had a significant correlation coefficient ($P \leq 0.05$). To evaluate our hypothesis that marine variables would be important after accounting for the effect of inland habitat, we also specifically searched for regression functions that were significant when a marine variable was combined with the most significant inland variable.

Because Oregon had a smaller map resolution (1.2-6 ha) than California (16 ha), map resolution may affect the variables that measure patch size. Therefore, we added minimum mapping unit to the regressions to see if they changed the results, which they did not.

RESULTS

When we correlated each variable separately with murrelet offshore abundance, we found abundance increased as old-growth forest fragmentation decreased in the regions (more old-growth and core area, more area in the largest patch, high proximity index; Table 3). The mean proximity index of old-growth, a measure of old-growth patch isolation (see Table 2), had the highest correlation with abundance. Specifically, closely spaced, large old-growth stands were associated with high bird numbers offshore. Abundance also increased with more medium-sized conifer forests in the regions. Trinidad, the region with the most birds had almost 5% of the land in old-growth core area (interior habitat) and 15% in medium-sized conifer forests (Table 4). No marine variables were positively correlated with murrelet numbers (Table 3). Annual marine nitrate concentrations were negatively correlated to murrelet abundance in California, but when Oregon was included, this relationship disappeared. Also, as latitude increased, murrelet densities increased. Such an increase may be an artifact of the greater nesting habitat availability farther north.

In the two variable regression model that best predicts murrelet offshore abundance, only inland variables were included (Table 5). The inland habitat variable with the most explanatory power (92% of the variance) was the mean proximity index, followed by either the percentage land in old-growth (California only) or the percentage land in the largest patch of old-growth (includes Oregon). No marine variables, except percent coastline in tidal flats were significant once an inland habitat variable was in the model. Once proximity index of old-growth was accounted

Table 2. Habitat variables measured in regions of California and southern Oregon.

Inland Fragmentation Variables (from FRAGSTATS)	
OG[1] (%)	Mean OG patch size (ha)
Mean proximity index of OG[2]	Largest OG patch (%)
OG core area (%) (50-m edge distance)	Edge old-growth per area of old-growth (m/ha)
Medium-sized conifer (%) (61-90 cm dbh)	
Marine Variables	
Tidal flats (% of coastline)	River mouths (no/km of coastline)
Mean (1978-1986) spring marine chlorophyll (mg/m^3 and % of coastline > 10 mg/m^3) (18-km pixel)	Mean (1978-986) summer marine chlorophyll (mg/m^3 and% > 10 mg/m^3 (from NASA coastal Zone Color Scanner)
Submarine canyons (no/km) within 22 km of shore (from NOAA bathymetry)	Sandy beach (% of coastline)[3]
Rocky coast (% of coastline)	Annual mean nitrate concentration (µmol/I from 1900-1990 (1-degree pixel along coastline, NOAA 1994)
Latitude (degrees at midpoint of region)	

[1]OG = old-growth forest.

[2]Quantifies size and distance of neighboring old-growth patches within a 5-km radius to distinguish sparsely spaced, small old-growth patches (low value) from clusters of large old-growth patches (high value). Large consolidated patches or fragmented, yet very closely spaced small patches, have a high mean proximity index (McGarigal and Marks 1995).

[3]This variable was only available in California (from a state shoreline map).

Table 3. Correlation coefficients (r) between number of murrelets offshore per km coastline and the highest ranked (using r) inland and marine (including latitude) habitat variables in California and Oregon or California alone.

Variable	California and Oregon (N = 9)	California (N = 8)
Mean proximity index OG[a]	0.95	0.96
OG (%)	0.85	0.91
OG core area (%)	0.91	0.90
Medium-sized conifer (61-90 cm dbh) (%)	-	0.86
Nitrate (mg/m^3)	n.s[b]	-0.86
Largest patch OG (%)	0.70	0.85
Latitude (degrees)	0.81	0.81

[a]OG = old-growth forests

[b]not significant

for, the partial correlation coefficient for tidal flats was 0.82. However, tidal flats explained only an additional 5% of the overall variance. The three best 2-variable regression models were highly predictive ($R^2 \geq 0.96$ and $P < 0.0001$; Table 5).

DISCUSSION

Inland habitat was by far more important than marine habitat in affecting murrelet regional numbers, accounting for up to 98% of the variance in offshore numbers (Table 5). Although we had expected that inland habitat would be more important, we had also expected the marine habitat to contribute to explaining a portion of the variation in murrelet abundance. The regions we selected for our study were relatively large scale. A smaller scale analysis may provide stronger relationships between marine habitat and offshore abundance.

Inland Habitat

As predicted, higher fragmentation of habitat inland would decrease murrelet abundance offshore. Regions with abundant murrelets contained some large blocks of contiguous old-growth forest, which increased old-growth clumping and percentage of land in the largest patch size (Fig. 1). Such large patches provide more core areas, which was also found to be important in our study of inland birds at smaller scales (Meyer *et al.* in press). Core area provides sites for nests away from the edge, where young are more likely to fledge successfully due to lowered predation rates (Paton 1994; Nelson and Hamer 1995).

Our prediction that the region with the most birds offshore would contain proportionally more forests with medium-sized trees than younger seral stage forests with smaller trees, was supported. Such a land-

Table 4. Offshore murrelets per km of coastline compared to average characteristics of old-growth (OG) and conifer forests, and coastline habitats of the regions in the study area.

Region name	Birds per km	OG (%)	OG core area (%)	OG mean proximity index	Largest patch OG (%)	Medium conifer (%)
South Oregon	17.0	7.49	4.40	305.25	0.20	—
Klamath	19.2	4.01	3.55	289.49	1.91	15.50
Trinidad	26.6	5.39	4.80	354.35	2.07	14.70
Humboldt Bay	11.0	4.55	4.19	41.86	2.07	12.00
Kings Range	4.5	0.43	0.29	31.31	0.09	7.40
Point Arena	2.7	0.51	0.43	0.45	0.17	9.24
Russian River	1.8	0.52	0.43	0.00	0.19	6.82
San Francisco	0.0	0.60	0.54	11.92	0.53	2.50
Santa Cruz	4.5	0.99	0.83	24.99	0.30	2.25

Table 5. Predictor variables and coefficient statistics in linear regression models of offshore murrelets per km of coastline in California alone or with southern Oregon included. Old-Growth conifer forest is represented in the table as "OG."

Variables	Unstandardized coefficient	SE	Standardized coefficient[1]	t-value	P<
California (N = 8)	$R^2 = 0.981$				
Mean proximity index OG[2]	0.0424	0.0074	0.636	5.7	0.002
% land in OG	1.807	0.5006	0.403	3.6	0.02
Constant	0.930	0.8863		1.1	n.s.
California/Oregon (N = 9)	$R^2 = 0.965$				
Mean proximity index OG	0.0494	0.0060	0.801	8.3	0.0002
% in largest patch OG[2]	2.946	1.0016	0.285	2.5	0.03
Constant	1.416	1.0595		1.3	n.s.
California (N = 8)	$R^2 = 0.974$				
Mean proximity index OG	0.0666	0.0049	0.999	13.6	0.0001
coastline in tidal flats	14.026	4.3681	0.235	3.2	0.03
Constant	1.666	0.8580		1.9	

[1]The standardized coefficient and P value show the relative importance of each variable.

[2]This variable was also highly predictive with mean proximity index in a two variable linear regression for California alone, but % land in OG was slightly better.

scape, with old-growth in a matrix of even-aged older second-growth forest, may support fewer nest predators as it would provide less edge contrast. However, forests with medium-sized trees did not significantly explain any additional variance in murrelet offshore abundance, once fragmentation of old-growth forest was considered. More research that targets old-growth areas, with and without surrounding medium-sized forests, is needed to determine the effects of various matrix habitats.

Marine Habitat

None of the marine variables were good predictors of offshore abundance. Nitrate concentration was the only marine variable with a significant simple correlation to abundance, and it decreased as murrelet numbers increased. We expected nitrate, an indicator of marine productivity, to be positively, rather than negatively, associated with the birds. Notably, the addition of the Oregon data removed the significant relationship. Because the addition of Oregon data negated the importance of nitrate, the nitrate result in California is likely a statistical artifact, rather than an important biological result. Of the marine habitat relationships we felt would be important, only our expectation that murrelet numbers would be highest in regions with more tidal flats was supported. Tidal flats were uncorrelated with the old-growth proximity index ($r = 0.17$) and thus independently contributed to murrelet abundance. Tidal flats are within the bays and estuaries, and are nutrient rich, highly productive areas providing food for potential murrelet prey.

When inland habitat fragmentation patterns were included in the models, marine habitat appeared to have little effect on murrelet offshore numbers, accounting for ≤5% of the variation in offshore numbers. On a smaller landscape scale (Meyer *et al.* in press), we found areas with consistently high chlorophyll, were near inland nesting areas. However, in the present study, increased primary productivity, as evidenced by chlorophyll in the ocean, did not significantly increase murrelet numbers over and above the effect of unfragmented inland habitat. Within our study area, murrelet abundance appears most limited by the amount and degree of fragmentation of old-growth nesting habitat. However, the marine environment may have a stronger influence on abun-

dance if nesting habitat increases. Our results suggest that conservation efforts for the Marbled Murrelet should focus on protecting or creating large, contiguous blocks of old-growth habitat, features which are uncommon in the study area.

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Land and Seascape Patterns Associated with Marbled Murrelet Abundance Offshore

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Abstract. —We measured offshore Marbled Murrelet (*Brachyramphus marmoratus*) abundance from April through October between 1989 and 1998, in northern California and southern Oregon and investigated its relationships with marine and terrestrial habitats. We found that higher murrelet abundance offshore was strongly related to the presence of large, clustered and unfragmented old-growth forests on nearby inland areas. Murrelets were most abundant offshore of contiguous old-growth forest adjacent to relatively abundant medium-sized, second-growth coniferous forests. Compared to the forest habitat, marine habitat was relatively unimportant in determining murrelet abundance offshore; high marine primary productivity and nutrients were not associated with high murrelet numbers. Tidal flat shorelines were weakly associated with more murrelets, independent of inland habitat. Our findings suggest management efforts to conserve the Marbled Murrelet should focus on protecting or creating large, contiguous blocks of old-growth habitat, features which currently are rare in the study area.

Key words.—*Brachyramphus marmoratus*, fragmentation, landscape, Marbled Murrelet, marine habitat, offshore habitat, seascape.

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The Marbled Murrelet (*Brachyramphus marmoratus*) is a seabird that forages in the northeastern Pacific Ocean from Alaska to central California, and breeds inland from April through September, mostly on large branch platforms in old-growth forests, and in second-growth forests that have residual large trees (Hamer and Nelson 1995). The species' decline and listing as a threatened species in the southern part of its range is believed to be primarily due to loss and fragmentation of its nesting habitat (Miller *et al.* 1997; Meyer and Miller in press; Meyer 1999). In southern Oregon and California, we have found murrelets are most likely to nest in unfragmented old-growth forests in a matrix of forests with mature second-growth (Meyer *et al.* in press). These forests were located relatively close to river mouths, fine sandy beaches, and marine waters with high chlorophyll concentrations, an indicator of high primary productivity (Joint and Groom 2000; Robinson 1990). Proximity to submarine canyons and bays were also important. Nesting is generally restricted to areas with frequent fog, such as the Coast Redwood zone in California and the Western Hemlock zone in southern Oregon (Meyer 1999). Although these features are associated with inland habitat, it is still unknown what broad-scale land- and sea-scape patterns affect murrelet abundance offshore in their marine habitat. Marine habitat characteristics that relate to offshore murrelet densities have not been well-defined. One objective of our research was to determine which marine characteristics and inland spatial patterns, measured in broad-scale regions of southern Oregon and California, were correlated with offshore murrelet numbers during the breeding season. A second objective was to determine which was more limiting to offshore abundance, the marine habitat or the inland nesting habitat. In particular, we wished to determine if the same characteristics that predicted inland nesting habitat use were important to predicting marine habitat use.

We predicted that regions with the highest offshore murrelet densities would have both high quality inland and offshore habitats. Specifically, we expected offshore murrelet densities to be positively correlated

with inland regions that contained closely-spaced, large blocks of old-growth forests and a high percentage of land with medium-sized trees (61-90 cm diameter at breast height). After taking into account the effect of inland habitat, we expected murrelet densities to be highest in regions with abundant sandy shorelines, tidal flats, river mouths, submarine canyons, and high spring and summer marine chlorophyll concentrations, as proximity to such characteristics are important in predicting nesting habitat (Meyer *et al.* in press). Murrelets should also be more abundant in marine waters with high nutrient levels, as such waters are indicative of coastal upwelling, a process which increases nutrient availability and prey density (Ainley and Boekelheide 1990).

Murrelets appear to show a delayed response to recent fragmentation and continue to use small forest fragments for several years before abandoning the area (Meyer *et al* in press). In our study area, large amounts of old-growth forest have been harvested in the last 20 years. The lowered reproductive success expected as a result of loss and fragmentation of inland nesting habitat would not strongly affect the offshore abundance until enough time had passed for substantial numbers of the adults to die and not be replaced. Therefore, offshore murrelet abundance, estimated from surveys in the 1990s, is expected to be more strongly related to vegetation conditions in the mid- to late 1980s than conditions in the 1990s. We addressed this potential lag in response to habitat changes by quantifying inland habitat during the mid-1980s. Unfortunately, we could not verify whether this mid-1980s map was more predictive than a map from the 1990s because habitat maps in the 1990s were not available at the same resolution and consistency across the study area. Nevertheless, we obtained very good results using the 1980s map.

STUDY AREA

The study area extends from Coos Bay, Oregon to Point Lobos at the southern end of Monterey Bay in California, 1,088 km of coastline (Fig. 1). The adjacent inland habitat is the southern extent of the known nesting range of the Marbled Murrelet (Ralph *et al.* 1995). Nesting habitat for the murrelet was generally restricted to within 40 km of the coast and to the inland fog zone (Meyer *et al.* in press). Old-growth forests adjacent to the coast in areas without fog were not occupied by murrelets. Within the murrelet nesting area, the vegetation was predominantly in the Western Hemlock zone in southern Oregon and the Coast Redwood zone in California (Franklin and Dyrness 1973, Agee 1993). The marine habitat in the study area comprises a 6-km wide strip along the coastline, where most murrelets forage (Ralph and Miller 1995; Strong *et al.* 1995).

