AN ABSTRACT OF THE THESIS OF

Blake A. Barbaree for the degree of Master of Science in Wildlife Science presented on April 15, 2011.

Title: NESTING SEASON ECOLOGY OF MARBLED MURRELETS AT A REMOTE MAINLAND FJORD IN SOUTHEAST ALASKA

Abstract approved:

_____________________________________________________________________

Bruce D. Dugger

This thesis focuses on the nesting ecology and marine space use of Marbled Murrelets (Brachyramphus marmoratus) during the 2007 and 2008 nesting seasons in and around Port Snettisham, a remote mainland fjord in Southeast Alaska. Marbled Murrelets (murrelets) are a declining species throughout most of their range, and their conservation is a challenging endeavor because they rely on relatively large expanses of terrestrial habitat for nesting and marine habitat for food. Murrelets are especially difficult to study because they place their nests at variable and often considerable distance from the sea in largely inaccessible locations; consequently, we know relatively little about their breeding ecology and overall life history compared to other seabirds. I used radio-telemetry to gather data on reproduction, behavior, and at-sea locations of murrelets. Herein, I describe individual and population-level marine space use, identify nesting habitat, estimate reproductive success, and characterize patterns of nest visits. Mean marine home range size for adult murrelets was significantly larger in 2008 (158.6 ± 103.7 km²) than 2007 (97.8 ± 59.4 km²),
suggesting that foraging conditions were relatively poor in 2008. Similarly, mean commuting distance from at-sea location to nest sites was significantly longer in 2008 (20.0 ± 2.0 km) than 2007 (12.0 ± 0.9 km), and murrelets nesting further from the coast likely reduced their foraging ranges in 2008. Central foraging hot spots were identified throughout Port Snettisham and near Holkham Bay and Tracy Arm to the south. Boundaries of these hot spots can be used to guide management of commercial fishing and tourism, and designation of marine protected areas. I located 33 active nests in mostly inaccessible sites within forest and non-forest habitat, including visually confirmed nest sites on the branches of large conifer trees and on ledges of steep cliffs near water (e.g., waterfall, lake, river, or glacier). Widespread use of rock cliff and subalpine nesting habitats (≥ 48.5% of located nests) indicated that nesting habitat models in Southeast Alaska should include these types of habitats. Nests were located further inland (range 1.0 - 52.0 km) and at higher elevations (range 42 - 1100 m) than previously documented in Alaska, including two nest sites > 15 km east of the USA/Canada border in British Columbia, Canada. The nesting season was ca. 113 days long (25 May - 16 September), and four late-season re-nesting attempts were documented. Apparent fledge success, derived by inference from behavior of radio-tagged adults, was 17.6% (n = 6 of 34). The low reproductive success at Port Snettisham was similar to estimates from south of Alaska, and unexpected because the area has relatively high densities of murrelets and seemingly ideal conditions for nesting. This information is noteworthy to future conservation planning because it provides evidence that murrelet reproduction may be low even when conditions for
nesting are relatively good. Despite an adaptation to high adult survival, murrelet populations cannot sustain themselves with similarly low levels of reproduction. Based on my results future research should focus on monitoring regional population trends, identifying causes of nest failure, estimating adult survival rates, and identifying sources of adult mortality.
NESTING SEASON ECOLOGY OF MARBLED MURRELETS AT A REMOTE MAINLAND FJORD IN SOUTHEAST ALASKA

by
Blake A. Barbaree

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

_____________________________________________________________________

Blake A. Barbaree, Author
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Chapter 1

GENERAL INTRODUCTION

Blake A. Barbaree
INTRODUCTION

Knowledge of reproductive ecology is fundamental to guide proper management practices and thus long-term conservation for any species. For birds, knowledge regarding nesting ecology is often gathered without great difficulty because adults are spatially restricted to areas near stationary nest sites. Most birds nest in locations relatively accessible to humans leading to well-documented nesting habits (Potter 1915, Kendeigh 1942, Nice 1957, Lack 1966, 1968, Ricklefs 1969); however, species that commonly nest in locations inaccessible to humans typically have poorly understood nesting ecology, as well as population demographics and trends. When a focal species uses mostly inaccessible areas for nesting, designing suitable conservation strategies can be difficult. Baseline information on spatial and temporal aspects of reproductive ecology are especially important because this knowledge allows biologists to design monitoring and research methodologies while properly administering terrestrial and marine habitat use permits.

Seabird research is often more difficult than research on terrestrial species because of logistical challenges presented by the marine environment at temperate and polar latitudes, where seabirds tend to aggregate (Hunt and Schneider 1987, Steele 1991). Nevertheless, nesting and foraging habits during the breeding season have been well-documented for most seabirds because of high fidelity to colonial nesting areas and central-place foraging habits. Non-colonial seabird species are less common and generally have secretive, poorly understood nesting habits. The family Alcidae
consists of 23 extant species of seabirds inhabiting oceans in the Northern Hemisphere, some of which have presented considerable challenge to researchers (Nettleship and Evans 1985, Udvardy 1963). The Alcidae family includes the genus *Brachyramphus*, which consists entirely of non-colonial species (*B. brevirostris* or the Kittletz’s Murrelet, *B. marmoratus* or the Marbled Murrelet, and *B. perdix* or the Long-billed Murrelet) that nest in relatively inaccessible inland habitats (Hamer and Nelson 1995). All three species are thought to be currently declining (Konyukhov and Kitaysky 1995, Kissling et al. 2007, Lynch et al. 2009), but management plans are either non-existent or partially based on presumed demographic rates.

In the absence of easily observable reproductive activity, researchers must rely on non-conventional methods to estimate reproductive success, which is imperative for assessing population stability in birds (Erwin and Custer 1982). While these estimates include caveats, information on reproductive output is crucial for identifying sources of variation and annual trends in demographic rates. Two primary methods are commonly used to estimate Marbled Murrelet reproductive rates: observational, at-sea surveys of the ratio of juveniles to adults (*e.g.*, Kuletz and Kendall 1998, Speckman et al. 2000) and radio-marking adults to locate and monitor active nests (*e.g.*, Bradley et al. 2004, Peery et al. 2004). Non-conventional methods, such as behavior-based inference, have been used to describe nesting activity and success based on direct observations of passerine species (*e.g.*, Vickery et al. 1992, Gunn et al. 2000). Research using radio-telemetry can potentially allow behavior-based
inferences of nesting activity and success in areas where preferred nesting habitat is largely inaccessible, while also identifying nesting areas and at-sea locations.

The Marbled Murrelet (hereafter murrelet) was listed as threatened in California, Oregon, and Washington under the U.S. Endangered Species Act (USFWS 1992, 1997), and in British Columbia (Rodway 1990) in the early 1990s. Murrelets are thought to be declining over much of their range primarily due to loss of older-aged forest nesting habitat, mortality from oil spills and gill-net fishing, and reduced reproductive success from spatio-temporal changes in prey distribution or quality (Burger 2002, McShane et al. 2004, Norris et al. 2007). Only a few decades ago, few murrelet nests had been located and observed. Their breeding ecology was once considered the “enigma of the Pacific” (Guiguet 1956) until the first scientifically confirmed nest was discovered in 1974 (Binford et al. 1975). This discovery was widely considered one of the last scientifically described nest sites for an avian species breeding in North America. Because of the historically late discovery of murrelet nesting habitat and the challenging nature of conducting research in that habitat, development of conservation strategies lagged due to limited knowledge of species biology. Management plans in regions where the species is listed spurred a rapid increase in overall knowledge, monitoring efforts, and reliability of trend estimates; however, relatively little is known about murrelet biology in Alaska where the species is not listed under the U.S. Endangered Species Act and not afforded added protection and management.
Alaska supports the majority of the population of Marbled Murrelets, but numbers appear to have declined an estimated 71% since the early 1990s (Piatt et al. 2007). Specific causes for the decline are unknown. Southeast Alaska, in particular, is generally considered the center of abundance for the species, but the region has no comprehensive management plan and knowledge of Marbled Murrelet ecology is limited (Piatt and Ford 1993, Piatt and Naslund 1995, DeGange 1996). Southeast Alaska is characterized by relatively productive marine waters (Weingartner et al. 2009) and large expanses of undisturbed forest (Campbell et al. 2004), providing theoretically ideal conditions to support murrelet populations. Knowledge of potential factors limiting reproduction and survival in these conditions would help focus management activities and enhance species conservation range-wide.

*Brachyramphus* murrelets are unlike most seabird species in that their marine ecology is better understood than their reproductive ecology. However, little is known about how individual murrelets use space within the marine environment because at-sea research has been mostly observational (see reviews in McShane et al. 2004 and Piatt et al. 2007). Intense monitoring of radio-marked murrelets can provide information on at-sea foraging locations and extent of movements between foraging and nesting locations. Managers require this information to develop marine management and at-sea monitoring strategies for murrelets, in addition to estimating potential energy requirements needed to sustain local populations. Improving our
understanding of at-sea habits of murrelets is crucial considering that murrelet population declines are partially associated with changes in the marine environment.

In this study, I used radio-telemetry during the nesting season to describe murrelet marine habitat use, characterize nesting habitat, and monitor reproductive success. My primary objective was to reveal information essential for preparing future management plans, monitoring protocols, and research. In the second chapter of this thesis, I used at-sea locations of radio-marked murrelets to describe space use in the marine environment. Chapter 2 provides the first estimates of marine home ranges in Alaska, identifies foraging hot spots, and investigates factors influencing foraging locations of nesting murrelets. In chapter 3, I used radio-marked murrelets to locate inland nest sites, monitor nesting behavior, and estimate nest success. Chapter 3 provides the first extensive information on murrelet nesting ecology in Alaska and documents unique aspects of murrelet nesting ecology in the study area. In chapter 4, I use results from chapters 2 and 3 to offer general conclusions and management recommendations, and identify directions for future research. Appendices contain unique information about murrelet nesting behavior and marine space use. Appendix A and B describe murrelet nest visitation patterns during the incubation and chick-provisioning phases, and characterize brood patch development at the time of capture. Appendix C contains results from individual fixed kernel density analyses on at-sea locations and maps showing population-level use of the marine environment in and around Port Snettisham.
STUDY AREA

This study was conducted at Port Snettisham (PS; 57°58’N 133°53’W), a relatively large, deepwater fjord on the mainland side of Stephens Passage, approximately 40 km south of Juneau, Alaska (Fig. 1.1). PS is located 150 km (overwater distance) from the open ocean and is protected from Gulf of Alaska circulation patterns by Admiralty and Chichagof islands. Inside the fjord, strong tidal action mixes saltwater with glacially influenced freshwater originating from the Speel and Whiting river basins along with numerous other smaller surrounding watersheds. Besides a few small private holdings, most adjacent land is part of the Tongass National Forest (USDA Forest Service) with the Taku River basin and US-Canada border 20-35 km inland to the north and east, respectively. The PS watershed is bordered by Tracy Arm-Fords Terror Wilderness Area to the south and the Kootznoowoo Wilderness Area (most of Admiralty Island National Monument) lies directly across Stephens Passage to the west. Research was focused in PS, but the surrounding inland and marine areas depicted in Figures 1.1 and 1.2 were routinely surveyed and considered part of the study area.

The rugged topography of the PS watershed has resulted in a relatively pristine environment; the land is road-less, forests are un-harvested, and inland areas are protected from long-term windthrow disturbance, an important factor influencing terrestrial ecosystems in Southeast Alaska (Kramer et al. 2001). Generally, the study area contains homogeneous forest cover at lower elevations with steep slopes leading
to a rapid transition to treeless and alpine habitat at higher elevations. Recent and ongoing glaciation on the mainland has left higher elevations dominated by exposed granite bedrock (USGS 2008); thus, the vast majority of land cover in the study area is not forested and instead dominated by alpine, ice, or rock cliff cover types (Fig. 1.2). Lower elevations, mostly within river valleys and along the coastline of the fjord, are dominated by volcanic and other sedimentary materials that support increased primary production and structural diversity (Schoen and Dovichin 2007) leading to fragments of high density productive old-growth forest. Forested lowlands in Southeast Alaska, including the study area, are mostly a mixed-conifer forest type (Campbell et al. 2004). Dominate tree species are western hemlock (Tsuga heterophylla) and Sitka spruce (Picea sitchensis) and subdominants typically include Alaskan cedar (Callitropsis nootkatensis), western red cedar (Thuja plicata), mountain hemlock (T. mertensiana), red alder (Alnus rubra), and black cottonwood (Populus trichocarpa). Dominant shrub species include Sitka alder (Alnus crispa sinuate), Alaskan blueberry (Vaccinium alaskensis), devil’s club (Opopanax horridum), salmonberry (Ribes spectabilis), and currents (Ribes spp.).
Figure 1.1. Study area map for Marbled Murrelet radio-telemetry project in 2007 and 2008 based at Port Snettisham, Southeast Alaska.
Figure 1.2. Land cover map of the study area for Marbled Murrelet radio-telemetry project in 2007 and 2008 based at Port Snettisham, Southeast Alaska. GIS data and classification by Schoen and Dovichin (2007). POG represents productive old-growth forests of all volume classes (VCs).
LITERATURE CITED


Chapter 2

MARINE SPACE USE OF MARBLED MURRELETS AT A REMOTE MAINLAND FJORD SYSTEM IN SOUTHEAST ALASKA

Blake A. Barbaree
ABSTRACT

At-sea research on Marbled Murrelets (*Brachyramphus marmoratus*) has been dominated by observational surveys, thus knowledge of individual space use is limited. To quantify spatially unbiased metrics of marine space use, I re-located individual Marbled Murrelets (murrelets) at-sea using radio-telemetry during the 2007 and 2008 nesting seasons in and around Port Snettisham (PS), a remote mainland fjord in Southeast Alaska. Mean (± SD) home range size (127.4 ± 88.8 km²) varied among 72 individuals and was significantly larger on average (± SE) in 2008 (158.6 ± 17.6 km²) than 2007 (97.9 ± 9.8 km²). Mean home range size in both years at PS was smaller than similar estimates from regions south of Alaska where murrelet populations are undergoing well-documented population declines. I identified population-level central foraging hot spots throughout PS and near the mouth of Tracy Arm to the south. The largest and most consistently used hot spot was within the fjord confirming that PS is an important foraging area for murrelets during the nesting season. Mean commuting distance from at-sea location to nest sites was significantly longer in 2008 (20.0 ± 2.0 km) than 2007 (12.0 ± 0.9 km), and murrelets nesting further from the coast likely reduced their foraging ranges in 2008. Differences in home range size and commuting distances to nests suggest that the cost of reproduction were higher because marine conditions within the fjord were less favorable for murrelets in 2008 than 2007. However, most reproductive rates did not differ between years (see Chapter 3); suggesting that factors other than marine
foraging conditions may limit murrelet productivity at PS. Nonetheless, the close proximity of central foraging areas to nest sites characterizes PS, and the adjacent marine and terrestrial areas to the south, as providing near ideal conditions for nesting murrelets.

INTRODUCTION

Marine management strategies for seabirds are uncommon, especially for species whose size and habits limit information on space use and therefore marine habitat requirements. Space use metrics are indicative of how an animal responds to its environment and can reveal potential factors constraining movement (Ford and Krumme 1979). In particular, information on home range (Worton 1987) and preferred foraging locations (Irons 1998) during the nesting season can improve our understanding of costs associated with nesting, foraging strategies, and requirements for marine resources. Inconsistent focus and methodology of at-sea research has limited inferences and comparisons between and within species. Without broad knowledge of intra-species variation of marine space use, developing spatio-temporal aspects of marine management strategies for focal species will be challenging.

