Brachyramphus murrelets at high latitude: behavioural patterns and new methods for population monitoring

by

Jenna Louise Cragg
B.Sc., University of Victoria, 2007

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of the Requirements for the Degree of

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in the Department of Biology

Supervisory Committee

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Outside Member

Abstract

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Developing cost-effective tools for population monitoring and research is fundamental to wildlife management programs. This is a major challenge for solitary-nesting, secretive seabirds distributed throughout remote areas of Alaska: the marbled murrelet (*Brachyramphus marmoratus*) and Kittlitz's murrelet (*B. brevirostris*). Both species have experienced major population declines in Alaska, which is the centre of the distribution of their global populations. In 2010-2012, I tested the reliability of two new remote-sensing approaches, marine radar surveys and autonomous acoustic monitoring, to assess population size, trends and distributions of *Brachyramphus* murrelets in the Kodiak Archipelago. The goals were to compare new and existing assessment tools, to identify differences in spatial and temporal patterns of activity by *Brachyramphus* murrelets at high latitudes, and to make recommendations for integrating remote-sensing methods into existing monitoring programs.

Autonomous acoustic sensors provided a reliable index of marbled murrelet abundance at fine spatial scales (2-3 ha forest stands). Detections of marbled murrelet vocalizations by acoustic sensors and human observers were not statistically different across weekly means. Because high temporal replication could be achieved at no extra cost, automated acoustic sampling provided the best seasonal resolution in patterns of murrelet activity. Radar surveys identified a prolonged (150 min) duration of pre-sunrise inland flight activity relative to lower-latitude populations, reflecting the longer duration of twilight at high latitude. A clear trend in seasonal activity, increasing from June to late July, was identified by radar, audio-visual, and acoustic surveys. The strong seasonal increase in activity detected by radar surveys appears to be an important factor to consider in planning population monitoring programs. Radar surveys could not distinguish between Kittlitz’s and marbled murrelets, but identified potentially greater frequency of inland flight by Kittlitz’s murrelets during darkness based on comparisons between sites. Spatial patterns of abundance, estimated by radar counts, were best predicted by combinations of marine and terrestrial habitat variables within 5 km of nesting flyways, including area of steep slopes (45-90°), area of old-growth forest, and at-sea densities < 200 m from shore in June. The largest murrelet populations occurred in both forested and unforested watersheds with steep topography; indicating that unforested steep slopes appear to be of greater importance to nesting marbled murrelets in Alaska than previously recognized, particularly in areas adjacent to marine productivity hotspots.

I recommend that radar sampling protocols be modified for high latitude surveys to begin 2 h before sunrise to accommodate longer activity periods, and that surveys be repeated at similar dates across years to avoid confounding population change with seasonal changes in abundance. I propose integrating new remote-sensing tools into existing monitoring programs to increase power to detect population trends, reduce costs and risks associated with field personnel, and increase capacity for long-term monitoring of murrelet response to environmental change at multiple spatial scales.

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Introduction

Background

Rare and secretive species pose challenges to researchers seeking to evaluate population size, trends and distributions, yet these species are often of conservation concern and most in need of study. Understanding patterns of abundance and habitat use, and developing cost-effective methods to census and monitor populations are crucial components of wildlife management and research. For rare species, the difficulties in achieving these goals are compounded when animals are found in remote areas, are highly mobile, and rely on spatially disjunct habitats.

Remote-sensing approaches in wildlife monitoring can provide cost-effective, non-invasive research and inventory tools (Pauli et al. 2009, Jewell 2013). Advances in technology have produced a variety of remote-sensing options that can be integrated into monitoring programs, including remote cameras (Rowcliffe & Carbone 2008), acoustic monitoring (Blumstein et al. 2011), vocalization identification (Terry et al. 2005), and radar systems (Gauthreaux & Belser 2003). Automated systems provide cost-savings by reducing field personnel requirements and allowing researchers to sample efficiently in situations that would otherwise be logistically challenging, such as in remote or poorly accessible sites, or for nocturnal observations of animal behaviour (Wrege et al. 2010, Buxton & Jones 2012). Radar scanning allows researchers to track the movements of aerial species over wide areas, and over all light levels (Hamer et al. 1995, Burger 1997). This technology has made major contributions to the field of migration monitoring in birds and bats, and has been applied to conservation projects to mitigate the impacts of development projects along flyways (reviewed in Gauthreaux & Belser 2003, Chilson et al. 2012).

This study tested two remote-sensing approaches for monitoring populations of rare, threatened seabirds in Alaska: radar and autonomous acoustic recording. The goal was to test the reliability of these new methods of population monitoring in comparison with established methods in Alaska, namely, at-sea vessel counts and audio-visual surveys in nesting habitat. New and established tools were tested in combinations to make recommendations for integrating methods to refine and improve population monitoring, and to gain understanding of high-latitude behaviours of these secretive seabirds.

Study species

This study examines two congeneric alcid species: the marbled murrelet (*Brachyramphus marmoratus*; Gmelin, 1789) and the Kittlitz's murrelet (*B. brevirostris*; Vigors, 1829) which are rare, solitary-nesting seabirds that breed sympatrically in parts of Alaska. The unique, non-colonial nesting strategy of *Brachyramphus* murrelets (in contrast to other genera of Alcids and in fact most other seabirds) has expanded the range of nesting habitats occupied by these species beyond the predator-limited offshore islands or cliffs typically occupied by colonial seabird species into forests and alpine habitats up to 80 km from the ocean. The low nesting density of *Brachyramphus* murrelets is mirrored at sea, where murrelets forage in small groups (mainly solitary birds or pairs) to exploit small prey schools in inshore waters (Ostrand et al. 1998, Kuletz 2005). Non-colonial nesting is accompanied by a suite of traits that have evolved to minimize detection by predators, including cryptic plumage and breeding sites, and secretive nest attendance patterns (Gaston & Jones 1998). *Brachyramphus* murrelets are long-lived, with low reproductive rates and slow population turnover (Beissinger 1995, Nelson 1997, Cam et al. 2003, Day & Nigro 2004, Peery et al. 2004a). The two Alaskan murrelet species have subtle differences in their nesting and foraging ecology, which likely reduces interspecific competition and allowing for coexistence across many areas of the Alaskan coast. Both species have experienced major population declines in Alaska, leading to conservation concerns and the need for increased monitoring efforts.

The global distribution of the Kittlitz's murrelet, as well as its nesting and foraging habitat selection reflect an association with glacially-influenced habitat, and this association is particularly strong during the breeding season (van Vliet 1993). Kittlitz's murrelets have a patchy distribution along the coast of Alaska and into the Russian Far

East, with a global population size estimated to be between 30,900-56,800 birds (USFWS 2010). Nesting is exclusively on the ground, on rocky talus slopes free of vegetation (Day et al. 1999). Suitable nest sites occur in recently deglaciated areas, glacial moraines, cliffs, and high-elevation alpine areas associated with glaciers. The preferred marine foraging habitat of Kittlitz's murrelets is also associated with glacial runoff and tidewater glaciers (Day & Nigro 2000, Arimitsu et al. 2012).

Marbled murrelets range from central California to the Aleutian Islands, generally nesting on mossy platforms on large limbs of old-growth conifers in forested areas (Nelson 1997), but also on the ground in areas with limited availability of tree-nest sites (Bradley & Cooke 2001). In Alaska, approximately 97% of marbled murrelets are thought to nest in trees (Piatt & Ford 1993), but the true proportion of ground-nesters may in fact be higher (Barbaree 2011, unpublished data from M. Kissling, U.S. Fish & Wildlife Service). The global population of marbled murrelets is approximately 359,200 (COSEWIC 2012), with approximately 66% of the global population occurring in Alaska (237,500; Piatt et al. 2007, M. Kissling pers. comm.). Marbled murrelets forage in nearshore marine waters and are associated with a variety of marine features across their range, including sandy beaches, kelp forests, sills and upwellings (Becker & Beissinger 2003, Yen et al. 2004, Kuletz 2005, Ronconi 2008).

Marbled and Kittlitz's murrelets have varying degrees of niche segregation and overlap across areas of coexistence in Alaska. A gradient of morphological and behavioural convergence is found between the two species despite an apparent lack of underlying genetic convergence (Pitocchelli et al. 1995, Congdon et al. 2000, Pacheco et al. 2002, Friesen et al. 2005). Marbled murrelets appear to have more phenotypic variation and behavioural plasticity than Kittlitz's murrelets. In areas without forests, marbled murrelets have adapted to nest on the ground, and these populations are morphologically intermediate between tree-nesting marbled murrelets and Kittlitz's murrelets (Pitocchelli et al. 1995). Across the latitudinal gradient from California to Alaska, marbled murrelet nest-site selection appears to reflect the local availability of potential nest platforms, with the proportion of ground-nesting apparently increasing with latitude, (Piatt et al. 2007, Barbaree 2011, unpublished data from M. Kissling, U.S. Fish & Wildlife Service). Comparatively, Kittlitz's murrelets appear to be confined to a relatively narrow ecological niche; nesting is exclusively on the ground, and apparently tied to areas with recent or current glaciation. It is not known to what degree interspecific competition influences behaviour, phenotypic plasticity, local persistence and abundance of each species in areas of overlap.

Both species of murrelets are of conservation concern in Alaska; marbled murrelet populations have declined by 70% over the last 25 years (Piatt et al. 2007), while Kittlitz's murrelet populations have declined in core population areas by as much as 85% in recent years (63% from 1989-2004 in Prince William Sound, Kuletz et al. 2011a; 84% from 1993-1999 in Lower Cook Inlet, Kuletz et al. 2011b; 85% from 1991-2008 in Glacier Bay, Piatt et al. 2011), although an overall rate of decline in Alaska has not been estimated. The marbled murrelet is federally listed as Threatened under the U. S. Endangered Species Act (ESA), although this does not apply to the Alaska population. The Kittlitz's murrelet has been a Candidate species for listing under the ESA since 2004, and a decision on its status is expected in September 2013.

Threats to both species in the marine environment include changes in marine food webs (Becker & Beissinger 2006, Norris et al. 2007), fisheries bycatch (reviewed in Piatt et al. 2007), oil spills (Piatt et al. 1990, Van Vliet 1994), other marine contaminants (Kaler et al. 2013), and disturbance from boat traffic (Agness et al. 2008, Marcella et al. 2013). Recent evidence suggests that a neurotoxin produced by dinoflagellates (saxitoxin) can bioaccumulate in sand lance, the main prey of Kittlitz's murrelets in the Kodiak Archipelago, resulting in significant mortality in Kittlitz's murrelet chicks (Lawonn 2013). On land, both species are threatened by loss of nesting habitat. The terrestrial nesting habitat of marbled murrelets is declining due to logging of old-growth forests, and subsequent forest fragmentation, which further decreases quality of nesting habitat due to increased densities of potential nest predators (Malt & Lank 2007, Peery & Henry 2010). Kittlitz's murrelets are particularly vulnerable to climate change due to their association with glaciers in both terrestrial and marine environments; as glaciers retreat, terrestrial habitat becomes unsuitable for nesting as vegetation succession proceeds, and specialized marine foraging habitat also disappears (Kuletz et al. 2003). Additionally, climate-induced changes in glacial fjords result in increased predation pressure on Kittlitz's murrelets from peregrine falcons (*Falco peregrinus*) and bald eagles (*Haliaeetus leucocephalus*; Lewis et al. 2013).

Study site

This study was conducted in the Kodiak Archipelago, Alaska, on its three largest islands: Kodiak, Afognak and Shuyak (Figure 1). Large areas of archipelago are protected within the Kodiak National Wildlife Refuge (encompassing two thirds of Kodiak Island and parts of Afognak), and state parks, which protect all of Shuyak Island and parts of northern Afognak Island. The archipelago is characterized by a climatic gradient from northeast to southwest, with warmer, wetter weather systems in the northeast and colder weather more characteristic of the Aleutian Islands in the southwest. The archipelago is divided into three ecological sections along this northeast to southwest axis: the Sitka spruce section, Montane-fjord section, and southern Heath section (Fleming & Spencer 2007). The Sitka spruce section dominates Shuyak, Afognak and the northern tip of Kodiak Island. Sitka spruce forests are expanding southwards across the archipelago following recolonization in the northern archipelago within the last 800 years. These forests are dominated by a single conifer species – Sitka spruce – with variable epiphyte development and undergrowth complexity depending on local site conditions and stand age. Older, more protected stands have extremely high epiphyte development, with high densities of potential murrelet nest platforms; meanwhile, stands on outer coastal fringes are often stunted, with very little epiphyte growth. Forest cover is generally below 300 m elevation, giving way to alpine meadows at higher elevations. At the southern edge of the Sitka spruce section, patches of young spruce trees are interspersed with willow, alder and salmonberry thickets. Central Kodiak Island is in the Montane-fjord section, dominated by granite peaks up to 1326 m and remnant glaciers, with steep-sided, short fjords to the east and deep inlets to the west. Vegetation of valley bottoms is characterized by wetland-meadow complexes and stands of cottonwood, birch, alder and willow. On low-elevation slopes, dense willow, alder, salmonberry-elderberry form nearly impenetrable thickets up to 200-300 m elevation. Prostrate alpine vegetation (alpine heath and tundra) is dominant above approximately 400-500 m elevation, giving way to exposed bedrock, scree, and snow cover. Southern Kodiak Island plant communities are more characteristic of sub-arctic Aleutian heath, with wide valleys of heath hummocks (mainly crowberry) and low rolling hills. Heath communities include dwarf willows and shrubs: crowberry, blueberry, cranberry, Labrador tea and bearberry (Fleming & Spencer 2007).

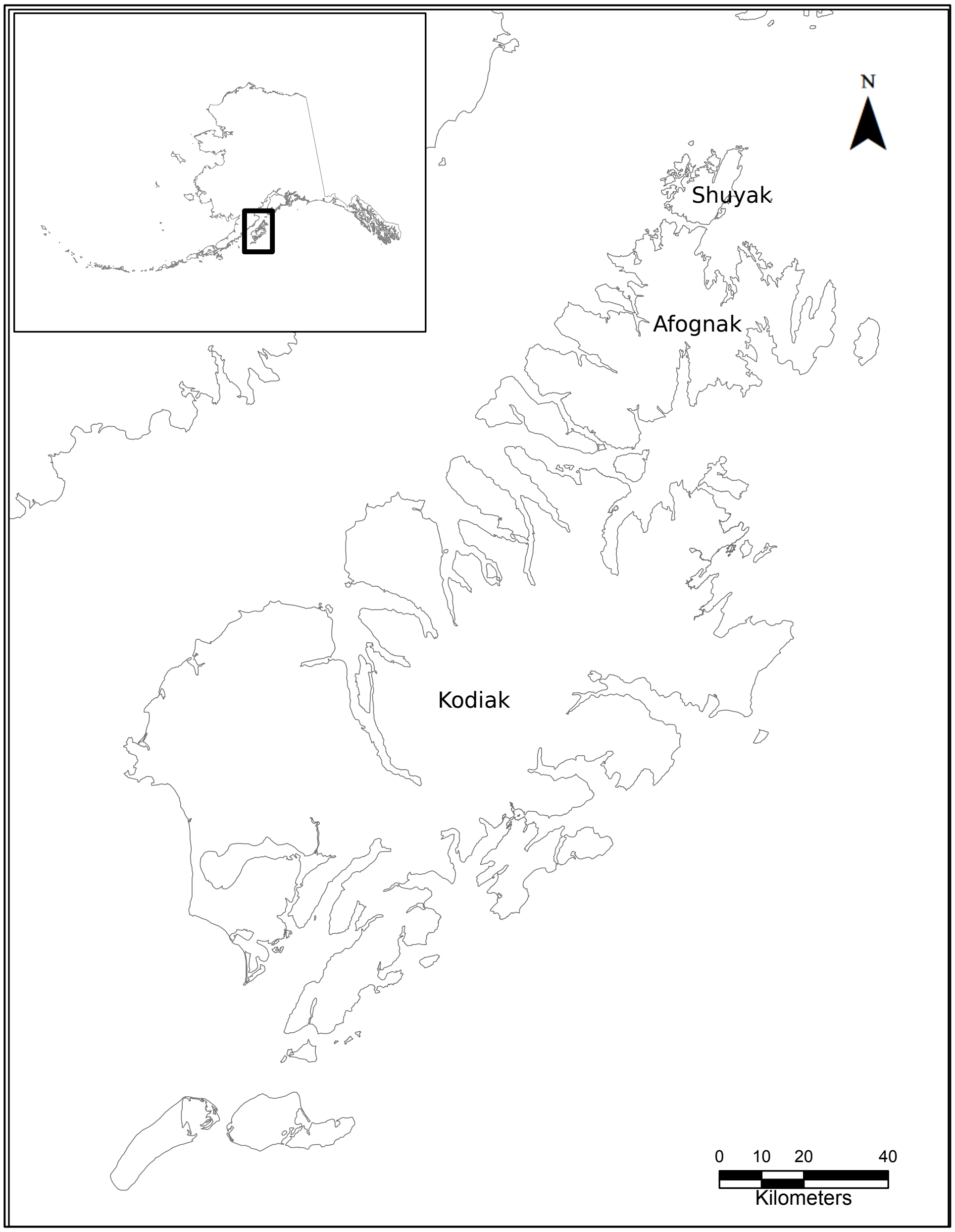

Figure 1: The Kodiak Archipelago's three largest islands: Kodiak, Afognak and Shuyak. The archipelago is located in the northern Gulf of Alaska.

The marine environment around the Kodiak Archipelago is exceptionally productive due to the upwelling of cold, nutrient-rich waters from currents striking the northern tip of the archipelago (Piatt 2011). This hotspot of marine productivity supports a higher abundance of seabirds than the rest of the Gulf of Alaska combined (Piatt 2011). One of the most numerically abundant seabird species in the archipelago is the marbled murrelet, second only in abundance to black-legged kittiwakes (*Rissa tridactyla*; unpublished data from Kodiak National Wildlife Refuge). At-sea vessel counts have identified the Kodiak Archipelago as one of three main concentrations of breeding marbled murrelets in Alaska, containing approximately 14% of the total Alaskan population (Piatt & Ford 1993, Piatt et al. 2007). Surveys of nesting habitat for marbled murrelets in southcentral Alaska identified Afognak Island as having the highest potential nesting densities in the region (Kuletz et al. 1995, Naslund et al. 1995). Kittlitz's murrelets are comparatively rare (< 1% of all *Brachyramphus* murrelets) in the archipelago, but both adults and hatch-year birds have been observed consistently over >30 years of at-sea surveys, scattered throughout the archipelago (Stenhouse et al. 2008, Madison et al. 2011). The first confirmed breeding record for Kittlitz's murrelets in the Kodiak Archipelago was in 2006 (Stenhouse et al. 2008). Following this, evidence of nesting on southwest Kodiak Island spurred intensive research in this unusual glacial refugium habitat. From 2008-2011, as part of an ongoing project, 53 Kittlitz's murrelet nests were found on Kodiak Island and monitored throughout the breeding season to investigate breeding ecology and nest site selection (Lawonn 2013).

Thesis outline

This study compared four methods of population monitoring of *Brachyramphus* murrelets across a variety of spatial scales and habitat types. I used marine radar, autonomous acoustic sensors, audio-visual surveys, and at-sea vessel counts to investigate spatial and temporal patterns of abundance in *Brachyramphus* murrelets at 27 sites in the Kodiak Archipelago, Alaska, from 2010-2012. The primary goal of the study was to test the suitability of using marine radar for tracking flying *Brachyramphus* murrelets as a tool for population monitoring in Alaska. This method has been established as a reliable way to census and monitor marbled murrelet populations south of Alaska. The challenges with adapting this technique to Alaskan conditions included the presence of two murrelet species that are indistinguishable on radar, as well as frequent extreme weather conditions affecting flight behaviour (strong wind), and latitudinal effects on murrelet behaviour due to light regime and seasonality. A secondary goal was to use autonomous acoustic sensors and at-sea vessel counts to detect the relative proportions of

Brachyramphus species in each radar survey site, to estimate the relative proportion of each species detected by radar.

Autonomous acoustic sensors were also tested on their own as a cost-effective alternative to audio-visual surveys of murrelet presence, abundance and behaviour (Chapter 1). The effectiveness and reliability of acoustic sensors for measuring an index of murrelet abundance was tested by comparing autonomous acoustic, audio-visual and radar surveys (Chapter 2). The combination of these methods was used to describe diurnal, seasonal, and spatial patterns of commuting flight behaviour during the breeding season, as well as potential differences in flight behaviour between marbled and Kittlitz's murrelets. The final objective of this study (Chapter 3) was to determine if spatial patterns of abundance from radar surveys could be predicted by marine (at-sea density) or terrestrial (area of potential nesting habitat types) variables, and at which spatial scales these predictors were most important. The final chapter (Synthesis) synthesizes findings about *Brachyramphus* murrelet ecology and behaviour, makes recommendations for murrelet monitoring programs in Alaska, and describes an ideal population monitoring design along with a preliminary power analysis of radar counts (Appendix B).