METHODS

The study area was divided into nine regions, which ranged from 2,121 to 6,504 km^2 and extended 40 km inland (Fig. 1), a distance which contained all known occupied nesting areas (Meyer *et al.* in press). Regions were centered on major clusters of old-growth forest, and the boundaries were selected to minimize high rates of bird movement between regions, assuming birds do not frequently travel much more than 20 km north and south of their nesting habitat (F. Cooke, unpublished data in British Columbia, Canada; Kuletz

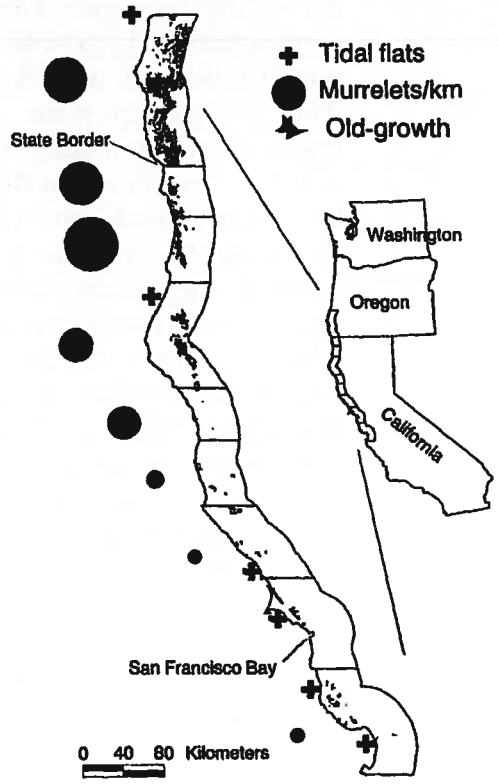

Figure 1. Study area divided into nine regions in southern Oregon and northern California. Potential old-growth nesting habitat for the murrelet is shown. Tidal flat locations and murrelet densities (proportional to areas of circles) are also shown.

et al. 1995; E. Burkett, unpublished data in central California). Within regions, the 6-km strip of marine habitat ranged from 366 to 1230 km^2 (Fig. 1).

We compiled available Geographic Information System (GIS) databases of marine features, marine water quality, old-growth forest and other land cover types within the nine regions. Using ARC/INFO (Environmental Systems Research Institute, Inc., Redlands, California, USA, v. 7.1), we calculated marine and terrestrial habitat variables including old-growth fragmentation patterns within each region and searched for relationships between habitat variables and offshore murrelet densities. Below we describe in more detail how we obtained our datasets.

Estimates of Murrelet Regional Numbers

We used methods detailed in Ralph and Miller (1995) to estimate the numbers of murrelets offshore for eight regions in California (883 km). Sections of the coast, 20 to 30 km in length, were surveyed and counts recorded for each 2-km segment of line transect. We estimated a 200-m effective survey width using line transect methods (Buckland *et al.* 1993). Estimates of the number of murrelets in each region were based on 5,739 two-km segments surveyed during April through October, from 1989 to 1998. The entire coastline was surveyed repeatedly using line transects parallel to the coastline at 800 m and 1,400 m from the shore. In addition, to determine the murrelet distribution at right angles to the shoreline, 25% of the coastline in the three northern regions of California and one location south of San Francisco Bay were intensively surveyed at increasing distances (400 m, 800 m, 1.4 km, 2 km, 3 km and 5 km) from the shore, in coastal sections 6 to 8 km long. Based on the intensive surveys, a linear regression was developed to estimate the number of murrelets in each of the eight regions. The independent variables were the average murrelet counts per 2-km segment at 800 m and 1,400 m transect distances for all intensive survey locations and the response variable was the extrapolated number of murrelets in a 6 km wide x 2 km coastal segment. The resulting regression equation and the mean counts at 800 m and 1,400 m were then used to estimate the total number of murrelets for each coastal section in California:

$$\text{Estimate of numbers in section} = 6.417 + 4.189 \cdot \bar{x}_{800m} + 5.190 \cdot \bar{x}_{1400m}$$

We summed the section numbers within each region to estimate the number of murrelets in the region (Table 1).

We obtained an estimate of numbers for the southern Oregon region by averaging those reported by Strong (1996). Strong's density estimates for southern Oregon were based on 343 transects, each 2 km long and with an effective survey width (Buckland *et al.* 1993) of 0.2 km. Surveys parallel to the coastline were conducted during June and July in 1992, 1993, and 1995 from boats at 300 to 750 m from the shore (Strong *et al.* 1995; Strong 1996). Additional surveys were conducted in 1995 at right angles to the shoreline in two 4-km long intensive survey areas to determine the proportion of murrelets offshore compared to the inshore (300-750 m) transect. Murrelet density was calculated in each transect by adding the proportion estimated to be farther offshore to the inshore counts. Densities were

Table 1. Murrelet offshore region population numbers and survey effort from April to October 1989 to 1998 for regions in California and southern Oregon.

Region name	Coastline length (km)	No. 2-km segments surveyed 800 m from shore	No. 2-km segments surveyed 1,400 m from shore	Total estimated birds	SE	Total birds per km coastline
South Oregon	205	343[1]	5	3495	243	17.0
Klamath	61	823	764	1178	42	19.2
Trinidad	72	534	576	1904	79	26.6
Humboldt Bay	127	1302	1257	1406	33	11.0
Kings Range	61	23	44	275	16	4.5
Point Arena	73	44	25	199	—[2]	2.7
Russian River	98	43	42	180	—[2]	1.8
San Francisco	233	35	33	0	0	0
Santa Cruz	158	109	85	717	93	4.5
Total	1088	3256	2831	9354	134	8.6

[1]These surveys were conducted between 300 and 750 m from shore in Oregon. Total surveyed lengths exceed coastline length because coastlines were repeatedly surveyed.
[2]Standard errors were not calculated for these regions because errors are based on number of pairs of 800 m and 1,400 m counts (Ralph and Miller 1995), but no 2-km segments were ever surveyed at both 800 m and 1,400 m distances from the shore for these areas.

extrapolated to the area surveyed in the region to obtain an estimate of numbers. For California and Oregon, we divided the estimate of total birds by the length of coastline in each region to obtain numbers of murrelets per km of coastline (Table 1).

Vegetation Databases

To map murrelet habitat, we created GIS maps from several sources. For California, we used an old-growth 1985-86 vegetation map developed from aerial photographs (Redwood Mapping Project, Larry Fox, Humboldt State University, 16 ha minimum mapping unit). For Oregon, we used two 1988 databases (Congalton *et al.* 1993 and BLM Western Oregon Digital Image Project, 1.2 to 6 ha minimum mapping unit) based on LANDSAT TM imagery. The final GIS maps for both states included old-growth only, defined as having >40% canopy cover and ≥10% cover in old, large trees present before Europeans arrived (typically >91 cm diameter at breast height in California). We used a third LANDSAT TM-based GIS map (CTTF 1993) to calculate percentage of land with medium-sized trees (61-90 cm diameter at breast height) in California.

Variables Sampled

Within each entire region, we quantified the major old-growth fragmentation and marine habitat variables that we found were important in Meyer *et al.* (in press) using FRAGSTATS (raster version, McGarigal and Marks 1995; Table 2). Because the area outside the Coast Redwood and Western Hemlock zones had very low murrelet use, we calculated old-growth variables only after eliminating any old-growth forest in the region that fell outside those zones (Fig. 1). We also included annual marine nitrate concentration, sampled at the surface of the ocean in 1 degree blocks along the coastline (NOAA 1994), as a variable because of its importance as an indicator of potential year round marine productivity (Granéli *et al.* 1990; Maranon *et al.* 2000) Nitrate concentrations during just the murrelet breeding season (spring and summer) were not available from NOAA for our entire study area. Latitude of the center of the region was included as an index of north to south changes in climate, which might affect murrelet abundance.

Data Analyses

Because the map resolution and methods used to calculate regional numbers were different in Oregon than California, we analyzed the data using California alone, and then with southern Oregon included. First, we calculated simple Pearson correlation coefficients between each variable and murrelets per km of coastline (Neter *et al.* 1989). Then we used best subsets linear regression to determine two-variable functions that best predicted murrelets per km. Best subsets regression calculates all possible subsets of the candidate variables. The adjusted R^2 and Mallows' C_P (C_P estimates bias and random error to assess fit) were the criteria used to select the best subset of variables (following Neter *et al.* 1989). Because we had only nine data points (regions), we needed to limit the number of candidate variables. Therefore, the inland variables included as candidates in the two-variable regressions were only those that had a significant correlation coefficient ($P \leq 0.05$). To evaluate our hypothesis that marine variables would be important after accounting for the effect of inland habitat, we also specifically searched for regression functions that were significant when a marine variable was combined with the most significant inland variable.

Because Oregon had a smaller map resolution (1.2-6 ha) than California (16 ha), map resolution may affect the variables that measure patch size. Therefore, we added minimum mapping unit to the regressions to see if they changed the results, which they did not.

RESULTS

When we correlated each variable separately with murrelet offshore abundance, we found abundance increased as old-growth forest fragmentation decreased in the regions (more old-growth and core area, more area in the largest patch, high proximity index; Table 3). The mean proximity index of old-growth, a measure of old-growth patch isolation (see Table 2), had the highest correlation with abundance. Specifically, closely spaced, large old-growth stands were associated with high bird numbers offshore. Abundance also increased with more medium-sized conifer forests in the regions. Trinidad, the region with the most birds had almost 5% of the land in old-growth core area (interior habitat) and 15% in medium-sized conifer forests (Table 4). No marine variables were positively correlated with murrelet numbers (Table 3). Annual marine nitrate concentrations were negatively correlated to murrelet abundance in California, but when Oregon was included, this relationship disappeared. Also, as latitude increased, murrelet densities increased. Such an increase may be an artifact of the greater nesting habitat availability farther north.

In the two variable regression model that best predicts murrelet offshore abundance, only inland variables were included (Table 5). The inland habitat variable with the most explanatory power (92% of the variance) was the mean proximity index, followed by either the percentage land in old-growth (California only) or the percentage land in the largest patch of old-growth (includes Oregon). No marine variables, except percent coastline in tidal flats were significant once an inland habitat variable was in the model. Once proximity index of old-growth was accounted

Table 2. Habitat variables measured in regions of California and southern Oregon.

Inland Fragmentation Variables (from FRAGSTATS)	
OG[1] (%)	Mean OG patch size (ha)
Mean proximity index of OG[2]	Largest OG patch (%)
OG core area (%) (50-m edge distance)	Edge old-growth per area of old-growth (m/ha)
Medium-sized conifer (%) (61-90 cm dbh)	
Marine Variables	
Tidal flats (% of coastline)	River mouths (no/km of coastline)
Mean (1978-1986) spring marine chlorophyll (mg/m^3 and % of coastline > 10 mg/m^3) (18-km pixel)	Mean (1978-986) summer marine chlorophyll (mg/m^3 and% > 10 mg/m^3 (from NASA coastal Zone Color Scanner)
Submarine canyons (no/km) within 22 km of shore (from NOAA bathymetry)	Sandy beach (% of coastline)[3]
Rocky coast (% of coastline)	Annual mean nitrate concentration (µmol/I from 1900-1990 (1-degree pixel along coastline, NOAA 1994)
Latitude (degrees at midpoint of region)	

[1]OG = old-growth forest.

[2]Quantifies size and distance of neighboring old-growth patches within a 5-km radius to distinguish sparsely spaced, small old-growth patches (low value) from clusters of large old-growth patches (high value). Large consolidated patches or fragmented, yet very closely spaced small patches, have a high mean proximity index (McGarigal and Marks 1995).

[3]This variable was only available in California (from a state shoreline map).

Table 3. Correlation coefficients (r) between number of murrelets offshore per km coastline and the highest ranked (using r) inland and marine (including latitude) habitat variables in California and Oregon or California alone.

Variable	California and Oregon (N = 9)	California (N = 8)
Mean proximity index OG[a]	0.95	0.96
OG (%)	0.85	0.91
OG core area (%)	0.91	0.90
Medium-sized conifer (61-90 cm dbh) (%)	-	0.86
Nitrate (mg/m^3)	n.s[b]	-0.86
Largest patch OG (%)	0.70	0.85
Latitude (degrees)	0.81	0.81

[a]OG = old-growth forests

[b]not significant

for, the partial correlation coefficient for tidal flats was 0.82. However, tidal flats explained only an additional 5% of the overall variance. The three best 2-variable regression models were highly predictive ($R^2 \geq 0.96$ and $P < 0.0001$; Table 5).

DISCUSSION

Inland habitat was by far more important than marine habitat in affecting murrelet regional numbers, accounting for up to 98% of the variance in offshore numbers (Table 5). Although we had expected that inland habitat would be more important, we had also expected the marine habitat to contribute to explaining a portion of the variation in murrelet abundance. The regions we selected for our study were relatively large scale. A smaller scale analysis may provide stronger relationships between marine habitat and offshore abundance.

Inland Habitat

As predicted, higher fragmentation of habitat inland would decrease murrelet abundance offshore. Regions with abundant murrelets contained some large blocks of contiguous old-growth forest, which increased old-growth clumping and percentage of land in the largest patch size (Fig. 1). Such large patches provide more core areas, which was also found to be important in our study of inland birds at smaller scales (Meyer *et al.* in press). Core area provides sites for nests away from the edge, where young are more likely to fledge successfully due to lowered predation rates (Paton 1994; Nelson and Hamer 1995).

Our prediction that the region with the most birds offshore would contain proportionally more forests with medium-sized trees than younger seral stage forests with smaller trees, was supported. Such a land-

Table 4. Offshore murrelets per km of coastline compared to average characteristics of old-growth (OG) and conifer forests, and coastline habitats of the regions in the study area.

Region name	Birds per km	OG (%)	OG core area (%)	OG mean proximity index	Largest patch OG (%)	Medium conifer (%)
South Oregon	17.0	7.49	4.40	305.25	0.20	—
Klamath	19.2	4.01	3.55	289.49	1.91	15.50
Trinidad	26.6	5.39	4.80	354.35	2.07	14.70
Humboldt Bay	11.0	4.55	4.19	41.86	2.07	12.00
Kings Range	4.5	0.43	0.29	31.31	0.09	7.40
Point Arena	2.7	0.51	0.43	0.45	0.17	9.24
Russian River	1.8	0.52	0.43	0.00	0.19	6.82
San Francisco	0.0	0.60	0.54	11.92	0.53	2.50
Santa Cruz	4.5	0.99	0.83	24.99	0.30	2.25

Table 5. Predictor variables and coefficient statistics in linear regression models of offshore murrelets per km of coastline in California alone or with southern Oregon included. Old-Growth conifer forest is represented in the table as "OG."

Variables	Unstandardized coefficient	SE	Standardized coefficient[1]	t-value	P<
California (N = 8)	$R^2 = 0.981$				
Mean proximity index OG[2]	0.0424	0.0074	0.636	5.7	0.002
% land in OG	1.807	0.5006	0.403	3.6	0.02
Constant	0.930	0.8863		1.1	n.s.
California/Oregon (N = 9)	$R^2 = 0.965$				
Mean proximity index OG	0.0494	0.0060	0.801	8.3	0.0002
% in largest patch OG[2]	2.946	1.0016	0.285	2.5	0.03
Constant	1.416	1.0595		1.3	n.s.
California (N = 8)	$R^2 = 0.974$				
Mean proximity index OG	0.0666	0.0049	0.999	13.6	0.0001
coastline in tidal flats	14.026	4.3681	0.235	3.2	0.03
Constant	1.666	0.8580		1.9	

[1]The standardized coefficient and P value show the relative importance of each variable.