Estimates of home range size for breeding seabirds represent the constraints of central place foragers that must nest on land, yet forage at sea. Breeding seabird home ranges can be further limited by costs associated with flight, especially when wing-propelled diving behavior has led to energetically expensive flapping flight
(Pennycuick 1987). In theory, seabirds should respond to clumped and predictable food resources by selecting nest sites in close proximity to minimize foraging ranges (Wittenberger and Hunt 1985, Kotliar and Wiens 1990, Gibbs 1991). This strategy would minimize commuting time between foraging areas and nest sites, thereby increasing potential foraging time (Orians and Pearson 1979, Hunt et al. 1999). Variation in the location and frequency of favorable foraging areas relative to individual nest sites should create variation in space use metrics between and within seabird populations (McNab 1963). Home range size should be a good general indicator of food resources because food availability typically displays an inverse relationship to the extent of space use by animals (Schoener 1983).

Because food resources in the marine environment have patchy and hierarchical distributions (Russell et al. 1992), seabirds typically use space within the marine environment unevenly. Seabirds are therefore considered reliable and convenient indicators of marine productivity at most spatial scales (Cairns 1988, Croxall et al. 1999), and they are increasingly being used to identify areas of relatively high prey densities or hot spots (e.g., Cairns and Schneider 1990, Piatt et al. 2006, Suryan et al. 2006). Hot spots more generally represent areas of elevated energy transfer rates between trophic levels due to relatively high primary productivity. Although a variety of analytical methods are available to identify marine hot spots (see review in Nelson and Boots 2008), locating individually-marked seabirds at-sea is the only unbiased field method for identifying aggregations of marine predators and
consequently highly available forage resources that characterize central foraging areas (Adams et al. 2004, Piatt et al. 2006). Seabird telemetry research is also a versatile management tool for defining boundaries of fishing zones, ecologically important areas, and marine protected areas (Wilson et al. 2009).

When distances between seabird foraging and nesting habitats are highly variable, such as in Marbled Murrelets (*Brachyramphus marmoratus*; hereafter murrelets), some individuals fly great distances over land to reach potential foraging habitat (Whitworth et al. 2000, Bloxton and Raphael 2009), resulting in substantial energetic investment in commuting costs during the nesting season (Hull et al. 2001). Murrelets nest solitarily up to 88 km from the coast (Nelson and Hamer 1995, see Chapter 3), unlike most seabird species that nest on islands or coastal colonies. While factors driving murrelets to nest at varying distances inland are unknown, nesting further inland will increase travel-related costs to nesting adults and affect energy allocation to their nest (Ricklefs 1977, Ricklefs 1983, Eberl and Picman 1993). Nesting murrelets could adopt behavioral strategies to optimize foraging efficiency and compensate for increased commuting costs such as foraging closer to inland flyways (Peery et al. 2009), altering provisioning rates or payload size, or replenishing body reserves during the post-breeding period (Hull et al. 2001). Whether the increased commuting costs from nesting further from the coastline limits productivity is unknown. However, an energetic limitation might be evident if murrelets nesting
further from the coast have different foraging strategies than those nesting near the coast, particularly during years with less favorable foraging conditions.

In this study, I used radio-telemetry to locate individual murrelets at-sea and address several questions using metrics of murrelet marine space use. First, I estimated individual home range size and tested the hypothesis that home range size will differ by sex and breeding status. Second, I examined space use at the population level to identify foraging hot spots with enhanced food availability and significance as foraging habitat. Lastly, I tested the hypothesis that murrelets nesting further inland from the coast will mitigate commuting costs associated with increased travel over land by reducing the distance they travel over water to reach foraging areas.

METHODS

Capture and Radio-Telemetry

I used night lighting (Whitworth et al. 1997) to capture murrelets in or at the mouth of Port Snettisham, Southeast Alaska (PS), on nights around the new moon that coincided with the beginning of their breeding season during 15-16 May 2007 (n = 39) and 26-28 May 2008 (n = 40). I attached VHF radio transmitters (Model A1555 ATS, Isanti, MN) weighing approximately 2.5 g (~1% of murrelet body weight) to the dorsal surface of the bird using a subcutaneous anchor (Newman et al. 1999), and drew blood samples to determine sex (Zoogen 2007) and assess overall health status (see Newman et al. 2008). Two murrelets captured in 2007 whose sex could not be
determined were excluded from analyses involving gender but were included otherwise.

During May-July of each year, I used aerial-, boat-, and ground-based radio-telemetry to track murrelets and locate nest sites, monitor daily nest attendance, and determine at-sea locations of individual murrelets. Using an aerial telemetry technique known as boxing (relative signal strength received by antennas on each wing of the aircraft was compared to determine the signal direction and circle an area around the radio-marked murrelet), I recorded locations at-sea and identified nesting areas (within which the nest was located). Boat-based surveys occurred periodically to fill spatial and temporal gaps in aerial survey data during 2008 (e.g., searches outside of PS on days with no aerial surveys). During boat surveys, I used triangulation (Nams 1990) with hand-held telemetry equipment to determine locations. Ground-based hand-held telemetry was used to confirm incubation at eight accessible nest sites. Data logger receivers (R4500; ATS, Isanti, MN) were deployed at six strategic locations (stations) inside PS to record presence/absence data 24 h/day. Murrelet presence and movements were monitored throughout the fjord during the entire study by placing data logger antennas at prominent shoreline locations along known flyways (Fig. 2.1). Using methods described in Chapter 3, I later determined the breeding status and daily nesting stage (pre-breeding, incubation, chick-provisioning, or post-breeding) for active breeders.
GIS spatial analyses were conducted in ArcGIS 9.3.x (Environmental Systems Research Institute, Inc., 2008) with ArcCatalog used to manipulate spatial data files and ArcMap used for spatial analyses and map production. Hawth’s Tools (Beyer 2005) were used for home range, polygon area, and straight-line distance calculations. Spatial data layers representing the study area were extracted from a GIS database compiled by Schoen and Dovichin (2007). All means are reported ± standard deviation, unless otherwise noted (Streiner 1996).

Fixed kernel density estimates (FKDE) were derived to estimate home range size for those individuals with ≥ 12 at-sea detections (n = 37 of 39 in 2007; and n = 35 of 40 in 2008; see Fig. C.4 for illustration). Kernel density estimation is the only widely accepted home range estimator (Kernohan et al. 2001) that produces a smoothed, continuous intensity surface representing an animal’s utilization distribution (UD) based on presence-only point locations (Worton 1989). I defined the breeding season home range (or the area an individual actually used) as 95% of the UD (Seaman and Powell 1996, Kernohan et al. 2001) and the core use area(s) as the 50% contour portion of each UD. I calculated the smoothing parameter for each FKDE in Animal Space Use 1.3 (Horne and Garton 2009) using least squared cross-validation (Seaman and Powell 1996, Horne and Garton 2006, Gitzen et al. 2006).

Because gathering at-sea locations from boat-based surveys in 2008 increased sample sizes (i.e., at-sea locations used to calculate an individual’s home range), I first
tested for an affect of sample size (explanatory) on home range size (response) using a multiple regression model with an interaction (sample size*year) in PROC REG (SAS Institute 2003). Second, I hypothesized that home range would be smaller for females and breeding individuals, when compared to males and non-breeders, respectively (Hèbert and Golightly 2008). I then used separate general linear models (PROC GLM, SAS Institute 2003) to investigate effects of sex, breeding status, and year (explanatory variables) on murrelet home range size and core use area (response variables). Finally, I tested for within-year effects of sex and breeding status on home range size and core use area by including interaction terms in the models (year*sex + year*breeding status).

*Marine Hot Spots*

An individual core use area (50% FKDE) represents an area of preferred foraging habitat (Adams et al. 2004) for a member of a population, so I used core areas to identify population-level foraging hot spots. GIS was used to identify hotspots by: (1) converting individual core use areas to raster data layers (spatial extent = 206.9 x 146.8 km) and defining cell values (core use area = 1; all other cells = 0); (2) combining raster data layers using Raster Calculator (+) before converting back to vector (polygon) data layers prior to analyses; (3) assessing spatial autocorrelation of polygon values using Moran’s I coefficient (Moran 1950); and (4) detecting clusters of polygons with higher values than expected by random chance using the Getis-Ord \( Gi^* \) statistic (or Z-score; Getis and Ord 1992, Ord and Getis 1995, Swenson and
Howard 2005). I considered polygons with Z-scores > 1 as hot spots (Swenson and Howard 2005), and further categorized hot spots as medium (1 to 1.9) and high (> 2; Santora et al. 2010). I characterized hot spot locations separately by year, sex, and breeding status to visually inspect the effects of these factors on hot spot locations.

Foraging Locations of Nesting Murrelets

I summarized at-sea locations from aerial surveys for nesting murrelets to determine if daily at-sea (foraging) locations differed by stage of the nesting cycle and distance of the nest site from the coastline via drainages. I assumed that murrelets selected at-sea locations to optimize at-sea foraging efficiency relative to energy requirements at the nest and costs of daily commutes between foraging areas and the nest site (Orians and Pearson 1979, Hunt et al. 1999). First, I hypothesized that murrelets would forage closer to nests during chick-provisioning than during incubation. Second, I hypothesized that murrelets that nested further inland from the coastline would compensate by foraging closer to the mouths of drainages used to access nest sites. I tested these hypotheses by measuring the distance from each at-sea location to the individual’s nest site and partitioning that distance into two measures of commuting distance: marine commuting distance and terrestrial commuting distance. I created pivot points to aid with distance calculations (Fig. 2.1). Pivot point locations ensured marine distances did not cross land, and terrestrial distances were measured along drainages used as flight paths to access each nest site.
I used multiple linear regression models to test whether mean marine commting distance (response) was related to terrestrial commuting distance, year, and nesting phase (PROC REG, SAS Institute 2003). Mean marine commuting distance was the response metric because there were multiple at-sea locations for each nesting murrelet. I calculated separate individual means for each nesting stage (pre-breeding, incubation, provisioning, and post-breeding), and a single individual mean for all locations while nests were active (incubation and chick-provisioning pooled). I only included individual stages with at least three at-sea locations in the analyses investigating effects of nesting stage and individual birds with at least five at-sea locations (while nests were active) for the analysis investigating effects of terrestrial commuting distance. Terrestrial commuting distances were not normally distributed (Shapiro-Wilk Normality Test; $W = 0.782, p < 0.0001$), so I log transformed the raw data to achieve normality. First, I tested for differences in mean marine commuting distance of at-sea locations to nest sites (response) among pre-breeding, active, and post-breeding stages of the nesting season (explanatory). Second, I tested for differences in mean marine commuting distance within the active nesting stages (incubation and chick-provisioning). Lastly, I removed the nesting stage variable and tested for effects of terrestrial commuting distance on marine commuting distance and included an interaction term (terrestrial distance*year) to test for differing effects between years.
RESULTS

I located radio-marked individuals an average of 24.5 ± 4.4 times during aerial surveys in 2007 (range 17 to 31; n = 37) and 29.7 ± 12.8 times during aerial and boat-based surveys in 2008 (range 12 to 55; n = 35). All radio-marked individuals were regularly detected at-sea during aerial surveys until their last detection (96.8% of possible detections in 2007; 95.3% in 2008) unless they were attending an inland nest site. Murrelets were located at-sea most often inside PS, closer to the mainland in Stephens Passage, or near the convergence of Tracy Arm and Endicott Arm (Fig. 2.2).

Marine Home Range

Mean home range size was 127.4 ± 88.8 km² (range 31.3 to 443.6 km²; n = 72; Appendix C). Mean core use area was 35.6 ± 25.6 km² (range 6.4 to 132.4 km²; n = 72). Sample size of at-sea locations did not influence estimated home range size for individuals (t = -0.73, p = 0.47). Murrelets had significantly larger home ranges (F₃,₆₉ = 7.85, p = 0.007) and core use areas (F₃,₆₉ = 5.33, p = 0.024) in 2008 than in 2007 (Fig. 2.3), but these estimates did not differ by sex (both p > 0.65) or breeding status (both p > 0.38). Home range size or core use area did not differ by sex or breeding status between years (all p > 0.27), although there was a trend in 2008 toward slightly larger home range size and core use area for males and non-breeders compared to females and breeders, respectively.
**Marine Hot Spots**

In 2007, at least 56.8% of individual core use areas overlapped in central PS, where the arms of the fjord converge, and a single large foraging hot spot was identified in that area (Fig. 2.4). Less overlap occurred in central PS in 2008, although a similar size hot spot was identified. Additional smaller hot spots were also identified in 2008 near the mouth of PS and the mouth of Tracy Arm to the south (Fig. 2.4). Hot spots for breeding murrelets were mostly within PS near high density nesting areas, while hot spots for non-breeders were less concentrated (Fig. 2.5). Conversely, hot spot location did not appear to differ by sex within each year (Fig. 2.6). The total size (medium + high) of population-level hot spots (all birds) increased from 24.7 km² in 2007 to 37.0 km² in 2008 (Table 2.1). Total size was similar (< 10 km²) between sexes in 2007 and 2008, and between breeding categories in 2007, but in 2008 hot spots for non-breeders (50.5 km²) were relatively large compared to hot spots for breeders (30.8 km²).

**Foraging Locations of Nesting Murrelets**

I documented 824 at-sea locations (342 during active nesting) for 36 nesting murrelets, including three radio-marked pairs, whose terrestrial commuting distances to nest sites ranged from 0.1 to 52.0 km (n = 33). Marine commuting distances from at-sea locations to nest sites ranged from 0.4 to 54.7 km during active nesting. Total commuting distances to nests (marine + terrestrial) from at-sea locations ranged from
1.5 to 94.2 km, and averaged 27.7 ± 14.7 km (n = 19) in 2007 and 29.4 ± 10.1 km (n = 10) in 2008.