Chapter 1: Automated acoustic monitoring of marbled murrelets (*Brachyramphus marmoratus*)

Introduction

The marbled murrelet (*Brachyramphus marmoratus*) is a solitary-nesting seabird of the family Alcidae that breeds along the west coast of North America from central California to the Aleutian Islands. The dispersed, cryptic nests of marbled murrelets, as well as their secretive nest attendance behaviours probably evolved as an anti-predator strategy (Gaston & Jones 1998). Marbled murrelets visit their nests during dark twilight, flying at high speed, often silently. Throughout most of their range, marbled murrelets nest in high mossy limbs of old growth conifers (Nelson 1997), although cliff ledge and subalpine ground nesting is relatively more common in the northern range of its distribution (Barbaree 2011, M. Kissling, pers. comm.). This secretive breeding behaviour makes it difficult to conduct studies of behaviour and habitat use, which are needed to monitor threatened and declining populations. Historical studies (1850-1980) suggest that marbled murrelet populations have declined drastically across their range (McShane et al. 2004), followed by major recent declines: by 70% in the last 25 years in Alaska and British Columbia (Piatt et al. 2007) and 30% in the last 10 years in Washington, Oregon and California (Miller et al. 2012). Logging of old growth nesting habitat has been identified as a main factor in population declines (COSEWIC 2012), and consequently a major focus of recovery planning is identifying high-quality forest nesting habitat for protection (USFWS 1997, Burger 2004a, CMMRT 2003). Monitoring patterns of habitat use by murrelets in forest stands can provide important information for managers attempting to identify and map high quality nesting habitat (Meyer & Miller 2002, Meyer et al. 2002, Burger and Bahn 2004, Meyer et al. 2004, Stauffer et al. 2004, Bigger et al. 2006a, Silvergieter & Lank 2011a,b).

The goal of this study was to develop a cost-effective automated system to monitor murrelet habitat use, vocal behaviour and relative abundance in forest stands. Currently, murrelet habitat use is evaluated at the forest stand-level through standardized audio-visual or radar surveys (Evans Mack et al. 2003, Burger 1997, Cooper et al. 2001) conducted by human observers. The major limitation of these surveys is that it is costly to support field crews, especially in remote areas. Observers can survey only one site at a time; therefore spatial and temporal replication is reduced. Furthermore, human audio-visual observers are subject to observer bias and additionally, differences in viewing conditions between sites are also a source of bias in observing murrelet behaviour (Bigger et al. 2006a).

Automated acoustic recording systems have recently been tested as a cost-effective alternative to deploying personnel for monitoring remote, nocturnal, rare, and elusive populations of seabirds (Borker et al. 2013, Buxton & Jones 2012, McKown et al. 2012, McKown et al. 2013). A pilot study in California showed that marbled murrelet vocalizations recorded by acoustic sensors were highly correlated with human audio-visual observer detections (Borker et al. 2013). The marbled murrelets is a suitable candidate for automated acoustic monitoring because of its conspicuous vocal behaviour during the breeding season, involving prolonged vocal and flight displays near nesting habitat shortly before sunrise (Nelson 1997, Dechesne 1998). The vocal repertoire of marbled murrelets is complex, including 8-12 distinct calls that are often combined in graded call series (Dechesne 1998). The complexity of the vocal repertoire reflects the need to communicate in two different acoustic environments (over forest or at sea), as well as multiple purposes for communication (territoriality or deterrence advertising, courtship, pair bonding; Dechesne 1998). Each call type is composed of combinations of distinct elements that contribute to vocal individuality, and are used for different communication purposes. Pure tones (such as in “keer,” “keheer,” ad “ay” calls) transmit better over long distances, while harmonics (e.g., “quack” calls) are highly localisable in noisy environment but attenuate more quickly with distance (Dechesne 1998). The most common call types (“keer” and “keheer”) are thought to be mainly contact calls, often observed when pairs reunite; while the harsher, harmonic “quack” call type is thought to be associated with arousal or aggression (Dechesne 1998). The large vocal repertoire of marbled murrelets and its potential for understanding murrelet behaviour remains relatively understudied, but the development of low-cost, weatherproof automated sensors provides a novel opportunity to pursue this avenue of research.

I tested the viability of acoustic monitoring for murrelets using automated sensors (Song Meters, Wildlife Acoustics Inc., Concord, MA) to record murrelet vocalizations across a range of habitat types in the Kodiak Archipelago, Alaska. My objectives were to determine whether sensors could reliably detect murrelet vocalizations and patterns of relative abundance, and to develop an efficient means of processing long recordings using automated call recognition software (Song Scope, Wildlife Acoustics, Inc., Concord, MA).

Methods

Collection of field recordings

I collected field recordings using automated acoustic sensors in the Kodiak Archipelago during the murrelet breeding season (June-August) in 2011 and 2012. In 2011, six sensors were deployed across a variety of habitat types at Monashka Bay on Kodiak Island (Table 1, Figure 2), from 15 June - 3 September. This site was selected as an intensive survey location because it contained both high quality forested nesting habitat where murrelets engaged in complex social interactions, and unforested areas that were identified as murrelet commuting flight paths through radar surveys (see Chapter 2). These habitat types provided the opportunity to compare vocal activity between commuting flight behaviour and social interaction above potential nesting habitat, and this difference in vocal activity was then compared to counts of flying murrelets obtained by radar (Chapter 2). In 2012, the study was expanded to five additional sites in the northern Kodiak Archipelago that were simultaneously surveyed by radar, with acoustic sensors placed in the most likely forested nesting habitat at four of these sites, and along a commuting flight path at the remaining site because there was no forest in the area (Chapter 2).

Two types of Song Meter (Wildlife Acoustics, Inc.) acoustic sensors were used: SM2 Terrestrial sensors (mounted at 1 m above ground), and SM2 Night Flight sensors mounted at 3-4 m above ground. Night Flight sensors are designed to increase sensitivity to distant calls from above, while attenuating noise from below; however, because this specialized microphone is also more costly than the base model, I tested whether this system provided an advantage in recording murrelet sounds. Song Meters were programmed to record for 2 hours each day, starting 2 hours before sunrise.

In forested habitat sensors were mounted on trees, while in unforested habitat sensors were mounted on 1 m posts and the surrounding vegetation was cleared within a 1.5 m radius to reduce noise interference. To compare the performance of the two sensor types, I deployed the SM2 Terrestrial and SM2 Night Flight sensors at the same tree in likely murrelet nesting habitat in 2011. In 2012, one recording was collected in potential forested nesting habitat at each of six sites in the northern Kodiak Archipelago (Figure 3); at one site no forested nesting habitat was available and the sensor was placed along a commuting flight path. Three sensors were deployed throughout the breeding season at Monashka Bay on Kodiak Island from 1 June – 27 August 2012. Two of the locations used in 2011 were re-used in 2012 based on preliminary results (relatively low noise interference and consistent presence of murrelets). These included sensor "Forest 1", located in high quality forested potential nesting habitat, and sensor "Flight path 5", located along a high-traffic commuting flight corridor identified by radar surveys. A third sensor (Forest 3) was added to census a separate patch of high-quality forested potential nesting habitat in 2012.

Table 1: Summary of Song Meter locations, sensor types, habitat descriptions and sampling effort at Monashka Bay, 2011-2012.

					Recordings (2 h pre-sunrise)		
Year	Site name	Site code	Sensor type	Habitat	Number subsampled	Mean detections	Mean false positives (%)
2011	Forest 1	FOR1	SM2 Terrestrial	Old growth forest	15	57.4	66.1
	Forest 2	FOR2	SM2 Night Flight	Old growth forest	28	55.2	57.0
	Flight path 1	FP1	SM2 Terrestrial	Grass & shrub	4	8.0	98.6
	Flight path 2	FP2	SM1 Terrestrial	Grass	4	2.0	99.4
	Flight path 3	FP3	SM1 Terrestrial	Alder shrub	4	22.5	96.2
	Flight path 4	FP4	SM1 Terrestrial	Grass & shrub	4	3.5	99.3
	Flight path 5	FP5	SM2 Night Flight	Sparse conifers	11	17.5	64.9
2012	Forest 1	FOR1	SM2 Terrestrial	Old growth forest	16	91.0	27.0
	Forest 3	FOR3	SM2 Terrestrial	Old growth forest	21	62.0	35.0
	Flight path 5	FP5	SM2 Night Flight	Sparse conifers	21	12.0	65.0

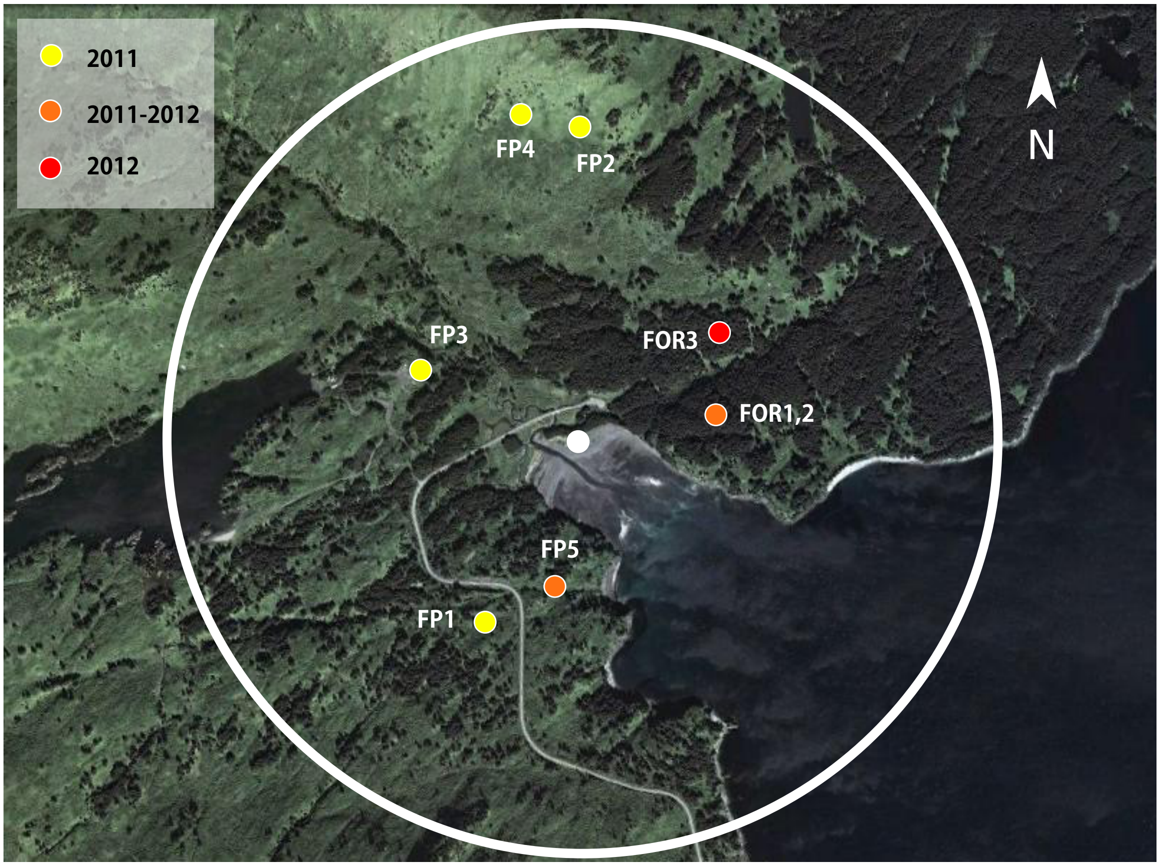

Figure 2: Song Meter locations within the scanning radius of the radar (white circle, diameter 1.5 km, see Chapter 2) at Monashka Bay radar station in 2011 and 2012 (codes correspond to Table 1; FOR1, 2 were deployed at the same tree). See example of murrelet flight paths in Figure 11, Chapter 2.

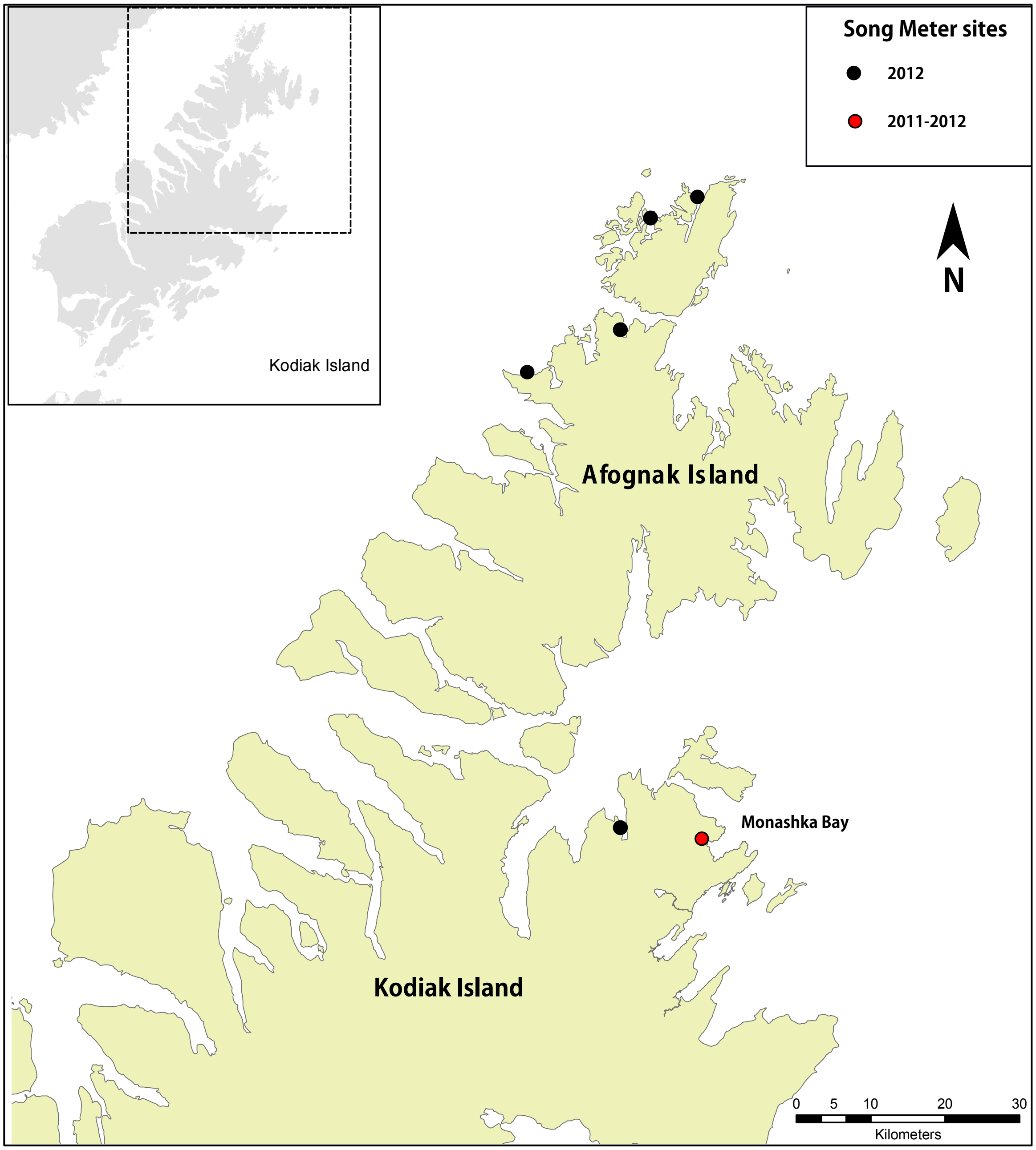

Figure 3: Song Meter sites in the northern Kodiak Archipelago, 2011-2012.

Field calibration of acoustic sensors

I conducted a field calibration to estimate the maximum distance at which murrelet calls could be detected by Song Meters in different acoustic environments. A 20-s series of 35 marbled murrelet calls, including the four call types detected in field recordings on Kodiak Island (keer, keheer, ay, quack) was played from an iPhone speaker at increasing

20-m intervals (0-80 m) from the Song Meter (SM2 Terrestrial model). A loud call (92 dB) and soft call (83 dB) were played at each distance. Call amplitude was measured using a separate iPhone microphone (Decibel Meter®). Because the amplitude of marbled murrelet calls is not known, I estimated a conservative minimum decibel level from field recordings. The loudest marbled murrelet calls recorded by Song Meters in field recordings from this study reached 90 dB (amplitude measured by the Song Meter microphone), and were most likely produced by murrelets flying no closer than 10 m from the Song Meter, therefore the true call amplitude is likely louder than 90 dB. Thus the loud call used in these experiments was likely to produce conservative estimates of the detection range of Song Meters. Two trials were conducted in both forested and open habitat: one with +12 dB gain adjustments to both microphones on the Song Meter (to amplify weaker calls) and one without gain adjustment, to test whether gain adjustment increased the detection distance of murrelet calls.

Automated scanning of recordings

I subsampled a random selection of field recordings throughout the 2011 and 2012 breeding seasons from each sensor, and scanned these recordings using automated recognition models called "recognizers" in the program Song Scope 4.1.3A (Wildlife Acoustics, Inc.; Agranat 2007, Buxton & Jones 2012). Recognizers were developed using the principles of "feature reduction", a process that selects features of vocalizations that distinguish one species from another. Elements of vocalizations that do not contribute to identification are removed, while maintaining enough model flexibility to accommodate individual variation in vocalizations (Wildlife Acoustics 2011).

Recognizers were built in an incremental process (Table 2) beginning with a "basic recognizer" that was gradually improved through feature reduction. The basic recognizer was built with "training data" consisting of Song Scope "annotations" (murrelet calls that were identified and labelled by call type). Initially, a subset of recordings was reviewed and all murrelet sounds were identified, tallied and categorized; including four marbled murrelet call types based on Dechesne (1998), and two non-vocal sounds (wing beats and jet sounds). These non-vocal sounds are generally produced in aerial flight displays: wing beats are heard when murrelets fly at low altitude (for example, below the forest canopy), while jet sounds are produced by wing feathers during aerial dives, which occur during flight displays with two or more birds. For simplicity, and because murrelet calls are variable, graded, and often distorted by echoes and Döppler effects (Dechesne 1998), I lumped what were potentially different call types together into four categories: 1) “keer”, 2) “keheer”, 3) “quack”, which included other “groan” and “hay” sounds, and 4) “ay” calls which included “whistles” (Figure 4). These four categories were developed on the basis of differences in structure (combinations of elements) that were easily distinguished from each other even in distant calls, described in Dechesne (1998). For example, “keer” calls have a simple “eyebrow” shape, which is modified in “keheer” calls with a “kick” element. The “ay” calls have a distinctive sinusoidal curve, while “quack” group calls have harmonics as their distinctive characteristic. Occasionally in graded call series, a single call had elements of more than one call type; when this occurred, the call was identified based on which element was “dominant” (i.e. of greater duration within the call). These call groupings were designed to allow rapid identification of calls during audits of recordings, rather than to provide a detailed inventory of murrelet calling behaviour.

The “keer” and “keheer” call types greatly outnumbered other murrelet sounds (>90% of all murrelet sounds) and were selected for annotation and recognizer development. Less common sounds such as “quack” calls were unsuitable for recognizers because of their rarity in recordings, which resulted in few correctly identified calls and generated high false positive rates when recognizers were applied.

Table 2: Summary of recognizer development, application and assessment using Song Scope software (Buxton & Jones 2012) to scan recordings for murrelet sounds.

	Step	Process	Outcome
1	Collecting annotations	Visually scanned recordings for all murrelet sounds to create sound categories and identify most common sounds.	Four marbled murrelet call categories identified and two non-vocal sounds (see text). "Keer" and "Keheer" calls selected for recognizer development.
2	Basic recognizer building	Collected and imported annotations (sound clips) of known "Keer" and "Keheer" calls.	Basic recognizers for "Keer" and "Keheer" with high false positive detections.
3	Recognizer improvement	Used feature reduction principles in Song Scope to adjust recognizer parameters that highlighted important elements of each call. Discarded poor annotations.	Iterations of improved recognizers were assessed using the cross-training feature in Song Scope and by comparison with results of a visually reviewed spectrogram.
4	Selection of final recognizer	The final recognizer was selected when the cross-training score was 67-68%, the false positive detection level was <60%, and the number of detections approximated the visual count.	The final "Keer" and "Keheer" recognizers that were used to scan recordings.
5	Scanning of recordings	Recordings were scanned with both "Keer" and "Keheer" recognizers simultaneously.	Recognizers generated a list of automated detections of suspected murrelet calls.
6	Review of recognizer detections	Visually reviewed all recognizer detections; labelled and tallied correctly identified murrelet sounds.	List of murrelet sounds ordered in time.
7	Grouping call series together	Murrelet sounds were grouped into call series if separated by < 5 seconds, following Evans Mack et al. (2003).	Number of call series "detections" per recording: this was the unit used to compare with detections from radar and audio-visual surveys.
8	Assessing recognizer performance	Compared recognizer detections to a visual review of 12 h of recordings.	Estimate of the mean proportion of false positives (incorrectly included non-murrelet sounds) and false negatives (missed call series).

Basic recognizers were built with large numbers of annotations (59 keer, 159 keheer) collected from different sensor types and acoustic environments, including a broad range of call amplitudes, lengths, frequencies and overall structures (shape) so that the final models would ultimately accommodate more variation. Initial recognizers generated a high proportion of false positives, and were incrementally improved to reduce false positives using two strategies (Table 2: Step 3): 1) adjusting model parameters to improve feature reduction, and 2) removing annotations that created too much variation in the model (e.g., annotations with background noise, or calls too weak to be detected correctly). Improved iterations of the recognizers were evaluated through two methods of assessment: first, the "cross-training" score was used to measure how well the model was expected to perform, through a feature in Song Scope that withholds a portion of annotations from the recognition model which are then tested against the algorithm (Wildlife Acoustics 2011). Second, the recognizer's performance was compared to a visual audit (visual review of spectrograms) of two recordings (each recording 2 h; 1049 and 151 murrelet calls respectively). I adjusted the following parameters to improve the recognizers: frequency minimum and range, maximum syllable, syllable gap, and song length, dynamic range, maximum model complexity and resolution (Appendix A: Table A-1). The final version of each recognizer (Appendix A: Table A-2) was achieved once the cross-training score approached 70%, and when the results of recognizer scans of the two test recordings had a proportion of false positive detections below 60%, with correctly identified calls approximating the true number of detections observed by visually reviewing the spectrograms. The false positive rate was not reduced beyond this level, in order to avoid making the recognizer too specific (called "over-training"). Overtraining can resulting in more missed calls because the recognition model rejects a greater proportion of atypical calls.