[2]This variable was also highly predictive with mean proximity index in a two variable linear regression for California alone, but % land in OG was slightly better.

scape, with old-growth in a matrix of even-aged older second-growth forest, may support fewer nest predators as it would provide less edge contrast. However, forests with medium-sized trees did not significantly explain any additional variance in murrelet offshore abundance, once fragmentation of old-growth forest was considered. More research that targets old-growth areas, with and without surrounding medium-sized forests, is needed to determine the effects of various matrix habitats.

Marine Habitat

None of the marine variables were good predictors of offshore abundance. Nitrate concentration was the only marine variable with a significant simple correlation to abundance, and it decreased as murrelet numbers increased. We expected nitrate, an indicator of marine productivity, to be positively, rather than negatively, associated with the birds. Notably, the addition of the Oregon data removed the significant relationship. Because the addition of Oregon data negated the importance of nitrate, the nitrate result in California is likely a statistical artifact, rather than an important biological result. Of the marine habitat relationships we felt would be important, only our expectation that murrelet numbers would be highest in regions with more tidal flats was supported. Tidal flats were uncorrelated with the old-growth proximity index ($r = 0.17$) and thus independently contributed to murrelet abundance. Tidal flats are within the bays and estuaries, and are nutrient rich, highly productive areas providing food for potential murrelet prey.

When inland habitat fragmentation patterns were included in the models, marine habitat appeared to have little effect on murrelet offshore numbers, accounting for ≤5% of the variation in offshore numbers. On a smaller landscape scale (Meyer *et al.* in press), we found areas with consistently high chlorophyll, were near inland nesting areas. However, in the present study, increased primary productivity, as evidenced by chlorophyll in the ocean, did not significantly increase murrelet numbers over and above the effect of unfragmented inland habitat. Within our study area, murrelet abundance appears most limited by the amount and degree of fragmentation of old-growth nesting habitat. However, the marine environment may have a stronger influence on abun-

dance if nesting habitat increases. Our results suggest that conservation efforts for the Marbled Murrelet should focus on protecting or creating large, contiguous blocks of old-growth habitat, features which are uncommon in the study area.

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Pacific Seabird Group

DEDICATED TO THE STUDY AND CONSERVATION OF PACIFIC SEABIRDS AND THEIR ENVIRONMENT

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March 24, 2010

Del Waters, Director
California Department of Forestry and Fire Protection
1416 Ninth Street
PO Box 944246
Sacramento, CA 94244-2460

Re: Impacts to the Marbled Murrelet from loss of suitable nesting habitat in California

Dear Mr. Waters:

On behalf of the Pacific Seabird Group (PSG), we are providing comments on proposed harvesting of suitable Marbled Murrelet (*Brachyramphus marmoratus*) nesting habitat in northern and central California. We are concerned that the cumulative impacts of multiple timber harvests in both occupied and unoccupied habitat could significantly impact conservation efforts for the Marbled Murrelet, which is listed as threatened under the federal Endangered Species Act (ESA) and listed as endangered under the California Endangered Species Act.

PSG is an international, non-profit organization that was founded in 1972 to promote the knowledge, study, and conservation of Pacific seabirds. It has a membership drawn from the entire Pacific basin, including Canada, Mexico, Russia, Japan, China, Australia, New Zealand, and the USA. Among PSG's members are biologists and scientists who have research interests in Pacific seabirds, government officials who manage seabird refuges and populations, and individuals who are interested in marine conservation. For two decades, PSG has taken an active lead in resolving many scientific aspects of the biology and conservation of Marbled Murrelets. PSG has served as an unbiased forum for government, university, and private sector biologists to discuss and resolve such issues.

The U.S. Fish & Wildlife Service listed the Marbled Murrelet in 1992 primarily because of significant losses of nesting habitat through logging and development in coastal forests of

Washington, Oregon, and California (USFWS 1992). An objective of the Marbled Murrelet recovery plan (USFWS 1997) is to stabilize and then recover the population by maintaining and/or increasing productivity and removing and/or minimizing threats to survivorship. Protecting terrestrial habitat, both occupied and unoccupied, including maintaining nesting habitat, protecting and enhancing blocks of contiguous forest cover as large as possible, and maintaining and enhancing buffer habitat is essential for the long-term recovery of this species (USFWS 1997:131-146). In fact, because so much murrelet habitat has been lost or depleted in California, remaining suitable habitat is especially important, regardless of its size, if murrelets are to have a good chance of surviving over the next 100 years.[1]

Marbled Murrelet Nesting Habitat

The amount of mature and late-seral habitat suitable for murrelet nesting in coastal areas is significantly below historic minima. The current amount of old-growth forest in California has been reduced by more than 96% from pre-logging levels (Larsen 1991). This is especially true from Mendocino county south through San Mateo county, where Marbled Murrelet populations have been particularly impacted by the reduced amount of remaining suitable nesting habitat. This reduction in suitable habitat could result in reduced population dispersal and create a "genetic bottleneck."

Suitable habitat should be well-distributed to reduce the probability that natural or human-caused catastrophe will threaten the survival of the species (USFWS 1996, 2006). Additionally, large contiguous blocks of nesting habitat are important for minimizing the effects of predation and windthrow. However, while large contiguous blocks create the best habitat, remaining unoccupied habitat is important, regardless of its size, in light of the fact that so little old-growth remains in California. Moreover, without a long-term strategy for Marbled Murrelet habitat conservation on State and private lands in northern and central California, the demise of the murrelet population will likely be accelerated. Allowing projects in suitable but unoccupied habitat to proceed will likely result in unacceptable habitat losses which will hinder the recovery of the Marbled Murrelet in California.

Continued Loss of Marbled Murrelet Habitat

Despite the listing of the Marbled Murrelet as a threatened species, the amount of suitable murrelet habitat has continued to decline throughout its range. The loss and degradation of habitat has resulted from: (1) harvesting on private and State lands; (2) federal/private land

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[1] Suitable murrelet habitat includes stands of any size with at least one tree with limb diameters or platform structure >10 cm, or a residual/remnant tree with limb diameters or platform structure >10 cm. From research on Marbled Murrelet habitat use, it is clear that the species can utilize small patches of suitable habitat. Murrelets can also nest in large residual trees that often remain from past fire and management activities. These residual trees are often found at low densities, sometimes less than one tree/acre. Therefore, any assessment of habitat must include a walk-through of every acre of the area in question. Without this detailed assessment it is easy to miss small patches of habitat and residual trees (excerpted from PSG's 1996 letter defining murrelet habitat).

exchanges; (3) logging (including selection logging and thinning) in suitable habitat and in buffers to suitable habitat; (4) misguided habitat conservation plans; (5) fragmentation effects from adjacent harvests and thinnings; and (6) a variety of natural and anthropogenic causes including fire, windthrow, and disturbance. The total loss of suitable nesting habitat between 1992 and 2003 was estimated to be about 226,000 acres or 10% of the estimated 2.2 million acres of suitable habitat (2003 estimate; McShane et al. 2004). Under the Northwest Forest Plan (USDA and USDI 1994a, b), habitat conservation plans, and other habitat management plans, new murrelet habitat will not be suitable for 50 to 200 years or more. The inability to create new murrelet habitat in the short term, combined with the continued harvesting of occupied and unoccupied habitat, ensures a downward trend in suitable murrelet habitat into the future. For these reasons it is imperative that current and potential nesting habitats be conserved.

Marbled Murrelet Populations Continue to Decline

The Washington, Oregon, and California murrelet population is estimated to be 22,000 birds (McShane et al. 2004). Population modeling indicates that this population is declining and will be extinct in parts of Washington, Oregon and California within 100 years without changes in the amount and quality of nesting habitat and in demographic trends (McShane et al. 2004). Low fecundity levels across Washington, Oregon, and California as measured by nest success indicate a population that cannot currently maintain itself (Beissinger and Peery 2003, McShane et al. 2004, http://www.reo.gov/monitoring/mm-overview.shtml). In addition to the serious habitat loss that has occurred, murrelets are also experiencing poor nest success due primarily to nest predation, which in turn is significantly affected by forest fragmentation and proximity to human developments (Raphael et al. 2002, McShane et al 2004). Thus, in order to diminish the threat of nest predation, and increase murrelet reproduction, the forest landscape and its surroundings must be protected to provide blocks, contiguous blocks of suitable nesting habitat. It is thus critical to ensure that any remaining occupied and unoccupied murrelet habitat in California is protected, and enhanced when possible.

In summary: (1) murrelet populations continue to decline due to habitat loss, low fecundity, high nest predation rates, and low adult survival; (2) most current recovery efforts rely on a system of reserves on federal land that is extremely limited in central and northern California, and, with the loss of occupied and unoccupied murrelet habitat continuing, State Lands and private lands with potential habitat play a crucial role in maintaining nesting habitat and ensuring future murrelet recovery; and (3) land use contrary to recovery objectives must be avoided within and adjacent to suitable habitats, especially ones significant to the stability and recovery of regional populations of imperiled species. Continued loss and fragmentation of habitat will increase the risk of extinction of this unique seabird in California. We agree with the Evaluation Report on the 5-Year Status Review for the murrelet that:

> It is unrealistic to expect that the species will recover before there is significant improvement in the amount and distribution of suitable nesting habitat (McShane et al. 2004: 6-34).

Without protection from further loss of suitable habitat and removing and/or minimizing threats to survivorship to allow for increased productivity, the Marbled Murrelet is likely to become extirpated in central and northern California in the foreseeable future.

Sincerely,

Craig S. Harrison

Craig S. Harrison
Vice Chair for Conservation

cc: Ren Lohoefener, Director, US Fish and Wildlife Service Region 8
John McCamman, Director, California Department of Fish and Game
Lester Snow, Secretary, California Natural Resources Agency
California Department of Forestry and Fire Protection, Santa Rosa

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Individual legacy trees influence vertebrate wildlife diversity in commercial forests

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Abstract

Old-growth forests provide important habitat elements for many species of wildlife. These forests, however, are rare where lands are managed for timber. In commercial forests, large and old trees sometimes exist only as widely-dispersed residual or legacy trees. Legacy trees are old trees that have been spared during harvest or have survived stand-replacing natural disturbances. The value of individual legacy trees to wildlife has received little attention by land managers or researchers within the coast redwood (*Sequoia sempervirens*) region where 95% of the landscape is intensively managed for timber production. We investigated the use of individual legacy old-growth redwood trees by wildlife and compared this use to randomly selected commercially-mature trees. At each legacy/control tree pair we sampled for bats using electronic bat detectors, for small mammals using live traps, for large mammals using remote sensor cameras, and for birds using time-constrained observation surveys. Legacy old-growth trees containing basal hollows were equipped with 'guano traps'; monthly guano weight was used as an index of roosting by bats. The diversity and richness of wildlife species recorded at legacy trees was significantly greater than at control trees (Shannon index = 2.81 versus 2.32; species = 38 versus 24, respectively). The index of bat activity and the number of birds observed was significantly greater at legacy trees compared to control trees. We found no statistical differences between legacy and control trees in the numbers of small mammals captured or in the number of species photographed using remote cameras. Every basal hollow contained bat guano and genetic methods confirmed use by four species of bats. Vaux's swifts (*Chaetura vauxi*), pygmy nuthatches (*Sitta pygmaea*), violet-green swallows (*Tachycineta thalassina*), and the long-legged myotis (*Myotis volans*) reproduced in legacy trees. As measured by species richness, species diversity, and use by a number of different taxa, legacy trees appear to add significant habitat value to managed redwood forests. This value probably is related to the structural complexity offered by legacy trees. The presence of a basal hollow, which only occur in legacy trees, was the feature that appeared to add the greatest habitat value to legacy trees and, therefore, to commercial forest stands. The results of our study call for an appreciation for particular individual trees as habitat for wildlife in managed stands. This is a spatial resolution of analysis that, heretofore, has not been expected of managers. The cumulative effects of the retention of legacy trees in commercial forest lands could yield important benefits to vertebrate wildlife that are associated with biological legacies.

Keywords: Biodiversity; Legacy tree; Biological legacy; Forest management; Managed forests; Northwestern California; Redwood; *Sequoia sempervirens*; Basal hollows; Wildlife communities; Bats; Small mammals; Birds

1. Introduction

The conservation of old-growth forests has received much attention in recent decades with the heart of the

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debate focusing on the value of old-growth as habitat for wildlife. Structural components of old-growth forests, such as snags, living trees with decay, hollows, cavities and deeply furrowed bark, provide habitat for many species (Bull et al., 1997; Laudenslayer, 2002). However, remnant old-growth trees and snags are rare in landscapes that are intensively managed for wood products. Homogenous young stands lacking structural and compositional complexity reduce the habitat value for species associated with old-growth forests (McComb et al., 1993; Carey and Harrington, 2001). The value of individual old-growth structures to wildlife in managed landscapes has received little attention by land managers or researchers (Hunter and Bond, 2001).

In some forest ecosystems, lands managed for timber production occupy all but a small portion of the landscape. In coast redwood (*Sequoia sempervirens*) forests, only 3–5% of the original old-growth redwood forest remains, largely as fragments scattered throughout a matrix of second and third-growth forests (Fox, 1996; Thornburgh et al., 2000). The remnants vary in size from large, contiguous forest patches protected in state and federal parks to patches of only a few hectares in size, to individual legacy trees in managed stands. Individual old-growth trees that have, for one reason or another been spared during harvest, or have survived stand-replacing natural disturbances, are referred to as "legacy" trees (Franklin, 1990). We define legacy trees as having achieved near-maximum size and age, which is significantly larger and older than the average trees on the landscape. This distinguishes them from other 'residual' trees, which may also have been spared from harvest but are not always larger and older than the average trees in the landscape.

The rarity of old-growth forests in managed landscapes combined with the rising economic value of old-growth redwood increases the likelihood that legacy stands and individual legacy trees will be harvested. At this time, there is no specific requirement for the retention of legacy trees during timber harvests on private or public lands in California. Exceptions occur on lands owned by companies that are certified as sustainable forest managers (Viana et al., 1996; Smart-Wood Program, 2000) and as such, are required to maintain and manage legacy old-growth trees.