Mean marine commuting distance for nesting individuals during pre-breeding (13.8 ± 7.3 km; n = 31) was similar to when nests were active (14.8 ± 6.2 km; n = 32), but mean post-breeding commuting distance (24.7 ± 10.6 km; n = 12) was greater than during other stages of the nesting cycle (F= 10.16, p < 0.001; t = 2.88, p = 0.005; Fig. 2.7). Mean marine commuting distance for nesting individuals did not differ between incubation (12.2 ± 4.0 km; n = 9) and chick-provisioning (16.8 ± 9.0 km; n = 9). The model with log (terrestrial distance) + year + log (terrestrial distance)*year was significant ($R^2 = 0.50, F_{3,29} = 8.35, p < 0.001$), and suggested inclusion of the interaction term explained more variation in the data. Mean (± SE) individual marine commuting distance was significantly greater (t = 3.32, p = 0.003) in 2008 ($\bar{x} = 20.0 ± 2.0$ km; n = 10) than in 2007 ($\bar{x} = 12.0 ± 0.9$ km; n = 19). The interaction term (log[terrestrial distance] * year) was not significant (t = -1.63, p = 0.115), but there was a tendency for birds with greater terrestrial commuting distances to have shorter average marine commuting distances in 2008, but not in 2007 (Fig. 2.8).
Figure 2.1. Examples of measurement procedure for distance between at-sea locations and nest site for nesting Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska.
Figure 2.2. At-sea locations recorded during aerial and boat-based surveys for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska.
Figure 2.3. Home range size (km²) and core use area (km²) for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Home range size was calculated using 95% fixed kernel density estimation (top) and core use area was calculated using 50% fixed kernel density estimation (bottom). Boxes indicate interquartile ranges, bars are median values, and Os indicate maximum outlier value.
Figure 2.4. Core use areas (50% fixed kernel density estimate) overlapped by year (top) and spatial analysis results (Getis-Ord Gi* statistic; bottom) to identify hot spots for Marbled Murrelets radio-marked in 2007 (left) and 2008 (right) at Port Snettisham, Southeast Alaska. Z-scores categorized according to Santora et al. (2010).
Figure 2.5. Results from hot spot analyses (Getis-Ord $G_i^*$ statistic) of core use areas (50% fixed kernel density estimate) by breeding status for Marbled Murrelets radio-marked in 2007 (top) and 2008 (bottom) at Port Snettisham, Southeast Alaska. Z-scores categorized according to Santora et al. (2010).
Figure 2.6. Results from hot spot analyses (Getis-Ord Gi* statistic) of core use areas (50% fixed kernel density estimate) by sex for Marbled Murrelets radio-marked in 2007 (top) and 2008 (bottom) at Port Snettisham, Southeast Alaska. Z-scores categorized according to Santora et al. (2010).
Figure 2.7. Mean individual marine commuting distances from at-sea locations to nest sites during pre-breeding ($n = 31$), active nesting ($n = 32$), and post-breeding ($n = 12$) stages of the nesting cycle for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Boxes represent the interquartile range; lines in boxes were median values; and O was an outlier.
Figure 2.8. Mean marine commuting distance from at-sea locations to nest sites (y-axis) relative to terrestrial commuting distance (x-axis) for Marbled Murrelets (n = 36) radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Error bars represent ± standard error for each individual mean. Boxes contain equations for linear regressions lines calculated for each year.

2007: $y = -0.0326x + 12.124$
$R^2 < 0.001; p = 0.97$

2008: $y = -2.6494x + 24.202$
$R^2 = 0.2895; p = 0.11$
Table 2.1. Hot spot size from individual core use areas (50% fixed kernel density estimate) by year for population segments of Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham Southeast Alaska. Hot spots determined by Z-score (Getis-Ord Gi* statistic) and categorized according to Santora et al. (2010). Medium hot spots had Z-scores of 1.0 to 1.9 and High hot spots had Z-scores of ≥ 2.0. (n = number of individuals used in each analysis)

<table>
<thead>
<tr>
<th>Population Segment</th>
<th>Year</th>
<th>n</th>
<th>Hot Spot Size (km²)</th>
<th>Medium</th>
<th>High</th>
<th>Total</th>
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</thead>
<tbody>
<tr>
<td>All</td>
<td>2007</td>
<td>37</td>
<td>15.0</td>
<td>9.7</td>
<td>24.7</td>
<td></td>
</tr>
<tr>
<td>All</td>
<td>2008</td>
<td>35</td>
<td>20.9</td>
<td>16.1</td>
<td>37.0</td>
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</tr>
<tr>
<td>Male</td>
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<td>19</td>
<td>15.4</td>
<td>14.0</td>
<td>29.5</td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>2007</td>
<td>16</td>
<td>15.5</td>
<td>11.4</td>
<td>27.0</td>
<td></td>
</tr>
<tr>
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<td>15.3</td>
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<tr>
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<td>28.3</td>
<td>17.5</td>
<td>45.8</td>
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<tr>
<td>Breeders</td>
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<td>12.9</td>
<td>10.4</td>
<td>23.3</td>
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<tr>
<td>Non-breeders</td>
<td>2007</td>
<td>16</td>
<td>22.3</td>
<td>10.2</td>
<td>32.5</td>
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<tr>
<td>Breeders</td>
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<td>19.8</td>
<td>11.0</td>
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<tr>
<td>Non-breeders</td>
<td>2008</td>
<td>18</td>
<td>31.6</td>
<td>18.9</td>
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</table>
DISCUSSION

Radio-marked murrelets generally foraged near the mainland and within the more protected deep fjords and bays where glacially influenced freshwater runoff and saltwater were mixed by currents and tides. When not located within Port Snettisham, murrelets typically used marine areas directly to the south. In particular, a region where two larger fjord systems converge (Tracy Arm, Endicott Arm, and Holkham Bay) was used predominately by several radio-marked murrelets and many others often commuted between the fjord systems. Murrelets within these neighboring fjord systems apparently comprised a large inter-mixing breeding population and prey densities were likely greater than adjacent marine areas further to the north (Taku Inlet) and south (bays associated with southern Stephens Passage). However, radio-marked murrelets were captured at night, near the mouth of Port Snettisham, and the proportion of murrelets that commuted to the study area to forage during the daytime from nesting areas further away remains unclear.

Home range size, core use area, and commuting distance were significantly greater on average in 2008 than 2007 for radio-marked murrelets in this study. Seabirds use the marine environment at varying scales depending on prey densities (Vlietstra 2005) and this trend was confirmed for murrelets at Port Snettisham during boat-based visual and hydroacoustic surveys throughout Port Snettisham in 2007 (Haynes et al. in press). Therefore, my results suggest that marine conditions were less favorable for foraging murrelets in Port Snettisham during the 2008 nesting
season (i.e., reduced foraging efficiency). Many factors likely influenced marine conditions within Port Snettisham because Southeast Alaska can experience large inter-annual variation in marine conditions due to large differences in winds and coastal freshwater runoff (Weingartner et al. 2009). I used previous studies and broad-scale information on factors that influence oceanographic properties, foraging efficiency, and prey accessibility to interpret the annual differences in home range size and commuting distance between years.

Rates of freshwater runoff, along with tidal stage (Haynes et al. in press), may be the main drivers of murrelet foraging efficiency within fjords like Port Snettisham. High levels of glacially-influenced freshwater runoff in fjord systems of the region will affect prey accessibility (Etherington et al. 2004) by influencing marine stratification, decreasing chlorophyll-a levels, and increasing turbidity. These conditions can reduce food availability and foraging efficiency for visual marine predators (Robertis et al. 2003). Port Snettisham was particularly susceptible to rapid increases in freshwater influx after heavy precipitation because the geography of the fjord channels runoff exiting numerous surrounding watersheds. High runoff events were more common in 2008, after a shift in the Pacific Decadal Oscillation Index (PDO), which drives regional weather patterns and broad-scale marine conditions in the Gulf of Alaska, from a warm anomaly to a cold anomaly in fall 2007 (NOAA 2011). Cold-PDO winters have been linked to increased freshwater runoff the following summer in Southeast Alaska (Neal et al. 2002), and more days with rainfall
≥ 2.5 cm were recorded in June-August 2008 (11% of days with records) than in 2007 (5%; NOAA 2010) at a weather station in Speel Arm. A PDO regime shift (from warm to cold) coincided with increased reproductive success in central California (Becker et al. 2007). Fluctuations in large-scale ocean anomalies likely have a considerable influence on local murrelet populations, but long-term data sets are needed to identify specific effects in Southeast Alaska.

My estimate of home range size is the first for murrelets in Alaska. Two previous radio-telemetry studies estimated home range size in northern California (505 km² in Hèbert and Golightly 2008) and Washington (742 km² in Bloxton and Raphael 2009) using minimum convex polygons (MCP). I re-calculated my home ranges sizes using MCP for comparison purposes and found that home range size of Port Snettisham murrelets was much smaller (154 ± 98 km² from Barbaree unpubl. data) than in California or Washington. This large disparity in home range size suggested more concentrated prey resources in my study area. I had anticipated that the higher energy demands of egg production and nesting (Drent and Daan 1980) would limit home range size for females and breeders, as was found by a study in northern California (ratio of male to female home range size = 682 km²:334 km²; ratio of non-breeder to breeder home range size = 655 km²:240 km²; Hèbert and Golightly 2008). In contrast, home range size did not differ by sex or breeding status in the present study. Home range results indicate that the marine environment around Port
Snettisham provided high quality foraging conditions compared to California and Washington, even during the relatively poor year of 2008.

Individual murrelet home ranges were not randomly distributed in the marine environment, but rather were clumped to form several population-level marine hot spots. All hot spots were near the confluence of distinct marine systems; the large hot spot that occurred during both years of the study in central Port Snettisham was located where three arms of the fjord converge. Two of the three arms were essentially large estuaries with glacially-influenced freshwater runoff, and the third is a deep channel leading to Stephens Passage that permitted high tidal mixing of freshwater outflow with saltwater forced in by prevailing currents and tides. This hot spot coincided with higher densities of murrelets on the water and marine forage fish in the water column, as indicated by boat-based transect surveys (Haynes et al. in press). Additional hot spots in 2008 were located near the mouth of Port Snettisham and near the mouth of Tracy Arm. These two adjacent fjord systems appear to support similar oceanographic processes that result in reliable a food supply for murrelets during the nesting season. If researchers can quantify oceanographic features and processes that produce high quality foraging conditions for murrelets, a marine habitat suitability model could be produced and would serve as a powerful tool for conservation. Therefore, future research comparing forage fish densities and oceanographic variables in areas with high murrelet densities during the nesting season is recommended.
The distribution of core use areas across the study area indicated that Port Snettisham and marine areas to the south represent regionally significant foraging habitats for murrelets. Marine hot spots identified in this study indicated locations of consistently high forage availability and central foraging areas for murrelets. Total size and concentration of hot spots was directly related to home range size, so greater total size of hot spots also reflected lower prey densities. Murrelet core use areas and hot spots should be used to help define spatial boundaries of commercial fishery restrictions and marine protected areas in and around Port Snettisham (Fig. 2.4).

Furthermore, gill-net fisheries have been identified as a considerable source of adult murrelet mortality (McShane et al. 2004) and I recommend that gill net fishing be excluded from Port Snettisham and locations within two kilometers of the mainland coastline to the south of Point Styleman (at the northern mouth of the fjord).

The distance an individual bird will be required to commute from its nest for food may change over time. Murrelets engaged in chick-provisioning must meet the food requirements of nestlings while meeting their own requirements for maintenance; therefore, they should commute to the foraging area where foraging efficiency is highest until commuting costs outweigh the benefits of increased foraging efficiency. Body fat reserves of seabirds are generally depleted during chick-rearing, partly due to more frequent commutes between foraging areas and nest sites with an increased payload in the form of chick meals (Ricklefs et al. 1986, Roby and Ricklefs 1986, Golet and Irons 1999). Seabirds therefore typically require sufficient body reserves
prior to initiating nesting attempts (Weimerskrich 1992, Chastel et al. 1995). The ability to maintain reserves and avoid mortality risks may depend on the costs of commuting, as determined by proximity of food resources to nest sites.

My method of averaging the marine commuting distance for an individual murrelet to visit its nest site eliminated daily variation, and the estimate represented the general willingness to travel further from the nest site to find food. Estimates of commuting distance to nest sites support the hypothesis that Port Snettisham provides relatively high quality marine foraging habitat for murrelets because estimates were shorter when compared to previous studies. Total commuting distances (terrestrial commuting distance + marine commuting distance) in this study (29 ± 18 km, \( n = 342 \) at-sea locations) were shorter than at Auke Bay, Southeast Alaska (78 ± 27 km, maximum distance 124 km, \( n = 46 \); Whitworth et al. 2000), and British Columbia (39 ± 23 km, range 12-102 km, \( n = 23 \) individuals; Hull et al. 2001). However, straight-line commuting distances from nest sites to foraging locations for six murrelets radio-marked at Port Nellie Juan, in Prince William Sound, Alaska (Kuletz 2005), were somewhat similar to estimates in this study, suggesting commuting costs between foraging areas and nest sites at Port Nellie Juan were similar to Port Snettisham.

I predicted that murrelets would forage closer to nest sites after nesting began and closer during chick-provisioning than incubation. Contrary to my prediction, the only detectable difference in foraging range occurred after nesting activity had ceased; therefore, murrelets foraged in similar locations prior to and after nest initiation.
Potential explanations for this result include: (1) the payoff at the foraging area mitigated the added commuting costs because high quality food resources were present near nest sites during both periods, (2) the range of commuting distances recorded during nesting did not place measurable energetic limitation on murrelets, (3) body reserves were sufficient for nesting upon arrival at the breeding grounds and social behaviors compelled foraging near nest sites, (4) foraging distance from the nest site was restricted prior to nesting as compensation for added costs of egg production, courtship, or prospecting for nest sites (Nelson and Hamer 1995), and (5) murrelets relied on a similar food source to build body reserves prior to nesting and to maintain reserves during nesting activities (i.e., an “income” breeding strategy, Drent and Daan 1980). Regardless of the explanation, murrelets nesting around Port Snettisham generally relied on the same foraging areas to meet their energetic needs immediately prior to and throughout the nesting season.

Foraging locations were not influenced by terrestrial commuting distance to nest sites (inland distance) in 2007 when core foraging areas were predominately in central Port Snettisham, a relatively short marine commuting distance to nest sites within the fjord. However, in 2008 when foraging conditions were apparently relatively poor in the fjord, marine commuting distances appeared to decrease as the inland distance to nest sites increased. Adequate self-maintenance should require behavioral trade-offs during nesting and compensation strategies may become more evident during years when food resources are less abundant. Behavioral compensation
for nesting further inland was likely not necessary in 2007, when the average marine commuting distance to nest sites was shorter on average. A reduction in marine commuting distance to the nest may be more evident in areas where murrelets are frequently required to commute long distances to feed (Whitworth et al. 2000), areas with lower prey abundance or quality (Becker and Beissinger 2006, Norris et al. 2007), and areas more heavily influenced by up-welling systems (Peery et al. 2009) or Pacific Ocean oscillation regimes (Chavez et al. 2003). If local prey distributions require long-distance foraging commutes during nesting, fewer individuals within a population will have sufficient reserves to accommodate the added costs of reproduction. Therefore, energy expended commuting to nest sites likely increased (Hull et al. 2001) at Port Snettisham in 2008 and productivity may have declined (Peery et al. 2004; see Chapter 3).

Murrelet behavioral plasticity to mitigate costs from larger marine home ranges and an increase in commuting costs is not well understood, and likely depends on the amount and type of food available. Murrelets and numerous other marine predators were repeatedly documented targeting Capelin (*Mallotus villosus*; Haynes et al. *unpubl. data*), a preferred, high energy prey resource (Montevecchi and Piatt 1984), within the fjord and nearby areas. A study on Common Murres (*Uria aalge*) found that capelin abundance and quality impacted reproductive rates (Davoren and Montevecchi 2003). A similar relationship may be present at Port Snettisham because
murrelets appeared to rely on Capelin as their primary prey, because high densities were often observed in vicinity of the hot spots.