Recordings were scanned with both Keer and Keheer recognizers simultaneously (Table 2: step 5), using default Song Scope sensitivity filter settings to reject candidate signals that were least likely to fit the model (Minimum Quality: 20%) as well as those with the lowest model fit (Minimum Score: 50%). The resulting recognizer detections of suspected murrelet calls were then visually reviewed to confirm correct identification (any murrelet sound), or identify false positive detections (other species or background noise). Correctly identified murrelet calls were labelled by call type and tallied for each recording. These murrelet sounds were then grouped together into "call series detections," a unit of detection based on audio-visual protocols (Evans Mack et al. 2003) that could be used in later analyses and comparisons with radar and audio-visual surveys, hereafter “detections”. Call series consist of murrelet sounds separated by < 5 s, based on audio-visual survey standards (Evans Mack et al. 2003). A special category of recognizer detection was created for false-positive detections occurring within murrelet call series, often the result of noise interference from other birds, to aid in correctly grouping murrelet calls together from the same call series. To test whether the number of detections increased as a linear function of all murrelet sounds detected, I plotted the number of call series as function of total calls, fitting the data using local polynomial regression.

Assessing recognizer performance

I determined false positive proportions as the percentage of non-murrelet calls within the total number of automated detections. False positive proportions were plotted across the season to detect a seasonal trend in noise interference, particularly from competing vocalizations of other bird species. Overall mean false positive rates were compared between sensor locations to assess the effects of noise interference on call recognition in different acoustic environments. To determine the proportion of false negatives (i.e., missed murrelet calls within a call series, and call series missed by the recognizers), I selected a random subsample of six recordings from different Song Meter units and acoustic environments to review (total sample 12 h of recordings, 2117 recognizer detections, 330 call series). I first calculated the proportion of missed calls within a call series to understand how this contributed to a single call series being counted as multiple detections. The false negative proportion was the number of murrelet call series missed by the automated recognizers relative to the total number found from visual inspections of the sub-sampled recordings. The false negative proportion was calculated for missed call series (rather than individual calls) because this was the relevant unit of comparison between acoustic sensors and audio-visual surveys, whereas the false positive proportions were calculated for individual calls to describe how efficiently the recognizer could distinguish murrelet sounds from other noise.

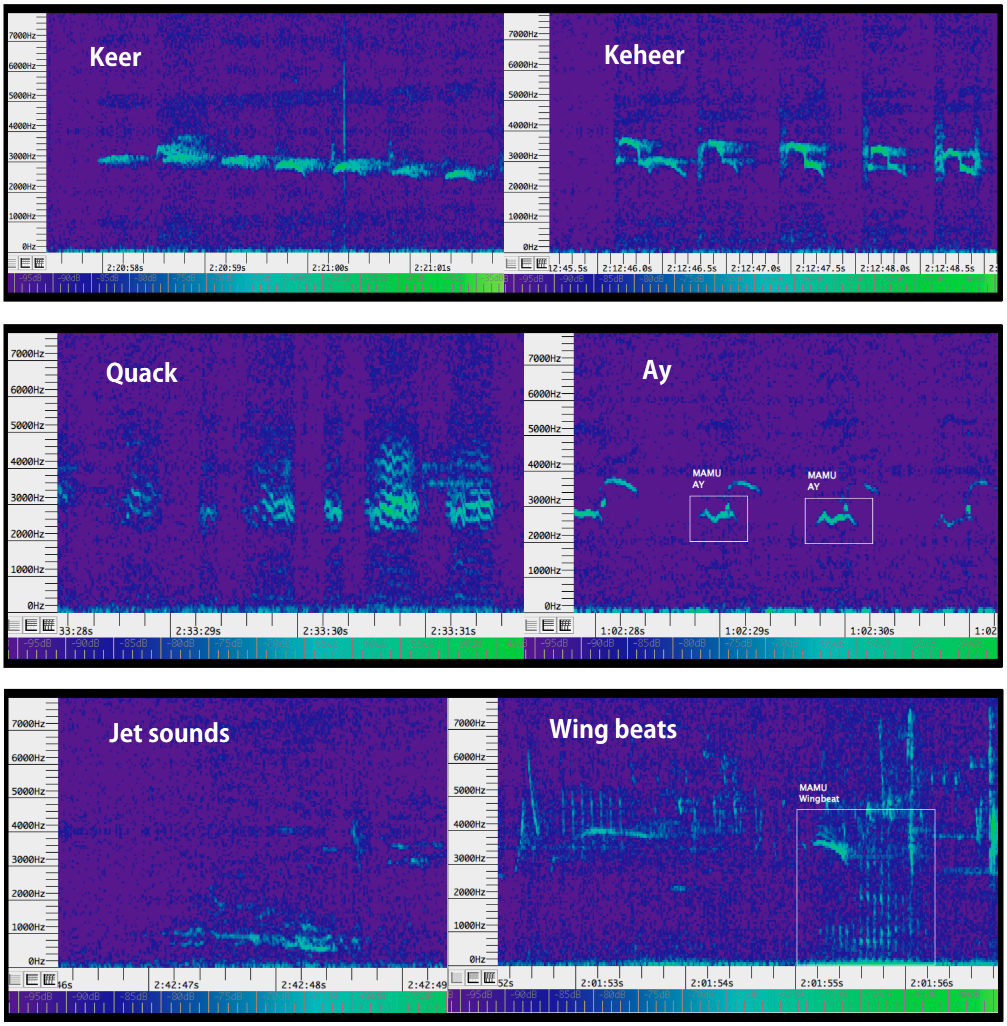

Figure 4: Spectrogram images of six marbled murrelet sounds: 4 vocalizations (Keer, Keheer, Quack, Ay) and 2 sounds produced by wings (jet sounds and wing beats) found in acoustic recordings. Frequency is on the y-axis (Hz), with time on the x-axis (s) and amplitude depicted by the colour spectrum on the bottom of the image.

Data analysis

I analyzed total detections per morning for each sensor, as the unit for comparing detections between sites, habitats, and the proportions of false positive or negative detections. A Wilcoxon signed rank test was used to compare detections between the two sensor types deployed at the same tree (sensors Forest 1 and Forest 2) in 2011 to test whether there was a difference in sensitivity between Night Flight and the Terrestrial Song Meter models. Detections recording by all sensors at forested sites at Monashka

Bay in 2011 and 2012 were plotted using non-parametric smoothing (generalized additive models) to visualize the seasonal trend; however, only the Forest 2 sensor recorded continuously throughout the breeding season in 2011, and therefore only this sensor was used to compare murrelet detections and false positive detections across the breeding season. In 2012, sensors were deployed on 1 June but due to a programming bug, they did not record daily until 14 July. To assess whether sensors in different locations at Monashka Bay were tracking the same seasonal trend within each year, I performed Spearman's Rank correlations between detections for pairs of sensors for each of the two years. In 2011, daily counts from two sensors (Forest 2 and Flight path 5) were compared from 24 July-17 August. In 2012 three sensors were compared (Forest 1, Forest 3, and Flight path 5) for recordings from 16 July-24 August. To assess whether seasonal trends were similar between years, I used Friedman Test (a non-parametric repeated-measures ANOVA) with sensor as the blocking factor to compare differences in counts between years. This test was performed on two sets of sensors that provided the longest series of daily counts: a) "Forest 2" (2011) and "Forest 1" (2012) which were deployed at the same tree in 2011 and 2012, and b) sensor "Flight Path 5" (2011, 2012). Finally, to test whether detections differed between the two sensors in nearby patches of likely forested nesting habitat, I used a paired t-test with observations paired by date to compare sensors Forest 1 and 3 in 2012. Data analysis was performed in the statistical software R (v. 3.0.0; R Development Core Team 2013).

Results

Summary of calling behaviour

Recognizers detected 20,632 murrelet sounds, yielding 5,870 detections (Table 3). The most frequent call type identified by recognizers was "keheer" (73% of calls), followed by "keer" (25%). Other vocalizations incidentally recorded ("ay" and "quack") made up the remaining 2% of calls detected. While reviewing recognizer detections of calling bouts, I found 14 recordings of non-vocal murrelet sounds (wing beats and jet sounds).

Table 3: Summary of murrelet calls, non-vocal sounds ("jet" sounds and wing beats), and call series detected by Song Meters in 2011 and 2012.

Year	Number of mornings sampled (2 h each)	Number of calls				Wing beats & Jet sounds	Total number of call series detections
		Keheer	Keer	Quack	Ay		
2011	70	6,285	2,221	117	39	13	2,725
2012	64	8,721	2,995	72	168	1	3,145
Total	134	15,006	5,216	189	207	14	5,870

Detection distance

The field calibration of Song Meters revealed the relative importance of factors affecting the detection distance of murrelet calls. Visual scanning of the spectrogram could detect murrelet calls approximately 20 m farther than call recognizers, which performed poorly at detecting faint calls (Figure 5). Second, the +12 dB gain adjustment did not appear to significantly affect the number of calls detectable by visual scan or by recognizers. The most important factor affecting detection distance was the acoustic environment: calls were detectable by both recognizers and visual scans at least 20 m farther from the Song Meter in open habitat than in forest. Loud (92 dB) calls could be detected by visual scan of the spectrograms up to 60 m in forest, while recognizers could only detect loud calls up to 40 m from the Song Meter. In open habitat 47% of loud calls could be visually detected on the spectrogram at 80 m, yet only one call (3%) was detected by the recognizer at this distance. Soft calls were more easily lost in background noise clutter in both environments, especially beyond 20 m. The call types recognized at the greatest distance from the Song Meter were "keer," "keheer" and "ay" calls, while "quack" calls were rarely detected beyond 20 m.

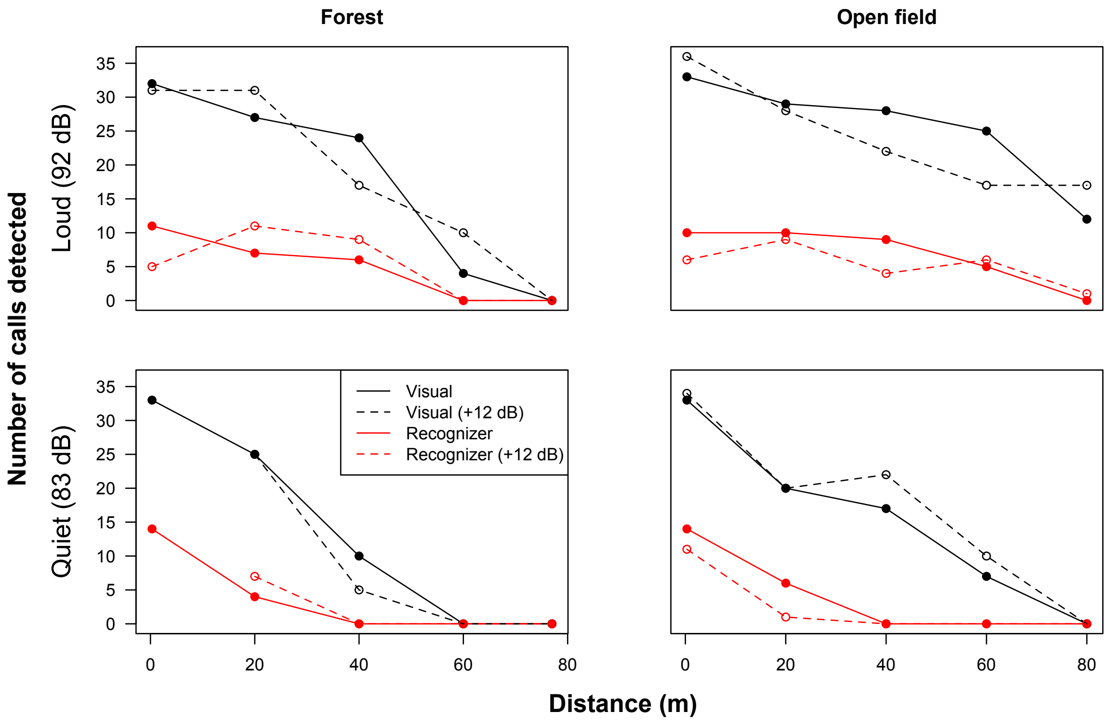

Figure 5: Song Meter field calibration results showing the number of calls (loud, 92 dB; quiet, 83 dB) detected by visual scans of spectrograms and by automated recognizers in Song Scope at increasing distance from the Song Meter in two acoustic environments (forest and open habitat), with 12 dB gain amplification (dashed lines) or without (solid lines).

Performance of sensor types

When the performance of two types of Song Meter deployed at the same tree in 2011 (SM2 Terrestrial vs. SM2 Night Flight) was compared, contrary to expectation, the Night Flight model had significantly lower mean detections than the Terrestrial model (Wilcoxon signed rank test: V = 96, p = 0.043). Although the Night Flight model is designed to increase sensitivity of the microphone to calls from above, it appeared that this increased sensitivity may have resulted in greater interference from background noise which reduces overall counts of murrelet detections. Alternatively, since the Night Flight sensor was mounted higher in the tree amongst branches, the microphone may have been closer to potential perch sites for songbirds that generated noise interference during the dawn chorus. In future, the utility of this microphone configuration could be tested by mounting it near the top of the forest canopy, where perching songbirds might be less abundant.

Audit of recognizer detections

Song Scope recognizers detected similar numbers of detections (call series) compared to the audit by visual scan in a review of six randomly selected recordings (12 h of recordings, 330 detections; Table 4). Excluding two recordings with significant noise interference, the recognition models detected 96% of the call series detected visually ($n = 299$). However, this apparent match in identification is misleading because automated recognition missed many short call series (1-3 calls) and counted many long call series as multiple detections when faint calls were missed. The mean proportion of calls detected by the recognizers within a call series was 30% (299 visually detected call series, 3809 total calls); thus in long call series (many series exceeded 50 calls) the recognizer was likely to miss enough calls to result in multiple detections within the series. The false negative rate (percentage of murrelet call series that the recognizers failed to detect) was 31% ($n = 299$ call series), mainly weak calls and short call series.

A comparison of the number of calls detected by recognizers and the number of call series counted after calls were grouped together (according to the 5-s rule) revealed a non-linear relationship (Figure 6), with fewer call series detections relative to calls as the number of calls increased. The variance in numbers of detections relative to calls also increased as the number of calls increased. I tested for non-linearity in the data by plotting a generalized additive model of the number of detections relative to calls, which revealed that there was a linear trend in the relationship when the number of calls was small (< 150), but this relationship became non-linear as the number of calls increased. I plotted a smoothed trend line (local polynomial regression fitting) to compare with the linear regression line for values of calls < 150 (Figure 6). The curve of the smoothed trend line was not affected by the removal of outliers. This non-linear relationship between the number of detections vs. calls could be due to a saturation effect, where during high murrelet vocal activity calling bouts overlap more frequently; alternatively, when vocal activity is greatest, each call series may contain more calls.

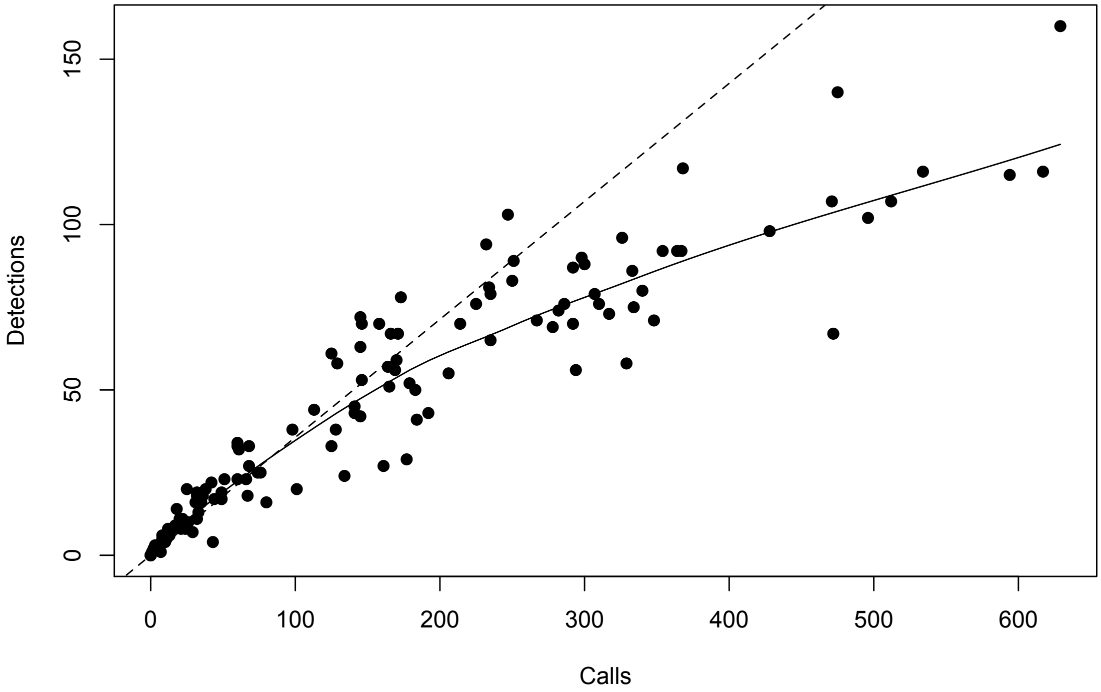

Figure 6: Comparison of the number of detections (call series) with calls detected by recognizers in all recordings with smoothed trend line (local polynomial regression fitting), and linear regression line (dashed line). The number of detections relative to calls decreased as the number of calls detected in the recording increased, producing a non-linear relationship.

Table 4: Sample of spectrograms comparing detections of murrelet calls and call series by visual spectrogram review vs. recognizer detections, with and without noise interference from other bird species or heavy rain and wind. The false negative rate (%) indicates the proportion of call series identified by visual review that were missed by the recognizer, per recording.

Recording date	Sensor	Noise interference	(A) Number of automated detections	(B) Visually confirmed murrelet calls detected by recognizer	False positives (%)[1]	(C) Count of call series detections (recognizer)[2]	(D) Count of call series detections (visual)	(E) Call series detections missed by recognizer	False negatives (%)[3]
10-Jul-11	Forest 1	None	443	234	47	81	72	20	28
12-Aug-11	Forest 2	None	186	179	4	52	53	17	32
16-Jul-12	Forest 3	None	382	158	59	70	81	28	35
16-Aug-12	Forest 1	None	440	340	23	80	93	29	31
25-Jun-11	Forest 1	Bird vocalizations	575	33	94	13	24	12	50
12-Aug-12	Flight path 5	Heavy rain/wind	91	1	99	1	7	6	86
Total	-	-	2,117	945	1,026	297	330	112	-

[1] Percentage false positives calculated as 100*(A-B)/A: calculated as a proportion of calls to describe the efficiency of recognizer in distinguishing murrelet sounds from other noise.

[2] The number of call series detected by the recognizer includes call series counted multiple times due to missed calls in the middle of the series, therefore the number of call series detections is sometimes larger than the number detected visually, while some call series were still missed.

[3] Percentage false negatives calculated as 100*E/D: calculated as a proportion of detections, because this was the relevant unit of comparison between radar, audio-visual and Song Meter surveys (see Chapter 2).

Noise interference and false positive detections

Two types of noise interference generated false positive recognizer detections in Song Meter recordings: competing vocalizations from other bird species and noise generated by strong wind and heavy rain. The relative abundance and proportion of false positives (out of all automated detections) varied seasonally and between sites, as a function of two factors: the relative abundance of murrelet calls (more calls meant a lower proportion of false positive detections) and noise interference. Forested sites had higher rates of murrelet detections than unforested sites, while competing bird vocalizations were greater at sites with brushy habitat supporting high densities of songbirds (Table 5). The highest ranked potential forest nesting habitat had the lowest mean false positive detection rate (47%), whereas lower-ranked potential nesting habitat had higher false positive detections (77-95%). Potential forest nesting habitat quality was ranked on the basis of density of potential nest platforms (branches ≥ 15 cm diameter with moss cover; CMMRT 2003, Burger 2004b). Low quality forest had no potential nest platforms within a 50 m radius of the Song Meter, while “marginal” quality forest had very few platforms (1-5), and high quality forest had high platform densities, with multiple platforms on each tree. In general, unforested sites had few murrelet detections and a high proportion of false positive detections (97-99%) because of high densities of songbirds, with the exception of one high-traffic flight corridor located in sparsely forested habitat which had a mean rate 65% false positive detections (Flight path 5 at Monashka Bay).

Table 5: Proportions of false positive detections (non-murrelet sounds selected by Song Meter recognizers) by habitat type or forest habitat quality (ranked according to nesting habitat potential; Burger 2004b).