A number of studies have demonstrated the importance of legacy and residual trees to wildlife. In Douglas-fir (*Pseudotsuga menziesii*) forests, flying squirrel abundance and nest locations were most often found in second-growth forests containing residual trees (Carey et al., 1997; Wilson and Carey, 2000). In addition, horizontal structural complexity increased in stands containing residuals (Zenner, 2000). In eastern hardwood forests, residual trees provided important habitat elements to forest birds in regenerating clear-cut stands (Rodewald and Yahner, 2000). In young and homogenous stands of regenerating redwood forests, residual old-growth legacy trees appear to be important roosting, foraging, resting, and breeding sites for spotted owls (*Strix occidentalis*), fishers (*Martes pennanti*), bats, Vaux's swifts (*Chaetura vauxi*), and marbled murrelets (*Brachyramphus marmoratus*) (Folliard, 1993; Klug, unpublished data; Thome et al., 1999; Zielinski and Gellman, 1999; Hunter and Mazurek, in press). In the preceding studies, the value of legacy structures was identified only as a consequence of studies on the individual species of wildlife. Our goal was instead to focus our research effort on the rare habitat element itself (the legacy tree) and determine how a variety of wildlife taxa may use it, compared to commercially-mature trees in the same stand.

2. Methods

2.1. Study area

The research was conducted during 2001 and 2002 in Mendocino County, California, in the central portion of the redwood range (Sawyer et al., 2000) in the Northern California Coast ecoregion (Bailey, 1994). The study area was approximately 1750 km^2 in size and included lands owned and managed by the Mendocino Redwood Company (MRC), the California Department of Forestry and Fire Protection-Jackson State Demonstration Forest (JSDF), and Hawthorne Timber Company (HTC)/Campbell Timberland Management (Campbell). These landowners manage approximately 65% of all coast redwood timberlands in Mendocino County.

MRC lands comprise 94,089 ha of timberlands in Mendocino and Sonoma Counties and are certified as sustainable under the Forest Stewardship Council and the Smart Wood Programs (Certificate No. SW-FM/COC-128). HTC/Campbell land includes 74,264 ha of

commercial redwood forest. JDSF is 20,639 ha of primarily second and third-growth redwood and Douglas-fir forests. Silvicultural prescriptions for each of the ownerships include about equal measures of even and uneven-aged harvest.

Elevations ranged from 44 to 576 m. Seasonal temperatures range from 18.2 to 9.4 °C in summer and from 13.3 to 5.5 °C in winter. Forests in this region are dominated by coast redwood. Other common trees species include Douglas-fir, grand fir (*Abies grandis*), tan oak (*Lithocarpus densiflora*), bigleaf maple (*Acer macrophyllum*), and Pacific madrone (*Arbutus menziesii*).

2.2. Site and tree selection

For the purposes of our research, we defined a legacy tree as any old-growth redwood tree that was >100 cm diameter at breast height (dbh) and possessed at least some of the following characteristics: deeply furrowed bark, reiterated crown, basal fire-scars, platforms, cavities, and one or more 'dead-tops'. Many legacy trees also had basal hollows ('goose pens') but absence of this trait did not exclude a tree from consideration. Legacy trees were represented by other species than coast redwood (e.g. Douglas-fir) but were not included in this study.

Thirty legacy trees were discovered using information provided by the landowners/managers and by our own reconnaissance. For a legacy tree to be selected for study the stand surrounding it must not have undergone timber operations at least 1 year prior to sampling nor could the stand have been proposed for alteration during the course of the study. The most recent harvest method varied from stand to stand but the majority of stands ($n = 27$) had been harvested under some type of selection method.

Legacy trees included those with and without basal hollows. Basal hollows occur as a result of periodic fires that produce repeated scarring and healing (Finney, 1996). To qualify as a hollow, the internal height must have been greater than the external height of the opening. Otherwise, the structure was considered a fire-scar when the cambium of the tree showed clear signs of effects from fire. We assumed that legacy trees did not need to have basal hollows to be of value to wildlife, therefore 15 legacy trees were selected that contained hollows and 15 did not.

The first step in selecting a control tree was by locating several (range = 3–10) of the largest commercially-mature trees from 50 to 100 m of a legacy tree. The set of candidates was reduced by eliminating from consideration all trees that did not share the same general environmental features with the legacy tree (i.e., similar distance to water and roads, similar slope and aspect). One control tree was randomly selected from the candidates that remained.

2.3. Wildlife sampling

2.3.1. General

An initial inspection was conducted of all trees that contained basal hollows ($n = 15$) and fire-scars ($n = 14$) by examining the interior of the hollow or fire-scar using a flashlight. These surveys were conducted during the initial portion of the study so as to not interfere with protocols designed to sample focal taxa (i.e., bats, small mammals). The hollow ceiling was searched for bats and nests of birds and mammals. The interior substrate of the hollow or fire-scar was inspected for evidence of use (e.g., feces, feathers, hair, prey remains, rest sites). Legacy and control trees were also visited regularly during the application of taxa-specific survey methods. Each time a tree was visited, field personnel would conduct an initial inspection for signs of use by wildlife.

2.3.2. Bats

We used Anabat II bat detectors (Titley Electronics, Australia) to record bat vocalizations at the trees, following the methods of Hayes and Hounihan (1994). The total number of vocalizations ('bat passes': Krusic et al., 1996; Hayes, 1997) was used to compare activity in the immediate vicinity of the legacy and control trees. To account for temporal variation in bat detections, we used a paired design and sampled simultaneously at the legacy and control trees at each site (Hayes, 1997). Bat detectors were located between 5 and 10 m from the trees, placed 1.4 m above the ground and at a 45° angle directed at the tree, a configuration that maximizes detection rates (Weller and Zabel, 2002). Each pair was sampled four times for two consecutive nights each (total = 8 nights), between either June (2002) or July (2001) and September.

Guano sampling occurred only at trees with basal hollows, using guano collection methods outlined by Gellman and Zielinski (1996). In addition to sampling guano in the 15 legacy trees with basal hollows, we also installed traps in three legacy trees with fire-scars. The oven-dried weight of guano served as a monthly index of bat use. A sample of 100 guano pellets was selected and subjected to genetic analysis to identify species. Species-specific genetic markers were developed from a 1.56 kilobase region of mitochondrial DNA spanning the majority of the 12S and 16S ribosomal RNA genes (Zinck et al., in press). We selected pellets for analysis by choosing one pellet from each tree sampled each year, and then selecting one pellet per tree sampled each season (i.e., spring and summer) until we reached 100 pellets. All trees sampled contributed at least one pellet for analysis. Eight species that occur in our study area can be identified using this method and one group of three species (*Myotis evotis*, *M. lucifugus*, and *M. thysanodes*) can be distinguished from others but not from each other (J. Zinck, pers. comm.).

2.3.3. Small mammals

We sampled non-volant mammals using live traps. Each tree selected for study was sampled using six Sherman live traps (8 cm × 9 cm × 23 cm) and two Tomahawk live traps (13 cm × 13 cm × 41 cm) placed at the base. Also, two Sherman traps and one Tomahawk trap were elevated 1.5 m and attached to the sides of the tree in an attempt to capture arboreal mammals. Traps contained seed bait and a small amount of polyester batting for insulation and bedding. We recorded the species, age, sex, reproductive status, and weight (g) of each mammal captured. A small amount of fur was clipped from the rear hindquarter (on the left if captured at the legacy tree; on the right if captured at the control) to distinguish individuals. Two, 5-day trapping sessions were conducted at each tree between June and August.

2.3.4. Time-constrained visual observation

Time-constrained observations were conducted from May to September. We observed each legacy and control tree for evidence of use or occupancy by wildlife. In 2001 we conducted one 30 min observation session in each of the three time intervals: (1) 2 h centered at dawn, (2) mid-day centered between 1100 and 1400 h, and (3) 2 h prior to sunset. In 2002, we conducted one 30 min observation session within 2 h of sunrise and sunset. All wildlife observed on, or within 5 m of the tree was recorded. Each time an animal was observed, the observer would note one occurrence (incident) per individual, the species, the amount of time spent at the tree, and the activity. Observations were categorized as perching, fly/perch, foraging, roosting, fledging, or 'present' (for non-avian species).

2.3.5. Remote photographic sampling

Animals present at the base of each tree were photographed using a remotely-triggered camera system (Trailmaster TM550, Trailmaster Infrared Trail Monitors, Lenexa, KS). The combination infrared and activity sensors and cameras were directed at the base of each tree from a distance of a few meters. We restricted the field of view of the sensor such that only animals directly in front of the tree base would be detected. Cameras were checked one day after installation and then approximately every 5 days for 3 weeks. Cameras operated simultaneously at each legacy and control tree in a pair. Each photo of an animal was considered a single detection, but we excluded all but one of a set of photographs of the same species taken consecutively during any 24 h period. This eliminated instances where animals would be present at the tree for several hours. We also excluded photographs of all small mammal species that were captured during the trapping sessions. All cameras operated during April–September.

2.4. Vegetation sampling

We collected physical measurements of each tree and of all basal hollows using variables described in Gellman and Zielinski (1996). We also measured vegetation attributes in the immediate vicinity of a random sample of 15 pairs of trees to determine whether the structure of the vegetation surrounding legacy and control trees differed. If such differences existed, it is possible that they would affect the use of the trees by wildlife, independent of the characteristics of the legacy and control trees themselves. We used variable-radius plot methods to estimate basal area (20-factor prism), and each tree that was included in the prism sample was also identified to species and its

diameter, height, and condition was recorded. Within an 11.3 m fixed radius plot, and centered on the legacy or control tree, all logs >25.4 cm diameter were recorded by species and their length and diameter measured. Canopy, shrub, herbaceous, and ground cover (duff and downed wood) were estimated visually within a 5 m fixed radius plot.

2.5. Species diversity

We used the Shannon index (Magurran, 1988, p. 34) to characterize the diversity of species detected at legacy and control trees. Diversity indices were calculated separately for the results from the small mammal sampling, time-constrained observation surveys, remote camera surveys, and for these three survey methods combined. We used the number of individuals captured (small mammal surveys), the number of detections (camera surveys) and the number of incidents (visual observation surveys) to calculate the proportion of individuals observed for all species. Our diversity calculations for the visual observation surveys (both individual and combined with the two other surveys) excluded species that were engaged in nesting activities that included frequent forays to and from a nest site (i.e., pygmy nuthatches (*Sitta pygmaea*) and violet-green swallows (*Tachycineta thalassina*)). We also calculated species evenness, a measure of the ratio of observed diversity to maximum diversity (Pielou, 1969), for each survey type described above.

2.6. Statistical analyses

Species diversity indices were statistically compared using the methods of Hutcheson (1970), which calculates a variance for each diversity statistic then provides a method of calculating t-values to test for significant differences between samples (Magurran, 1988, p. 35). Small mammal trapping, time-constrained observation and remote photograph (medium and large mammals only) data were analyzed using matched-pair t-tests. We were unable to normalize the results of the camera (all animals) data and thus used a non-parametric signed-rank test (S) to compare the number of detections by photograph at legacy and control trees. We used a mixed-effects analysis of variance model to compare bat detections between legacy and control trees.

Vegetation characteristics in the immediate vicinity of the legacy and control tree were compared using either t-tests (continuous variables) or χ^2-tests (categorical variables). All statistical analyses were conducted using SAS, Version 8.2 (SAS Institute, 2001, Cary, NC). Statistical significance was implied if P was <0.05.

3. Results

As expected, legacy trees were larger in diameter (mean dbh = 293 cm (S.D. = 82.3)) and height (mean = 53 m (S.D. = 14.8)) than the control trees (mean dbh = 73 cm (S.D. = 15.2), mean height = 32 m (S.D. = 10.2)). However, the mean diameter of control trees was 72.5 cm dbh, which is considered a commercially-mature size (R. Shively, pers. comm., 2001, Mendocino Redwood Company).

3.1. General wildlife observations

Initial examinations of the trees indicated that most of the hollows and fire-scars in legacy trees ($n = 19$; 63%) had evidence of small mammal use on the basis of the discovery of feces, food remains, or nest evidence (usually dusky-footed wood rat *Neotoma fuscipes* middens, $n = 5$). One hollow contained four roosting bats and six hollows (40%) contained guano, evidence of bat use. Four hollows or fire-scarred legacy trees (13%) had evidence of use (i.e., claw marks) by large mammals and feces or nests indicated that 10 legacy trees (33%) were used by birds.

The general inspection of trees resulted in several noteworthy observations of reproductive activity:

(1) On 16 June 2002, two adult pygmy nuthatches were observed repeatedly entering and exiting a cavity in a legacy tree. The birds were observed entering the cavity with food, which was followed by vocalizations of young.
(2) A legacy tree contained a large cavity that was occupied by barn owls (*Tyto alba*) during both years of the study. Fresh feces and food pellets were observed during each visit to the tree.
(3) On 16 July 2002, violet-green swallows were observed repeatedly entering and exiting a cavity in a legacy tree. These behaviors, and the time of

year, suggest the birds were nesting within the cavity.

(4) Vaux's swifts nested for two consecutive years in the basal hollow of a legacy tree.

(5) On 23 July 2002 a large number of bats was observed in a hollow that had conspicuous guano accumulation and in which was discovered, on 31 July 2001, a dead juvenile long-legged myotis. Collectively, this evidence suggests that this legacy tree was used as a maternity colony.

3.2. Bats

3.2.1. Acoustic sampling

We recorded a total of 10,799 bat passes over the two sample years. The mean index of bat activity was significantly greater at the legacy trees compared to the control trees ($F_{1,45.7} = 17.66, P < 0.0001$) (Fig. 1). The mean index of bat activity at legacy trees with and without hollows was 34.8 (S.D. = 33.4, $n = 15$) and 22.6 (S.D. = 15.9, $n = 15$), respectively, a difference that was not statistically significant ($t = 1.27$, $P = 0.21$).

3.2.2. Guano sampling

We collected guano monthly from July to October 2001 and April to October 2002. All hollows and fire-scars showed evidence of bat use during some portion of the survey period. Average guano weight declined from August to October during both years (Fig. 2).

Sixty-eight of the 100 guano samples submitted for analysis amplified adequate amounts of DNA for species analysis. Four species were verified to use legacy trees, with the long-legged myotis the most common (46%) (Table 1). The California myotis (*Myotis californicus*) was the species detected at the greatest number of hollow-bearing trees (73%) and the total number of trees (hollow-bearing and fire-scarred (66%)). The big brown bat (*Eptesicus fuscus*) and the California myotis were the only species identified from the four guano samples that originated from fire-scars (Table 1).

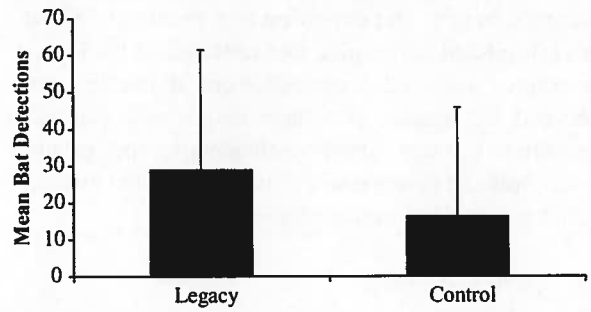

Fig. 1. Mean bat detections and standard deviation for legacy and control trees ($F_{1,45.7} = 17.66$, $P < 0.0001$) in Mendocino County, California, 2001 and 2002.