My study suggested that Port Snettisham and nearby areas provided favorable foraging conditions compared to all previous studies on murrelets at sea. In addition, Haynes et al. (in press) and M. Kirchhoff (unpubl. data) documented high densities of murrelets at Port Snettisham compared to other areas in Southeast Alaska, which suggests this fjord and surrounding marine areas are a critical habitat for murrelets. Mainland fjords in Southeast Alaska likely provide nearly ideal marine conditions for murrelets during some years, but the frequency of these conditions is unknown. Other fjord systems and areas with similar hydrography, freshwater influx, and low levels of disturbance should provide similar marine conditions that result in higher densities of murrelets during the nesting season and higher productivity. The confluence of Icy Straight and Glacier Bay to the northwest fits this description and high densities of murrelets have been observed there throughout the nesting season (Piatt et al. 2007). Murrelets also nest on islands in Southeast Alaska (see review in Piatt et al. 2007), which account for a large proportion of the ice-free land area in the region. However, the terrestrial and marine environments of islands in the archipelago are different from mainland fjords, because glacial influence is lower and human-induced habitat disturbance is more common (i.e., development, natural resource extraction, and recreation). Future research to describe the differences in marine and terrestrial
habitat on islands and the mainland is needed to design effective murrelet conservation strategies.

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Chapter 3

NESTING ECOLOGY OF MARBLED MURRELETS
AT A REMOTE MAINLAND FJORD IN SOUTHEAST ALASKA

Blake A. Barbaree
ABSTRACT

Gathering new data on reproductive ecology for a species of conservation concern is imperative for designing effective management and monitoring strategies, particularly in unstudied parts of their range, where habitat quality is excellent and abundance is high. In 2007 and 2008, I used radio-telemetry to locate and monitor nests of Marbled Murrelets (*Brachyramphus marmoratus*) at a remote mainland fjord in Southeast Alaska with mostly pristine terrestrial and marine habitat. I located 33 active nests within forested (tree; \( n = 15 \)), non-forested (cliff; \( n = 16 \)), and undetermined \( (n = 2) \) habitat types. Nests were located further inland (range = 1.0 - 52.0 km) and at higher elevations (range = 42 - 1100 m) than previously documented in Alaska. Nest initiation rate was 46.1\% (35 of 76), hatch success was 47.4\% \((n = 18 \text{ of } 38)\), and apparent fledge success was 17.6\% \((n = 6 \text{ of } 34)\). Regional murrelet nesting habitat models should include rock cliff and alpine nesting habitat (≥ 48.5\% of nests in this study) when characterizing nest-site availability, but the occurrence of non-forest nesting outside of Port Snettisham is unknown. It is of conservation concern that reproductive rates were so low in a region with high Marbled Murrelet abundance and seemingly ideal terrestrial and marine habitat for breeding murrelets. Predation pressure or food limitations may explain the low reproductive rates, but causes were not evident. A difference in ocean conditions between years coincided with shorter nesting attempts and lower hatch success in 2008, suggesting birds were more food limited in 2008. However, predation levels were unknown. Identifying the causes of
low reproductive rates for murrelets in Southeast Alaska will be imperative to understanding population declines range-wide. Because adult Marbled Murrelets need to maximize the number of breeding opportunities within their lifetime, reducing the impacts of adult mortality will be paramount for effective species preservation.

INTRODUCTION

Information on the reproductive rates of a species helps us understand fundamental life-history traits by determining its overall investment into reproduction. The life history of all seabirds is characterized by long life spans and relatively low investment into any single reproduction, mostly due to inter- and intra-annual variability in food availability (Lack 1968, Ashmole 1971, Ricklefs 1977). These traits have been well-documented for most colonial nesting seabird species, but life-history traits are difficult to for assess non-colonial and secretively nesting species, such as the Marbled Murrelet (Brachyramphus marmoratus; hereafter murrelet). Non-colonial nesting seabirds may be adapted to even higher survival and lower reproduction than colonial nesting species (Wittenberger and Hunt 1985), making them extremely vulnerable to naturally occurring or human-induced variation in resources. Widespread decline of murrelet populations resulted in the species being listed as federally threatened in California, Oregon, Washington, and in British Columbia (USFWS 1992, Rodway 1990), and considered endangered by the International Union for the Conservation of Nature (IUCN 2011). Loss of older-aged
nesting habitat is considered the primary driver of significant population declines (Lynch et al. 2009). Most large expanses of remaining older-aged forest nesting habitat are in Alaska, where up to 90% of the world population of murrelets breed, but population declines of up to 70% are suspected in Alaska since 1970 (McShane et al. 2004).

Seemingly large and undisturbed populations of an imperiled species are seldom given research priority, but the ecology of these populations can provide valuable insight into a species’ life-history adaptations. Southeast Alaska is considered the center of abundance for murrelets (Piatt et al. 2007); mostly due to a highly productive marine environment and associated high prey abundance (Hunt 1995), and minimal anthropogenic disturbance to terrestrial habitat on the mainland. Port Snettisham, a remote mainland fjord in Southeast Alaska, has extremely high murrelet abundance during the nesting season relative to most areas (111 ± 35 murrelets km\(^{-2}\) in Haynes et al. in press), and foraging conditions are relatively good compared to studies south of Alaska (see Chapter 2). Considering that apparently ideal nesting habitat is also present, the reproductive ecology of murrelets at Port Snettisham should represent the best possible insight into the species’ life-history adaptations.

The vast majority of research on murrelets has been conducted south of Alaska, where terrestrial land cover, topography, and land use practices differ significantly. In the southern portion of their range, adult murrelets fly up to 100 km
inland to nest sites located primarily on mossy platforms in older-aged trees (Carter and Sealy 1987, Nelson and Hamer 1995a, Nelson 1997). However, in southwestern Alaska, tree-less habitat dominates the landscape and nests are found only on the ground or on cliffs. Non-tree nests are considered uncommon in other regions of Alaska, and British Columbia (Day et al. 1983, McShane et al. 2004, Bradley and Cooke 2001, Piatt et al. 2007). In addition, evidence that murrelets have a low rate of nest initiation and low nest success has accumulated south of Alaska. Brood patch evaluation (McFarlane Tranquilla 2003a) and nest initiation rates during radio-telemetry studies (e.g., Bradley et al. 2004, Peery et al. 2004, Hèbert and Golightly 2006, Bloxton and Raphael 2009) suggested that reproductively mature murrelets do not nest every year. Factors that may cause murrelets to forego nesting are not clear. If murrelets have adapted a low rate of nest initiation, high nest success is needed to maintain populations (Lack 1954, Williams 1966, Ricklefs 1977). Conversely, all estimates of murrelet nest success or productivity have been low when compared to historical levels (Beissinger and Peery 2007) and to other Alcids (Gaston and Jones 1998), including estimates from nests located during ground-based surveys (e.g., Naslund et al. 1995, Nelson and Hamer 1995b), counts of juvenile to adult ratios at-sea (e.g., Anderson and Beissinger 1995, Lougheed et al. 2002, Kuletz and Kendall 1998, Peery et al. 2007), and during previously cited radio-telemetry studies. Continued decline of murrelet populations within listed regions has been documented despite conservation of nesting habitat (Lynch et al. 2009). This suggests that current
conservation strategies are insufficient and actions beyond preservation of nesting habitat will be necessary for recovery of the species.

As part of a larger, multi-faceted study on murrelets in Southeast Alaska from 2005 to 2008, I radio-marked murrelets in 2007 and 2008 to describe nest-site characteristics and reproductive rates at Port Snettisham, Southeast Alaska. Extensive radio-telemetry monitoring was intended to provide an understanding of murrelet nesting ecology in Southeast Alaska, because relatively few active murrelet nests have been found in the region, most opportunistically (DeGange 1996, Piatt et al. 2007). Only a single year radio-telemetry study has documented a spatially un-biased sample murrelet nest locations in Southeast Alaska (n = 6 in Whitworth et al. 2000), but descriptions of nest sites was not possible. Therefore, I addressed two central questions: (1) where and when were murrelets nesting? and (2) what was the nest initiation rate and success rate at murrelet nests?

METHODS

I used night lighting (Whitworth et al. 1997) to capture murrelets near the mouth of Port Snettisham (PS) on nights around the new moon that coincided with the beginning of their breeding season during 15 - 16 May 2007 (n = 39) and 26 - 28 May 2008 (n = 40). I attached VHF radio transmitters (Model A1555 ATS, Isanti, MN) that weighed approximately 2.5 g (~1% of murrelet body weight) using a subcutaneous anchor (Newman et al. 1999). A small amount of blood was also drawn
to later determine sex (Zoogen 2007) and overall health of birds (Newman et al. 2008).

Aerial-, boat-, and ground-based radio-telemetry were used to locate nest sites, monitor daily nest attendance, and determine at-sea locations of individual murrelets. Data logger receivers (R4500; ATS, Isanti, MN) were also deployed at strategic locations inside PS (Fig. 3.1) to record presence/absence data 24 h/day. Data loggers recorded date and time for all confirmed radio-transmitter detections. By placing data logger antennas at prominent shoreline locations along known flyways, radio-marked murrelet presence and directional movements were monitored throughout the fjord during the entire study.

I defined a murrelet as a breeder if it attempted to nest at least once, and I confirmed an attempt directly by finding an active nest or indirectly using telemetry data to identify behavior patterns consistent with incubation. Murrelets attend nests for 24-hr shifts during incubation resulting in an “on-off” pattern (Nelson and Hamer 1995a); thus, an incubating bird would be located at the nest site one day and at-sea the following day (incubation behavior). Based on this pattern, I defined a nest attempt as when a bird exhibited incubation behavior for at least four consecutive days (i.e., on-off-on-off). Nest initiation date was defined as the day incubation behavior began for each nesting murrelet. Nest initiation rate was defined as the percentage of radio-marked murrelets that bred. For this calculation, a radio-marked nesting pair of murrelets was considered one individual. I tested for an affect of sex and year on
breeding status using a generalized linear model with fixed effects (PROC GENMOD; SAS Institute, 2003).

Timing and duration of the murrelet nesting season was quantified using estimates of nest initiation dates and previously published information on the average duration of the incubation period (30 days) and the nestling period (28 days; Hamer and Nelson 1995). Nesting season duration was calculated as the period between the first nest initiation date and the extrapolated fledging date for the last nest initiated (Hamer and Nelson 1995, Carter and Sealy 1987, Lougheed et al. 2002). I also calculated mean nest initiation, hatch, and fledge dates (PROC MEANS; SAS Institute, 2003).

Nest sites were located during aerial surveys. I used an aerial telemetry technique known as boxing (comparing the relative signal strength received by antennas on each wing to determine the signal direction and circle an area around the radio-marked bird) to define a nest-site area (within which the nest was located) with an accuracy of approximately ± 100 m. For nests that were subsequently visited on the ground, I recorded nest-site type (tree or cliff) and elevation (using an altimeter). For nests not accessible by foot, nest-site type was recorded from the plane as tree, cliff, or undetermined, the latter category was used when habitat composition in the nest-site area was mixed or the exact nest location was unknown.

Elevation (m) was estimated for inaccessible nest sites using topographic mapping software (TOPO! v.4.0, National Geographic). Distance inland (km) was
calculated using straight-line distances along flight corridors determined by watershed topography with Hawth’s Tools (Beyer 2005) in ArcGIS 9.3.x (Environmental Systems Research Institute, Inc., 2008). I used two-tailed t-tests (PROC TTEST; SAS Institute, 2003) to compare nest elevation and distance inland by nest type. Nest elevation and distance inland were not normally distributed (Shapiro-Wilk Normality Test; elevation, W = 0.92, p = 0.02; distance inland, W = 0.79, p < 0.0001), so I log transformed the raw data and achieved normality.

I anticipated that reproductive rates for murrelets at PS would be higher than most previous estimates because of the seemingly good nesting and foraging habitat. However, I could not visit most nests to confirm their fate because they were placed in inaccessible locations. Therefore, I used telemetry data to infer reproductive success (Bradley et al. 2004), because murrelets have distinctly different movement patterns during incubation and chick-provisioning. I used patterns in the radio-telemetry data to infer two measures of success: hatching success and late-stage nestling or apparent fledge success. A nest was considered to have successfully hatched when incubation behavior patterns were documented for ≥ 28 consecutive days (Nelson 1997) with this pattern followed by chick-provisioning behavior. I detected individual movement patterns indicating chick-provisioning behavior by examining data logger detections over time. Specifically, chick-provisioning behavior was inferred when data loggers detected a murrelet moving towards its nest, followed by a brief period of no detections (30 – 120 min), before movement away from the nest was detected.
Murrelet chicks reportedly fledge at 27-40 days old (Nelson 1997), but detecting true fledgling dates from behavior patterns identified using telemetry was difficult because chick-provisioning rates by adult males and females can differ considerably during late-stages of the nestling period (Nelson and Hamer 1995a, Manley 1999, Bradley et al. 2002). Consequently, I adapted an approach used by Bradley et al. (2004), who defined chick rearing as successful if chick-provisioning behavior was observed for at least 20 days. That study confirmed that telemetry-based behavior patterns were a reasonable surrogate for physically visiting the nest. I defined hatch or fledge fate as “unsuccessful” when incubation or chick-provisioning behavior ceased for ≥ 3 consecutive days.

I used separate generalized linear models to test if hatch or fledge success, both binary response variables, varied between year (2007 or 2008) and nest-site type (tree or cliff; PROC GENMOD; SAS Institute, 2003). Nest sites with undetermined habitat type (n = 3) were excluded from both analyses and nests with unknown fledge fate (n = 4) were excluded from the model investigating effects on fledge success. I conducted post-hoc general linear models to test if hatch or fledge success varied by sex of the bird (PROC GENMOD; SAS Institute, 2003). Nest attempts were excluded from the post-hoc analyses if sex of the bird was unknown (n = 2) or both members of the pair were radio-marked (n = 3). All means are reported ± standard error.
RESULTS

I captured and radio-marked 79 murrelets during 2007 and 2008, including both members of three breeding pairs in 2007 (Table 3.1). I conducted 80 aerial telemetry surveys and 77 of 79 radio-marked murrelets were detected at least once. I conducted 33 boat-based telemetry surveys, recording 111 at-sea locations for 27 radio-marked murrelets. I tracked radio-marked murrelets for periods of 3 to 88 days. The mean individual tracking period was 61 ± 17 d (n = 39) in 2007 and 46 ± 24 d (n = 40) in 2008. Data logger stations recorded 69,464 detections in 2007 and 65,420 detections in 2008.

I located and described 33 active nest sites (Fig. 3.2 and 3.3). Data loggers indicated two additional murrelets nested, but I was unable to locate their nests during surveys. Nest initiation rate was 46.1% (35 of 76; Table 3.1). Nest initiation rate did not differ by year ($\chi^2 = 0.280, p = 0.60$), but male murrelets were more frequently involved with nesting attempts (66%) than female murrelets (34%; $\chi^2 = 10.69, p = 0.002$). Additionally, four birds renested during the study. Mean nest initiation date was 10 June ± 2 d (range = 25 May to 19 July), mean hatch date was 10 July ± 2 d (range = 24 June to 18 Aug.), and mean fledge date was 7 Aug. ± 2 d (range = 22 July to 16 Sept.). The observed nesting season lasted 113 days from 25 May to 16 Sept.

Nest sites were located in the Port Snettisham watershed (n = 28), on the Snettisham Peninsula (n = 2), in the Tracy Arm watershed (n = 1), and on the Glass Peninsula of Admiralty Island (n = 2). The majority of nests (75.8%) were within the
Whiting River \((n = 8)\) and Speel Arm/River \((n = 17)\) basins. Nest sites were divided almost equally between forested habitat (tree nests, \(n = 15\); Fig. 3.4) and rock cliff habitat (cliff nests, \(n = 16\); Fig. 3.5) with two nests classified as undetermined.