Habitat	Vegetation subclass or habitat quality rank	Number of recordings (2 h)	Mean false positive proportion (%)	Total recognizer detections	Total positively identified recognizer detections	Mean detections per day (call series)
Forest	Low quality	2	95	1,257	67	6
	Marginal	1	77	573	134	24
	High quality	80	47	40,277	18,656	64
Unforested	Grass	8	99	6,504	63	3
	Grass & shrub	8	97	9,089	215	13
	Sparse conifer	32	65	6,820	1,480	14

Noise interference created by vocalizations of other species constituted all false positive detections other than weather noise, and occurred in nearly all recordings. Songbird interference was most intense in the early to mid-breeding season (June and early July) when these birds were maintaining territories (Figure 7). Because marbled murrelet calls are relatively simple and often monosyllabic (e.g., “keer” and “ay” calls), recognizers often misidentified components of other, more complex bird calls as murrelet calls, generating large numbers of false positives. Many species contributed false positives, and their relative contributions depended mainly upon how close the calling bird was to the Song Meter as well as the length and complexity of calls; for all species, louder calls were more likely to be detected by the recognizer at the expense of more distant calls (including murrelet calls). For example, at the Forest 1 site, there were five species that contributed most to false positives: the fox sparrow (*Passerella iliaca*), hermit thrush (*Catharus guttatus*), varied thrush (*Ixoreus naevius*), Pacific wren (*Troglodytes pacificus*), and pine grosbeak (*Pinicola enucleator*). The two species with the most prolonged and complex calls appeared to generate the most false positives: fox sparrows generated 301 of 536 (56%) false positives one morning, whereas Pacific wrens generated 224 of 431 (52%) of false positives on another morning, depending on which species called loudest. Other species commonly detected by recognizers at other sites included golden-crowned sparrows (*Zonotrichia atricapilla*), savannah sparrows

(*Passerculus sandwichensis*) and white-winged crossbills (*Loxia leucoptera*). In addition to these species, the Song Meters recorded the vocalizations of other birds and animals that were not detected by the recognizers. This included other song birds (golden crowned kinglet, *Regulus satrapa*), seabirds (glaucous-winged gull, *Larus glaucescens*; American black oystercatcher, *Haematopus bachmani*) and potential predators of murrelets such as the bald eagle (*Haliaeetus leucocephalus*), common raven (*Corvus corax*) and red squirrel (*Tamiasciurus hudsonicus*). During the height of the dawn chorus in June and early July, competing vocalizations occasionally became so intense that murrelet calls could not be detected even by visually reviewing the spectrogram. These events were generally of short duration (< 30 s) and occurred relatively infrequently during recordings, amounting to 2-3 minutes of recordings where murrelet calls could not be detected. At the same time, recognizers often falsely detected loud calls made by other bird species at the expense of fainter murrelet calls, resulting in a higher proportion of false negatives (e.g. 50% on 25 June 2011) compared to other parts of the season when songbird calls were less frequent (31% averaged over 8 h of recordings, Table 4). Noise interference from rain and wind were significant only during extreme weather events (very heavy rain, strong winds). Heavy rain falls caused high proportions of false positives (up to 99% of all recognizer detections, Table 4), and generated broad-spectrum background “white noise” that appeared to drown out murrelet calls; strong wind produced a similar effect. These severe weather events were relatively rare, occurring on only three survey days in both (2011 and 2012) seasons.

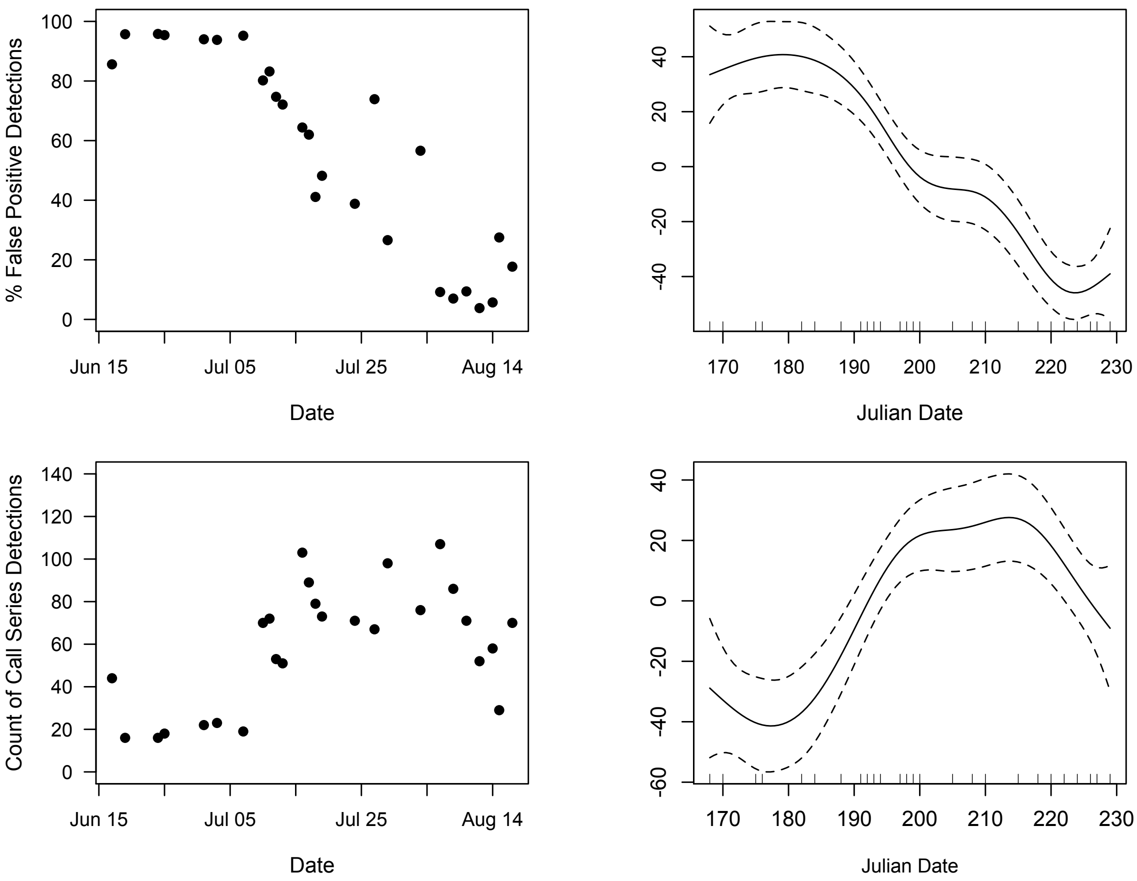

Figure 7: Seasonal trend of false positive detections (top) and murrelet call series detections (bottom) from acoustic sensor Forest 2, at Monashka Bay, 2011. Generalized additive models are shown on the right panels, with dashed lines indicating two standard errors or approximately 95% confidence limits of the prediction. The y-axis is the centred smooth value of the number of detections in logits; on the x-axis, the tick marks on the bottom indicate the sampling distribution.

Seasonal trends in calling

Vocal activity of murrelets detected by Song Meters in forested habitat at Monashka Bay increased from June through early July, with a peak in activity between 15 July and 5 August, followed by a decline in activity throughout the rest of August (Figure 8). The seasonal patterns of detections were not significantly different between years either in forested habitat (Friedman test; $S = 11.64$, df = 13, p = 0.557) or along a commuter flight path ($S = 6.476$, df = 10, p = 0.774) at Monashka Bay. When activity patterns recorded by sensors were compared within seasons, there was no significant correlation in 2011 between sensors Forest 2 (potential nesting habitat) and Flight path 5 (Figure 9; n = 10, $r_s = 0.50$, p = 0.1411), while in 2012, the seasonal pattern in detections was significantly correlated between all sensors (Figure 9; Forest 1 vs. Forest 3: n = 16, $r_s = 0.81$, p = 0.0001; Forest 1 vs. Flight path 5: n = 16, $r_s = 0.79$, p = 0.0003; Forest 3 vs. Flight path 5; n = 20, $r_s = 0.54$, p = 0.0131). When daily counts were compared between nearby forest sensors Forest 1 and Forest 3 (Monashka Bay 2012), there were significantly more detections at Forest 1 (Figure 9, paired t-test; t = 4.06, df = 15, p = 0.001).

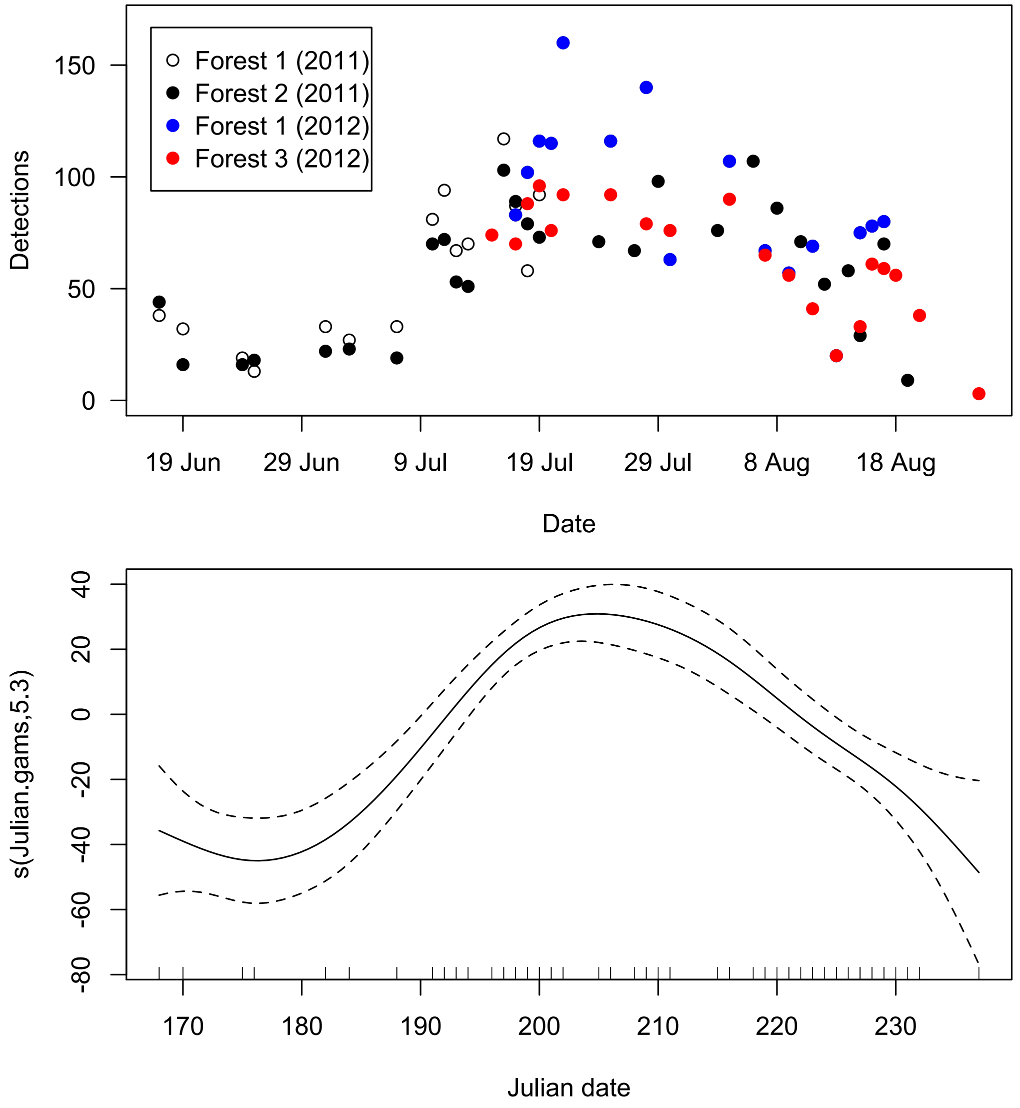

Figure 8: Song Meter detections from all forest sensors at Monashka Bay in 2011 and 2012 (top) and non-parametric smoothed model (generalized additive model) of detections from sensor Forest 2 from both years of data (bottom). The dashed lines indicate two standard errors above and below the mean, or approximately 95% confidence of the prediction. The y-axis is the centred smooth value of the number of detections in logits; on the x-axis, the tick marks on the bottom indicate the sampling distribution.

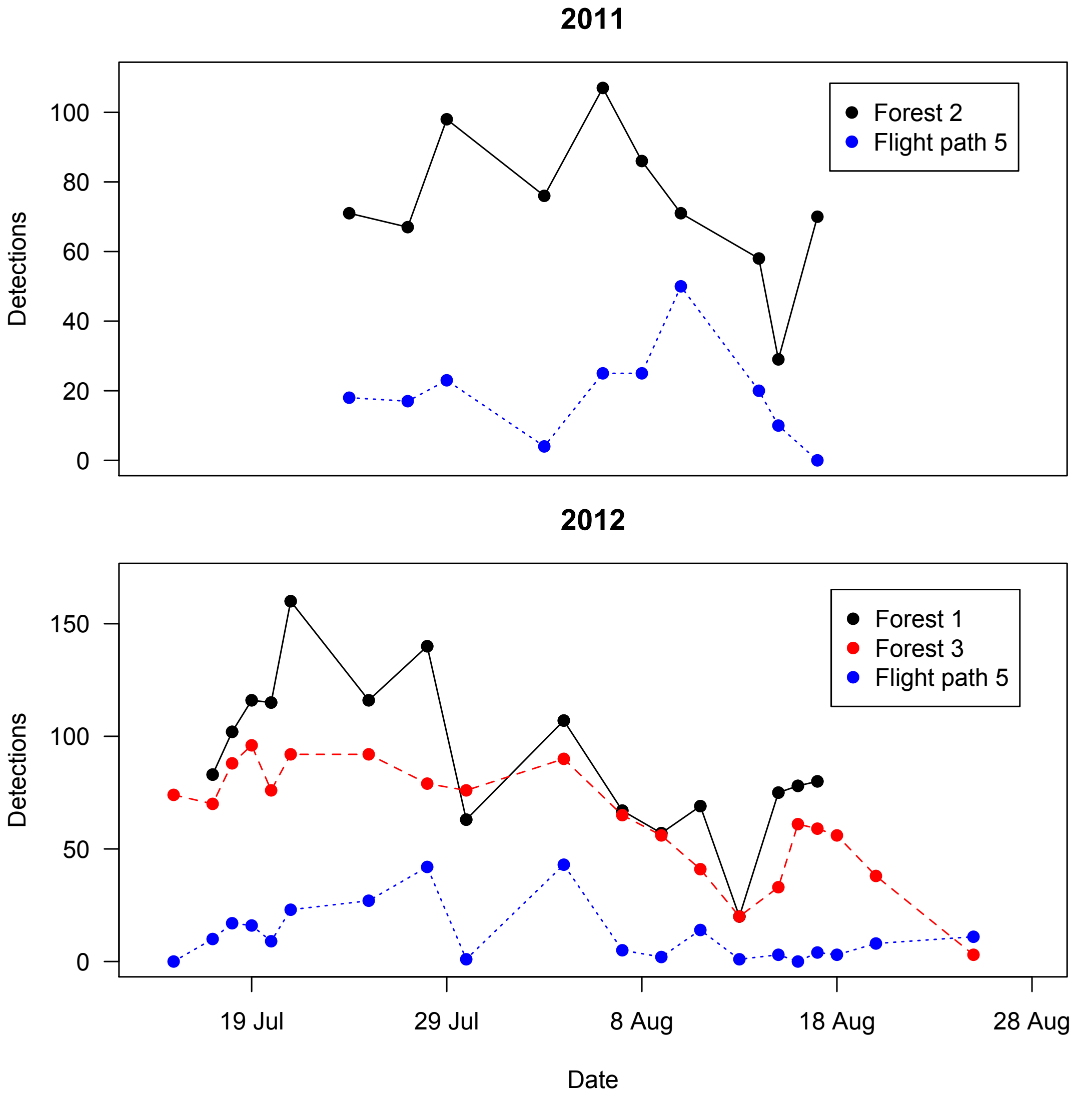

Figure 9: Comparison of Song Meter counts across the season for sensors recording simultaneously at Monashka Bay: 2 sensors in 2011 (24 July-18 August) and 3 in 2012 (14 July-24 August).

Discussion

Application of autonomous acoustic recording and call recognition software

Autonomous acoustic recording devices, along with automated call recognition software provided an efficient and cost effective way to sample murrelet vocal activity. The detection range of Song Meters was conservatively 80-100 m, resulting in a sample area of approximately 2-3 ha. Because the amplitude of calls used in my tests was likely to be quieter than real murrelet calls, my results (detection distance of 80 m) probably underestimate the detection range of the Song Meter. These results are similar to a test of the Song Meter detection range of boreal forest songbirds, in which detection probability declined below 50% beyond 50 m (Venier et al. 2012). Detection curves such as these can be used to estimate the proportion of missed calls within a given area around acoustic sensors. However, the detection range of Song Meters appears to be significantly smaller than audio-visual surveys (detection rates decrease substantially beyond 200 m; Cooper & Blaha 2002). Other variables that were not tested in this experiment that would also affect Song Meter detections are wind speed and direction, flight direction of the birds and rain- or wind-generated rustling noise.

The relatively small sampling area of acoustic sensors is ideal for monitoring murrelet activity in relation to specific habitat attributes in a given forest stand. In this study, two nearby patches of high quality nesting habitat were sampled (sensors Forest 1 and 3 at Monashka Bay, 250 m apart) and recorded consistently different numbers of daily detections, indicating that acoustic sensors can detect subtle differences in habitat use, even if some of the same individual birds are detected at two nearby patches. Sensors at Monashka Bay also recorded similar patterns of seasonal activity both within and across years, with clear trends due to high temporal replication.

The use of automated call recognition software (recognizers in Song Scope) greatly increased the efficiency of processing recordings. It took approximately one hour to review and group automated call detections for every two hours of field recording, compared to approximately three hours to visually scan the same spectrogram to search for murrelet calls. Although recognizers did not perfectly sample recordings (missing some calls and counting some call series as multiple detections), their overall performance provided a reasonable approximation of the true vocalization rate in recordings and greatly improved the efficiency of collecting the data. A limited comparison (2 h of recordings) between Song Scope recognizers and spectrogram cross-correlation (XBAT, Cornell Lab of Ornithology) showed a nearly identical proportion of false positive detections between the two call recognition methods (A. Borker, pers. comm.). The efficiency of using recordings and automated detection software was greatest when Song Meters were placed in areas with high abundance of murrelet calls and low interference from other species, such as high quality potential nesting habitat. A comparison of sensor sites showed that noise interference could be reduced by avoiding complex understory habitat that provides perch sites for higher densities of songbirds; such leafy vegetation also amplifies noise from rain and wind, compared to moss-dominated sites.

Vocal behaviour of murrelets and implications for acoustic monitoring

Marbled murrelets engage in conspicuous vocal and flight displays in the dawn activity period during the breeding season, just after the peak of inland commuting flight observed by radar (Burger 1997, Cooper & Blaha 2002). The reasons for this uncharacteristic behaviour are not well understood, but it likely involves a combination of pair-bond maintenance and perhaps spacing (deterrence advertising) behaviours (Nelson 1997, Dechesne 1998). Because of the association between vocal flight displays and nesting habitat, audio-visual observations have been used as a measure of murrelet habitat use to inform habitat conservation planning. Audio-visual surveys have been used since the early 1990’s as the standard form of habitat assessment for marbled murrelets (Ralph et al. 1995) before the development of marine radar techniques for tracking flying murrelets (Hamer et al. 1995). Numerous audio-visual studies have found relationships between forest overflight displays, especially “occupied” behaviours, and various metrics of murrelet habitat quality (Meyer & Miller 2002, Meyer et al. 2002, Burger and Bahn 2004, Meyer et al. 2004, Stauffer et al. 2004, Bigger et al. 2006a).

Linking detections of vocalizations, either from audio-visual surveys or acoustic sensors, to murrelet abundance and habitat use has limitations compared to other survey techniques. These limitations include the relatively small area over which auditory signals can be heard, and high variation in auditory detections because of various forms of observer bias and inherent variability in murrelet vocal behaviour. Comparisons of detections in inland forest habitat between marine radar (tracking flying murrelets over a

1.5 km radius) and audio-visual surveys illustrate the limitations in using primarily auditory detections, through audio-visual surveys, in evaluating habitat use at the stand-level (Burger 1997, Cooper & Blaha 2002, Bigger et al. 2006a). Compared to radar, audio-visual surveys miss a large but variable proportion of silent commuting murrelets, especially during dark twilight, which is when the majority of commuting murrelets are active (Burger 1997). This makes auditory detections a poor method to estimate the number of murrelets using a given flyway as a way to estimate the breeding population size. The main strength of auditory detections is in evaluating murrelet activity that is relevant to a given forest stand, as an indication of nesting habitat suitability. However, audio-visual surveys detect a variable number of murrelets commuting past the survey station, whose presence is not associated with the local area (Cooper & Blaha 2002). This introduces a complicating factor into relating vocal activity to habitat; however, far fewer detections were recorded by Song Meters on commuting flight paths in this study compared to nesting habitat. An additional source of error comes from the variable probability of detecting murrelets across habitat types due to differences in murrelet behaviour (e.g. more conspicuous behaviour in habitat more likely to be used for breeding), which could inflate differences in detection rates between habitats (Bigger et al. 2006a). A final limitation in relying on auditory detections is that this results in a higher probability of detecting non-breeding murrelets, potentially introducing variability in counts that does not reflect the abundance of breeding murrelets in a given area (Jodice & Collopy 2000, Cooper & Blaha 2002). All in all, these sources of error in estimating the relative abundance of murrelets at a given forest site result in high variation in audio-visual counts relative to radar counts, and low power to detect population trends (Jodice et al. 2001).

Rather than using acoustic detections as a means to estimate population trends or absolute breeding population size, the strength of this small-scale census tool is to link murrelet activity, as an index of abundance, with specific forest attributes. Automated acoustic sensors could improve monitoring in forest stands in several ways: by supplementing audio-visual surveys to increase spatial and temporal replication; by eliminating variation due to observer bias; and by reducing variation due to site characteristics that result in differences in viewing conditions. In this study, subtle but consistent differences were identified in vocal activity of murrelets between nearby forest patches. Such differences between forest patches could be used as a way to measure habitat use, and rank forest stands of higher value to murrelets, especially when used in combination with other readily-available data showing forest structure (e.g., satellite imagery, aerial photographs or GIS forest cover data). Another use of acoustic monitoring would be in obtaining long-term datasets at key locations. These data sets could be used to investigate changes in habitat use by murrelets in response to changes in the environment produced by factors such as climate change, habitat fragmentation, or changes in predator abundance. Deploying multiple sensors simultaneously would allow long-term monitoring of larger habitat patches, and provide measures of local variability, compared to a single sensor.