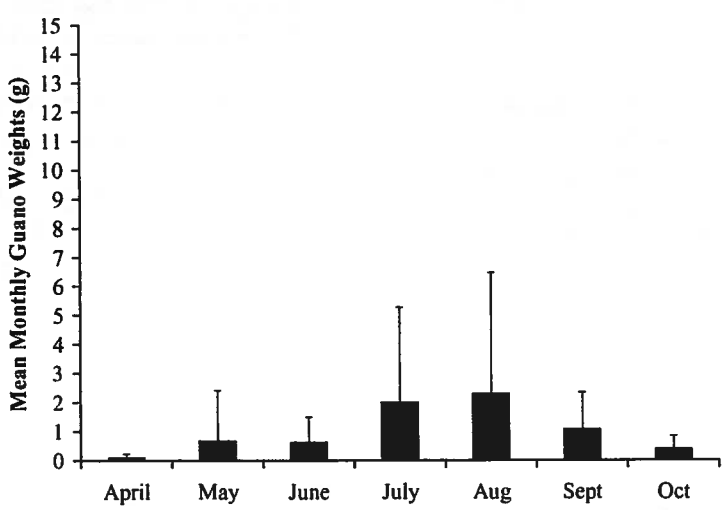

Fig. 2. Mean monthly guano weights (g) and standard deviation (April–October) at 14 hollow-bearing trees in Mendocino County, California, 2001 and 2002.

Table 1
Number of 68 guano samples collected from 15 basal hollows and three fire-scars that could be identified to species

Species	Guano sample		Hollows		Fire-scars		Trees total	
	Number	Percentage of samples	Number	Percentage of hollows	Number	Percentage of fire-scars	Number	Percentage of trees total
Big brown bat (*E. fuscus*)	9	13	5	33	3	100	8	44
California myotis (*M. californicus*)	17	25	11	73	1	33	12	66
Myotis 3[a]	11	16	5	33	0	0	5	27
Long-legged myotis (*Myotis volans*)	31	46	9	60	0	0	9	50

[a] *Myotis lucifugus*, *M. evotis*, and *M. thysanodes* are not currently distinguishable, but guano from these three species can be distinguished from other species.

3.3. Small mammal sampling

There was a slightly greater number of total small mammal captures at legacy trees compared to control trees (Table 2). There was also a greater number of individuals captured at the legacy trees compared to control trees, though this relationship was not statistically different ($t = 0.5$, $P = 0.62$). Two of the insectivores (shrew mole (*Neurotrichus gibbsi*) and Trowbridge's shrew (*Sorex trowbridgii*)) were the only species of small mammals that appeared to be trapped more commonly at the base of legacy trees.

3.4. Observation surveys

Each legacy and control tree was sampled at least twice, resulting in a total of 132 surveys and 114.5 h of survey effort (Table 3). There was a significantly greater number of incidents ($t = 16.6$, $P < 0.0001$) and time spent ($t = 4.05$, $P = 0.0004$) at legacy trees compared to control trees (Table 3). Wildlife (primarily birds) was observed about nine times as frequently at legacy trees compared to control trees and there were also more species observed at legacy trees compared to control trees (Table 4).

Of the activities observed, 82% was either perching or flying. There was twice as much foraging activity at legacy trees (22 incidents) compared to control trees (10 incidents). Woodpeckers, nuthatches, and some swallows were observed only at legacy trees; acorn woodpeckers used a legacy tree as a food storage location (i.e., granary). The majority of individuals observed were pygmy nuthatches, violet-green swallows, or unknown passerines.

Remote cameras operated a total of 1278 survey hours. We photographed 18 species at legacy and control trees; 13 species were detected only as a result of the camera surveys (Table 5). The total number of photographic detections was 38 at legacy trees (mean = 1.4, S.D. = 2.4, $n = 27$) and 17 at control

Table 2
Summary of small mammal captures by species at study sites in Mendocino County, California, 2001 and 2002

Species	Total captures		Total individuals captured		Individuals captured at both legacy and control pair
	Legacy	Control	Legacy	Control	
Trowbridge's shrew (*S. trowbridgii*)	33	18	30	16	0
Fog shrew (*S. sonomae*)	2	4	2	3	0
Shrew mole (*N. gibbsii*)	5	0	5	0	0
Short-tailed weasel (*Mustela erminea*)	0	1	0	1	0
Dusky-footed wood rat (*N. fuscipes*)	62	88	23	37	0
Redwood (yellow-cheeked) chipmunk (*Tamias ochrogenys*)	93	51	39	31	3
Deer mouse (*Peromyscus maniculatus*)	150	133	67	61	1
Western red-backed vole (*Clethrionomys californicus*)	20	37	13	19	0
Total	365	332	179	168	4

Table 3
Summary of visual observation results[a]

Tree type	Total			Survey period					
	Total survey effort (h)	min/h	Number of incidents	a.m.		Mid		p.m.	
				min/h	Number of incidents	min/h	Number of incidents	min/h	Number of incidents
Legacy	57.5	0.0998	188	0.1035	170	0.002	4	0.1938	14
Control	57.0	0.0105	34	0.0143	27	0.003	6	0.0024	1

[a] Total survey effort, duration (min/h of survey effort) that individuals were observed and the total number of incidents of wildlife observed for three time periods; a.m. (within 2 h of sunrise), mid (2 h centered around mid-day) and p.m. (2 h within sunset).

trees (mean = 0.63, S.D. = 1.3, $n = 27$); the means were not statistically different ($S = 37.5$, $P = 0.10$). When we restricted detections to include only medium and large mammals the total numbers of detections were 14 (mean = 0.52, S.D. = 0.64) and 10 (mean = 0.37, S.D. = 0.88) at legacy and control trees respectively, but were not statistically different ($t = 0.78$, $P = 0.44$).

Table 4
Species observed at legacy and control trees and the number of incidents (number of times a species was observed) during time-constrained visual observations in Mendocino County, California, 2001 and 2002

	Legacy	Control
Species at legacy only		
Acorn woodpecker	12	0
Common raven	2	0
Downy woodpecker	1	0
Hairy woodpecker	3	0
Northern flicker	2	0
Osprey	1	0
Pygmy nuthatch	25	0
Red-breasted nuthatch	1	0
Turkey vulture	1	0
Unknown flycatcher	1	0
Unknown owl	1	0
Unknown swallow	11	0
Unknown woodpecker	4	0
Vaux's swift	3	0
Violet-green swallow	52	0
Winter wren	2	0
Species at control only		
Golden-crowned kinglet	0	1
Hutton's vireo	0	8
Species at both legacy and control		
Brown creeper	4	2
Chestnut-backed chickadee	4	2
Hermit warbler	1	1
Pacific-slope flycatcher	1	1
Redwood chipmunk	1	1
Steller's jay	10	7
Unknown passerine	44	10
Western gray squirrel	1	1

3.5. Vegetation sampling

There were no differences in the vegetation characteristics in the area immediately surrounding the legacy and control trees. Basal areas, tree diameters, tree heights, log volumes, canopy cover, shrub cover, and herbaceous cover were statistically indistinguishable (Table 6). In addition, there were no significant

Table 5
List of species and the number of detections (photographs) at legacy and control trees during remote camera surveys in Mendocino, California, 2002[a]

	Legacy	Control
Species at legacy only		
Bat (species unknown)	1	0
Brush rabbit (*Sylvilagus bachmani*)	7	0
Sonoma vole (*Arborimus pomo*)	1	0
Winter wren (*Troglodytes troglodytes*)	1	0
Species at control only		
Gray fox (*Urocyon cinereoargenteus*)	0	2
Raccoon (*Procyon lotor*)	0	1
Species at legacy and control		
Black bear (*Ursus americanus*)	4	1
Black-tailed deer (*Odocoileus hemionus*)	1	1
Bobcat (*Lynx rufus*)	4	1
Douglas' squirrel (*Tamiasciurus douglasii*)	5	4
Spotted skunk (*Spilogale gracilis*)	1	1
Striped skunk (*Mephitis mephitis*)	4	3
Western gray squirrel (*Sciurus griseus*)	9	3

[a] Each detection represents only one photo per species per tree per 24 h period.

Table 6
Means and standard deviations (S.D.) for habitat variables sampled in the immediate vicinity of legacy (L) and control (C) trees in Mendocino County, California, 2001 and 2002[a]

Vegetation characteristic	Tree type				t	P
	L		C			
	Mean	S.D.	Mean	S.D.		
Basal area (m^2/ha)	55.6	22.5	56.8	27.5	0.17	0.87
Tree dbh (cm)	46.7	23.2	49.2	23.6	0.38	0.71
Tree height (m)	24.6	7.7	26.2	8.3	0.87	0.40
Log volume (m^2)	1.27	1.4	0.79	0.86	1.08	0.30
Canopy cover (%)	83.6	7.6	84.4	8.2	0.42	0.68
Shrub cover (%)	12.8	16.5	16.1	21.2	0.63	0.54
Herbaceous cover (%)	24.9	36.8	16.7	23.6	1.19	0.30

[a] Legacy and control trees were excluded from calculations. t-values and P-values are from the results of matched-pair t-tests.

differences in tree species, tree condition, log species, log condition, the amount of duff, or the amount of downed wood (Table 7). Thus, we concluded that there were no systematic differences in the physiognomy of vegetation surrounding legacy trees when compared to control trees.

3.6. Diversity indices

The number and diversity of species using legacy trees was greater than those using control trees using data from only the time-constrained observation surveys, or when we combined the results from the time-constrained observation surveys, camera surveys, and small mammal trapping (Table 8). Species richness was about 1.5 times as great at legacy trees ($n = 38$) than at control trees ($n = 24$) for all surveys. Using data from the timed observation surveys only, the species richness was more than twice as great at legacy

Table 7
Frequency of occurrence for habitat variables sampled in the immediate vicinity of legacy (L) and control (C) trees in Mendocino County, California, 2001 and 2002[a]

Vegetation characteristic		Frequency for tree type		χ^2	P
		L	C		
Tree species	Coast redwood	22	22	2.03	0.36
	Other conifer	15	12		
	Hardwood	20	10		
Tree condition	Live	40	33	2.42	0.3
	Declining	13	5		
	Dead	4	5		
Log species	Coast redwood	31	27	0.63	0.73
	Other conifer	10	9		
	Hardwood	4	6		
Log condition	Class 1	2	1	1.05	0.9
	Class 2	8	8		
	Class 3	15	11		
	Class 4	13	12		
	Class 5	7	9		
Downed wood	High	7	8	0.13	0.72
	Low	8	7		
Duff	High	13	12	NA	NA
	Low	2	3		

[a] Legacy and control trees were excluded from calculations. Statistical values are from χ^2 goodness of fit tests.

Table 8
Number of individuals (small mammals) or detections (other taxa), species richness, evenness and diversity indices by survey method for legacy (L) and control (C) trees in Mendocino County, California, 2001 and 2002[a]

Survey method	Tree type	Number of individuals or detections	Richness (number of species)	Evenness	Shannon diversity index	t statistic	d.f.	P
Observation	L	111	22	0.73	2.25	2.13	95	0.05–0.02
	C	34	10	0.82	1.88			
Trailmaster	L	38	11	0.88	2.11	0.64	54	>0.5
	C	17	9	0.93	2.04			
Mammal trapping	L	179	7	0.82	1.60	0.26	350	>0.25
	C	168	7	0.82	1.58			
Overall	L	328	38	0.77	2.81	5.05	481	<0.001
	C	219	24	0.73	2.32			

[a] Tests statistics refer to the Shannon diversity indices.

trees ($n = 22$) than at control trees ($n = 10$). The Shannon diversity indices were statistically higher at legacy trees (2.81) than control trees (2.32) for the combined surveys and for the observational surveys (human observer) (Table 8), but we did not find differences in the richness or diversity of small mammals captured in traps or for the species detected by cameras, when these data sets were analyzed separately (Table 8). Evenness was greater at legacy trees compared to control trees for the combined surveys only (Table 8).

4. Discussion

As measured by species richness, species diversity, and use by a number of different taxa, legacy trees appear to add important foraging and breeding habitat value to redwood forests managed for timber. The use of legacy trees by wildlife was demonstrated by evidence of their nesting, roosting and resting; behaviors which were not observed at control trees. This difference is probably related to the structural complexity offered by redwood legacy trees (Bull et al., 1997; Laudenslayer, 2002). Control trees were smooth-boled with very few large horizontal limbs, few cavities, and no basal hollows. Legacy trees possess these structural features, which probably account for their greater attractiveness to a variety of wildlife species.

The presence of a basal hollow, which only occur in legacy trees, was the feature that appeared to add the greatest habitat value to legacy trees and, as a result, to commercial forest stands. However, we did not sample specifically for wildlife that may benefit from the presence of large horizontal branches (e.g. platform nesting wildlife). Basal hollows were used by every taxa sampled, but appear to be particularly important to bats and birds. In addition to the fact that guano was collected at every hollow we sampled, individual bats were observed in hollows, and reproduction was documented. Use of basal hollows by bats has been observed in other redwood regions (Gellman and Zielinski, 1996; Zielinski and Gellman, 1999; Purdy, 2002) and there are several previous reports of basal hollows used by bats for reproduction (Rainey et al., 1992; Mazurek, in press). Hollows also appear to be important nest sites for some bird species, in particular Vaux's swifts (Hunter and Mazurek, in press). Because roost and nest availability can limit the populations of birds and bats (Humphrey, 1975; Kunz, 1982; Brawn and Balda, 1988; Christy and West, 1993; Raphael and White, 1984), basal hollows may play a critical role in the redwood region if they provide roost and nest sites in forests that are otherwise deficient. The increased use of legacy trees by insectivorous birds and bats may also be because the rugosity of the bark may harbor a greater diversity and abundance of insects (Ozanne et al., 2000; Willett, 2001; Summerville and Crist, 2002). Bark gleaners, such as brown creepers (*Certhia americana*), have been correlated with the abundance of spiders and other soft-bodied arthropods that are significantly associated with bark furrow depth (Mariani and Manuwal, 1990); this may also explain the disproportionate use of legacy trees by nuthatches and woodpeckers. Finally, basal hollows not only benefit the wildlife that use them but the trees in which they are found. The feces of animals that are attracted to hollows can be an important source of nutrients for trees that may be on nutrient-poor sites (Kunz, 1982; Rainey et al., 1992).

The mammal data (bats excluded) did not suggest a disproportionate association with either legacy or control trees. Possible exceptions include two insectivores, which were captured more at legacy trees, and the dusky-footed woodrat, whose nests were found in five of 15 basal hollows. Shrew moles are associated with older forests (Raphael, 1988; Carey and Johnson, 1995) and are infrequently found in logged areas (Tevis, 1956). Several studies also found that Trowbridge's shrews have a similar association with mature forest conditions (Gashwiler, 1970; Hooven and Black, 1976; Carey and Johnson, 1995).