Nest-site type was visually confirmed from the ground for seven tree nests and one cliff nest. Five of the accessible tree nests in the PS watershed were located within low-diversity western hemlock \((Tsuga heterophylla)\) forests intermixed with Sitka spruce \((Picea sitchensis)\). Two accessible tree nests on Admiralty Island were within forests dominated by western hemlock with western red cedar \((Thuja plicata)\) and red alder \((Alnus rubra)\) intermixed at lower elevations, and mountain hemlock \((T. mertensiana)\)-mixed conifer at higher elevations. Six of seven nest trees were identified to species: western hemlock \((n = 4)\), mountain hemlock \((n = 1)\), and Sitka spruce \((n = 1)\). The unidentified nest tree was suspected to be Sitka spruce.

Cliff nests were found in an assortment of non-forest habitat types. Cliff nests were characterized by steep rock faces with sparse epiphyte and vegetation cover. Snow or ice cover commonly surrounded cliff nesting areas, particularly earlier in the nesting season at higher elevations. Nest position on the cliff face ranged from near the talus at the cliff base to > 500 m above the base. Presumably, most nests were on ledges; however, one cliff nest may have been located underneath overhanging rock because the transmitter signal was only detectable at a horizontal angle during aerial surveys. A cliff nest in 2008 was on a 400 m high cliff face with a base accessible by foot \((\sim 1.0 \text{ km from the coast}; \text{Fig. 3.5B})\). The nest site was approximately 300 m
above the base of the cliff with 15-20% vegetation/epiphyte cover on the cliff face. Vegetation and epiphyte cover was dominated by Alaskan blueberry (*Vaccinium alaskensis*) intermixed with grass and mosses, which was typical for steep rocky areas near the coast or in mid to lower elevation river valleys of the PS area. In contrast, several high elevation cliff nests much further inland (*e.g.*, Fig. 3.5A and E) were several kilometers from the nearest tree and located high on cliff faces with sparse vegetation and epiphyte cover in association with active glaciers. Other cliff nest sites were on intermediate or alpine cliffs with sparse tree cover nearby, but extreme slopes or harsh conditions preventing dense tree growth (*e.g.*, Fig. 3.5C, D, F, G, and H).

Median nest-site elevation was 376 m (range = 30 - 1,100 m) and median distance inland (via flyways) was 9.6 km (range = 1.0 - 52.0 km; Fig. 3.6). Predictably, cliff nests were generally found at higher elevations (491 ± 64 m; *n* = 16) than tree nests (272 ± 53 m; *n* = 15; *t*-value = 2.98; *p* = 0.006). However, distance to coastline did not influence nest-site type (*t*-value = 0.75; *p* = 0.46). Sixteen of 33 (48.5%) nest sites were > 10 km from the coast and four (12.1%) nest sites were > 30 km from the coast. Two nest sites 1.5 km apart in the Whiting River basin (one tree nest and one cliff nest; Fig. 3.3) were > 52 km from the coast and > 15 km east of the USA/Canada border in British Columbia, Canada.

Hatch success was 47.4% (*n* = 18 of 38) and apparent fledge success was 17.6% (*n* = 6 of 34; Table 3.2). Hatch success was higher in 2007 (66.6%) than 2008 (30.0%; *χ*² = 4.46, *p* = 0.035). Nest-site type did not affect hatch success (*χ*² = 0.88, *p*
= 0.35). Apparent fledge success was similar between years ($\chi^2 = 0.55, p = 0.46$). However, there was evidence that fledge success was higher at tree nests than at cliff nests ($\chi^2 = 3.64, p = 0.057$; Table 3.3). Sex of the radio-marked bird did not affect hatch success ($\chi^2 = 0.59, p = 0.44$) or fledge success ($\chi^2 = 0.53, p = 0.47$). Mortality of three murrelets was suspected during incubation, leading to nest failure. Nest failure was verified at one tree nest in mid-July 2007 when an empty nest bowl was visually confirmed two days after chick-provisioning behavior ceased.

Four of 20 (20%) nest attempts that failed during incubation resulted in re-nesting attempts. All re-nest attempts occurred within 20 days after incubation behavior ceased for the first attempt. Time elapsed between periods of incubation behavior was 11 to 20 d. All re-nest attempts were pinpointed to the same location as initial attempts, but re-use of the same nest bowl, limb, or tree could not be determined due to the inaccessibility of the nest locations. A successful hatch was inferred for one of four re-nesting attempts, but apparent fledge success could not be determined.
Figure 3.1. Map of six stationary data logger receiver locations during Marbled Murrelet radio-telemetry project in 2007 and 2008 at Port Snettisham, Southeast Alaska.
Figure 3.2. Map of nest locations by year for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska.
Figure 3.3. Map of nest locations by nest-site type for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska.
Figure 3.4. Photographic examples of nine nest locations in forested (tree) habitat for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Photos by Dan Cushing (A) and Blake Barbaree (B-H). (continued on next page)
Figure 3.4. Continued from previous page.
Figure 3.5. Photographic examples of eight nest locations in non-forested (cliff) habitat for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Photos by Blake Barbaree (A-H). (continued on next page)
Figure 3.5. Continued from previous page.
Figure 3.6. Elevation (top) and distance to coastline via flyways (bottom) of Marbled Murrelet nest locations by nest-site type for birds radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Boxes represent interquartile values, lines in boxes are median values, and Os are maximum outlier values.
Table 3.1. Results of capture efforts by sex and breeding status for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska.

<table>
<thead>
<tr>
<th>Year</th>
<th>Capture Dates</th>
<th>Total Male</th>
<th>Total Female</th>
<th>Breeders Male</th>
<th>Breeders Female</th>
<th>Non-breeders Male</th>
<th>Non-breeders Female</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>15 May-16 May</td>
<td>20 (51.3%)</td>
<td>19 (48.7%)</td>
<td>14 (66.7%)</td>
<td>7 (33.3%)</td>
<td>6 (33.3%)</td>
<td>12 (66.7%)</td>
</tr>
<tr>
<td>2008</td>
<td>26 May-28 May</td>
<td>17 (42.5%)</td>
<td>23 (53.7%)</td>
<td>11 (64.7%)</td>
<td>6 (35.3%)</td>
<td>6 (26.1%)</td>
<td>17 (73.9%)</td>
</tr>
</tbody>
</table>
Table 3.2. Nest success estimates for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Hatch and fledge success are presented as percent successful and include four re-nest attempts. One nest attempt in 2007 is not included due to unknown hatch and fledge fate. * Four nest attempts with successful hatch but unknown fledge fate in 2007 are not included in fledge success estimates.

<table>
<thead>
<tr>
<th>Year</th>
<th>Nest Attempts</th>
<th>Hatch Success</th>
<th>Nest Attempts</th>
<th>Fledge Success</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>19</td>
<td>63.2%</td>
<td>15*</td>
<td>20.0%</td>
</tr>
<tr>
<td>2008</td>
<td>19</td>
<td>31.6%</td>
<td>19</td>
<td>15.8%</td>
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<tr>
<td>Total</td>
<td>38</td>
<td>47.4%</td>
<td>34</td>
<td>17.6%</td>
</tr>
</tbody>
</table>
Table 3.3. Nest success estimates by nest-site type for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Hatch and fledge success are presented as percent successful and include four re-nest attempts. * Four nest attempts with successful hatch but unknown fledge fate in 2007 are not included in fledge success estimates.

<table>
<thead>
<tr>
<th>Nest-Site Type</th>
<th>Hatch Fate</th>
<th></th>
<th>Fledge Fate</th>
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<tbody>
<tr>
<td></td>
<td>Nest Attempts</td>
<td>Hatch Success</td>
<td>Nest Attempts</td>
<td>Fledge Success</td>
</tr>
<tr>
<td>Tree</td>
<td>17</td>
<td>58.9%</td>
<td>13*</td>
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<tr>
<td>Cliff</td>
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<td>33.3%</td>
<td>3</td>
<td>33.3%</td>
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<tr>
<td>Total</td>
<td>38</td>
<td>47.4%</td>
<td>34</td>
<td>17.6%</td>
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</tbody>
</table>
DISCUSSION

New information on Marbled Murrelet nesting habitat in Southeast Alaska

Murrelets nested in surprisingly diverse locations and habitats at Port Snettisham. Almost half (48.6%) of nests were located in cliff or alpine habitat (i.e., not in trees), which is more than any previous study of murrelet nesting biology. The use of cliff nest sites was unequivocal due to the absence of suitable trees in the vicinity of the transmitter signals from incubating murrelets. However, some tree nests could have occurred on tree roots or on the ground near ravines covered by forest canopy, as documented in Southeast Alaska by Ford and Brown (1995) and Willson et al. (2010). Radar surveys of inland flight activity in south-central Alaska (Marks and Kuletz 2001) and British Columbia (Burger 1997) found higher murrelet activity levels in forested versus non-forested areas. However, I documented murrelets accessing cliff nests using forested lowland watersheds, suggesting the presence of murrelets in forested flyways does not always indicate tree nesting in areas where extensive cliff or alpine habitat is available nearby.

The use of cliff habitat for nesting is likely more common than hypothesized in Southeast and south-central Alaska (see McShane et al. 2004, Piatt et al. 2007), but only in locations where suitable cliff habitat is widely available near preferred marine foraging areas. Terrestrial and marine habitats within mainland fjords have very different physical- and bio-geographical features than most locations throughout Southeast and south-central Alaska, particularly on islands and other areas where late-
successional habitat types or human-induced disturbances are more widespread. Nesting in trees may predominate in areas with large expanses of forest habitat, and the occurrence of non-forest nesting may be related to the amount of suitable non-forest land cover available (i.e., steep, higher elevation rock cliff and alpine habitat) within a reasonable distance from the coast. Unfortunately, I had no direct access to cliff nests, so the physical characteristics of these sites (e.g., width of ledge, cover type) remain unknown. Nesting on cliffs may exclude certain forest dwelling nest predators, but exposure to aerial predators may increase. Differences in predation levels could have resulted in tree nests having somewhat higher nest success compared to cliff nests, although the small number of successful nests in this study limited conclusions. In addition, natal philopatry may also play an important role in choice of nest-site type, but secretive habits have limited the understanding of natal dispersal for non-colonial seabirds. To better understand the costs and benefits of nesting in forested and non-forested habitat, research investigating predation levels and small-scale nest-site structure is required, particularly for non-forest nests.

Murrelets at Port Snettisham were documented nesting farther inland and at higher elevations than previous studies in Alaska. Most nests described from Alaska have been located within 10 km of the coast (Piatt et al. 2007), but I found that 16 of 33 nests were > 10 km inland. At the extreme, two nest sites were located at approximately 51 and 52 km inland (1.5 km apart) in the Whiting River basin and > 15 km east of the USA/Canada border inside British Columbia, Canada. This is the
first documentation of murrelets foraging in Alaska, but nesting in Canada, where the species is considered federally threatened. Based on my observations during aerial surveys and those of A. Burger (pers. comm.), murrelets foraging in Alaskan waters are also suspected to nest in Canada along the Taku and Stikine River basins. The occurrence of murrelets crossing international boundaries during commutes to nest sites presents a challenge and opportunity for collaboration between wildlife management agencies from the U.S. and Canada.

Numerous nest sites in this study (37.8%) were at elevations ≥ 400 m, including two nests at > 800 m above sea-level. On the Olympic Peninsula in Washington, murrelets have been detected at elevations above 1000 m during audio-visual surveys (Bloxton and Raphael 2009). Increasing documentation of this behavior suggests that high elevation nesting is not common, but will occur when the topography allows. Additionally, three nests on cliffs in the Speel Arm watershed were at high elevations, far above cliff bases near glaciers, and > 5 km from the nearest tree (Fig. 3.6A and E). Of the seabirds in this area, this habitat type was previously considered as nesting habitat only for the closely related Kittlitz’s Murrelet (B. brevirostris; Day et al. 1999). If this nesting behavior is indicative of the local murrelet population, 8% or more of murrelets nesting at Port Snettisham may nest in tree-less landscapes near active glaciers. Nesting further inland and at higher elevation increases energy costs during commutes and the added costs are presumably
offset by other benefits (Hull et al. 2001), which may include reduced predator abundance (e.g., Bradley 2002, DeSanto and Willson 2001).

Taken together, my observations indicate that murrelet nesting habitat models from other regions are not applicable to mainland Southeast Alaska. Regional managers should expand their definition of murrelet nesting habitat to include non-forested habitat, habitat farther from the coast, and habitat at higher elevation. Generating a region-specific nesting habitat model is necessary for appropriate classification of murrelet nesting habitat. Using remotely sensed data and aerial photograph interpretation methods, similar to methods in Burger et al. (2010) and Waterhouse et al. (2011), to characterize coarse landscape-scale preferences is a viable approach to quantify and predict the potential for non-forest nesting in other areas.

**Timing and rate of Marbled Murrelet reproduction**

The murrelet nesting season at Port Snettisham was slightly longer (113 days) than predicted for Alaska (108 days in Hamer and Nelson 1995), while the earliest nest initiation date (25 May) and peak incubation period (June 22) were comparable to previous estimates for Alaska (Hamer and Nelson 1995, Kuletz and Kendall 1998, Speckman et al. 2000). Re-nesting was responsible for the extended nesting season and re-nests accounted for four of six nest attempts initiated after 21 June. One re-nest attempt in 2008 began particularly late in the season (18 July) and accounted for the latest potential fledging date (16 Sept.). This late nest initiation date was similar to the
last date observed in Desolation Sound, British Columbia (Lougheed et al. 2002) and western Oregon (S. K. Nelson unpubl. data).

Murrelet reproduction outside of peak breeding periods may be considerably greater than once believed and re-nesting was a significant factor in murrelet nesting ecology at Port Snettisham. Re-nesting accounted for 9.5% of all nest attempts, which was similar to an estimate in British Columbia (14% in McFarlane Tranquilla et al. 2003b). I also noted that birds only re-nested after failure during incubation, no birds re-nested after failure during chick-provisioning, which is consistent with general expectations regarding replacement nests for seabirds (Nelson 1979). The prevalence of re-nesting should be dependent on age structure and seasonal foraging conditions. The likelihood of a long-lived seabird re-nesting depends on individual quality, usually associated with age, experience, body condition (Hipfner et al. 1999), and reliability of a late season food supply (Hipfner 2001). The range of nest initiation dates and re-nesting rates observed during this study suggest that Port Snettisham and nearby areas provide reliably good foraging conditions from July through September.

Nest initiation rate and nest success at Port Snettisham were low and similar to estimates from areas with well-documented population declines (Lynch et al. 2009). All previous estimates of reproductive success from radio-marked birds were from south of Alaska. Regional differences in reproductive rates should be expected due to variation in nesting and feeding habitat quality (see review in McShane et al. 2004); given the relatively pristine conditions in Southeast Alaska, I predicted that
reproductive rates would be comparatively high to research conducted farther south in the murrelets breeding distribution. Moreover, the criteria I used to infer fledge success would potentially over-estimate nest success (see Bradley et al. 2004 for further details). Yet my estimates were low.