Strengths and limitations of autonomous acoustic monitoring

Autonomous acoustic sensors have several practical advantages of over other types of surveys: the relatively low cost of units, automation (greatly reducing costs of field personnel), portability, and efficient use of power (battery life generally lasts > 2 months for daily 2-h recordings). Acoustic monitoring also provides a permanent recording of each survey, which has several advantages over field surveys. First, each recording can be reviewed multiple times by the same observer or multiple observers to check for errors, which reduces observer bias. Recordings also allow the observer to use spectrograms to distinguish between murrelet call types (such as “keer” and “keheer”) which are virtually indistinguishable by ear, providing a more detailed record of vocal activity. Finally, the recordings can be stored for future use, providing an enormous repository of data on marbled murrelet vocal activity (e.g., in this study, a subsample of 268 h of recordings yielded 20,632 marbled murrelet calls). Recordings also contain information about the presence of other species that may be of interest to biologists (e.g., presence and relative abundance of potential predators such as corvids, or other species of management concern that can be detected by their vocalizations).

Automated acoustic monitoring can be applied in forestry management and land-use planning. Acoustic sampling of specific forest patches can contribute to habitat suitability rankings; alternatively, habitat use can be monitored following forest harvesting to investigate the effects of harvesting practices (e.g., selective logging, size of variable retention patches) on habitat use by murrelets. Long-term monitoring could simultaneously record changes in the relative abundance of nest predators such as corvids that would be likely to increase in population density following forest fragmentation (Malt & Lank 2007).

The application of automated acoustic monitoring is limited by small sample area, significant time and effort to process large volumes of data, and lower efficiency and effectiveness of recording target species in certain types of sites due to competing noise. Since the main strength of acoustic monitoring is in collecting large volumes of data at low cost, it needs to be recognized that even using automated call recognition software, processing long recordings can be very time consuming (in this study, processing time was approximately ½ the duration of recordings). Processing could be streamlined for marbled murrelet recordings by simply reviewing spectrograms for murrelet calls and eliminating the grouping of call series (this step was only done to make comparisons with audio-visual surveys), since the relationship between calls and grouped call series only deviated slightly from a linear correlation (Figure 6). Another option is to subsample smaller time intervals each morning (e.g., Wimmer et al. 2013), based on exploratory sampling to determine the most representative portion of the pre-sunrise activity period.

Processing efficiency in this study was also affected by the number of false positive detections generated by the complex vocalizations of songbirds. In brushy areas, the number of false positive detections per 2-h recording regularly exceeded 1,000, which significantly increased time needed to review each spectrogram. Additionally, during the early breeding season songbird vocalizations occasionally saturated the recording, potentially resulting in missed detections of murrelet calls. Although this problem occurred on relatively rare occasions (2-3 min periods per recording, over a period of 3 weeks in June-early July), saturation of recordings could be a more serious problem at locations outside of Kodiak Island where songbird density is greater. The relatively sparse understory of the old-growth Sitka spruce forest where recordings were collected on Kodiak Island had apparently lower densities of songbirds than habitats with more brushy vegetation. Forests in the Kodiak Archipelago are relatively young (the earliest colonization of the archipelago by Sitka spruce is thought to have occurred within the last 800 years), and have less understory vegetation than might be found forests in the murrelet's range that are more successionally advanced and have complex understory development. Such forests may provide habitat for higher densities of songbirds which could detrimentally affect signal recognition by acoustic processing software.

Finally, inferences about habitat use by murrelets from automated acoustic sensors should be limited to an index of activity or abundance, rather than estimates of absolute abundance. In the absence of visual observations of behaviours indicative of nesting (e.g., below-canopy flight, circling; Evans Mack et al. 2003), inferences about the likelihood of nearby nests or nesting density should be avoided.

Future development of acoustic monitoring and potential applications

The development of autonomous acoustic sensor systems and vocal recognition software is proceeding rapidly, making acoustic monitoring of remote animal populations increasingly efficient. New transmitting devices incorporated into acoustic sensor systems offer the potential to deploy sensors in remote locations and monitor the status of equipment in real time via satellite (power, memory space), and to upload recordings remotely via cellular networks (McKown et al. 2012, Wildlife Acoustics 2013). Coordinated systems of sensors now available can triangulate sounds to provide detailed information on the direction and distance of signal sources (Wildlife Acoustics 2013). The advancement of computer processing techniques for recordings includes the potential for vocal fingerprinting of individuals. Given that vocal fingerprinting of marbled murrelets is possible with carefully selected call recordings (low distortion from Döppler effects and echoes; Dechesne 1998), advances in both microphone quality and processing techniques could provide a means to identify individual murrelets recorded at forest sites. Such refinement in monitoring of murrelet vocal behaviour would provide major breakthroughs in understanding murrelet behaviour and ecology. Combining recordings with visual observation of murrelet flight behaviours could also increase our understanding of the complex vocal repertoire (Dechesne 1998) of this species.

Chapter 2: Comparing novel techniques for monitoring populations of *Brachyramphus* murrelets in Alaska

Introduction

Kittlitz's (*Brachyramphus brevirostris*) and marbled murrelets (*B. marmoratus*) are small diving seabirds of the family Alcidae that breed sympatrically in parts of Alaska. Murrelets of the genus *Brachyramphus* are unique among the alcids in their non-colonial nesting, cryptic breeding sites, camouflaged plumage and secretive nest attendance, all thought to have evolved as anti-predator strategies (Gaston & Jones 1998). Kittlitz's and Marbled murrelets exhibit varying degrees of niche overlap in Alaska (Day & Nigro 2000, Nelson et al. 2013), but have subtle differences in their nesting and foraging ecology (Day et al. 2003). Marbled murrelets generally nest in mossy limbs of old growth conifers (Nelson 1997); in Alaska, 97% of their at-sea distribution during the breeding season occurs adjacent to suitable forest habitat (Piatt & Ford 1993). Kittlitz's murrelets are spatially associated with glaciers across their range (van Vliet 1993, Kuletz et al. 2003) nesting on bare ground in high-elevation unvegetated rocky terrain (Day et al. 1999, Lawonn 2013) and foraging in turbid glacial runoff (Day & Nigro 2000, Day et al. 2003). Both species are of conservation concern in Alaska due to evidence of large population declines over the last 25 years (Piatt et al. 2007, Kuletz et al. 2011a,b, Piatt et al. 2011).

The primary goal of this study was to develop improved methods for monitoring populations and distributions of *Brachyramphus* murrelets in Alaska. I tested the effectiveness of combinations of established murrelet population monitoring methods (marine radar surveys, audio-visual surveys) and a new monitoring technique (automated acoustic sensors) to monitor relative abundance and spatial and temporal trends of breeding murrelets. A secondary goal was to use all three methods to investigate behavioural differences between Kittlitz's and marbled murrelets.

Current population monitoring of *Brachyramphus* murrelets in Alaska is conducted through at-sea vessel counts, which have produced imprecise population estimates and have low power to detect population trends (USFWS 2010, Kissling et al. 2007, 2011). Inherent difficulties with population monitoring through at-sea vessel counts include the highly mobile nature of these species, the large non-breeding component of the population (Kittlitz's murrelet in particular), logistical and budgetary constraints to visit remote areas, difficulty in distinguishing between the two *Brachyramphus* species at sea, observer sensitivity to weather conditions and observer bias (USFWS 2010, Kissling 2011). Additionally, information from at-sea vessel surveys on population size and trends is relevant to large, regional scales, and it is therefore difficult to infer relationships between at-sea counts and specific areas of adjacent inland breeding habitat.

South of Alaska, marine radar surveys have become an established method to census and monitor populations of marbled murrelets (Hamer et al. 1995, Burger 1997, Cooper et al. 2001), with high power to detect population trends (Burger 2001, Arcese et al. 2005, Bigger et al. 2006b, Cooper et al. 2006). Radar counts also provide information on habitat associations and inferred relative nesting density at the watershed level (Burger 2001, Raphael et al. 2002). Given the uncertainties around population status and trend for Alaskan murrelets, radar monitoring techniques could provide a valuable tool for managers to refine and focus conservation efforts. I conducted radar surveys in the Kodiak Archipelago from 2010 to 2012 in order to develop radar monitoring protocols suitable for Alaskan conditions. Alaska poses unique challenges such as two species of murrelets overlapping in their breeding habitat, extreme weather events, including high winds that affect flight behaviour, large variation in nesting habitat, an exposed coastline, and latitudinal effects on light regime and seasonality. This study provides the first high-latitude assessment of seasonal trends in murrelet inland flight behaviour by radar. During the "core" breeding period, seasonal trends in inland flight behaviours were detected by radar in some low-latitude populations (Cooper et al. 2001), but not in others (Burger 2001). Breeding season length is shorter in Alaska (Piatt et al. 2007, Nelson et al. 2013), perhaps promoting greater synchrony in breeding phenology, which could produce seasonal patterns in radar counts during the core breeding period (June-July).

Automated acoustic recording techniques provide a complementary tool for monitoring of murrelet populations in remote areas. A major limitation of murrelet population monitoring is the high cost of supporting field crews, which often reduces spatial and temporal replication of surveys. I compared detection rates of murrelet vocalizations from automated acoustic sensors (Song Meters, Wildlife Acoustics Inc., Concord, MA) to radar observations of relative abundance and flight behaviour. The objective of this comparison was to determine whether acoustic detections provided a reliable index of the relative abundance of murrelets, and to test whether acoustic detection reliability differed between likely nesting habitat compared to commuting flight paths over unsuitable habitat. Finally, combined radar and acoustic surveys were tested to differentiate marbled and Kittlitz's murrelets on the basis of differences in patterns of flight and vocal behaviour.

Methods

To compare radar, audio-visual and automated acoustic surveys I applied these methods in the Kodiak Archipelago during the murrelet breeding season (June-August) from 2010 through 2012. The murrelet "detection" was the common unit of comparison between survey methods. In radar surveys, a murrelet detection is defined as a series of radar echoes (3 or more) that have the appearance, flight speed and flight pattern characteristic of a murrelet (Manley 2006). For audio-visual surveys, a murrelet detection is defined as "the sighting or hearing of one or more murrelets acting in a similar manner" (Paton et al. 1995, Ralph et al. 1994), with gaps between calls of > 5 s considered separate detections (Evans Mack et al. 2003). An automated acoustic murrelet detection was similarly defined as a series of murrelet calls separated by < 5 s (Evans Mack et al. 2003, Borker et al. 2012).

Radar and audio-visual surveys: data collection

I used marine radar (Hamer et al. 1995, Burger 1997) to observe flying murrelets at 27 sites in the Kodiak Archipelago from 2010-2012 during the core breeding period, early

June through the first week of August (Figure 10). The radar unit was a Furuno 1954C (X-band, 12 kW transmitter, 9410 MHz, 2 m array) modified by tilting the scanner upwards by ~15˚ according to standard adjustments for murrelet surveys (Burger 1997, Harper et al. 2004). In 2010, all surveys were conducted at Grant Lagoon on southwest Kodiak Island (57.461º N, 154.657º W). This site is located at the mouth of the Ayakulik River valley, an area that has been intensively searched for Kittlitz's murrelet nests from 2008-2013, yielding 91 nest discoveries (Lawonn 2013, R. Corcoran, pers. comm.). This is the largest known concentration of Kittlitz's murrelet nests on Kodiak Island and no marbled murrelet nests have been found here. Thus, radar surveys conducted at Grant Lagoon were likely to be tracking a higher proportion of Kittlitz's murrelets relative to marbled murrelets than other radar sites in the archipelago. At this site, surveys of 6 h were conducted in randomized periods throughout the 24 h cycle to investigate diurnal activity and to permit visual identification during daylight of other species detected by radar. In 2011-2012, repeated surveys were conducted at Monashka Bay, on northern Kodiak Island. Exploratory surveys were also conducted opportunistically throughout the archipelago as part of a nearshore marine bird monitoring program with the Kodiak National Wildlife Refuge. In 2011, surveys were conducted along the southern and eastern coasts of Kodiak Island, mainly within the Kodiak National Wildlife Refuge, while in 2012 surveys were conducted on northern Kodiak Island, and on Afognak and Shuyak Islands. Based on the 2010 data, the surveys conducted in 2011 and 2012 were only at night and twilight, beginning 30 minutes before sunset and ending one hour after sunrise or 10 minutes after the last murrelet detection (sunrise and sunset times from www.sunrisesunset.com).

For each murrelet detected by radar I recorded flight behaviour in order to distinguish potential murrelets from other species. Targets were identified on the basis of four criteria: flight speed ≥ 50 km h^{-1}; flight type (direct or sinusoidal); flight path consistent with the likely route used for commuting flight between potential nesting areas and marine foraging sites; and number of sequential images of the target (hits) ≥ 4. If all four criteria were met the target was recorded as a "murrelet", if three of the four it was considered a "possible murrelet" (Figure 11). Targets with fewer than three of these criteria were recorded as an unknown species. The actual species was recorded if verified by the audio-visual observer. In addition, murrelet flight direction was categorized as inbound (landward), outbound (seaward) or circling (which generally occurs in likely nesting habitat). Typical murrelet flight paths were identified, so that it was possible to place acoustic sensors in areas used by murrelets, and to estimate the number of detections associated with a specific area such as the location of acoustic sensors and audio-visual observers. Weather conditions (% cloud cover; cloud type; air temperature; wind speed, measured with an anemometer; and wind direction) were recorded at the start and end of each survey, plus weather events during the survey that would affect the reliability of data (e.g., high winds or rain showers).

Audio-visual surveys were conducted in conjunction with radar surveys at dusk (from radar survey start until civil twilight) and at dawn (starting 1 h before sunrise until 1 h after sunrise). I used standard audio-visual protocols (Evans Mack et al. 2003) to record murrelet detections, including species identity when possible, along with vocalizations, flight behaviour, and murrelet group size. Detections were considered to be indicative of habitat occupancy (i.e., possible nearby nest site) if murrelets flew below tree canopy height (or below ~ 5 m in unforested habitat), circled, landed or took off, or called from a stationary point (Evans Mack et al. 2003). Audio-visual surveys were also used to monitor the presence and behaviour of other coastal bird species, such as eagles, waterfowl, gulls and shorebirds, that were likely to appear on the radar. In 2010, murrelet audio-visual detections were rare, and therefore I recorded detailed characteristics of flight behaviour of other bird species identified by the audio-visual observer that were likely to be confused with murrelets.

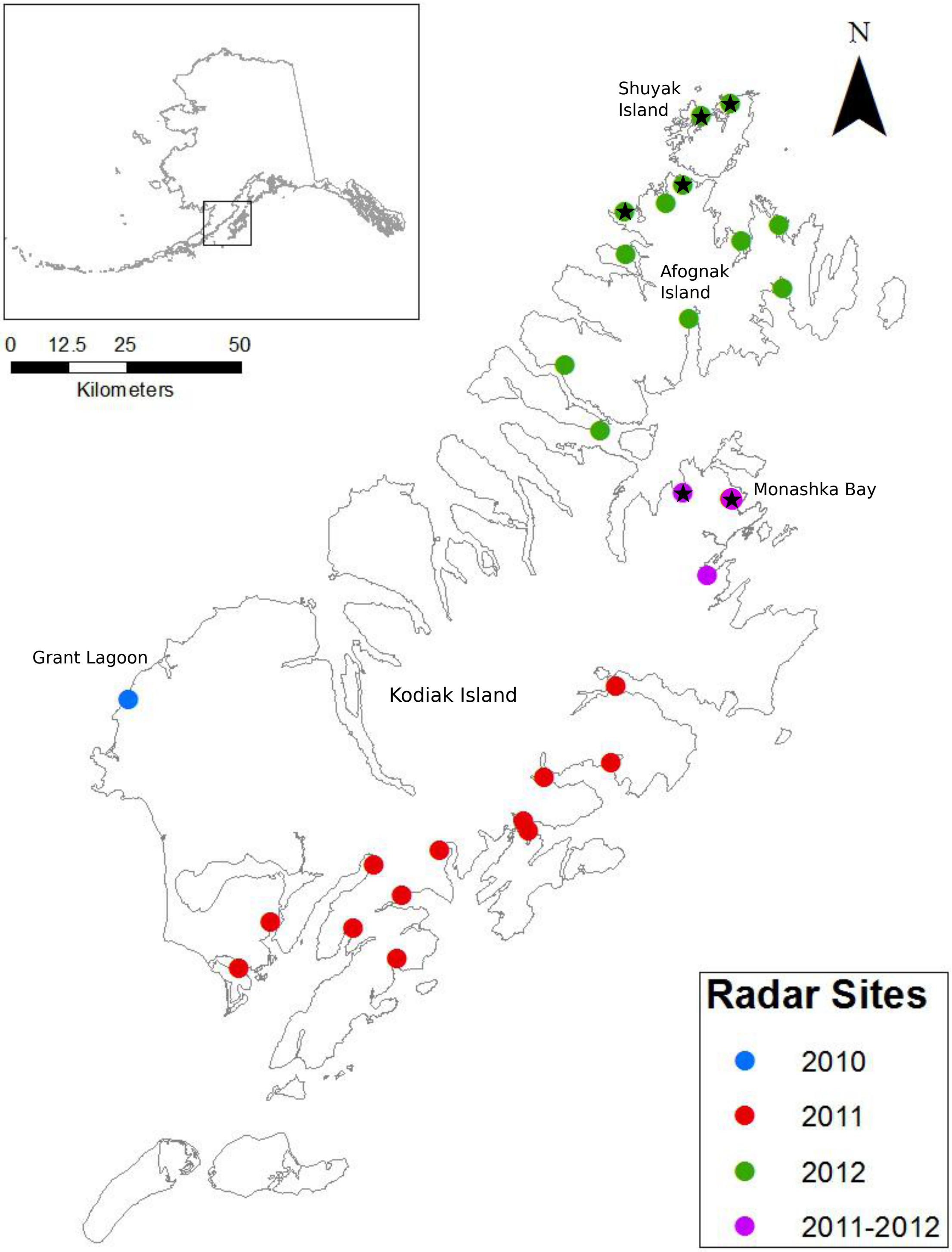

Figure 10: Radar sites surveyed from 2010-2012 in the Kodiak Archipelago. Sites with both radar and automated acoustic surveys indicated by stars.

Radar and audio-visual surveys: data analysis

To examine diurnal activity patterns in radar and audio-visual surveys, I calculated the proportion of each survey's counts within 30-min intervals (relative to sunrise), calculated the mean proportion in each interval across all sites, and used the coefficient of variation of the mean as a measure of variability in activity.

The only site that was sampled by radar across most of a breeding season was Grant Lagoon (14 overnight surveys, 3 June- 27 July 2010). There was high variation in diurnal activity patterns at this site; therefore mean murrelet counts per hour for each survey were used to visualize the seasonal trend in activity. Diurnal activity patterns at Grant Lagoon were summarized by calculating the mean radar count of murrelets for each 1-h time interval relative to sunrise for the 24 h cycle; this diurnal pattern of commuting flights was compared to the mean fish delivery rates detected by cameras at Kittlitz's murrelet nests inland of the radar station (Lawonn 2013).

Audio-visual detections of circling murrelets (an indication of occupied behaviour) were compared to circling detections by radar at Monashka Bay using pooled detections for 2011 and 2012 and a Wilcoxon signed rank test. The trend in circling detections for both methods during the period of sampling was described with linear regression.

Acoustic field recordings

I collected field recordings using automated acoustic sensors in the Kodiak Archipelago during the murrelet breeding season (June-August) in 2011 and 2012. Detailed methods for data collection and analysis of recordings by Song Meters are described in Chapter 1. Song Meters were programmed to record for 2 hours each day, starting 2 hours before sunrise, to match the peak of murrelet activity observed by radar. In 2011, sensors were placed at six sites across a variety of habitat types within the radar scanning area at Monashka Bay on Kodiak Island (Table 1 from Chapter 1, Figure 11A) from 15 June-3 September. In 2012, sensors were deployed in the most likely potential forested nesting habitat within the radar scanning area at six sites in the northern Kodiak Archipelago (Figure 10); at one site no forested nesting habitat was available and the Song Meter was placed along a commuting flight path. Three sensors were deployed at Monashka Bay on Kodiak Island from 1 June – 27 August 2012.