The camera data did not reveal disproportionate use of legacy trees by mammals. Relatively few mammalian carnivores were detected at either type of tree, perhaps because some species (i.e., the marten (*Martes americana*) and the fisher (*M. pennanti*)) are sensitive to forest habitat loss and fragmentation (Buskirk and Powell, 1994) and have been either extirpated from the region or are very rare (Zielinski et al., 1995, 2001). With the exception of the two insectivores and wood rats, none of the non-volant mammals we sampled appeared to be strongly associated with the legacy trees. Unlike the passerine birds, which use the structurally complex bark of

legacy trees for foraging and cavities for nesting, and the bats, which roost in hollows and bark crevices, our data do not indicate that legacy trees have exceptional value for rodents or for the species of carnivorous mammals that still occur in the region.

Our conclusions about the value of legacy trees to wildlife in the redwood region are supported by the results of studies on individual species of wildlife elsewhere. Legacy trees (also described as old-growth residuals) are used by northern (*Strix occidentalis caurina*) and California (*S. o. occidentalis*) spotted owls for nesting and roosting (Moen and Gutiérrez, 1997; Irwin et al., 2000). Fishers use legacy conifers, and residual hardwoods, as daily rest sites in public Douglas-fir forests (Seglund, 1995) and private redwood forests (R. Klug, pers. comm.). Flying squirrels were twice as abundant when legacy trees were retained in managed areas (Carey, 2000) and their diet was found to be more diverse in legacy stands (Carey et al., 2002).

Our work was directed at assessing the value of individual *legacy* trees in stands, but there is a considerable body of research on the related question of what value *residual* trees and patches have in maintaining wildlife diversity in forests. Residual structures may not be as old as the legacy structures we studied, but they can add important structural diversity to which many species of wildlife respond. Songbirds in a variety of coniferous mixed, and hardwood forest types have benefited from the retention of residual trees (Hobson and Schieck, 1999; Rodewald and Yahner, 2000; Schieck et al., 2000; Tittler et al., 2001; Whittman et al., 2002; Zimmerman, 2002). Southern red-backed voles (*Clethrionomys gapperi*), a late-successional associated forest species, are also more common in harvested areas as the basal area in residual trees increases (Sullivan and Sullivan, 2001). The retention of residual structure during logging appears to have benefits to wildlife, but additional research will be necessary to distinguish the effects of retaining commercially mature—but relatively young—trees for wildlife from retaining and managing legacy trees, which are typically much older.

The goal of this study was to document the pattern and frequency of use of legacy and control trees so that we might better understand how young and old elements are used within the matrix of commercial redwood forests. To do so we compared the occurrence of species and individuals, but did not evaluate how individual trees contribute to *survival* or *reproduction* (i.e., fitness) of individual species. Measures of abundance, or indices of abundance, are not sufficient to completely evaluate the effects of variation in habitat on wildlife populations; in some cases they can even mislead because not all places where animals occur are suitable for reproduction (Van Horne, 1983). Our observations of reproductive behavior by a number of birds and at least one species of bat, however, suggest that legacy trees may influence the fitness of some species as well. We also believe that the potential survival value of access to legacies was probably underestimated in our study because we evaluated use only during the climatically benign summer months. We expect that benefits of access to legacy trees would be the greatest during the winter when they would be used as refuges from inclement weather (e.g., Carey, 1989).

If legacy trees provide one of the few choices for nesting and reproductive sites, and they are rare, then it is possible that they may be easily located and searched by predators making them population 'sinks' (Pulliam, 1988). Tittler and Hannon (2000) did not find increased predation in this respect, but their study evaluated residual trees, which were more numerous and probably not as distinctive and obvious foraging locations as are the more structurally distinctive redwood legacy trees. It is clear, however, that the risks that wildlife may be subjected to when using, and perhaps congregating at, legacy structures will need to be evaluated with respect to the benefits.

5. Conclusions

Our traditional view of conservation reserves is of large protected areas. However, few landscapes provide us with the opportunity to preserve large tracts of land and we must consider conserving biodiversity within the matrix of multiple use lands (Lindenmayer and Franklin, 1997). Given the fragmented nature of mature forests in the redwood region, remnant patches of old-growth and individual legacy trees may function as 'mini-reserves' that promote species conservation and ecosystem function. Legacy structures increase structural complexity in harvested stands

and, as a result, can provide the 'lifeboats' for species to re-establish in regenerating stands (Franklin et al., 2000). Although the lifeboat function may not be entirely fulfilled for vertebrates with large area needs, these habitat elements may make it possible for some species to: (1) breed in forest types where they may otherwise be unable, and (2) secure a greater number of important refuges from climatic extremes and predators. In addition, these functions may allow legacy trees to provide some measure of habitat connectivity ('stepping stones') to larger more contiguous tracts of old-growth forests (Tittler and Hannon, 2000; Noss et al., 2000).

Because of their rarity in commercial forests, the first step in the management of legacy trees is to determine their locations and protect them from logging or from physical degradation of the site. Because legacy redwoods with basal hollows are even more rare, locating and protecting these should be the highest priority. In addition, the circumstances that lead to their genesis will be difficult to recreate, especially on commercial timberland. Hollows form by repeated exposure of the base of trees to fire (Finney, 1996), and because most fires on private land are suppressed, prescribed fire would need to be repeatedly applied to trees that would be designated as 'future legacies' and which would be excluded from harvest in perpetuity. We hasten to add, however, that legacy trees without basal hollows appear to have significant benefits to wildlife. Even without management to encourage basal hollows we suggest that managers plan for the recruitment of trees that are destined to become legacies. This will require their protection over multiple cutting cycles. We expect that new silvicultural methods will be required to prescribe the process of identifying, culturing, and protecting residual legacy trees. Although we do not believe that any one tree will protect a species, we do believe that the cumulative effects of the retention, and recruitment, of legacy and residual trees in commercial forest lands will yield important benefits to vertebrate wildlife and other species of plants and animals that are associated with biological legacies.

The results of our study beg us to consider habitat at a spatial scale that is smaller than that of habitat patches or remnant stands; we conclude that *individual trees* can have very important values to wildlife. More research would be helpful, however, to specify the level of individual tree retention required to maintain biodiversity in managed lands (Lindenmayer and Franklin, 1997). It would help to know, for example, whether the fitness of individual species, and the diversity of wildlife communities, is greater in landscapes in which legacy trees are common compared to landscapes with very few legacy trees. It is possible that because legacy trees are rare—despite their apparent values to wildlife—that they do not affect wildlife diversity or productivity over large areas. It would also advance our knowledge to determine whether legacy trees in legacy-rich landscapes can function to maintain connectivity between protected stands of mature and old-growth forests. If so, the landscape context will be an important component of managing residual legacy trees and planning their recruitment across landscapes. For now, however, this study makes clear that protecting legacy trees will protect important habitat features that receive disproportionate use by many wildlife species. The protection and management of these trees can enhance wildlife conservation on lands where the opportunities to do so can be limited.

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Chapter 37

Population Trends of the Marbled Murrelet Projected From Demographic Analyses

Steven R. Beissinger[1]

Abstract: A demographic model of the Marbled Murrelet is developed to explore likely population trends and factors influencing them. The model was structured to use field data on juvenile ratios, collected near the end of the breeding season and corrected for date of census, to estimate fecundity. Survivorship was estimated for the murrelet based on comparative analyses of allometric relationships from 10 species of alcids. Juvenile ratios were generally low, and were higher for counts made from shore or in kelp beds (typically 10 percent) than conducted offshore (<5 percent). Annual survivorship was strongly related to body size in alcids. Survival for the Marbled Murrelet was predicted to be 0.845 and range to 0.90. Lambda, the expected annual growth rate of the population, was estimated for likely combinations of fecundity and survival, and indicated that under all combinations murrelet populations are expected to be declining. Based on the best data, rates of decline are predicted to be 4-6 percent per year, but the rate of decline could conceivably be twice as large. Studies in Alaska and British Columbia suggest population declines at 3-5 percent per year, supporting model predictions. Results are discussed in relation to the factors affecting murrelet population growth, and the use of juvenile ratios for monitoring murrelet populations.

Recovering a threatened or endangered species depends on determining its rate of population change and correcting the factors that limit population growth. Despite the important information on the biology and life history of the Marbled Murrelet (*Brachyramphus marmoratus*) that has been brought together in this volume, population trends for the murrelet remain elusive because little long term data are available. Christmas bird counts from five sites in Alaska found a 50 percent decline in the population over a 20 year period (Piatt and Naslund, this volume). Murrelet censuses conducted in Clayoquot Sound, British Columbia 10 years apart found a 40 percent decline in the population (Kelson and others, in press). Comparison of historic and current data suggests that the murrelet has disappeared or become very rare in large portions of its nesting range in California, Oregon, and Washington (Carter and Morrison 1992). But current population trends in the Pacific Northwest remain unknown.

Demographic modeling can give indications of likely population trends and play an important role in the conservation of the Marbled Murrelet. Simple demographic models based on estimates of annual survival and fecundity can be used to determine the rate of decline or increase of a species. They can also help focus attention on critical demographic information that needs to be gathered for future studies. Sensitivity analyses, where demographic values are altered to see the effect on population growth, can indicate which components of the life history are most likely to affect population growth and where the potential for management may be greatest.

Unfortunately, only a little is known about the demography of the murrelet. There are no estimates of survivorship for birds of any age. Reproduction is slightly better understood. Clutch size is known to be one egg, and a substantial proportion of nests are known to fail (Nelson and Hamer, this volume b). However, neither the age of first breeding nor the proportion of adults that breed is known. The ratio of young-of-the-year (hereafter juveniles) to after-hatch-year birds (subadults and adults) has been monitored at-sea and is often very low (e.g., Ralph and Long, this volume).

This paper represents an initial attempt to model the demography of the Marbled Murrelet to explore likely population trends. Although few data are available, there is enough reproductive information from murrelets to use, in conjunction with predictions of survivorship derived from analyses of past studies of alcids, to yield crude estimates of the rate and direction of change of the murrelet population.

Model Structure

The model was structured to take advantage of the one population parameter that could be best estimated from field data - fecundity. In the absence of detailed data, the simplest way to model the murrelet population is based on three life stages: adults (birds that are breeding age or older), subadults (birds that are greater than one year old but younger than the age of first breeding) and juveniles (fledged young that have reached the ocean but have not yet survived their first year of life). The latter stage takes particular advantage of one of two estimates of productivity available from field data - namely the ratio of young to after-hatch-year birds surveyed at sea. The virtue of this scheme - simplicity - is also its weakness. Undoubtedly there may be age variation among the demographic rates of murrelets, as there is with other seabirds (Hudson 1985, Nur 1993, Wooller and others 1992). But without any specific information on the age structure of vital rates, assigning age structure to them would be arbitrary. For the moment, simplicity has its virtue.

The simplified population life cycle given in *figure 1* is based on post-breeding season censuses with a projection interval of one year (Caswell 1989, Noon and Sauer 1992) and is typical for long-lived monogamous birds (McDonald and Caswell 1993). The flow of events is (1) censuses are conducted at the end of the breeding season, (2) birds must then survive to the next breeding season, (3) all individuals are aged one year, (4) surviving adults then breed, and (5) post-breeding censuses are conducted again. Circles or nodes

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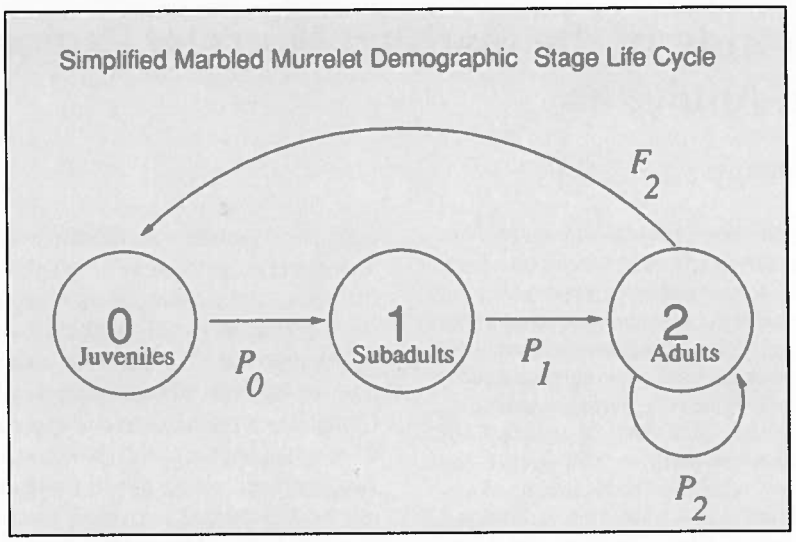

Figure 1—A simplified life cycle diagram for the Marbled Murrelet used in developing predictions of demographic trends: P_0 = Probablity of annual survival for fledglings that have reached the oceans; P_1 = Probablity of annual survival for subadults; P_2 = Probablity of annual survival for adults; and F_2 = annual fecundity, i.e., the number of young reaching the ocean per pair.

(Caswell 1989, McDonald and Caswell 1993) represent the stage classes: juveniles (0), subadults (1), and adults (2). P_0 is the probability of annual survival for fledglings that have reached the ocean. P_1 is the annual survivorship of subadults. Note that this stage may take several years for birds to mature and additional nodes would need to be added for each year that the age of first breeding exceeded 2 years old. The annual rate of adult survival is given by P_2. By definition, only adults breed and their average annual fecundity (i.e., the number of young reaching the ocean per pair) is given by F_2.

I explored only the simplest deterministic version of the model because no data yet exist on the magnitude of fluctuations of demographic characteristics from year to year. The model assumed: (1) survivorship and fecundity would change little from year to year; (2) populations were near a stable age structure; (3) a 1:1 sex ratio, supported by Sealy (1975a); (4) no density dependence; and (5) no senescence occurs and adult birds have no maximum life span. Such assumptions, although sometimes violated to varying extents in real populations, are typical for models of this nature (Lande 1988, Noon and Biles 1990). Usually such models are constructed only for females, since it is often difficult to know much about male fecundity. Thus, all rates needed for *figure 1* were expressed on a per female basis. Since there are little data available for murrelets, the model was evaluated for a range of feasible demographic values.

Methods

Survivorship estimates were derived from the literature, because there have been no studies of individually-marked murrelets. A comparative analysis of survivorship of auks was conducted by Nadav Nur (1993). Allometric relationships and multiple regression models between body size (32-8000 g), reproductive rate (which is clutch size [1–2 eggs] times brood number [1–2 broods per year]), and annual survival were developed for 10 species of Alcidae. Estimates of annual survival for adult murrelets were then made assuming an adult body size of 222 g (Sealy 1975a) and a clutch size of 1 egg. Estimates of annual survival for juveniles and subadults were assumed to be proportional to adult survival as revealed from the literature survey of other seabird species.