Nest initiation rate (48.1%) was low relative to other alcids (DeSanto and Nelson 1995), but within the range reported in other murrelet radio-telemetry studies (e.g., 65% in Bradley et al. 2004; 31% in Peery et al. 2004; 33% in Hèbert and Golightly 2006). Low initiation rates could be the result of my sample including subadults or non-breeding adults, which may include between 15 - 30% of the population for a given year (Sealy 1975, Piatt and Ford 1993). Several research-related factors may have biased the rate low, including that some birds were captured after their nest had already failed, nests failed before day four of incubation and were not detected, or that capture, handling, and radio-marking caused some birds to forego nesting. If the latter were true, the stress should disproportionately affect females because they incur the cost of egg formation, which is typically 15 days for alcids (Gaston and Jones 1998). The fact that males had a higher initiation rate than females suggests that at least some females may have been affected by capture and handling. However, there was no difference in hatch or fledging rates at nests of males and females indicating that if birds initiated a nest, subsequent incubation and chick-provisioning behavior would continue as expected. Consequently, our estimate of nest initiation rate for males (66%) was likely more accurate for our population of
murrelets, and estimates of hatch and fledging success are representative of the population of murrelets breeding in Port Snettisham. Radio-marking only male murrelets during future research would eliminate the potential bias of capture during egg formation.

I anticipated relatively high rates of apparent nest success, but my estimate for at Port Snettisham (17.6%) was much lower than reported in British Columbia by Bradley et al. (2004; 65.7%, n = 108) or Zharikov et al. (2006; 58.6%, n = 29), despite using the same methods. My estimate was more comparable to radio-telemetry studies in northern Washington (5%, n = 40 in Bloxton and Raphael 2009), northern California (22.2% in Hèbert and Golightly 2006), and central California (0% in Peery et al. 2004). Low reproductive rates were somewhat expected during studies south of Alaska because murrelets were nesting in highly fragmented and disturbed nesting habitat, but suitable nesting habitat with low levels of disturbance was almost certainly not limited at Port Snettisham. Previous estimates of murrelet productivity in Alaska were derived using HY:AHY ratios from at-sea surveys. Two estimates in south-central Alaska were variable and site-specific (2 - 13% in Kuletz and Kendall 1998; 16% in Kuletz and Piatt 1999), but generally represented higher levels of reproduction than observed at Port Snettisham. However, low levels of productivity were observed in Auke Bay, Southeast Alaska (0.4 - 3.1% in Anderson and Beissinger 1995), and the nest success rate at Port Snettisham probably resulted in a similar level of annual productivity.
The causes of nest failure at Port Snettisham are not clear and should be the focus of follow up research. Depredation is a common cause of failure for forest nesting passerines in Southeast Alaska (Willson and Gende 2000), and predation pressures may explain the diel shifts in the distribution of murrelets at sea where birds typically leave the fjord at night (Haynes et al. 2010). However, no information on predator abundance is available for non-forest habitat in Southeast Alaska or remote locations with extreme topography like Port Snettisham. As with many seabirds, nest failure could also be linked to marine conditions related to foraging efficiency. A shift in the Pacific Decadal Oscillation (PDO) regime, from a warm to a cold anomaly, was recorded in fall of 2007 (NOAA 2011). PDO regime influences regional weather patterns and a cold-PDO anomaly significantly increases freshwater discharge in Southeast Alaska, particularly in mainland locations (Neal et al. 2002). The geography of Port Snettisham makes the fjord susceptible to rapid fluctuations in glacially influenced freshwater runoff. High runoff events result in murky and turbid water conditions prevailing throughout the fjord. The cold-PDO regime coincided with significantly lower hatch success in 2008 compared with 2007. I also documented larger marine home range sizes and longer average commuting distances from at-sea foraging locations to nests in 2008. Finally, central foraging hot spots expanded outside of the fjord in 2008, after being located entirely within the fjord in 2007 (see Chapter 2). Together, these results are consistent with the hypothesis that nesting murrelets experienced better foraging conditions on average in 2007 (Peery et
Whether the differences in marine home range size and commuting distances were large enough to influence reproductive output remains unclear, but nest initiation rate and nest success were similar between years. Research confirming the causes of murrelet nest failure is needed to better inform managers about factors limiting murrelet reproduction in Southeast Alaska.

I provide evidence that murrelets in Southeast Alaska are less specialized in their choice of nesting habitat than birds breeding south of Alaska, but this finding does not advocate that murrelets will commonly utilize non-forest nesting habitat elsewhere. A clear definition of suitable non-forest nesting habitat is needed before its occurrence can be predicted elsewhere. Murrelets will not adapt to non-tree nesting in areas where anthropogenic disturbance has destroyed or reduced the quality of older-aged forest nesting habitat. Conservation of suitable older-aged forest nesting habitat is necessary in Southeast Alaska, especially if murrelet nest success is higher for tree nests as my findings suggest. Furthermore, factors other than nesting habitat availability apparently already limit murrelet reproduction at Port Snettisham. Identifying the factors that may limit reproduction throughout the region should be a high priority. If murrelets are currently limited by environmental factors, further loss of nesting habitat may be extremely detrimental to population stability.

All evidence to date suggests that murrelets have adapted a life-history strategy to maximize adult survival, regardless of consequences to reproductive output. Conservation of nesting habitat, while necessary, will not be sufficient to avoid further
population declines without incorporating a strategy to reduce adult mortality. In theory, every breeding pair of murrelets must breed successfully twice within their lifetime to maintain a stable population. Populations adapted to high survival and low reproduction should benefit most from an increase in survival because longer life spans result in more breeding opportunities (Stearns 1992). Therefore, decreasing adult mortality may be a viable conservation strategy to mitigate low reproductive output. Potentially beneficial conservation actions include protection of critical marine habitat near nesting habitat, predator deterrence, and minimizing mortality from gill-net fishing, oil spills, and other human-induce sources of mortality. Finally, this study provides a foundation for conservation of murrelets in Southeast Alaska and pathways for future research to better understand beneficial and limiting factors for murrelets range-wide.

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Chapter 4

CONCLUSIONS

Blake A. Barbaree
My study was the first multi-year radio-telemetry study on murrelet breeding ecology entirely in an area where anthropogenic impacts are minimal in both the terrestrial and marine habitats. New information on nesting ecology allowed for biologically important comparisons to areas south of Alaska where humans have influenced murrelet habitat and behavior for centuries. Most notably, murrelets at Port Snettisham commonly used forested and non-forested habitat for nesting. Murrelets nesting in and near Port Snettisham represent the first population documented to be widely using two fundamentally different nest-site types with diverse landform and vegetation structure.

Previous studies with comparatively large samples of nest sites were conducted south of Alaska, confining the understanding of potential nesting habitat on the mainland of Alaska. Murrelets at Port Snettisham were generally less specialized when selecting habitat type for nest sites than murrelets to the south, probably because multiple types of nesting habitat were readily available within close proximity to nest sites. Spatially separated avian populations are known to adopt unique life-history strategies depending on the surrounding landscape (Hansen and Urban 1991), and my study area provided large expanses of forested, alpine, and rock cliff habitat for nesting. Nesting habitat choice is likely influenced by natal philopatry and small-scale structural preferences that provide protection from predation and weather. Windthrow events and other abiotic disturbance events (i.e., landslides and avalanches) are the main drivers of terrestrial vegetation structure in Southeast Alaska (Kramer et al.)
2001), and the frequency of abiotic disturbance events may be an important factor influencing the choice of nest sites at Port Snettisham.

Compared to previous studies, home range size and commuting distance for murrelets at Port Snettisham were small, suggesting that foraging conditions were comparatively good. However, the levels of reproduction observed in this study were not sufficient to maintain the population and were similar to estimates from areas with well-documented population declines (Lynch et al. 2009). Factors driving low reproduction at Port Snettisham remain unclear. Rates of depredation at nest sites may have been considerable, but specific causes of nest failure are unknown. Relatively low prey abundance or prey quality may have contributed to the low rates of reproduction at Port Snettisham, and the extent that marine conditions influence murrelet behavior at sea can vary considerably between years in Southeast Alaska. The Pacific Decadal Oscillation (PDO) regime shifted from warm to cold fall of 2007 (NOAA 2011), which likely caused environmental variation, and may explain the increased average home range and average commute from foraging to nest sites observed in 2008. Consistent with this explanation, hatch success was higher in 2007 than 2008. However, my study was only conducted for two years, so placing these results in long-term context is difficult.

The accumulating data on murrelet productivity suggest it is, on average, relatively low. This could indicate fundamental problems for breeding murrelets throughout their range and possibly that murrelets have evolved a life-history that
includes a bet-hedging reproductive strategy (Seger and Brockman 1987), where long-lived adults experience high reproductive output during infrequent favorable years. During other years adults forego breeding or experience lowered success, making populations highly dependent on maintaining adult survival (Sæther et al. 1996). In theory, population declines may be inevitable if bet-hedging species are exposed to historically uncommon factors that lower reproduction or increase adult mortality. The loss of nesting habitat and increased sources of adult mortality are considered the primary causes for population declines south of Alaska (Rodway 1990, Lynch et al. 2009), and murrelets in Alaska should be susceptible to similar threats. In addition, variable food availability often results in a bet-hedging reproductive strategy, and high prey densities are likely infrequent near most murrelet nest sites. Murrelet diet quality has been reduced considerably over the last century in California (Becker and Beissinger 2006) and British Columbia (Norris et al. 2007), suggesting that years with favorable conditions for nesting are increasingly infrequent. If murrelets rely on a bet-hedging reproductive strategy, minimizing sources of adult mortality and promoting murrelet reproduction will be the most effective conservation strategies.
MANAGEMENT IMPLICATIONS

Several specific management recommendations flow from the results of my research. Managers in Southeast Alaska should incorporate rock cliff and alpine habitat into their definition of murrelet nesting habitat, particularly on the mainland and at higher elevations. Both forested and non-forested habitat types may be equally important to murrelet conservation at some locations. Piatt et al. (2007) suggests that murrelet populations in Alaska have declined more than 70% since the 1970s. Reproductive rates for the population of murrelets nesting in and around Port Snettisham were unexpectedly low and this may be contributing to population declines. The specific reasons for low reproduction are unknown and until better data are available, I recommend that managers implement population surveys in Southeast Alaska to monitor population trends. Based on my results for timing of nesting, such surveys should consider the first week of June as peak nest initiation and end no later than 31 July. If productivity surveys using juvenile to adult ratios at-sea are desired, they should be conducted during August and September to incorporate peak (2-10 August) and late potential fledging dates (16 September). Previous surveys at Auke Bay likely missed a portion of hatch year birds because potential fledging dates for 30% of nests at Port Snettisham were 15 August or later (Speckman et al. 2000).

Marine management actions that seem prudent include some seasonal fishery closures in and immediately nearby Port Snettisham. Gill-net fisheries have been identified as a considerable source of adult murrelet mortality (McShane et al. 2004),
and stocked predatory fish populations can compete with murrelets for food. My results identifying murrelet core use areas and hot spots can be used to help define spatial boundaries of commercial fishery restrictions and marine protected areas in and around Port Snettisham (Fig. 2.4 and Appendix C).

FUTURE RESEARCH

This study poses new information needs regarding murrelet nesting ecology and habitat requirements in Southeast Alaska. Specific information needs include: (1) research to identify sources and importance of nest failure; (2) work to estimate adult survival and identify sources of adult mortality; (3) research linking marine foraging conditions to reproductive rates; (4) work to develop a GIS model to quantify landscape-scale nesting habitat preferences allowing for identification of nesting habitat in other areas; (5) also develop of a fine-scale (< 30 m pixel) regional land cover GIS database, to employ the nesting habitat model, and address other natural resource-related questions; (6) research to document predator abundance within different habitat types; and (7) research to identify nest-site locations and nest success on islands in the Southeast Alaska where the landscape can vary considerably from mainland fjords.

My study indicates that given proper geography, vhf radio-telemetry and data loggers have utility for investigating aspects of murrelet breeding biology. Locating nests with radio-marked birds provides the most unbiased method for characterizing
murrelet nesting habitat preferences, reproductive behavior, and nest success, while avoiding observer related disturbance and minimizing effort (Piatt et al. 2007).

However, given the difficult locations of murrelet nests advancing this research agenda completely may require improvements on current technology. Smaller and longer-lasting tracking devices will give researchers potentially cost-effective methods to document and monitor murrelet nest-sites. Improved tracking devices will also allow researchers to identify potential limiting factors using at-sea locations during fall and winter, time periods when information on murrelet ecology is scarce.

LITERATURE CITED


NESTING SEASON ECOLOGY OF MARBLED MURRELETS
AT A REMOTE MAINLAND FJORD
IN SOUTHEAST ALASKA

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Appendix A

NESTING BEHAVIOR PATTERNS OF MARBLED MURRELETS  
AT PORT SNETTISHAM, SOUTHEAST ALASKA

Blake A. Barbaree
ABSTRACT

Measuring the environmental cues used by Marbled Murrelets to time daily activities is important for understanding species ecology and designing appropriate population surveys. I used radio-marked birds and a series of stationary data loggers to record patterns of nesting behavior for Marbled Murrelets at fjord in Southeast Alaska. The timing of inland flights by adults to nests during the incubation and chick-provisioning periods were significantly related to photoperiod, being most synchronized with civil twilight ($\bar{x} = -1 \pm 21$ min, $n = 357$, $R^2 = 0.321$). The amount of time between civil twilight and sunrise varies by day and latitude, and monitoring surveys should record both civil twilight time and sunrise time to incorporate variation in peak periods of flights to nest sites.

INTRODUCTION

Development of monitoring protocols for avian species is a significant challenge for managers in areas with no local information on nesting ecology. Marbled Murrelets (*Brachyramphus marmoratus*; hereafter murrelets) are listed as federally threatened in California, Oregon, Washington, and British Columbia (USFWS 1992, Rodway 1990), and monitoring protocols have been established and implemented in these areas since the mid-1990s. Nesting murrelets are cryptic, secretive, and primarily crepuscular in their flights from the sea to nest sites. Thus,
little is known about their behavior patterns during nesting, particularly in Alaska, where the majority of the world population of murrelets breeds (Piatt et al. 2007).

General aspects of murrelet nesting behavior are known. Murrelet pairs exhibit nearly equal bi-parental care during nesting. Incubation shifts last roughly 24 hours with exchanges occurring during early morning hours (Nelson and Hamer 1995a); thus daily incubation exchanges result in a predictable pattern of incubation for each individual (“on” the nest one day and “off” the nest the next day). Chick-provisioning rates and timing are less regular but typically occur during early morning (02:00-06:00) or evening (18:00-22:00). The exact time that breeding individuals initiate daily activities will vary by date and latitude. Monitoring protocols refer to time of sunrise when scheduling daily surveys in known and suspected nesting habitat. However, the time of between first light and sunrise increases with latitude and timing of murrelet peak activity could also vary. The exact environmental cues murrelets use to time flights to nest sites and variability associated with that behavior is not known.