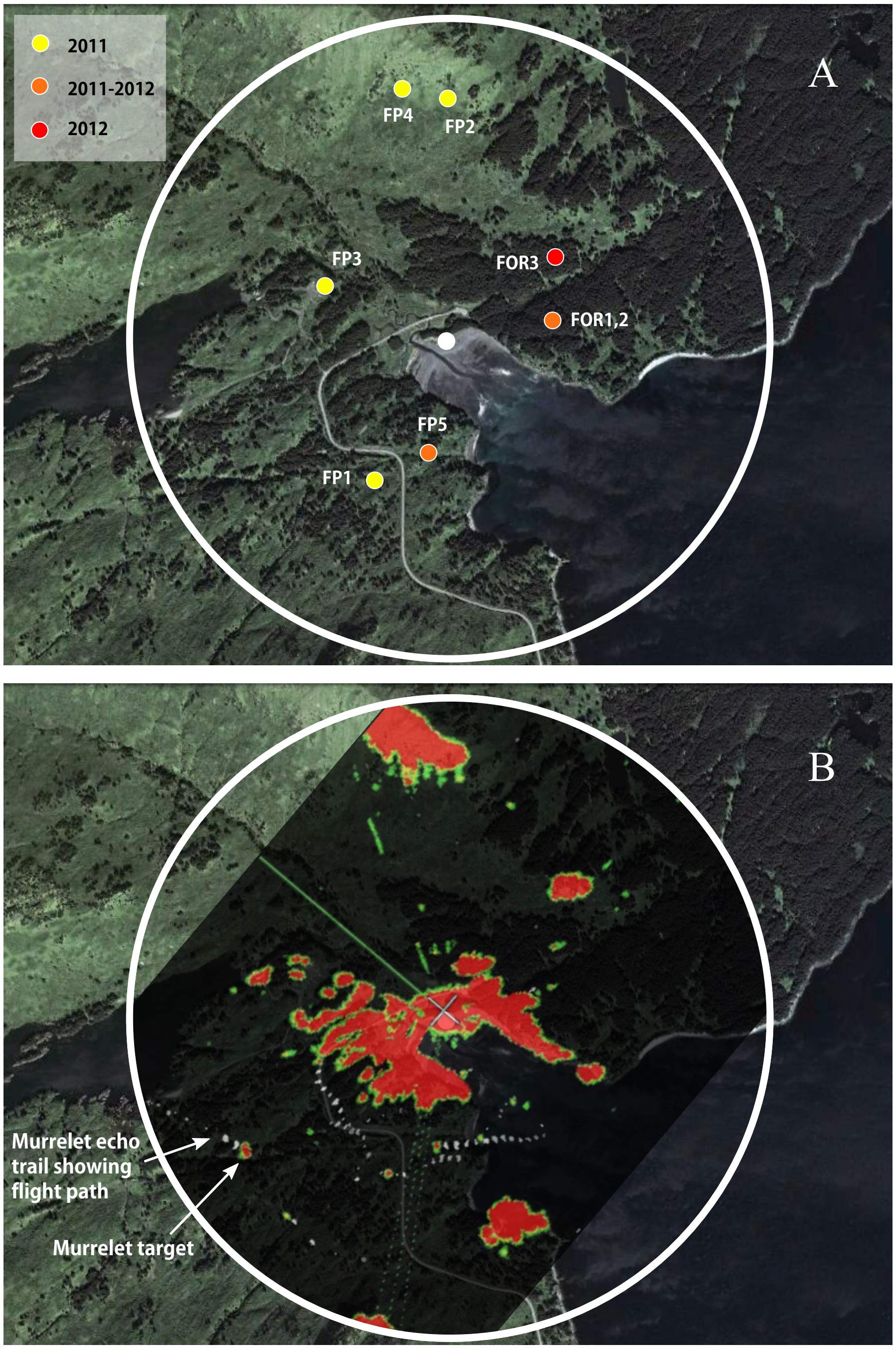

Figure 11: A) locations of Song Meters within the scanning radius of the radar (white circle). Song Meter names correspond to codes in Table 1, Chapter 1. FOR 1,2 were located on the same tree. B) Radar screen image overlaid over a satellite photo of Monashka Bay, showing murrelet targets commuting along a flight corridor in the lower left side of the circle. Large red patches are areas of land detected by the radar scanning beam. Red dots are murrelet targets with echo trails (whitish dots) showing their flight path and speed (distance between white dots).

Comparison of radar, audio-visual and autonomous acoustic detections

Audio-visual and Song Meter detections were compared for surveys conducted at Monashka Bay, the only location where audio-visual observers were within 300 m of the Song Meter. Simultaneous surveys were conducted on six mornings in each year: 2011 (10-18 July) and 2012 (16-24 July). The total number of audio-visual detections was compared to Song Meter detections during the period starting one hour before sunrise when surveys overlapped. To test if there was a relationship between audio-visual and Song Meter counts across all surveys at Monashka Bay, pooled counts from 2011 and 2012 were used to test for correlation. Data were collected slightly earlier in the season in 2011 and had lower overall counts than 2012, therefore the mean Song Meter and audio-visual counts for each year were compared separately using two-sample t-tests to avoid the potentially confounding effects of seasonal differences in abundance.

Radar and Song Meter counts were compared at six sites where surveys were conducted simultaneously in 2012 to test for correlations in counts across sites. At two sites (Monashka Bay, Red Fox Bay), I observed two discrete murrelet flight paths by radar, one of which was > 800 m from the Song Meter and therefore excluded from the comparison. At the other four sites, flight paths were variable and it was not possible to exclude distant murrelets from the comparison with Song Meter counts. Because radar surveys focused on counting all commuting birds rather than tracking only the murrelets passing within 100-200 m of the Song Meter, a strict comparison of targets within the likely Song Meter detection range and the Song Meter counts could not be conducted. Instead, the abundance of vocal detections from Song Meters (total detections per morning) was compared to the total number of incoming commuting murrelets observed by radar at each site (with the exception of excluded flight paths noted above). Five of the six sites were visited only once as part of a nearshore marine bird monitoring program, while many surveys were conducted at Monashka Bay; therefore, in order to avoid pseudoreplication, a mean count of daily Song Meter and radar detections from Monashka Bay was used in this analysis. A Spearman's rank test was used to test for correlation between radar and Song Meter detections across the six sites.

A within-site comparison of radar and Song Meter counts was conducted at Monashka Bay, where concurrent radar and Song Meter surveys were repeated on multiple mornings in 2011 and 2012. To test whether radar and Song Meter counts were correlated temporally (across all survey days), Song Meter counts from the sensor location Forest 1 (Table 1, Figure 11A) were compared with radar counts for the flight path closest to this sensor using a Spearman's rank test for pooled counts from both years, and for 2012 separately.

Vocalization rates from Song Meter recordings were compared between two habitats at Monashka Bay: first, a likely nesting area, where 24% of murrelet targets observed by radar (n = 587) engaged in circling flight, and second, a high-traffic commuting flight corridor where 96% of murrelet targets (n = 926) were commuting (fast direct flight). Mean Song Meter and radar counts (2 h pre-sunrise) were compared in likely nesting habitat for sensors Forest 1 and 2 (located at the same tree in 2011-2012 and 2011, respectively), and for sensor Flight path 5 (2011-2012) using Welch's two-sample t-tests. Pooled daily counts for 2011 and 2012 from radar, Song Meter (sensor Forest 1) and audio-visual surveys were compared using a one-way ANOVA for the period during which all three surveys were conducted simultaneously (1-h pre-sunrise). Radar counts in this test were limited to murrelets flying within the area sampled by the audio-visual observer and acoustic sensor.

Seasonal trends in murrelet activity were compared between the three types of surveys by plotting repeated counts across the breeding season from Grant Lagoon (radar; 2010), and Monashka Bay (radar, audio-visual, and Song Meter; 2011-2012). To describe seasonal trends in murrelet flight behaviour, the number of circling detections by radar and audio-visual surveys at Monashka Bay was plotted across the season using pooled counts from 2011-2012.

Results

Survey effort

I completed radar, audio-visual and Song Meter surveys at multiple sites in the Kodiak Archipelago from 2010-2012 (Table 6). In total, 97 radar surveys (including the dawn activity period), 124 audio-visual surveys (dawn and dusk), and 134 dawn Song Meter surveys were completed, yielding 26,375 murrelet detections.

Table 6: Summary of survey effort (2010-2012) by survey type and total murrelet detections. See Figure 10 for the locations of sites.

Survey type and year	Location	Dates	Number of Surveys	Hours	Sites	Detections Murrelets	Detections Possible murrelets*	Detections Total
Radar								
2010	Grant Lagoon	4 June-27 July	35	181.7	1	1,230	868	2,098
2011	East Kodiak & Monashka Bay	5 June-20 August	30	159.6	14	6,628	607	7,325
2012	Northern Kodiak Archipelago & Monashka Bay	1 June-24 July	32	194.3	15	10,408	644	11,081
Total			97	535.6	27	18,266	2119	20,504
Audio-visual								
2010	Grant Lagoon	4 June-27 July	36	73.5	1	22	-	22
2011	East Kodiak & Monashka Bay	5 June-3 August	36	57.5	12	576	-	576
2012	Northern Kodiak Archipelago & Monashka Bay	1 June-24 July	52	83	14	1,641	-	1,641
Total			124	214	23	2,239		2,239
Song Meter								
2011	Monashka Bay	15 June-3 September	70	140	1	2,725	-	2,725
2012	Northern Kodiak Archipelago & Monashka Bay	1 June - 27 August	64	128	6	3,145	-	3,145
Total			134	268	6	5,870		5,870

*These were radar detections that fulfilled three of the four selection criteria for murrelets and identification was therefore less certain (see Methods).

Radar surveys: differentiating murrelets from other species, weather effects

It was possible to differentiate murrelet targets from those of other species on the basis of flight speed and behaviour under most weather conditions. Murrelet targets flew on average 35 km h^{-1} faster than commonly seen, relatively fast-flying non-murrelet targets such as red-throated loons (*Gavia stellata*), red-breasted mergansers (*Mergus serrator*), and bald eagles (*Haliaeetus leucocephalus*; mean murrelet flight speed ± SE: 83.0 ± 0.5 km h^{-1}, n = 1796; Figure 12). Murrelets had direct or sinusoidal flight paths 89.9 % of the time (n = 2330), while circling behaviour was observed mainly when radar stations were located near potential forested nesting habitat (9.1% of observations, n = 212).

During high wind events, the reliability of using flight behaviour to differentiate murrelets from other species was reduced. With a strong tail wind, other bird species flew with higher ground speeds and more direct flight paths, making them difficult to distinguish from murrelets, and resulting in falsely inflated murrelet counts. In 2010 surveys at Grant Lagoon, a weak positive relationship between murrelet counts and wind speed ($F_{1,17} = 10.94$, $R^2 = 0.39$, $p = 0.004$) was driven by two high wind events (Figure 13). When these events were removed from the analysis, the relationship disappeared; indicating that above a threshold wind speed (18 km h^{-1}) murrelet counts become unreliable.

Although high tailwinds resulted in an apparent increase in murrelet detections, headwinds appeared to reduce murrelet detections, either because murrelets appeared to fly too slowly and were not counted, or because they used alternative flight paths to reach their nest sites. At the Monashka Bay radar station, there were two commuting flight paths with differing trajectories into inland nest sites; murrelets using one flight path flew directly west when commuting landward and were more exposed to strong westerly winds. Although strong winds from both the south and west occurred between 9-18 July, 2011, only westerly wind (18 July) affected counts of commuting murrelets (Figure 14), resulting in unusually low counts of incoming murrelets. The ratio of outgoing to incoming detections (6.8 outgoing birds per incoming bird) was highly skewed compared to the normal ratio (0.6); this was entirely due to the unusually low number of murrelet flying inland against the headwind, and not because of a falsely inflated number of outgoing murrelet targets flying with a tailwind. No effect of this wind event was observed along the second flight path. High winds (> 20 km h^1) were recorded during 10 surveys (9.6% of all surveys attempted in 2010-2012) and prevented 3 surveys; surveys with unreliable counts due to wind were not used in other analyses.

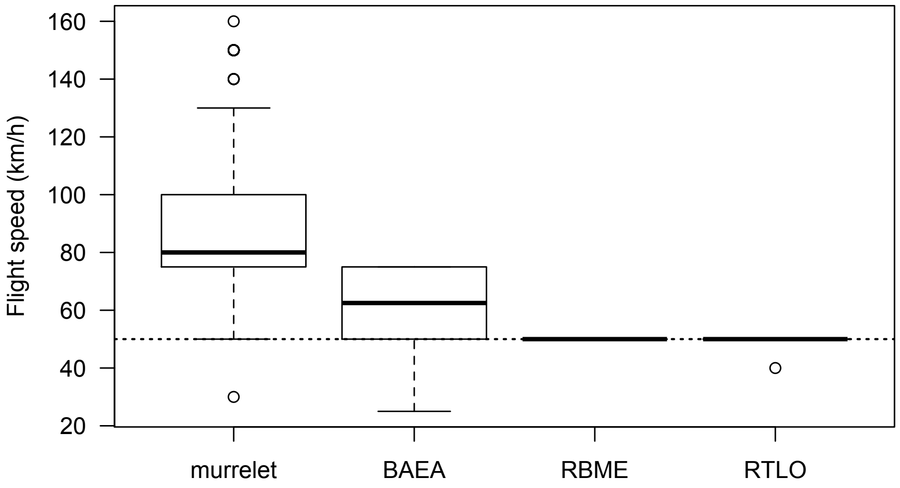

Figure 12: Boxplot of flight speeds (box shows median and interquartile range, whiskers indicate maximum and minimum speed values) of murrelets (n = 1787) and other fast-flying common coastal birds (bald eagle BAEA, n = 10; red-breasted merganser RBME, n = 4; and red-throated loon RTLO, n = 7). Cut-off speed for murrelet detections (50 km h^{-1}) is indicated by the horizontal dashed line.

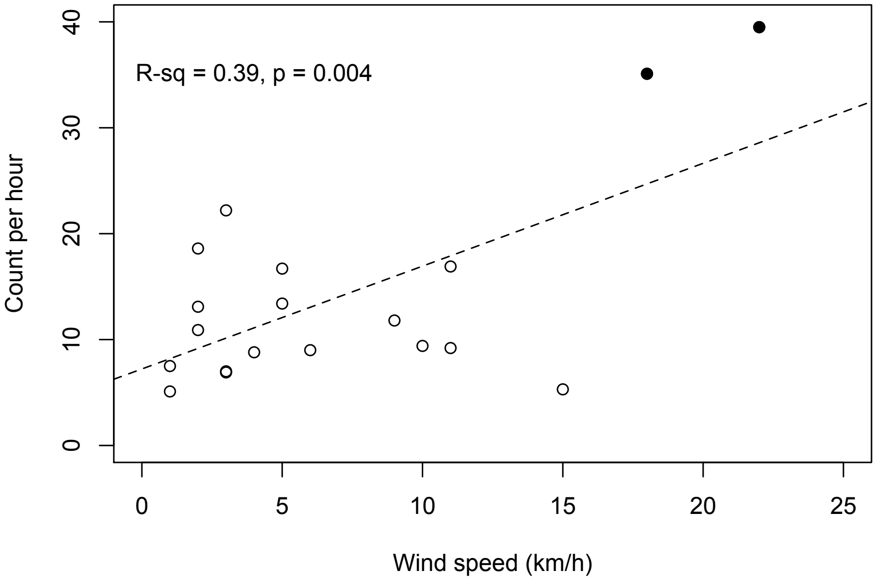

Figure 13: In 2010 radar surveys at Grant Lagoon, there was a weak positive relationship (R^2 = 0.39, p = 0.004) between mean murrelet count per hour and average wind speed over the survey (estimated using the Beaufort Scale) when all wind speeds were included in the analysis; this relationship disappeared when two high-wind events were removed (filled circles).

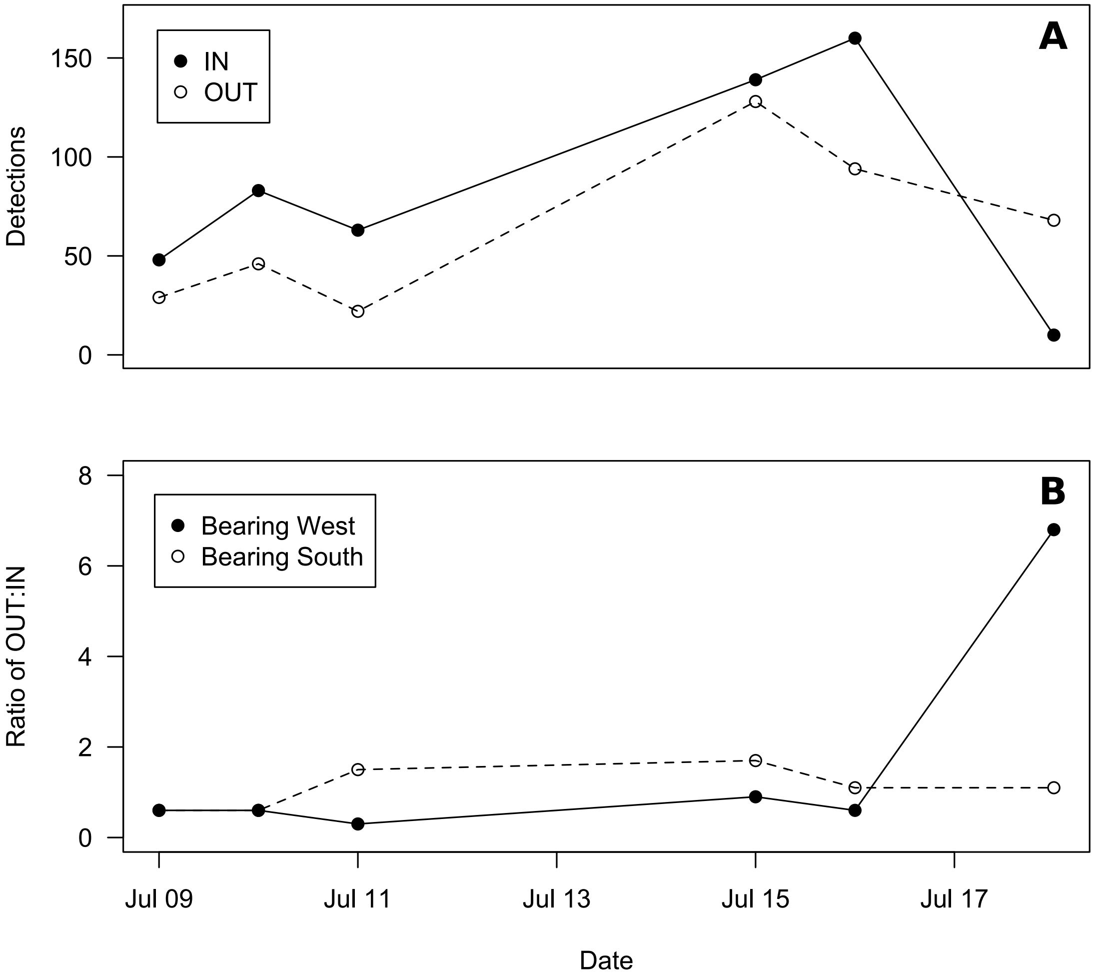

Figure 14: Effects of wind on the number of murrelets detected by radar along two flight paths (one bearing W, one bearing S) at Monashka Bay, 9-18 July, 2011. (A) a strong westerly wind on 18 July reduced the number of inbound (landward) murrelet detections along the flight path bearing west, resulting in a skewed proportion of outbound to inbound detections (OUT:IN ratio) along this flight path (B).

Differentiation between Kittlitz's and marbled murrelet targets by radar was not possible, because murrelet targets were rarely confirmed with visual or aural observation. Visual observations of flying murrelets (fast-flying silhouettes) did not permit species identification, while aural observations were exclusively marbled murrelets. When commuting flight behaviour was compared between murrelets detected at Grant Lagoon (presumed to have a higher proportion of Kittlitz's murrelets nesting nearby) to other sites, there was no difference in the proportion of direct vs. sinusoidal flight in commuting birds (mean of 30.8% sinusoidal flight at both Grant Lagoon and averaged across all other sites). The mean flight speed of murrelets was slightly slower at Grant Lagoon compared to the mean of all other sites (mean ± SE of 81.2 ± 0.66 km h^{-1}, n = 939, and 84.1 ± 0.72 km h^{-1}, n = 805 respectively), and this difference was statistically significant (Welch two sample t-test: t = 2.969, df = 1691.8, p = 0.003). This small difference in speed (< 4%) could be indicative of slower flight speeds in Kittlitz's murrelets; however, this result could have been generated by confounding factors such as wind speed, topography and observer bias.

Radar surveys: diurnal activity patterns

Diurnal activity patterns observed by radar showed that murrelets had activity peaks at dawn and dusk, with a much greater peak at dawn (Figure 15). The proportion of activity occurring during the pre-sunrise activity peak also had the lowest coefficient of variation (Figure 15). Landward flight activity peaked 84 ± 3 min (mean ± SE; n = 49) before sunrise whereas seaward flight activity peaked 48 ± 6 min pre-sunrise (n = 47).

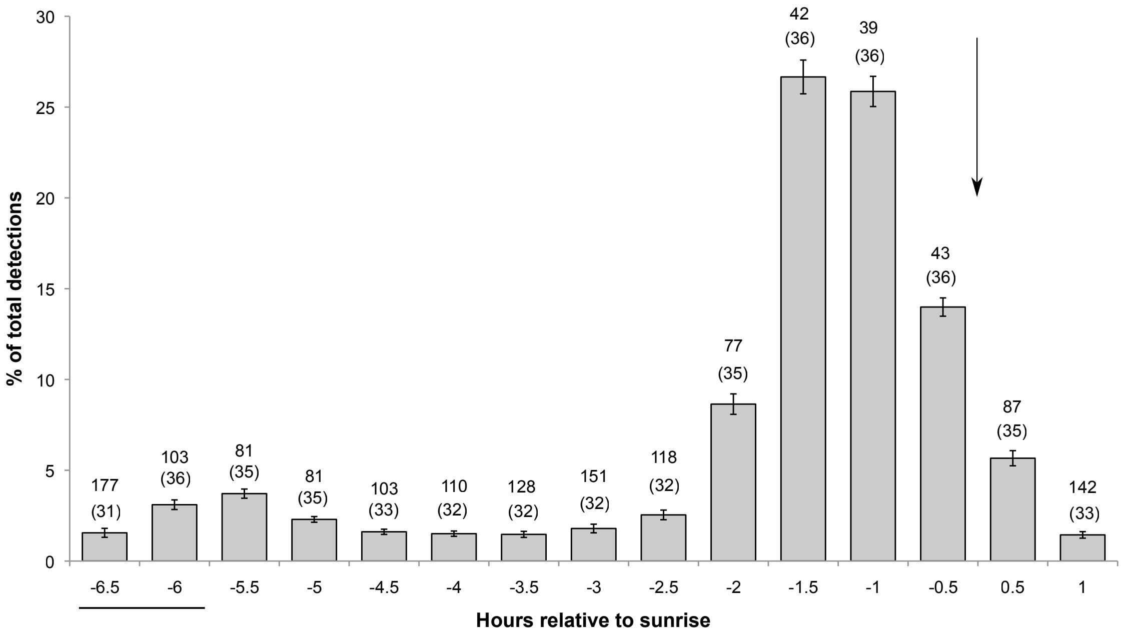

Figure 15: Diurnal activity pattern in 30-minute intervals for pooled 2011 and 2012 murrelet detections observed by radar shown as the mean (± SE) of the percentage of total detections per survey relative to sunrise (indicated by arrow). Labels above each column show the coefficient of variation with sample size below (the period from -6.5 h pre-sunrise to 1.5 h post-sunrise was sampled equally across sites). Sunset time relative to sunrise varied across the season and is indicate by the black bar (bottom left).