Fecundity values indicate the average number of female young produced annually by a female that has reached or exceeded the age of first breeding. The only murrelet demographic data that I have found pertains to the reproductive potential of the species: ratios of juveniles to after-hatch-year birds (adults and subadults) in the ocean (hereafter called the "juvenile ratio"), and an estimate of nesting success (the number of young produced per nesting pair). Information on nesting success was derived from Nelson and Hamer (this volume b).

Arguably the best data on reproductive potential are ratios of juveniles from at-sea surveys. If measured at the end of the breeding season, these ratios act like a "snapshot" census of recruitment rates because they implicitly incorporate all of the parameters needed to estimate fecundity: clutch size, the proportion of nests fledging young, the proportion of birds nesting, the number of nesting attempts per year, and the survivorship of fledglings to the sea until the time of census. Because this "snapshot" is taken immediately near the end of the breeding season, a

post-breeding population model was used. Similar ratios have been used to examine population trends in a variety of other wildlife studies (Hanson 1963, Lambeck 1990, Paulik and Robson 1969, Roseberry 1974).

At-sea surveys should be conducted before subadults and adults begin to molt into winter plumage and become difficult to distinguish from young-of-the-year (Carter and Stein, this volume). In most years, molting adults and subadults are first detected in mid- to late August (Carter and Stein, this volume; Ralph and Long, this volume). Therefore, I used survey data collected on or before 16 August, and pooled results for two week periods to yield reliable sample sizes. However, fledging of young can occasionally occur until late September (Hamer and Nelson, this volume a). When the at-sea surveys were conducted, it is likely that some young had not yet fledged (and thus would not be detected), but most adults were censused since they were in the ocean gathering food to feed young. Therefore, this ratio will tend to underestimate recruitment. To correct for this problem, I used the cumulative frequency distribution for estimates of "known" fledging dates for all nests or young found throughout the range (Hamer and Nelson, this volume a). From this distribution, I determined what proportion of young would have fledged by the end-point of the census date and then adjusted the juvenile ratio upwards by this factor.

There is one problem with using juvenile ratios to estimate fecundity. Fecundity is the number of female young per *adult female* produced annually. But during the censuses, *subadults* can not be distinguished from adults that are capable of breeding. Therefore, just using the ratio of juveniles to after-hatch-year birds from the censuses will tend to underestimate fecundity because the proportion of adults will be overestimated. This can be seen by conducting a deterministic projection of a population for 25 years and looking at the proportion of the population that fledglings comprise. Just using the value from the ratio usually results in a lower ratio of young-of-the-year birds to older birds than expected. Fortunately, the ratio can be corrected by increasing it incrementally until the population projection yields the proper starting ratio of juveniles to older birds.

Alcids typically exhibit delayed ages of first breeding (Croxall and Gaston 1988, Hudson 1985). One of the earliest recorded ages of first breeding is for Cassin's Auklet (*Ptychoramphus aleuticus*) where some birds begin at 2 years but most start at 3 years of age (Croxall and Gaston 1988). Hudson (1985) estimated 5 years in general for Atlantic alcids. The age of first breeding of individuals, however, ranged between 3 and 15 years (Harris and others 1994). Given its small body size, it is unlikely that the murrelet would require 5 years to reach sexual maturity, although it could require longer to obtain a nest site if sites were limiting. On the other hand, nest sites were probably much more abundant historically than they are today as a result of deforestation. Thus, in comparison to most other seabirds, which nest colonially on islands where obtaining a breeding site can sometimes be difficult (Hudson 1985), it seems likely that the Marbled Murrelet would have a young, rather than old, age of first breeding. I suspect that an age of first breeding would be 3 years, but explored ages from 2 to 5 in the model.

Once demographic traits were selected, values were used to calculate lambda (the expected annual growth rate of the population) and the stable stage distribution. Populations decline when lambda is less than 1 and increase when lambda exceeds 1. The stable stage distribution is the proportion of the total population that is comprised of each stage class and can be used to yield an expected juvenile ratio. Lambda and the proportion of juveniles in the stable age distribution were calculated: (1) analytically by constructing Leslie matrices and solving for the dominant eigenvalue and right eigenvector (Caswell 1989) using MATLAB (1992); and (2) numerically using spreadsheets to project population changes over 25 years (Burgman and others 1993). I used these same methods to explore what levels of adult survival and fecundity are required to yield estimates of lambda equal to 1 for different ages of first breeding and the juvenile ratios that these combinations would produce. A sensitivity analysis was conducted by determining the partial derivative of lambda with respect to each element in the Leslie matrix (Caswell 1989, McDonald and Caswell 1993).

Results

Estimating Fecundity

Reproduction in the marbled murrelet appears to be highly asynchronous. The cumulative frequency distribution for estimated dates of fledging throughout the range of the murrelet shows a regular increase during the breeding season (*fig. 2*). Fledging has occurred as early as the first week in June and very rarely as late as September, although 94 percent of the nests had fledged by the end of August. Fledging finished by the end of August in Alaska, British Columbia, and Washington, but in Oregon and California, it extended into September (see fig. 3 in Hamer and Nelson, this volume a). A linear model fit the data well, especially through the middle portions of the range of fledging dates (*fig. 2*). This model was used to estimate the cumulative proportion of nests that had fledged to adjust juvenile ratios for differences in the date of surveys.

Table 1 summarizes the ratio of juveniles for different localities, survey periods, and years for surveys made from shore or from a boat cruising only through kelp beds, which juveniles appear to frequent preferentially (Sealy 1975a). Similar data are shown for the juvenile ratio from boat surveys at sea (*table 2*). Several trends are evident. First, the proportion of juveniles encountered was much greater near shore (<800 m from shore) and on kelp bed surveys (*table 1*), than on boat surveys (*table 2*) of near shore (500-800 m) and distant waters (from 1400 m up to 5 km off shore in some cases). All at-sea surveys had adjusted ratios of juveniles of less than 5 percent, while onshore surveys typically had adjusted ratios of 9–16 percent juveniles. Juveniles were

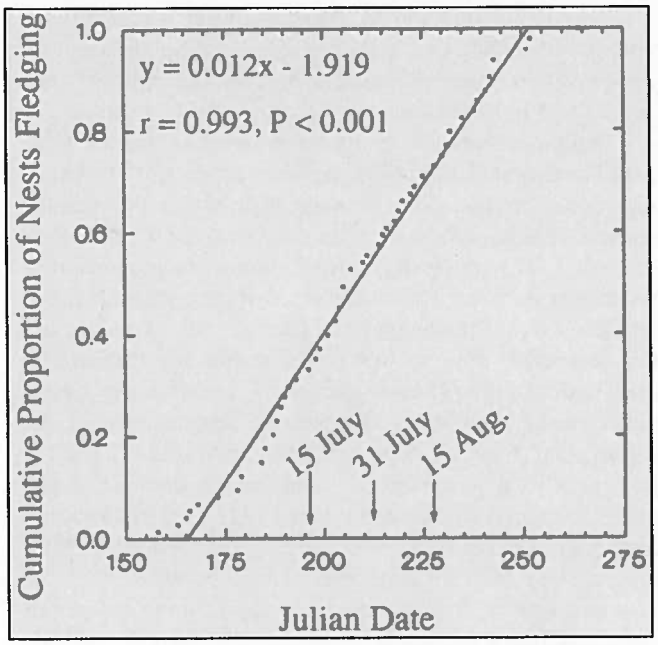

Figure 2—The cumulative probability distribution function for fledging dates of 74 Marbled Murrelet nests. Results of a linear regression of Julian date (x) on the cumulative proportion of nests that fledged (y) was fit to data and are given. No probability value can be calculated for the regression because cumulative fledging values are not independent. Data are from Hamer and Nelson (this volume a). Dates shown refer to the end point of censuses used to adjust the juvenile ratio.

rarely seen beyond 1 km offshore, whereas adults have frequently been seen up 3 km off shore and were still encountered up to 5 km (Ralph and Miller, this volume; Strong, pers. comm.). A good example of this effect is from studies in Clayoquot Sound, British Columbia (*tables 1* and *2*). Surveys through kelp beds where juveniles were known to forage found juvenile ratios 3–4 times greater than total area counts (surveys of all individuals in the sound). Thus, it seems likely that onshore surveys will overestimate the juvenile ratio, and at-sea surveys will underestimate them unless the at-sea surveys include some transects close to shore or through kelp beds.

Second, the juvenile ratio increased during the breeding season in every case at locations with repeated surveys (*tables 1 and 2*). This would be expected if nests in a population were asynchronously fledging young (*fig. 2*), and juveniles, subadults and adults remained in the general vicinity so that populations were being surveyed. The universal increase in juvenile ratios during the breeding season indicates that juvenile ratios may be useful tools for tracking productivity of a population. Third, sequential surveys often yielded similar juvenile ratios after the percentage of juveniles observed was adjusted for different survey dates using the linear model in *figure 2*. The closest values generally occurred for surveys conducted in late July and early August (*tables 1 and 2*). These adjusted ratios differed by about 3 percent or less, in 6 out of 7 instances. Thus, juvenile ratios appear to be sensitive to seasonal change, yet provide repeatable measures for fecundity estimates.

Table 1—Surveys of the ratios of juveniles to after-hatch-year birds (adults and subadults) for Marbled Murrelets conducted during the breeding season along shorelines or from boats cruising only along kelp beds. The percentage of juveniles (Pct. juv.) was adjusted for the timing of the survey (survey period) by using the cumulative frequency of fledging dates (fig. 2) to estimate an adjusted percentage of juveniles (Adj. pct. juv.) for the end of the nesting season

Region	Year	Survey period	*n*	Survey results: Pct. juv.	Survey results: Adj. pct. juv.	Source
British Columbia	1993	1–15 July	206	7.3	16.9	Manley and Kelson
		16–31 July	157	8.9	14.2	(pers. comm.)
Central Oregon	1988	16–31 July	107	2.8	4.5	Nelson
		1–15 Aug.	90	7.8	9.7	(pers. comm.)
	1989	16–31 July	112	5.4	8.6	
		1–15 Aug.	101	7.9	9.8	
	1990	1–15 July	555	0.4	0.9	
		16–31 July	200	7.0	11.2	
		1–15 Aug.	58	8.6	10.6	
	1991	1–15 July	391	1.3	3.0	
		16–31 July	486	9.9	15.8	
		1–15 Aug.	319	11.6	14.4	

Table 2—Surveys of the ratios of juveniles to after-hatch-year birds (adults and subadults) for Marbled Murrelets during the breeding season conducted from boats cruising at a variety of distances from shore. The percentage of juveniles (Pct. juv.) was adjusted for the timing of the survey (survey period) by using the cumulative frequency of fledging dates (fig. 2) to estimate an adjusted percentage of juveniles (Adj. pct. juv.) for the end of the nesting season

Region	Year	Survey period	*n*	Survey results		Source
				Pct. juv.	Adj. pct. juv.	
British Columbia	1993	16 Aug.	2732	4.0	4.9	Manley and Kelson (pers. comm.)
Central Oregon	1992	1–15 July	1609	0.1	0.2	Strong (pers. comm.)
		16–31 July	902	0.6	1.0	
		1–15 Aug.	1032	3.3	4.1	
Northern California	1993	15–31 July	355	1.4	2.2	Ralph (pers. comm.)
		15–30 Aug.	192	2.1	2.1	

The adjusted ratios of young-of-the-year murrelets to after-hatch-year birds were generally low, although there was considerable variation among juvenile ratios (*tables 1 and 2*). The most reliable ratios for estimating murrelet fecundity would come from at-sea surveys which covered long distances (>20 km) or large areas and surveyed close to shore (≤ 500 m) as well as farther away in order to have a better chance of encountering clumps or groups of juveniles. To the best of my knowledge, only two data sets fulfill both requirements - total area counts in Clayoquot Sound, British Columbia and surveys off the coast of central Oregon (*table 2*). Both studies had seasonally adjusted juvenile ratios around 4–5 percent, so I chose to use 5 percent as a realistic estimate of fecundity. Although Ralph and Long's (this volume) surveys indicate that juvenile ratios may be as low as 2 percent, their transects did not consistently extend closer than 800 m from shore and may have underestimated the true ratio. Likewise, the 15 percent ratios from onshore counts appear to greatly overestimate the proportion of juveniles because the vast majority of adults would have been too far from shore to be detected (Ralph and Miller, this volume). However, onshore counts do suggest that the 5 percent estimate of fecundity could be too low if at-sea surveys had missed many juveniles. Thus, I also evaluated optimistic estimates of adjusted juvenile ratios of 10 percent, twice the realistic value and similar to corrected nesting success derived below.

Fecundity might also be estimated from studies of nesting success, but this is more difficult to do for the murrelet. A total of 22 nests have been found in the Pacific Northwest—see table 2 of the study by Nelson and Hamer (this volume b). Only 36 percent of the murrelets successfully fledged young. This would yield an estimate of 0.36 young produced per nesting pair (since murrelets can fledge only 1 young), or 0.18 female young per nesting female, assuming half of the young fledging would be males based on the sex ratio found by Sealy (1975a).

This value overestimates fecundity for two reasons. First, many nests were found after the young had hatched. This would greatly overestimate overall nesting success because murrelet nests often fail (>50 percent) in the egg or early stages of chick-rearing before they are likely to be detected—see table 3 of the study by Nelson and Hamer (this volume b). The true number of female chicks fledging per female may be closer to 0.15. Second, it is unlikely that all females would attempt to nest every year and a significant proportion of the population (5–16 percent) may be nonbreeders (Hudson 1985). Third, the estimate of fecundity for the post-breeding model assumes that the young have safely reached the ocean. The long flight from the nest to the ocean can be expected to be hazardous for nestlings as exemplified by grounded young birds that have been found (Carter and Erickson 1992, Rodway and others 1992). Thus, to arrive at a fecundity value, the true number of female young per nesting female (0.15) would have to be corrected by multiplying it by: (1) the estimated proportion of adult birds nesting (averaged from the estimates of Hudson cited above to yield 0.9); (2) the proportion of young that survive from fledging to until the time of census (anybody's guess, but 0.9 might be a reasonable estimate); and (3) the number of nesting attempts per pair per year which is assumed to be 1 (Hamer and Nelson, this volume a). This would result in a fecundity value around 0.12, similar to average estimates from onshore juvenile ratios (*table 1*).