As part of a larger multi-faceted study on murrelets in Southeast Alaska, I radio-marked birds during 2007 and 2008 to characterize patterns of nest attendance. Specifically, I addressed three questions: (1) how often do irregular patterns of incubation occur? (2) what cues do breeding murrelets use to initiate commuting flights from at-sea locations to nest sites? and (3) does murrelet chick-provisioning behavior differ between the sexes?
METHODS

I used night lighting (Whitworth et al. 1997) to capture murrelets near the mouth of Port Snettisham (PS) on nights around the new moon that coincided with the beginning of their breeding season (15 - 16 May 2007 [$n = 39$] and 26 - 28 May 2008 [$n = 40$]; see Chapter 3 for detailed methods). The sample in 2007 included both members of three nesting pairs. I attached VHF radio transmitters (Model A1555 ATS, Isanti, MN) that weighed approximately 2.5 g (~1% of murrelet body weight) using the subcutaneous anchor method (Newman et al. 1999). Blood samples were also drawn and analyzed to determine sex (Zoogen 2007) and overall health of birds (Newman et al. 2008).

I tracked and located birds using aerial-, boat-, and ground-based radio-telemetry to: (1) locate nest sites; and (2) monitor daily nest attendance. Data logger receivers (R4500; ATS, Isanti, MN) were deployed at strategic locations (stations) inside PS (Fig. 2.1) to record presence/absence data 24 h/day. Data loggers recorded date and time for all confirmed radio-transmitter detections. By placing data logger antennas at prominent shoreline locations along known flyways, radio-marked murrelet presence and movements were monitored throughout the fjord during the entire study. Radio-telemetry data were pooled by individual to identify and confirm nesting behavior. Once behavior patterns associated with nesting were confirmed, I described abnormal nesting behaviors and quantified departure time from the sea and
frequency of nest-site visits. Means are reported ± standard deviation unless otherwise noted (Streiner 1996).

I used methods similar to Bradley et al. (2004) to identify nesting behavior from patterns in the radio-telemetry data. I used telemetry data to determine breeding status (breeder vs. non-breeder), and nesting phase (incubation vs. chick-provisioning), and document irregularities in nesting behavior patterns, such as irregular incubation shifts. Incubation shifts were considered irregular if a nesting murrelet was detected: (1) at-sea on consecutive days between incubation shifts (e.g., on/off/off/on pattern); (2) incubating for two consecutive days; or (3) at-sea after leaving the nest during an incubation day.

I used detections of radio-marked murrelets recorded by the data logger stations to estimate the timing of inland flights from the sea to nests. I detected flight patterns indicating nest visits by examining data logger detections. Nest attendance was confirmed on days coinciding with aerial surveys. Specifically, I estimated departure time for a flight to the nest as the last data logger detection prior to nest attendance. An incubation shift was inferred when data loggers detected movement towards the nest site and the bird was later detected at the nest during an aerial survey or not detected at-sea again for 24 hours (Nelson and Hamer 1995). I identified timing and frequency of chick provisioning by if a radio-marked bird was detected at-sea 1-3 hours after initial movement towards the nest site. Although murrelets are known to
provision chicks during daylight hours (Nelson and Hamer 1995), movements towards or away from the nest site from 06:00 to 19:00 were rarely consistent with definitive evidence of chick provisioning behavior. As a result, I have excluded apparent chick provisioning flights during mid-day hours. Chick provisioning rates were also separated by sex because males are thought to provision nestlings more frequently than females, particularly during late stages of the nesting period (Vanderkist et al. 1999, Bradley et al. 2002).

Because the exact cue that murrelets use to time their commuting flights to nest sites is not clear, I used simple linear regression models (PROC REG; SAS Institute, 2003) to investigate the relationship between time of departure to the nest site and official sunrise and civil twilight. Official civil twilight begins in the morning and ends in the evening when the sun is geometrically 6° below the horizon and generally coincides with the time ambient light at ground level exceeds or falls below zero lux (USNO 2010). I used mixed general model analyses with fixed effects (sunrise or twilight time, sex, and year) and individual murrelet as a repeated effect (PROC MIXED; SAS Institute 2003). Choosing an appropriate covariance structure for repeated effects was critical to producing powerful inference (Littell et al. 2000). In addition, not accounting for temporally dependent data may lead to improper validation or rejection of a research hypothesis (Carroll and Pearson 2000). I selected the auto-regressive moving average covariance structure (ARMA 1,1) based on
Akaike Information Criterion results from models using several applicable covariance structures (Burnett et al. 2010). ARMA (1,1) typically fits unbalanced longitudinal data and allowed a time-dependent covariance structure for each individual, while utilizing a minimal number of parameters (Rochon 1992). Finally, I used two-tailed t-tests (PROC TTEST; SAS Institute, 2003) to assess sex-specific differences in provisioning flight frequency and time of day.

RESULTS

Irregular incubation shifts were detected on 33 separate occasions at 15 of 42 (35.7%) nests with known hatch fate. Egg neglect (or a murrelet detected at sea during an incubation day) was also observed on several occasions. For example, a male murrelet was detected at-sea by data loggers from 13:03 to 22:28 on 20 June 2007 between definitive inland movements, including confirmation of nest attendance during an early morning aerial survey. Two radio-marked murrelet pairs also displayed irregular incubation behavior. On 18 June 2007, a female murrelet terminated an incubation shift 101 minutes prior to its mate flying inland to incubate, likely leaving the nest unattended for a short period. The same female murrelet did not return to incubate on 23 or 30 June 2007, while its mate was detected incubating for two consecutive days on both occasions. The same pattern was also observed when a different female murrelet did not return to incubate on 8 July 2007, leaving the
male murrelet incubating for two consecutive days. Radio-telemetry also indicated that this pair did not incubate on 13 June 2007 when both murrelets were detected at-sea by data loggers throughout the day.

Males accounted for 11 of 18 (61.1%) provisioning events for two radio-marked pairs whose nests failed during early chick-provisioning (< 10 days post-hatch). Conversely, the male for the third pair only accounted for 12 of 39 (30.7%) recorded events and ceased chick-provisioning behavior after 11 days, while the female continued provisioning behavior for at least an additional 14 days.

Data loggers recorded 357 departure times from the sea to nest sites during incubation, at least one observation for 33 of 38 nesting radio-marked murrelets. Undetected murrelets had nest-site flyways outside the range of my data loggers. Pooled mean daily departure time from the sea during incubation was 75 ± 20 min prior to sunrise and 0.6 ± 21 min prior to morning civil twilight (Table A.1). Departure time during incubation was significantly correlated with sunrise ($R^2 = 0.345; F_{1,323} = 101.9; p < 0.0001$; Fig. A.1) and civil twilight time ($R^2 = 0.321; F_{1,323} = 101.9; p < 0.0001$), but did not differ by sex or year.

Data loggers recorded 208 morning and 52 evening sea departure times during chick-provisioning for 19 nesting murrelets in 2007 and 2008. Pooled mean morning departure time during chick-provisioning was 72 ± 21 min prior to sunrise and 7 ± 33 min prior to civil twilight (Table A.2). Morning provisioning flight departure time
was significantly correlated with sunrise ($R^2 = 0.194; F_{1,188} = 27.29; p < 0.0001$; Fig. A.2) and civil twilight ($R^2 = 0.191; F_{1,188} = 25.82; p < 0.0001$), and less evidence that evening departure time was synchronized with sunset ($R^2 = 0.069; F_{1,38} = 9.55; p = 0.004$) or evening civil twilight ($R^2 = 0.069; F_{1,38} = 11.27; p = 0.002$). Again, departure times did not differ by sex or year.

Male murrelets had a higher rate of daily chick-provisioning events compared to females, and were more likely than females to provision chicks during evening hours (both two-tailed $p < 0.0001$; Table A.3). Both males and females fed chicks more frequently near sunrise than near sunset, with morning flights accounting for 79.9% of all provisioning events (Fig. A.3). Male provisioning flights occurred more often during evening hours ($n = 43$ of $160$) compared to females ($n = 13$ of $107$).

**DISCUSSION**

Use of stationary data loggers along flyways to monitor nest attendance provided useful information on incubation patterns and departure times from the sea to nests for a large sample of nesting murrelets. Murrelets nesting within the fjord were regularly detected traveling to and from nest sites because of the unique topography of Port Snettisham. Areas with similar topography should employ these methods when information on presence or movement patterns is of interest.
Irregular incubation patterns (murrelets remaining at-sea for two consecutive days) or egg neglect (murrelets leaving eggs unattended) was common (35.7%) for nesting murrelets in my study. Egg neglect has been documented in other murrelet studies (e.g., Nelson and Peck 1995) and is also common among other alcids (e.g., Astheimer 1991, Gaston and Powell 1989, Wolf et al. 2005). Murrelets that displayed irregular incubation patterns (and had successful hatch fate) incubated 4.2 days longer on average, which suggests these behaviors may prolong the incubation period. The secretive nesting habits of murrelets have restricted our knowledge of behavior at nests, but my findings identify a need for research regarding murrelet nest-site attendance and its influence on nest fate.

Departure times from the sea to nest sites during incubation were highly correlated with both sunrise and civil twilight; however, mean departure time was more directly centered on civil twilight. The relationship between departure time and civil twilight was much weaker during chick-provisioning, particularly during the evening when it appeared to have no biologically important association. Studies in British Columbia (Burger 1997) and Oregon (Cooper et al. 2001) also noted that the timing of peak movements inland was near morning civil twilight, ambient light appears to be the key zeitgeber for murrelet flights to their nest sites. Terrestrial and at-sea murrelet monitoring protocols schedule daily surveys based on time of sunrise, which is considered the peak of inland flight activity. However, the time period
between official civil twilight and sunrise varies daily at Port Snettisham (range = 42 - 79 min) from 1 May to 31 August, peaking on or near 21 June. Beginning daily surveys two hours prior to sunrise may miss a portion of inland flights in Alaska. My findings suggest that using that civil twilight is a more appropriate time to reference when scheduling surveys, particularly in Alaska.

Male murrelets provisioned chicks more often than females, particularly during evening hours. My results support previous findings in British Columbia where a significant male bias was reported for un-marked murrelets flying inland (Vanderkist et al. 1999) and total and evening provisioning events for radio-marked murrelets (Bradley et al. 2002). Data from all studies suggest that female chick-provisioning rates are more likely to decrease during late stages of nesting. However, I detected a the female member of a radio-marked pair actively attending a nest more than 14 days after the male ceased provisioning behavior. While male-biased provisioning appears to predominate in murrelets, a reduced role the male does occur. Female murrelets may reach an energetic threshold more often than males, where survival costs outweigh the benefits of provisioning offspring, as has been described in several smaller avian species (Bryant and Tatner 1991). If an investment threshold limits parental care in murrelets, nestlings are more at risk of abandonment or malnutrition during late provisioning due to a greater chance of decreased parental investment, dwindling adult energy reserves, or mortality of a provisioning adult.
LITERATURE CITED


Figure A.1. Departure times of adult Marbled Murrelets from the sea to nest sites during the incubation period (Y-axis) as a function of time of sunrise (top) and of civil twilight (bottom) for birds radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Lines represent least squares regression lines.
Figure A.2. Departure times of adult Marbled Murrelets from the sea to nest sites during the chick-provisioning period in the morning (top; 02:00 - 06:00) and in the evening (bottom; 19:00 - 23:00) as a function of time of sunrise/sunset and of civil twilight for birds radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Boxes contain values for least squares regression lines.
Figure A.3. Numbers of chick-provisioning events recorded for male ($n = 12$) and female ($n = 5$) radio-marked Marbled Murrelets during morning (02:00 - 06:00) and evening (19:00 - 23:00) hours in 2007 and 2008 at Port Snettisham, Southeast Alaska. The total column includes two birds of unknown sex.
Table A.1. Pooled mean departure time from the sea to nest sites during incubation for Marbled Murrelets radio-marked in 2007 ($n = 18$) and 2008 ($n = 15$) at Port Snettisham, Southeast Alaska. Means are reported ± SD.

<table>
<thead>
<tr>
<th>Year</th>
<th>Times ($n$)</th>
<th>Mean Time</th>
<th>Minutes +/- Sunrise</th>
<th>Minutes +/- Civil Twilight</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>224</td>
<td>2:42 ± 26 min</td>
<td>-74 ± 21</td>
<td>1 ± 21</td>
</tr>
<tr>
<td>2008</td>
<td>133</td>
<td>2:43 ± 25 min</td>
<td>-78 ± 19</td>
<td>-3 ± 20</td>
</tr>
<tr>
<td>Total</td>
<td>357</td>
<td>2:41 ± 26 min</td>
<td>75 ± 20</td>
<td>-0.6 ± 21</td>
</tr>
</tbody>
</table>
Table A.2. Mean departure time from the sea to nest sites during chick-provisioning for 19 Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Time of day reported as 02:00 - 06:00 (AM) and 18:00 - 22:00 (PM). Means are reported ± SD.

<table>
<thead>
<tr>
<th>Year</th>
<th>Time of Day</th>
<th>Times (n)</th>
<th>Mean Time</th>
<th>Minutes +/- Sunrise</th>
<th>Minutes +/- Civil Twilight</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>AM</td>
<td>131</td>
<td>3:24 ± 27</td>
<td>-50 ± 32</td>
<td>18 ± 34</td>
</tr>
<tr>
<td></td>
<td>PM</td>
<td>40</td>
<td>21:28 ± 41</td>
<td>-27 ± 36</td>
<td>-95 ± 36</td>
</tr>
<tr>
<td>2008</td>
<td>AM</td>
<td>77</td>
<td>3:07 ± 29</td>
<td>-72 ± 21</td>
<td>-11 ± 21</td>
</tr>
<tr>
<td></td>
<td>PM</td>
<td>12</td>
<td>21:39 ± 34</td>
<td>-23 ± 35</td>
<td>-76 ± 43</td>
</tr>
<tr>
<td>Total</td>
<td>AM</td>
<td>208</td>
<td>3:22 ± 33</td>
<td>-72 ± 21</td>
<td>-7 ± 33</td>
</tr>
<tr>
<td></td>
<td>PM</td>
<td>52</td>
<td>21:29 ± 38</td>
<td>-23 ± 35</td>
<td>-93 ± 47</td>
</tr>
</tbody>
</table>
Table A.3. Chick-provisioning event rates by sex (morning = 02:00 - 06:00; evening = 19:00 - 23:00) for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. Two birds of unknown sex were included in total row. Means are reported ± SD.

<table>
<thead>
<tr>
<th></th>
<th>Morning</th>
<th>Evening</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>0.78 ± 0.22</td>
<td>0.23 ± 0.22</td>
<td>1.0 ± 0.32</td>
</tr>
<tr>
<td>n = 12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>0.69 ± 0.20</td>
<td>0.04 ± 0.04</td>
<td>0.73 ± 0.23</td>
</tr>
<tr>
<td>n = 5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>0.74 ± 0.20</td>
<td>0.17 ± 0.20</td>
<td>0.91 ± 0.31</td>
</tr>
<tr>
<td>n = 19</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Appendix B

BROOD PATCH STATUS AND THE EFFECTS OF CAPTURE ON THE REPRODUCTIVE STATUS OF MARBLED MURRELETS AT PORT SNETTISHAM, SOUTHEAST ALASKA

Blake A. Barbaree
Evaluation of brood patch presence and stage is considered an indicator of reproductive status for most avian species. However, low nest initiation rates have been recorded for Marbled Murrelets (*Brachyramphus marmoratus*; hereafter murrelet), even for birds with well developed brood patches (see Chapter 3). The age at first nesting is not known for murrelet (Nelson 1997), and brood patch evaluation was not a good indicator of reproductive status for murrelets in British Columbia (McFarlane Tranquilla *et al.* 2003). Adult murrelets may undertake a reproductive strategy where nesting is not attempted every year, but no previous data on brood patches has been reported for Alaska. As part of a larger study on murrelet nesting ecology, I used information on brood patches collected during capture and subsequent documentation of nesting behavior to investigate: (1) the prevalence of non-breeding murrelets with brood patches; and (2) the effects of capture, handling and radio-marking on nesting.