Diurnal activity patterns at Grant Lagoon, where Kittlitz's murrelets were more likely to be sampled (not included in Figure 15), were different from other sites with greater murrelet abundance. Activity was greatest during the night (beginning approximately six hours before sunrise), with a slight peak in activity beginning one hour before sunrise (Figure 16). Unlike other radar sites, murrelet activity was relatively constant throughout the night and declined gradually following sunrise. This was also inconsistent with nest visitation patterns during the chick-rearing phase, documented by nest cameras at Kittlitz's murrelet nests inland of the radar station (Lawonn 2013). Nest cameras showed clear peaks in fish delivery rates occurring at dusk and dawn, with virtually no activity during the darkest hours of the night (approximately 1:00-3:00 am). This indicates that the radar was likely tracking some murrelets that were not associated with nests monitored by camera, including potentially non-breeding and immature murrelets involved in social interaction and nest prospecting, or marbled murrelets nesting elsewhere in the area.

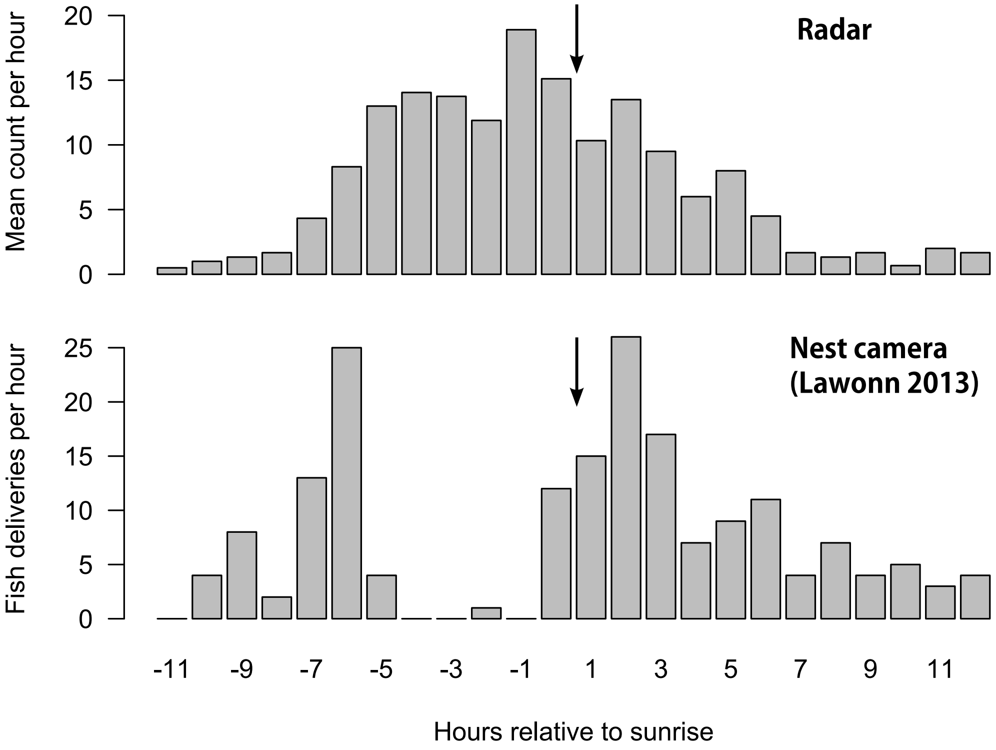

Figure 16: Comparison of the mean radar counts (6 June-27 July) of commuting murrelets (incoming and outgoing) at Grant Lagoon (2010) per hour relative to sunrise (marked by arrow), to mean Kittlitz's murrelet fish deliveries (15 June-8 August) per hour recorded by nest cameras inland of the radar over the 24-hour cycle.

Audio-visual surveys

Audio-visual surveys were useful in identifying potentially confusing species on radar such as loons, mergansers, cormorants and eagles; however, audio-visual observers were unable to determine the species identity of the majority of murrelet targets on radar. Over the three field seasons and >200 hours of observation, no Kittlitz's murrelets were positively identified by audio-visual surveys. All detections summarized in this study are of marbled murrelets or unidentified *Brachyramphus* murrelets. Audio-visual detections of murrelets were greatest at forested sites, where murrelets engaged in social interaction near potential forest nesting habitat, producing 653 detections of "occupied" behaviour (flying below canopy height, circling above the canopy, aerial dives) at forested sites in 2011 and 2012.

Acoustic recordings: summary of calling behaviour

Acoustic sensors recorded four types of marbled murrelet vocalizations and two non-vocal sounds (wing beats and jet sounds), yielding 5,870 detections (Chapter 1, this study). No Kittlitz's murrelet vocalizations were detected over 134 surveys (268 h of recordings).

Comparison of radar, audio-visual and autonomous acoustic detections

There was no significant difference in mean counts of detections between audio-visual and Song Meter surveys in either 2011 or 2012 (Two-sample t-test; $t = 1.453$, $df = 10$, $p = 0.177$, $t = 0.569$, $df = 10$, $p = 0.582$; Figure 17). In 2012, sampling occurred slightly later in the season (16-24 July compared to 10-18 July in 2011), which could be the reason that counts were slightly higher in 2012 for both methods; audio-visual counts were significantly higher in 2012 than in 2011 (Two sample t-test; $t = 3.593$, $df = 10$, $p = 0.005$). Although there was no difference in mean counts between survey methods, daily counts from the two methods were not correlated across the breeding season when detections from both years were pooled (Figure 18; $S = 168$, $r_s = 0.41$, $p = 0.185$).

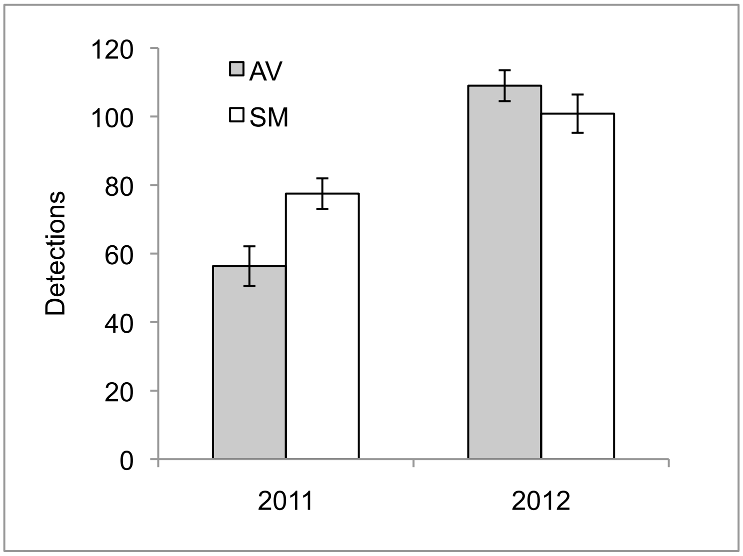

Figure 17: Annual mean audio-visual (AV) and Song Meter (SM) detections per survey ± SE at Monashka Bay in 2011 (6 concurrent surveys; 10-18 July) and 2012 (6 concurrent surveys; 16-24 July).

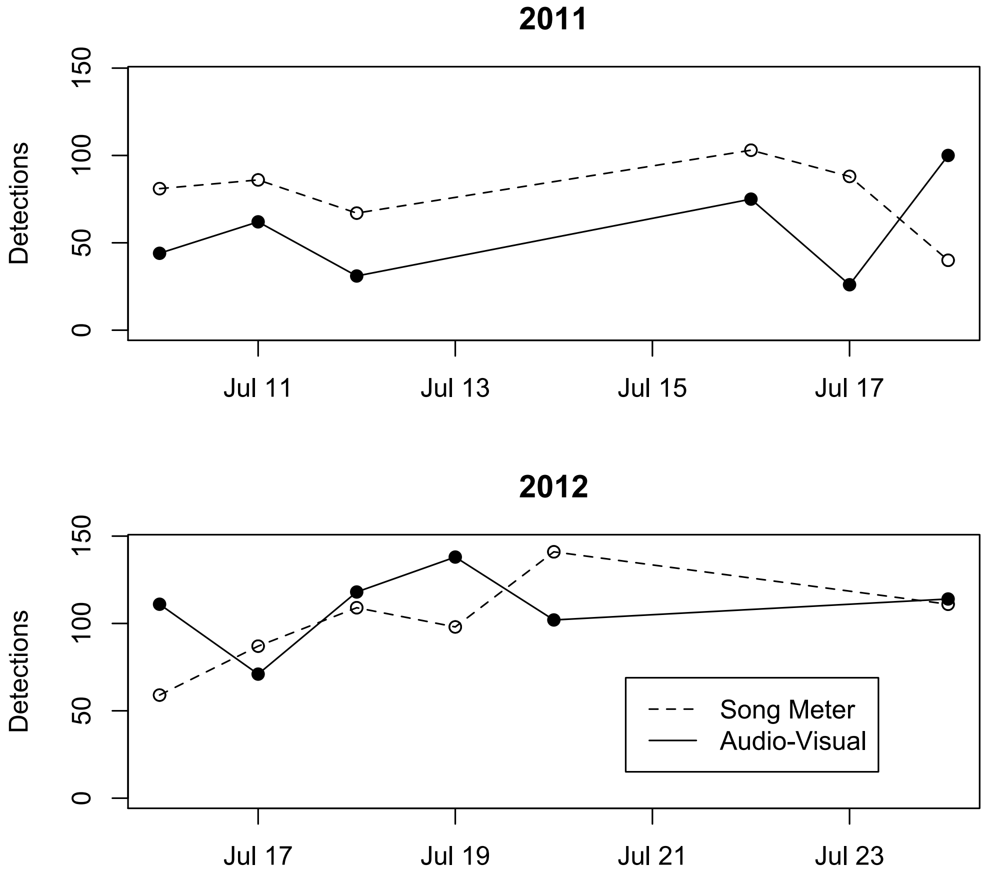

Figure 18: Daily counts of detections from audio-visual (AV) and Song Meter (SM) surveys in 2011 and 2012 at Monashka Bay.

There was no correlation between radar and Song Meter counts across the six sites sampled in 2012 (Figure 19; S = 8, $r_s = 0.77$, p = 0.103). A potential outlier was the comparison conducted at Devil's Inlet, where high counts on radar far exceeded Song Meter counts, but even with this site removed the correlation between radar and Song Meter counts was not significant (S = 2, $r_s = 0.90$, p = 0.083). There was no correlation between Song Meter and radar counts across the season at Monashka Bay (sensor Forest 1 and radar counts over forest), either in 2012 (S = 42.1, $r_s = -0.20$, p = 0.700) or with 2011 and 2012 surveys pooled (Figure 19; S = 111.8, $r_s = 0.32$, p = 0.364); however, sample sizes were small and therefore correlation tests lacked statistical power.

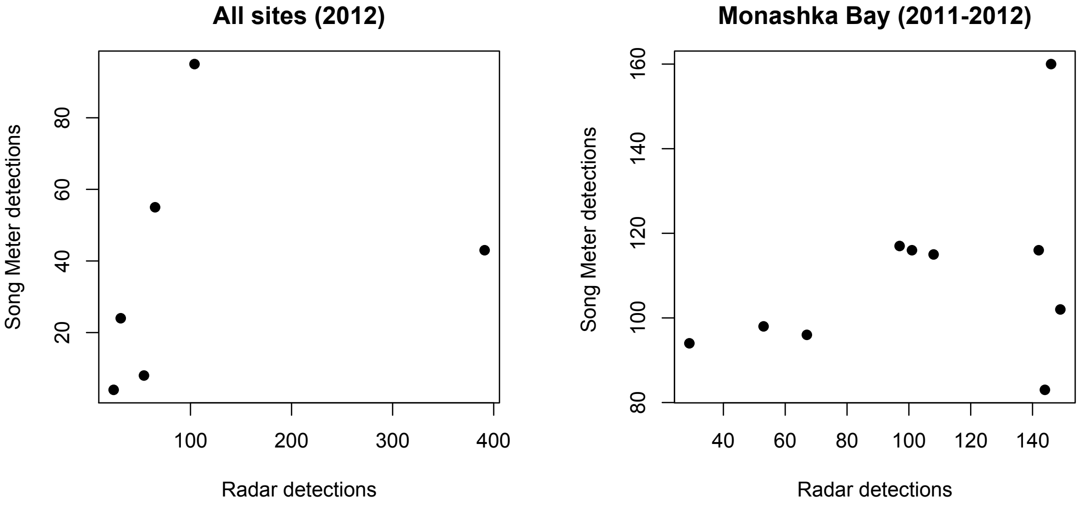

Figure 19: Spatial comparison of radar and Song Meter detections across all sites sampled in 2012 throughout the northern Kodiak Archipelago (left, includes 1 commuting site), and temporal comparison between radar counts above forested habitat and Song Meter Forest 1 located in forest (pooled for 2011-2012 at Monashka Bay, right).

A comparison of radar and Song Meter counts at Monashka Bay along a commuting flight path showed that murrelets were generally silent while commuting, with radar counts on average about eleven times greater than Song Meter counts (Figure 20). In contrast, there was no significant difference between the mean number of radar and Song Meter detections in likely forest nesting habitat ($t = 0.563$, $df = 11.8$, $p = 0.584$). When all survey methods were compared in likely nesting habitat at Monashka Bay, there was no difference in mean counts (Figure 21; 1-way ANOVA; $F_{2,27} = 0.579$, $p = 0.567$); however, variance in counts was higher for audio-visual and Song Meter surveys compared to radar. In addition to similar overall counts, similar behaviour was observed between radar and audio-visual surveys: there was no difference in the mean number of circling murrelets observed between radar (mean ± SE; 38.1 ± 7.6) and audio-visual surveys (33.4 ± 7.1) for pooled counts from 2011 and 2012 at Monashka Bay (Wilcoxon signed rank test; $V = 59.5$, $p = 0.683$). In general, Song Meter detections did not provide information on the flight behaviour of murrelets with the exception of rare detections of wing beats and jet sounds (0.4 detections per survey, $n = 148$ h) which could indicate below-canopy flight, a type of “occupied” behaviour (Evans Mack et al. 2003); by comparison, audio-visual surveys detected occupied behaviours (below-canopy flight, circling, aerial dives) on average 36 times per survey (n = 26 h).

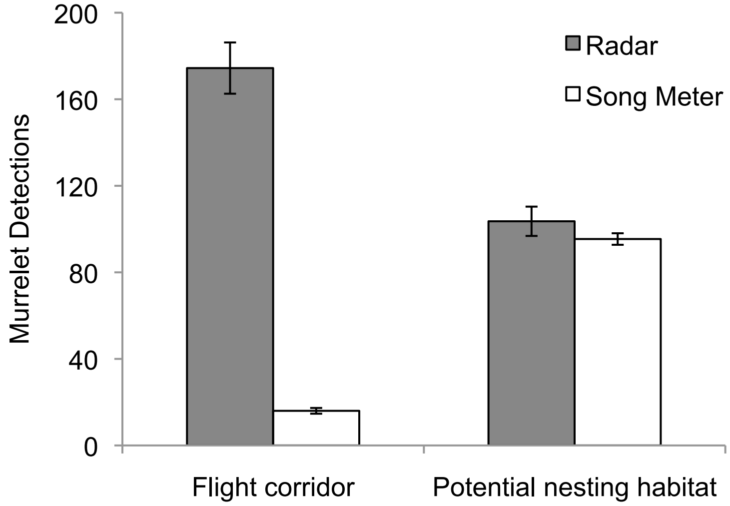

Figure 20: A comparison of mean Song Meter and Radar detections (± SE) along a commuting flight path and in potential nesting habitat at Monashka Bay for 2 h pre-sunrise (pooled detections from 2011-2012) showed that most commuting murrelets were silent, while more murrelets vocalized in potential nesting habitat.

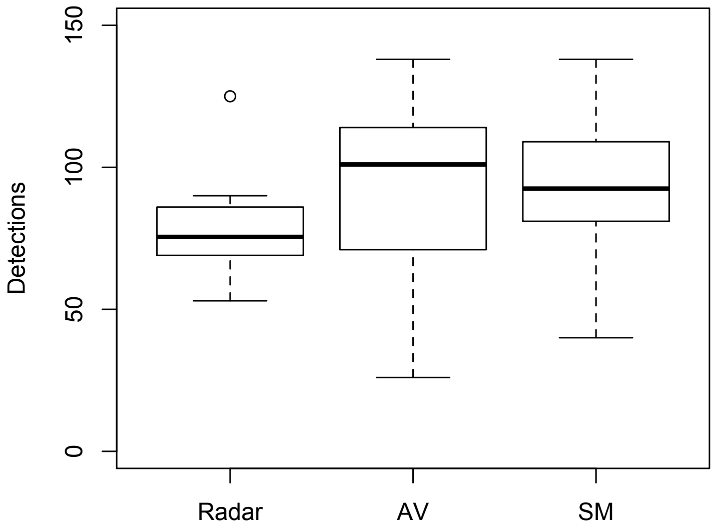

Figure 21: A comparison of daily murrelet detections occurring one hour before sunrise (when all three survey methods were used simultaneously) in forested habitat at Monashka Bay, 2011 and 2012 pooled, showed that there was no significant difference between methods, with higher variance in audiovisual (AV) and Song Meter (SM) counts. Boxplot indicates median and interquartile range, whiskers show minimum and maximum values.

An overall comparison of mean daily counts (both commuting corridor and forest habitat combined) made by radar, Song Meter and audio-visual surveys at Monashka Bay relative to sunrise shows that the radar detected many more murrelets than either Song Meters or audio-visual surveys during each time period, but especially during dark twilight (Figure 22). This is most likely due to two factors: the larger scanning area of the radar and its ability to detect silent birds. Both Song Meter and audio-visual surveys showed that the peak of conspicuous, vocal activity for murrelets occurred in the hour preceding sunrise.

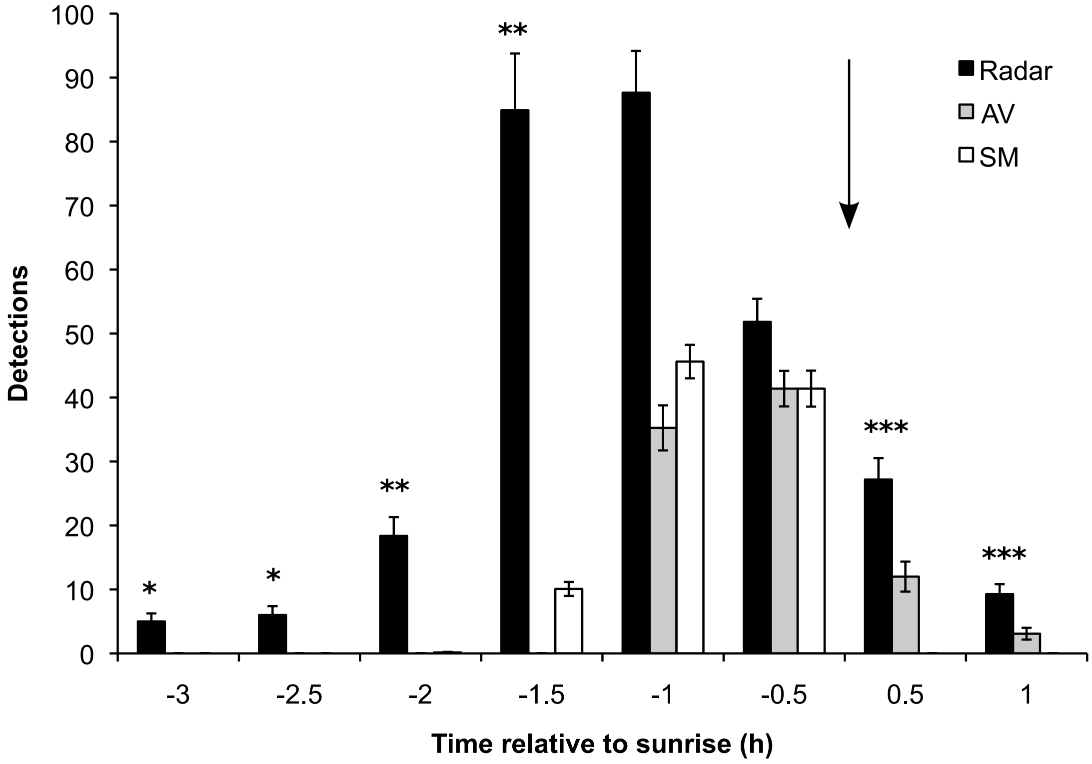

Figure 22: Comparison of mean ± SE of detections by radar, audio-visual (AV) and Song Meter (SM) surveys relative to sunrise (indicated by arrow). Radar surveys were conducted beginning 7 h before sunrise-1 h after sunrise, while AV surveys began 1 h before sunrise until 1 h after sunrise, and SM surveys began 2 h before sunrise until sunrise (* no AV or SM survey, ** no AV survey, * no SM survey).**

The seasonal activity trend was consistent across all three survey methods from 2010-2012 (Figure 23), with increasing activity throughout the months of June and July that peaked late July and early August, followed by a decline throughout the month of August. Logistical and funding constraints prevented sampling throughout the entire breeding season. Acoustic sensors provided the most complete picture of seasonal activity trends because multiple sensors were deployed autonomously throughout the breeding season, while logistical constraints limited the replication of radar and audio-visual surveys. The increased murrelet activity recorded in mid-July by all three survey methods indicated that there were more murrelets commuting to the nesting habitat (from radar counts), as well as more vocal activity during this phase of the breeding season (from Song Meters and audio-visual surveys). Radar and audio-visual surveys also recorded increasing counts of circling murrelets throughout the month of July in likely nesting habitat at Monashka Bay (Figure 24; Radar: $R^2 = 0.47$, $F_{1,12} = 10.69$, $p = 0.007$; audio-visual: $R^2 = 0.68$, $F_{1,12} = 29.16$, $p < 0.001$), a flight behaviour associated with nesting habitat.