Estimating Survivorship

Nur (1993) found that the annual probability of survival for adults (P_2) was positively related to body size for 10 species of alcids. Similar data are presented in *figure 1* of De Santo and Nelson (this volume). Adult survivorship ranged from about 0.75–0.77 for small-bodied Least Auklets (*Aethia pusilla*) and Ancient Murrelets (*Synthliboramphus antiquus*) to 0.91–0.94 for large-bodied Atlantic Puffins (*Fratercula arctica*), and Common and Thick-billed murres (*Uria aalge* and *U. lomuia*). Nur also found that adult survivorship was negatively related to annual reproductive effort (clutch size times broods per year) after controlling for the effects of body size. Together these two variables accounted for 72 percent of the variation in annual survivorship among the 10 species. Nur then derived a multiple regression model to

estimate an annual survival rate of alcids on the basis of body mass and clutch size. This resulted in an estimate of 0.845 for the Marbled Murrelet. Two standard errors of the estimate for the prediction, encompassing 95% of the likely values for typical murrelet survivorship (Steel and Torrie 1960), fell between 0.811 and 0.880. I used 0.85 for adult survival and also explored the possibility that the annual probability of survival might be as high as 0.90, a value typical for larger Atlantic alcids (Hudson 1985). Values of survivorship as low as 0.81 were not considered because they would have required extremely high fecundity values for populations to persist.

Annual survival for juveniles and subadults of most bird species is usually less than adult survival. Survival for juvenile and subadult alcids is not as well known as adult survival. These values are hard to estimate and can often be underestimated due to emigration. Frequently these values are simply given as the probability of surviving to the age of first breeding. Hudson (1985) gives a range for the probability of surviving to first breeding of 13-53 percent, with a mean close to 30 percent, but this is for large-bodied birds with late ages of first breeding. Nur (1993) suggested that survival of juveniles and subadults could be considered to be proportional to adult survival. Using data from Hudson (1985) for five populations of murres, Nur calculated that juveniles survive their first year of life at about 70 percent the rate of adult survival, first year subadults survived slightly less well than adults (0.888), and that after 2 years of age survivorship was approximately equal to adult survivorship. I used these proportions for juvenile and subadult survival estimates in the model.

Predicted Murrelet Population Trends

Figure 3 shows the possible combinations of adult survival and fecundity for populations experiencing no growth (lambda equal to 1) for different possible ages of first breeding. Combinations above the lambda isobar result in increasing populations and combinations below the lambda isobar result in declining populations. For the Marbled Murrelet, fecundity may not exceed 0.5 because females are thought to lay only 1 egg per year and, on average, only half of the young that fledge would be females. Note that the lambda isobars for different ages of first breeding converge as survivorship increases and fecundity declines. As fecundity values drop below 0.20 and survivorship rises above 0.90, our assumption of the age of first breeding will have little effect on the predicted population trends.

Likely combinations of adult survivorship and fecundity are shown for the murrelet in the box on *figure 3*. These estimates are well below the lambda isobars, and indicate that murrelet populations are likely to be declining. Given an annual survivorship of 0.85–0.90, murrelet fecundity would have to range from 0.20 to 0.46 to result in stable populations for different ages of first breeding. Such values would result in adjusted juvenile ratios of 15 percent to 22 percent, well below the values currently observed. Fecundity at these levels

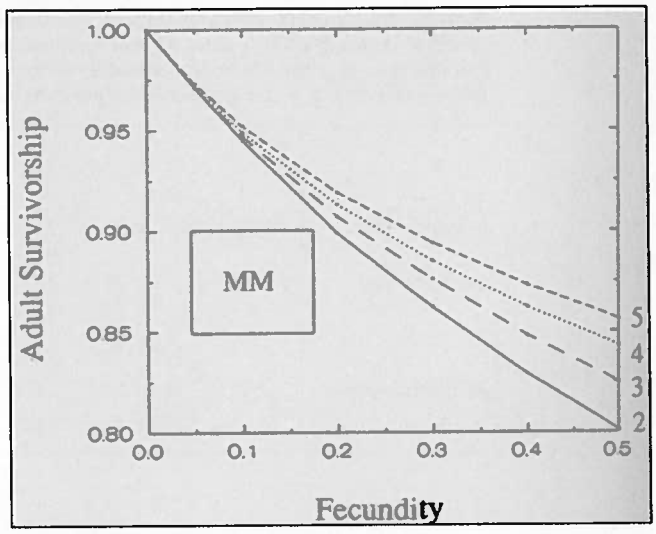

Figure 3—Sets of isobars where lambda equals 1 (i.e. populations are neither increasing or decreasing) for different combinations of fecundity and annual survivorship. Above the isobars populations should increase and below the isobars populations should decline. Isobars are shown for ages of first breeding from 2 to 5 years. Survivorship of juveniles and subadults was set at 0.700 and 0.888 times adult survivorship, respectively. Likely Marbled Murrelet values for survivorship and fecundity are delimited within the box. See text for details.

is typical for other auks, which generally experience nesting success in excess of 70–80 percent (Hudson 1985, Nur 1993). For example, if murrelets experienced nesting success similar to other seabirds (75 percent), nests were attempted by 90 percent of the potential breeding population each year, and 90 percent of the young survived to reach the ocean (i.e., fecundity = 0.30), then murrelet populations would grow when adult survivorship exceeded 0.862–0.894. These values fall well within the expected range of survivorship values. Unfortunately, even the most favorable estimate of fecundity, conceivable from current field data for the Marbled Murrelet (i.e., uncorrected nesting success = 36 percent), would require survivorship values to exceed 0.908–0.924 for populations to grow. Such survivorship values may occur during some years, but seem likely to be higher than the long term average expected for this species (Nur 1993).

The above analyses suggest a predicted rate of decline for the murrelet population that is substantial. Using the estimates of survival and fecundity obtained above, likely combinations of demographic rates and their resulting annual change in population size are compiled (*table 3*). It appears that murrelet populations are likely to be declining 2-4 percent per year and it is conceivable that the decline may even be 2-3 times larger.

A sensitivity analysis (*table 4*) indicated that estimates of lambda were most strongly affected by adult survivorship. Changes in fecundity had about half the effect on lambda that changes in adult survivorship had. Neither juvenile survivorship nor adult survivorship had strong effects on lambda.

Table 3—Predicted rates of annual change for Marbled Murrelet populations based on likely combinations of demographic rates based on three different scenarios of juvenile recruitment and nesting success measured in the field, and two levels of adult survival from comparative analysis. Lambda, the expected growth rate of the population, was virtually unaffected by changes in age of first breeding

Fecundity scenario	Resulting fecundity	Adult survival	Lambda	Annual pct change
At-sea juvenile ratio (5 pct)	0.06	0.85	0.88	−12
	0.06	0.90	0.93	−7
On-shore juvenile ratio (10 pct) or	0.12	0.85	0.91	−9
corrected nesting success (24 pct)	0.12	0.90	0.96	−4
Uncorrected nesting success (36 pct)	0.18	0.85	0.94	−6
	0.18	0.90	0.98	−2

Table 4—Sensitivity of lambda to changes in the Leslie matrix elements for the Marbled Murrelet based on the three different fecundity scenarios for an age of first breeding of 3 years. See Table 3 *for values used in each of the fecundity scenarios*

Parameter	At-sea juvenile ratio	On-shore juvenile ratio	Uncorrected nesting success
Fecundity	0.487	0.544	0.444
Juvenile survival	0.084	0.047	0.114
Subadult survival	0.066	0.037	0.090
Adult survival	0.890	0.937	0.854

Discussion

Model Parameter Estimates

There are a number of sources of uncertainty in the parameter estimates that may have affected model outcomes. Lambda was most sensitive to changes in adult survivorship (*table 4*), which is typical for potentially long-lived birds like the murrelet. Estimates of survival have the greatest uncertainty, since they were not derived from field data but instead were based on comparative analyses of allometric models. Nevertheless, there are reasons for confidence in the estimates evaluated. Survivorship is often strongly related to both body size and reproductive effort in birds (e.g., Gaillard and others 1989, Saether 1988), and this trend was also strong in the Alcidae (Nur 1993). The range of annual survivorship values for adults evaluated in the model (0.85-0.90) included more than two standard errors for the upper bound of the prediction from the regression, which should encompass > 95 percent of the variation in potential mean estimates. Higher annual survival rates (0.90-0.94) are typical only for three species of auks with body masses exceeding 600 g (Nur 1993; De Santo and Nelson, this volume), three times the size of the murrelet. Survivorship ranges from 0.75-0.88 for seven alcid species with medium and small body sizes (< 600 g); only the Atlantic Puffin had annual survival rates routinely above 0.90.

It is likely that annual survivorship for Marbled Murrelets will be among the upper range of values evaluated in this model (e.g., 0.87-0.90), because the murrelet's inherently low reproductive rate (1 egg per nesting attempt) requires high survivorship for populations to grow. On the other hand, because the murrelet's unusual life history strategy of nesting in old growth forests often far from the sea, it probably faces higher mortality risks than other seabirds. Field studies to determine survival rates are needed, and are becoming more feasible as marking and telemetry techniques are perfected for this bird (Quinlan and Hughes 1992; Priest and Burns, pers. comm.).

All measures of fecundity from field data for the Marbled Murrelet appear to be low. Arguably the most complete measures of fecundity were derived from juvenile ratios based on extensive at-sea censuses corrected for the date of census in relation to the timing of fledging (*table 2, fig. 2*). Extensive at-sea censuses conducted recently have universally produced low percentages of juvenile birds (*table 2*). Such low ratios indicate poor reproductive success that could be due to high nest failure rates from predation (Nelson and Hamer, this volume b), or a low proportion of adults attempting to breed, perhaps because they are unable to find suitable nest sites. Some portion of the low reproductive success could have been due to El Niño effects on food supplies. Although there is ample evidence that El Niño affects nesting success of

seabirds that nest and forage offshore (Ainley and Boekelheide 1990), there is no evidence that fish populations within 2 km of shore, which murrelets mostly utilize, are affected.

Some uncertainty in the measure of fecundity derived from juvenile ratios is associated with the timing of censuses. To convert juvenile ratios to a fecundity estimate, ratios had to be increased to account for young fledging after the date of census by using the cumulative frequency distribution for fledged nests with known dates (*fig. 2*). This distribution was comprised of nests from Alaska to California, because sample size was not large enough to partition nests among portions of the murrelet's range. Variation in the fledging dates exists between Alaska, British Columbia, and the Pacific Northwest (Hamer and Nelson, this volume a), although there is much overlap. Future research might employ bootstrapping techniques (Crowley 1992) to calculate an error estimate for the cumulative frequency by date, as one way to determine the inherent variability of the correction factor.

Other approaches to estimating fecundity also yielded low values, but are likely to have too many biases to be useful yet. Juvenile ratios measured only using on-shore counts tended to be higher than off-shore counts (*table 2*). But fecundity will be overestimated by using only on-shore counts because they undersample adults. Estimates of fecundity from nesting success are likely to be less useful than juvenile ratios because they must be corrected for many factors that are difficult to measure (such as the proportion of adults nesting, fledgling survival to the ocean, and renesting frequencies). Furthermore, for the foreseeable future, fecundity estimates based on nesting success are likely to depend on small sample sizes because of the difficulty in finding nests.

Predicted Rates of Decline of Murrelet Populations

All scenarios of the demographic model predicted that murrelet populations are likely to be declining (*table 3*). The estimated rate of decline varied from 2-12 percent per year, depending on the parameter estimates used. Based on the discussion of the parameters above, the most likely rate of decline would be based on fecundity values from juvenile ratios intermediate between offshore juvenile ratios (which may underestimate reproductive success) and nesting success (which certainly overestimates fecundity), used with an estimate of survival close to 0.90. These intermediate fecundity values would suggest a rate of decline around 4 percent per year.

A predicted decline of 4 percent per year is in close agreement with population declines documented in two field studies of murrelets. A 50 percent decline in murrelets detected over 20 years of Christmas Bird Counts in Alaska (Piatt and Naslund, this volume), despite an increase in observer effort during this period, would represent a 3.4 percent average annual decline. Similarly, the 40 percent decline in the Clayoquot Sound murrelet population in British Columbia over 10 years (Kelson and others, in press) would average to a 5 percent annual decline. These studies are based on either periodic but intensive sampling during few annual periods (British Columbia), or low intensity but extensive sampling every year (Alaska). Despite, the sampling shortcomings inherent in these two studies, the population trends that they have documented are in good agreement with trends predicted by the model in this paper.

Model results suggest that murrelet populations may even be declining at greater rates (*table 3*). A 7 percent annual decline would be predicted from juvenile ratios based on offshore counts in conjunction with high survival estimates. This value is certainly a possibility for Pacific Northwest populations of murrelets, which exhibit low offshore juvenile ratios. It is even conceivable that murrelet populations could be declining at 9-12 percent per year (*table 3*). However, this rate of decline is so high that it seems unlikely to go unnoticed by field researchers. Furthermore, it is based on the most pessimistic combinations of fecundity and survivorship. I interpret the model predictions, in conjunction with the field evidence, to suggest that murrelet populations are likely to be declining at least 4 percent per year and perhaps as much as 7 percent per year.

Use of Juvenile Ratios for Murrelet Conservation

Conservation efforts for Marbled Murrelets have been hampered in part because of a lack of reliable biological information. Demographic characteristics have been especially difficult to measure because nests are very hard to find and monitor, murrelets fly long distances both over the ocean and across land, and the birds are difficult to capture, mark, and telemeter (Quinlan and Hughes 1992). Juvenile ratios provide one estimator of murrelet population health that may be reasonably measured in the field.

Juvenile ratios have great potential as estimators of productivity. It is easy to obtain large sample sizes of juvenile ratios compared to the difficulty of finding and monitoring nests. It will be many years before enough nests are found to yield sample sizes sufficient for accurate estimates of nesting success. Additional information needed to convert nesting success into annual fecundity (the proportion of birds that nest and the number of attempts per year) will perhaps be even more difficult to obtain. Juvenile ratios implicitly incorporate these factors. Research will need to determine optimal protocols for sampling juvenile ratios at-sea that take into account apparent differences in habitat use by juveniles and adults (*tables 1* and *2*) as well as other factors that could bias these ratios.

Changes in juvenile ratios could be a useful tool to understand factors limiting murrelet population growth. Juvenile ratios could be monitored in a regional areas (e.g., over 30-50 kms of shoreline) and compared to landscape characteristics to determine the effects of forest management and other land use practices. Juvenile ratios may also be useful for monitoring murrelet population trends. However, changes in juvenile ratios can be caused either by changes in recruitment (increased nesting success results in greater proportions of juveniles) or changes in adult survivorship (decreased survivorship results in greater proportions of juveniles). Whether juvenile ratios change due to improved

recruitment or decreased adult survivorship should be apparent by examining year-to-year changes in population size. Increases in juvenile ratios coupled with increased population size should indicate increased productivity. However, if coupled with decreased population size, increased juvenile ratios would indicate decreased adult survivorship.

For making sound conservation decisions based on population trends and demography, there is no substitute for good field data based on direct estimates of population change, survival and fecundity. For the Marbled Murrelet, such information is likely to remain scarce. Future research should explore the strengths and weakness of using the ratio of juveniles to after-hatch-year birds as a proxy for direct demographic measurements.

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