I used night lighting (Whitworth *et al.* 1997) to capture murrelets near the mouth of Port Snettisham (PS) on nights around the new moon that coincided with the beginning of the breeding season (15 - 16 May 2007 [*n* = 39] and 26 - 28 May 2008 [*n* = 40]; see Chapter 3 for detailed methods). I attached VHF radio transmitters (Model A1555 ATS, Isanti, MN) that weighed approximately 2.5 g (~1% of murrelet body weight) using the subcutaneous anchor method (Newman *et al.* 1999) to all birds during 2006 to 2008. Brood patches were evaluated and scored based on Sealy (1974)
to assess reproductive status. Brood patch scores ranged from zero (no brood patch) to six (full regression) with a score of three representing a fully developed brood patch. Blood samples were also drawn and analyzed to determine sex (Zoogen 2007) and overall health of birds (Newman et al. 2008). To assess potential impacts of capture on female egg formation, I used a one-way ANOVA to test whether the number of days between capture and nest initiation varied by sex (PROC ANOVA, SAS Institute, 2003). To assess potential temporal or capture effects on female egg production, I tested for an effect of sex and year on breeding status using a generalized linear model with fixed effects (PROC GENMOD; SAS Institute, 2003).

I captured and radio-marked 119 murrelets during 2006 - 2008, including both members of three breeding pairs in 2007 (Table 3.1). A radio-marked murrelet from 2006 was re-captured in 2008 and radio-marked again; this murrelet was in good health when re-captured and the transmitter from 2006 was still attached to a small external skin flap. It nested at the same inaccessible cliff nest site in both years.

Brood patch evaluations indicated individual and annual variation in breeding stage at the time of capture (Table B.1). Most murrelets captured in late April 2006 (31 of 40) had a brood patch score of ≤ 1 indicating a pre-breeding phase. I delayed the capture period by several weeks during 2007 and 2008 to more closely coincide with peak nest initiation. Consequently, nearly all murrelets captured during 2007 and 2008 had developing or fully developed brood patches (83.5%, n = 66 of 79). During
2006 - 2008, 40.7% \((n = 33)\) of the murrelets with significant brood patch development \((\text{score} \geq 1)\) at the time of capture were subsequently classified as breeders and 20.7% \((n = 6)\) of the murrelets with no brood patch \((\text{score} = 0)\) were subsequently classified as breeders.

In 2007 and 2008, incubation behavior by female murrelets was first noted between 5 and 50 days after capture. Egg development in female alcids typically requires around 15 days (Gaston and Jones 1998), but the development period in murrelets was unknown. Capture likely occurred during egg formation for 38.5% \((n = 5\) of 13) of nesting female murrelets because incubation behavior began \(\leq 10\) days post-capture. Proportionally fewer male murrelets \((27.6%; \ n = 8\) of 29) began incubation behavior \(\leq 11\) days post-capture, although the number of days between capture and nest initiation did not differ by sex \((F_{1,39} = 0.49, p = 0.49)\). Male radio-marked murrelets \((66\%)\) were more frequently involved with nesting attempts than female radio-marked murrelets \((34\%; \ \chi^2 = 10.69, p = 0.002)\). Nest initiation rate did not differ by year \((\chi^2 = 0.280, p = 0.60)\).

My results suggest that brood patch presence and stage of development were not reliable indicators of murrelet reproductive status at Port Snettisham. Murrelets may undertake a reproductive strategy whereby reproductively mature individuals do not nest every year. Low nest initiation rates at Port Snettisham and during previous studies suggest this behavior is a strategy to increase survival rates (see Chapter 3).
Presence of a brood patch on a murrelet may indicate reproductive maturity, but the age at first breeding is not known. Reproductive maturity may occur before birds have developed sufficient behavioral or social capabilities to nest.

My results also suggest that the effects of capture, handling, and radio-marking were significant for some individuals, particularly females. The effects of capture related effects could be detrimental to egg development, particularly for birds closer to incubation. Radio-marking may also have effects beyond handling because transmitters may induce drag during flights or foraging dives. Regardless, the overall effects will vary by individual, likely depending on sex, quality of the bird, breeding stage, and handling time. Radio-marking only male murrelets may produce a more accurate measure of nest initiation rate and increase the number of documented nest-site locations. Developing a method to determine sex of murrelets in the field may increase the utility of radio-telemetry studies in search of nest locations and reproductive parameters. Finally, researchers should always attempt to reduce capture-induced stress by minimizing handling time and pursuit time during capture.

LITERATURE CITED


Table B.1. Brood patch development scores (based on Sealy 1974) assessed for all Marbled Murrelets captured from 2005 to 2008 at Port Snettisham, Southeast Alaska.

<table>
<thead>
<tr>
<th>Score</th>
<th>Late-June 2005</th>
<th>Late-April 2006</th>
<th>Mid-May 2007</th>
<th>Late-May 2008</th>
<th>Breeders</th>
<th>Non-breeders</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 = No brood patch</td>
<td>0</td>
<td>16</td>
<td>7</td>
<td>6</td>
<td>6</td>
<td>23</td>
</tr>
<tr>
<td>0.5 = Starting to de-feather</td>
<td>0</td>
<td>5</td>
<td>2</td>
<td>0</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>1 = Partially de-feathered</td>
<td>0</td>
<td>10</td>
<td>5</td>
<td>9</td>
<td>8</td>
<td>16</td>
</tr>
<tr>
<td>1.5 = 50% de-feathered</td>
<td>0</td>
<td>2</td>
<td>7</td>
<td>4</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>2 = Mostly de-feathered</td>
<td>0</td>
<td>4</td>
<td>11</td>
<td>12</td>
<td>14</td>
<td>13</td>
</tr>
<tr>
<td>2.5 = Nearly all de-feathered</td>
<td>0</td>
<td>3</td>
<td>6</td>
<td>2</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td>3 = Fully de-feathered</td>
<td>27</td>
<td>0</td>
<td>1</td>
<td>7</td>
<td>4</td>
<td>31</td>
</tr>
<tr>
<td>3.5 = Starting to regress</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
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<td>4 = Partial regression</td>
<td>2</td>
<td>0</td>
<td>0</td>
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<td>2</td>
</tr>
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Appendix C

FIXED KERNEL DENSITY ESTIMATES FOR MARBLED MURRELETS AT A REMOTE MAINLAND FJORD SYSTEM IN SOUTHEAST ALASKA: CORE USE AREA OVERLAP MAPS AND DATA TABLES

Blake A. Barbaree
Figure C.1. Core use areas (50% fixed kernel density estimate) overlapped for Marbled Murrelets \( n = 72 \) radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska.
Figure C.2. Core use areas (50% fixed kernel density estimate) overlapped for Marbled Murrelets radio-marked in 2007 ($n = 37$) at Port Snettisham, Southeast Alaska.
Figure C.3. Core use areas (50% fixed kernel density estimate) overlapped for Marbled Murrelets radio-marked in 2008 (n = 35) at Port Snettisham, Southeast Alaska.
Figure C.4. Illustration of methods for fixed kernel density estimation used for a Marbled Murrelet radio-marked in 2008 (ID = 041-08) at Port Snettisham, Southeast Alaska. A) At-sea detections or vector point data layer; B) fixed kernel density estimation results or raster data layer; C) final vector polygons with terrestrial portions erased.
Table C.1. Fixed kernel density estimates of home range (95%) and core use area (50%) size (km) for Marbled Murrelets radio-marked in 2007 at Port Snettisham, Southeast Alaska.

<table>
<thead>
<tr>
<th>Murrelet</th>
<th>Year</th>
<th>Sex</th>
<th>Breeder</th>
<th>n</th>
<th>95%</th>
<th>50%</th>
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<tr>
<td>001-07</td>
<td>2007</td>
<td>F</td>
<td>Y</td>
<td>22</td>
<td>87.34</td>
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</tr>
<tr>
<td>031-07</td>
<td>2007</td>
<td>-</td>
<td>Y</td>
<td>21</td>
<td>50.03</td>
<td>15.18</td>
</tr>
<tr>
<td>043-07</td>
<td>2007</td>
<td>M</td>
<td>Y</td>
<td>28</td>
<td>48.09</td>
<td>12.05</td>
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<td>051-07</td>
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<td>F</td>
<td>Y</td>
<td>20</td>
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</tr>
<tr>
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<td>Y</td>
<td>25</td>
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<td>Y</td>
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<td>Y</td>
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<td>M</td>
<td>N</td>
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<td>086-07</td>
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<td>N</td>
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<td>23.93</td>
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<td>2007</td>
<td>F</td>
<td>N</td>
<td>18</td>
<td>115.22</td>
<td>26.33</td>
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<td>2007</td>
<td>M</td>
<td>Y</td>
<td>19</td>
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<td>26.02</td>
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<tr>
<td>095-07</td>
<td>2007</td>
<td>F</td>
<td>Y</td>
<td>28</td>
<td>119.70</td>
<td>40.16</td>
</tr>
<tr>
<td>098-07</td>
<td>2007</td>
<td>-</td>
<td>Y</td>
<td>20</td>
<td>31.34</td>
<td>10.37</td>
</tr>
</tbody>
</table>
Table C.2. Fixed kernel density estimates of home range (95%) and core use area (50%) size (km) for Marbled Murrelets radio-marked in 2008 at Port Snettisham, Southeast Alaska.

| Murrelet | Year | Sex | Breeder | n  | Fixed Kernel Density Estimate |
|----------|------|-----|---------|----|-------------------------------|---|---|---|---|---|---|
|          |      |     |         |    | 95%  | 50%  |     |     |     |     |     |
| 041-08   | 2008 | F   | Y       | 41 | 120.04 | 33.00 |
| 062-08   | 2008 | M   | Y       | 44 | 133.93 | 35.84 |
| 081-08   | 2008 | F   | N       | 12 |  58.23 | 13.58 |
| 102-08   | 2008 | M   | Y       | 44 | 122.20 | 32.99 |
| 122-08   | 2008 | M   | N       | 12 | 443.59 |132.36 |
| 141-08   | 2008 | F   | N       | 17 |  86.16 | 22.86 |
| 161-08   | 2008 | M   | Y       | 18 |  98.00 | 32.20 |
| 181-08   | 2008 | F   | Y       | 15 |  63.88 | 19.62 |
| 202-08   | 2008 | F   | N       | 29 |  58.40 | 13.33 |
| 222-08   | 2008 | M   | Y       | 34 | 334.06 | 98.82 |
| 242-08   | 2008 | M   | Y       | 26 | 126.46 | 30.80 |
| 260-08   | 2008 | M   | Y       | 47 |  84.94 | 19.59 |
| 283-08   | 2008 | F   | N       | 21 | 144.52 | 50.09 |
| 304-08   | 2008 | M   | Y       | 24 | 231.79 | 53.17 |
| 321-08   | 2008 | F   | N       | 20 | 201.23 | 64.07 |
| 342-08   | 2008 | M   | N       | 37 | 384.86 | 88.29 |
| 360-08   | 2008 | F   | Y       | 36 | 203.27 | 51.61 |
| 381-08   | 2008 | F   | N       | 55 | 141.71 | 28.41 |
| 402-08   | 2008 | F   | N       | 53 |  38.20 |  6.39 |
| 421-08   | 2008 | M   | Y       | 32 | 178.85 | 46.66 |
| 442-08   | 2008 | M   | N       | 32 |  94.65 | 26.35 |
| 461-08   | 2008 | F   | N       | 35 | 179.46 | 42.74 |
| 483-08   | 2008 | F   | N       | 17 | 274.13 | 82.33 |
| 502-08   | 2008 | F   | N       | 16 | 240.59 | 85.42 |
| 522-08   | 2008 | M   | N       | 16 |  48.81 | 10.91 |
| 544-08   | 2008 | F   | N       | 32 | 335.91 | 77.24 |
| 562-08   | 2008 | F   | Y       | 37 | 311.55 | 98.48 |
| 585-08   | 2008 | M   | Y       | 23 | 127.66 | 35.94 |
| 623-08   | 2008 | F   | N       | 41 | 109.40 | 28.65 |
| 682-08   | 2008 | F   | N       | 14 | 155.50 | 43.93 |
| 742-08   | 2008 | F   | Y       | 18 |  43.81 | 11.82 |
| 804-08   | 2008 | M   | Y       | 36 |  64.79 | 15.46 |
| 832-08   | 2008 | F   | N       | 54 | 125.72 | 30.23 |
| 891-08   | 2008 | M   | Y       | 36 |  49.59 | 11.16 |
| 924-08   | 2008 | F   | Y       | 16 | 135.74 | 39.93 |
Table C.3. Fixed kernel density estimates (FKDE) of home range (95%) and core use area (50%) by year, sex, and breeding status for Marbled Murrelets radio-marked in 2007 and 2008 at Port Snettisham, Southeast Alaska. $n$ = number of individual estimates.

<table>
<thead>
<tr>
<th>Sample Segment</th>
<th>Year</th>
<th>$n$</th>
<th>95% FKDE (km²)</th>
<th>50% FKDE (km²)</th>
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<tr>
<td></td>
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<td></td>
<td>Mean ± SD</td>
<td>Min</td>
</tr>
<tr>
<td>All</td>
<td>2007</td>
<td>37</td>
<td>97.8 ± 59.4</td>
<td>31.3</td>
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<td>2008</td>
<td>35</td>
<td>158.6 ± 103.7</td>
<td>38.2</td>
</tr>
<tr>
<td>Male</td>
<td>2007</td>
<td>16</td>
<td>95.9 ± 63.1</td>
<td>38.0</td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>20</td>
<td>168.3 ± 124.6</td>
<td>48.8</td>
</tr>
<tr>
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<td>2007 &amp; 2008</td>
<td>34</td>
<td>127.9 ± 100.4</td>
<td>38.0</td>
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<tr>
<td></td>
<td>2007</td>
<td>19</td>
<td>107.2 ± 56.2</td>
<td>35.7</td>
</tr>
<tr>
<td>Female</td>
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<td>15</td>
<td>151.4 ± 87.7</td>
<td>38.2</td>
</tr>
<tr>
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<td>2007 &amp; 2008</td>
<td>36</td>
<td>131.8 ± 77.6</td>
<td>35.7</td>
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<tr>
<td></td>
<td>2007</td>
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<td>95.1 ± 50.7</td>
<td>31.3</td>
</tr>
<tr>
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<td>143.0 ± 85.0</td>
<td>43.8</td>
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<td>116.5 ± 71.4</td>
<td>31.3</td>
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<tr>
<td></td>
<td>2007</td>
<td>16</td>
<td>101.5 ± 70.9</td>
<td>35.7</td>
</tr>
<tr>
<td>Non-breeder</td>
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<td>173.4 ± 119.4</td>
<td>38.2</td>
</tr>
<tr>
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<td>2007 &amp; 2008</td>
<td>34</td>
<td>139.6 ± 104.6</td>
<td>35.7</td>
</tr>
</tbody>
</table>