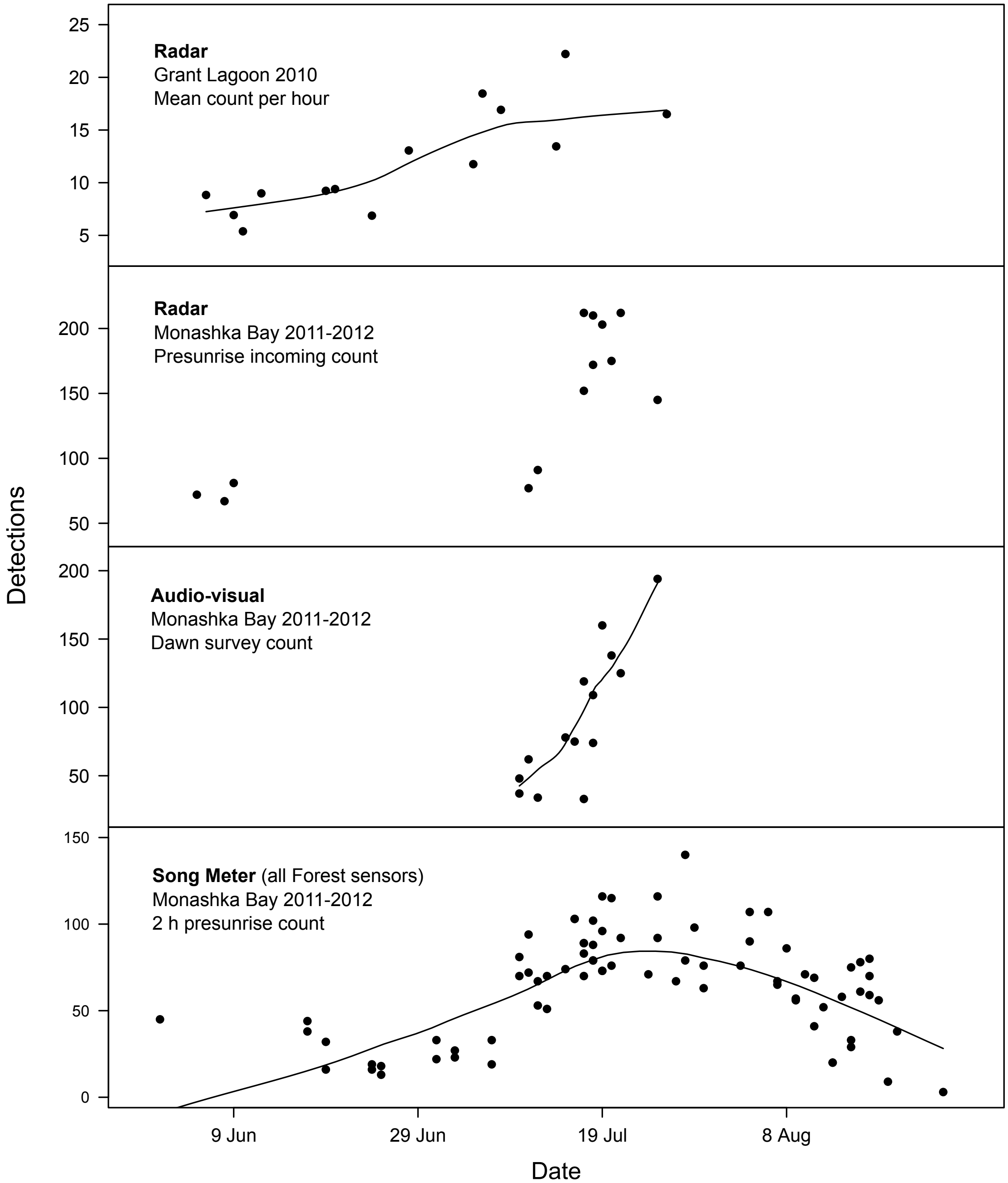

Figure 23: Seasonal trends in detections for radar, audio-visual and Song Meter surveys from 2010-2012, with smoothed trend line (local polynomial regression fitting). The data show an increase in murrelet activity from early June-late July, with a decline in August.

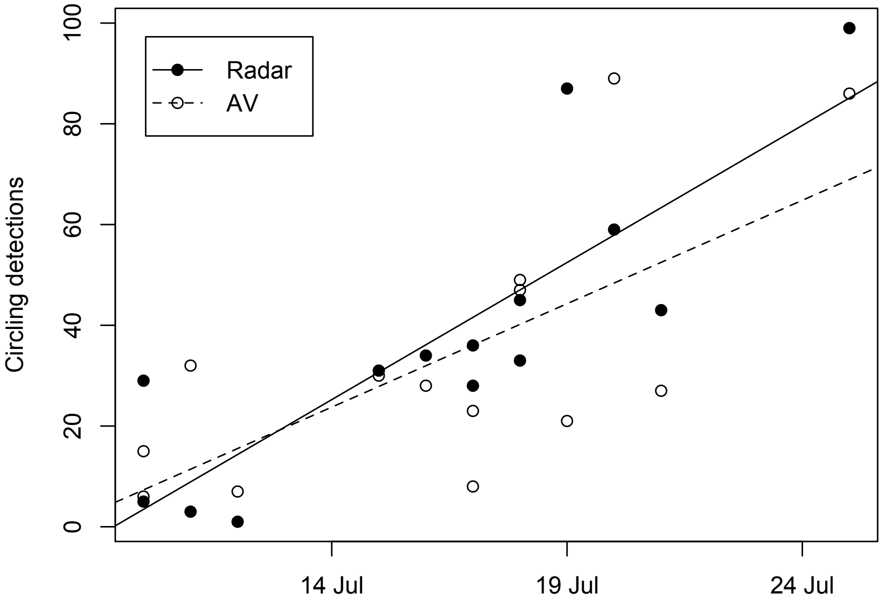

Figure 24: There was a significant linear increase in detections of murrelet circling flight behaviour by both radar ($R^2 = 0.47$, $F_{1,12} = 10.69$, $p = 0.007$) and audiovisual (AV; $R^2 = 0.68$, $F_{1,12} = 29.16$, $p < 0.001$) surveys from 10-24 July at Monashka Bay (2011 and 2012 pooled).

Discussion

Diurnal activity patterns

Diurnal activity trends described by radar surveys on Kodiak Island showed that commuting murrelets were active earlier and for longer periods relative to sunrise compared to populations at lower latitudes (Burger 1997, 2001, Cooper et al. 2001). Murrelet dawn activity peaks recorded in Clayoquot Sound, British Columbia (latitude of 49.4° N) began 50-70 minutes before sunrise and lasted approximately 60 minutes (Burger 1997, 2001), while the peak of dawn activity in the Kodiak Archipelago (approximately 57° N) began 120 minutes before sunrise and lasted approximately 150 minutes. Longer dawn activity periods at high latitude correspond to longer twilight periods: in Clayoquot Sound, civil twilight (sun angle < 6° below horizon) occurs 44 minutes before sunrise on the longest day of the year (21 June) compared to 74 minutes before sunrise in Kodiak. Furthermore, the onset of twilight is more gradual at high latitude, where nautical twilight (sun angle < 12° below horizon) does not occur at all during the murrelet breeding season. These results provide strong evidence that murrelets respond to light cues in timing their inland flight activity. This hypothesis is supported by murrelet response to other factors affecting light levels, such as the longer observed dawn activity periods on overcast, gloomy mornings compared to clear mornings seen in both radar (Burger 2001, Cooper et al. 2001) and audio-visual surveys (Rodway et al. 1993, Cooper & Blaha 2002). The secretive, crepuscular nest attendance of murrelets appears to be driven by predator avoidance (Rodway et al. 1993, Gaston & Jones 1998). An optimal period of twilight exists when murrelets can safely visits nests: during darkness, nest visits increase the risk of serious injury to a high-speed commuter navigating through dark forest, while daylight visits risk drawing the attention of potential predators both to the commuting adult and to the nest site itself. The diurnal activity patterns observed in this study support this optimal light level hypothesis, because murrelets appeared to time their commuting activity relative to the onset of twilight at either dusk or dawn.

Seasonal activity patterns

All three survey methods showed similar timing of seasonal trends in activity at two sites in different ecosystems (Grant Lagoon, tundra; Monashka Bay, mixture of old growth Sitka spruce forest and unforested land). The most complete seasonal trend data was provided by acoustic sensor detections. Seasonal activity increased gradually from June throughout the month of July and decreased rapidly in August. These trends reflected the timing of phases in breeding chronology identified from Kittlitz’s murrelet nests monitored on Kodiak Island (Lawonn 2013) and other studies of both murrelet species in Alaska (Hamer & Nelson 1995, Kuletz 2005); with the peak of activity corresponding to the onset of chick-rearing and early fledging stages. South of Alaska, seasonal trends in marbled murrelet activity have been detected in some cases by radar (Cooper et al. 2001) and audio-visual surveys (reviewed in O’Donnell et al. 1995), but not others (Jodice & Collopy 2000, Burger 2001). The absence of seasonal trends was perhaps due to the longer breeding season in more southerly latitudes resulting in a greater degree of breeding asynchrony, or due to more variation in at-sea conditions affecting the activity budgets of both breeding and non-breeding murrelets in relation to costly inland flight behaviour (Jodice & Collopy 2000). Radar sampling restricted to the core period of breeding activity (late May-late July) in southern British Columbia found no seasonal trend (Burger 2001), but during the same sampling period in Alaska, seasonal patterns were evident. The clear seasonal activity trend in high-latitude murrelet populations has implications for monitoring protocols, since population estimates made at different times during the season would be potentially very different. Acoustic monitoring could provide a useful way to identify the patterns of seasonal activity in different areas to inform the timing of radar surveys to monitor populations.

Differences in behaviour between marbled and Kittlitz's murrelets

Differences in flight behaviour between Kittlitz's and marbled murrelets were inferred from comparisons of radar observations between Grant Lagoon, with a nearby population of breeding Kittlitz's murrelets (up to 22 nesting pairs found per year; Lawonn 2013) and other radar sites assumed to have very low percentages of Kittlitz's murrelets (< 1% of all *Brachyramphus* murrelets counted at sea; Chapter 3, this study). At Grant Lagoon, inland flight activity was consistently high throughout the night from sunset until just after sunrise (Figure 15), while at other radar sites, activity was concentrated just before dawn (Figure 16). In contrast, remote cameras at Kittlitz's murrelet nests during the same period documented visits mainly after sunrise, with almost no visits occurring during dark periods of the night (Lawonn 2013).

The species identity and breeding status of murrelets commuting during darkness at Grant Lagoon is unknown, but remote camera data collected at nest sites over four years (2008-2011) indicates that this behaviour is not typical of nesting Kittlitz's murrelets in the area (Lawonn 2013). Even accounting for travel time between the coastal radar station and inland nest locations (up to 15 km from the radar, requiring 10-15 minutes of travel time), a large proportion of inland flight behaviour during darkness occurred outside of the likely window of commuting activity. Data collected in Icy Bay, Alaska provides evidence that non-breeding Kittlitz's murrelets engage in prospecting and courtship in the nesting habitat during darkness (unpublished data from M. Kissling, U.

S. Fish & Wildlife Service). Kittlitz's murrelets may time their inland flight behaviour differently from marbled murrelets due to different risks associated with open nesting habitat. Bare, open habitat could expose murrelets to greater predation risk than forested habitat, forcing them to engage in prospecting behaviour during darker twilight. Additionally, in open habitat compared to forests, murrelets face lower risks of collisions, and have better visibility of potential nest sites even in low light. Kittlitz's murrelets have larger eyes relative to skull size than marbled murrelets, and this has been proposed as an adaptation for foraging in darker marine environments (Day et al. 2003); it is possible that this adaptation is also important for navigating terrestrial nesting habitat in low light. Future radar sampling should be conducted in areas of high Kittlitz's murrelet abundance to determine whether this apparent pattern of nocturnal flight behaviour is common.

Comparison of radar, audio-visual and acoustic surveys: strengths and limitations

Radar surveys are considered the most reliable and least variable method to census and monitor murrelet populations at the watershed level (Burger 1997, Cooper et al. 2001, Cooper & Blaha 2002). Radar counts have high statistical power to detect population trends (Arcese et al. 2005, Bigger et al. 2006b, Cooper et al. 2006), and provide information on murrelet habitat associations (Burger 2001, Raphael et al. 2002). As in other studies (Burger 1997, Cooper et al. 2001, Cooper & Blaha 2002), radar surveys in the Kodiak Archipelago detected more murrelets than audio-visual methods (audio-visual and Song Meter), and provided much more detailed information on flight behaviour, including commuting flight direction, circling flight, and spatial patterns over a wide area (scanning radius 1.5 km). The incorporation of radar surveys into murrelet population monitoring programs in Alaska can offer improvements in population monitoring and provide insights into habitat associations. Despite the advantages of radar over other survey methods, radar studies can be limited by low spatial and temporal replication due to cost and logistical constraints, and the limiting effects of rain and high winds. Radar units are costly to purchase, and costly to operate because of the need for field personnel, and transportation; heavy, bulky equipment necessitates transport by boat, vehicle or floatplanes. Site access can be difficult in areas with few roads or a lack of suitable anchorages, and radar surveys also require a clear radar view, which can be problematic in forested areas. Other site features such as low topography can be unsuitable for radar counts because murrelet flight paths are dispersed over a wide area (Burger 1997, Raphael et al. 2002). Finally, radar surveys cannot detect below-canopy flight behaviours indicative of nesting, which reduces the likelihood of identifying stand occupancy.

Autonomous acoustic sensor systems provide a low-cost alternative to radar surveys for fine-scale assessments of relative abundance and seasonal patterns of activity. In this study, acoustic sensors provided the best information on seasonal trends in murrelet activity because data acquisition was not limited by the logistical constraints of human observers. However, audio-visual surveys provided more detailed visual observations of murrelet flight behaviour than acoustic sensors, which is important in assessments of stand occupancy (Evans Mack et al. 2003). Another advantage of audio-visual surveys is to provide real-time feedback for radar operators on potentially confusing species and their flight behaviours (e.g., mergansers and loons that occasionally make murrelet-like landward flights).

Integration of radar, audio-visual and acoustic monitoring

Combinations of radar, audio-visual and automated acoustic surveys can be used to maximize efficiency in monitoring activities of marbled murrelets for different purposes. The combination of radar and acoustic sensors can link population size and habitat use. Radar surveys can be used to identify large or important populations of murrelets at the watershed scale, followed by assessment of specific habitat patches by acoustic sensors. For example, the combined methods can be used to investigate poorly-known habitat-use by marbled murrelets in unforested watersheds, or to identify a gradient of habitat use in forested watersheds. Alternatively, acoustic sensors can be used for long-term monitoring of habitat patches used by important populations, to monitor the effects of changes to habitat, such as the effects of forest fragmentation or climate change on forest characteristics. Acoustic sensors can reduce the need for repeated audio-visual assessments of habitat, by providing an index of murrelet abundance in the study area that can be followed by targeted audio-visual surveys of likely habitat patches to determine stand occupancy. Finally, acoustic sensors can be used to provide a high-resolution image of murrelet seasonal activity patterns that can inform the timing of other surveys the following season, or can be used to calibrate surveys done within the same season with regard to seasonal activity peaks. Given that murrelet breeding phenology can differ between locations even at similar latitudes (McFarlane Tranquilla et al. 2005), the use of acoustic sensors to identify seasonal trends in each potential study area is valuable.

Chapter 3: Patterns of abundance in *Brachyramphus* murrelets in relation to at-sea density and potential nesting habitat

Introduction

Habitat selection by animals involves complex hierarchical decisions at multiple spatial scales, which produces spatial patterns of habitat use across the landscape (Lima & Zollner 1996). Seabirds face unique habitat selection challenges in the marine environment, where their prey is patchily distributed in space and time. During the breeding season, seabirds must also evaluate terrestrial habitat for nesting, increasing the complexity of habitat-selection decisions. Balancing the need for safety at nest sites with the energetic costs of travel to profitable foraging patches is a central problem for seabirds and other central place foragers. Most seabirds have evolved a strategy of colonial breeding that can facilitate habitat selection, both at sea and on land, through information transfer between conspecifics (Danchin & Wagner 1997). In contrast to this strategy of spatial aggregation, *Brachyramphus* murrelets are unusual non-colonial seabirds that nest in dispersed, hidden nests up to 50 km from the ocean, and forage solitarily or in small groups in nearshore marine waters on small schools of forage fish (Nelson 1997, Kuletz 2005). Two species of *Brachyramphus* murrelets are sympatric across large areas of Alaska: the marbled murrelet (*B. marmoratus*), which generally nests in high mossy limbs of old growth conifers (Nelson 1997), and the Kittlitz's murrelet (*B. brevirostris*), which nests on bare rocky ground, generally at high elevations (Day et al. 1999).

The marine distribution of *Brachyramphus* murrelets during the breeding season reflects the distribution of their preferred nesting habitats at large (regional) spatial scales (Piatt & Ford 1993, Day et al. 1999, Miller et al. 2002). Conversely, large-scale patterns of terrestrial habitat use are related to the proximity of productive marine habitat (Meyer et al. 2002). Coarse-scale patterns of habitat selection (< 100 km) in the marine environment also correspond to proximity to nesting habitat (Ronconi 2008, Becker &

Beissinger 2003). However, the quantitative link between spatial patterns of abundance observed at sea and the use of specific areas of adjacent terrestrial habitat is not well understood. Only radiotelemetry studies have been able to directly link murrelet habitat use between marine and terrestrial habitats (e.g. Lougheed 1999, Hull et al. 2001, Kuletz 2005, Peery et al. 2004b, 2009, Barbaree 2011, unpublished data from M. Kissling, U. S. Fish & Wildlife Service). However, radiotelemetry is costly, and only tracks patterns of fine-scale habitat use by individuals, providing limited information on watershed-scale habitat use.

The goal of this study is to link spatial patterns of murrelet abundance at sea to areas of adjacent breeding habitat using counts of murrelets commuting along nesting flyways. Because *Brachyramphus* murrelets are secretive breeders, population census and monitoring has been conducted across many parts of their range through at-sea vessel counts (Piatt et al. 2007, Kissling et al. 2011, Kuletz et al. 2011a,b, Piatt et al. 2011, Miller et al. 2012). Relationships between these at-sea distributions and use of adjacent habitats can be inferred by tracking murrelets as they commute between nest and ocean using marine radar. Counts of commuting murrelets from radar surveys have become a standard method to census local populations of murrelets in forested watersheds south of Alaska (Burger 1997, Cooper et al. 2001), and these population estimates have a positive linear relationship with area of suitable nesting habitat inland of the radar station (Burger 2001, Raphael et al. 2002). Thus, radar counts can provide a quantitative link between local patterns of abundance at sea and use of adjacent terrestrial habitats.

This study was conducted in the Kodiak Archipelago, Alaska, which has breeding populations of both marbled and Kittlitz's murrelets. In 2011-2012, I conducted radar surveys and adjacent at-sea vessel counts of *Brachyramphus* murrelets at 21 sites, with a variety of potential nesting habitats inland of radar stations. The relationships between at-sea counts, terrestrial habitat types, and radar counts are explored within three spatial scales: 5, 10 and 15 km from radar stations. First, I examined relationships between radar counts and at-sea density to determine which measures of at-sea density (nearshore, offshore, or the combination thereof) are most strongly correlated with radar estimates of local population size, and at which spatial scale the correlations are strongest. Next, I compared the relationships between radar counts and potential nesting habitat types to assess which habitats are important for breeding murrelets. Finally, I compared models including both marine and terrestrial variables to determine which combinations of variables best predict population estimates from radar counts, and whether these variables differ across spatial scales.

Methods

Radar counts

Radar surveys were conducted following methods described in Chapter 2. To compare with habitat variables and at-sea counts, the number of incoming murrelets counted within two hours pre-sunrise was selected as the an index of the local nesting population size at each radar site. At sites with multiple radar counts, the mean count was used; however, only radar counts conducted in June and July were used in population estimates. Counts in August were significantly lower than June counts, and were only conducted at 5 sites; therefore they were not used. Survey sites encompassed a variety of terrestrial habitat types. Many radar sites had low-lying coastal topography, with no clear boundaries between drainages; unlike the forested watersheds south of Alaska where radar sampling is used to monitor populations of marbled murrelets in discrete watershed units (Burger 2001, Raphael et al. 2002). Because drainages had no clear delineations or boundaries, I created artificial circular boundaries with radii of 5, 10 and 15 km to compare radar counts with marine and terrestrial variables. These spatial scales were selected to reflect a range of possible commuting distances between ocean and nest in an island environment where no point on land was greater than 20 km from the ocean.

At-sea vessel counts

In collaboration with the Kodiak National Wildlife Refuge, I conducted at-sea vessel counts of *Brachyramphus* murrelets in 2011 and 2012 in the Kodiak Archipelago as part of a long-term monitoring program for nearshore seabirds in the Gulf of Alaska. Study design and protocols were developed by the National Parks Service, southwest Alaska Network (Coletti et al. 2009) and the U. S. Geological Survey (Dean & Bodkin 2009). In 2011, at-sea transects were conducted on east Kodiak Island, and in 2012 the survey area covered the northernmost coast of Kodiak Island, as well as Afognak and Shuyak Islands (Figure 25).

Two types of transects were used to sample the marine habitat of *Brachyramphus* murrelets: nearshore transects running 100 m offshore and parallel to shoreline, and offshore transects running perpendicular to shore. All nearshore transects were approximately 5 km long, but length was varied for offshore transects from 4-5 km. Transects were occasionally truncated due to navigational hazards such as dense kelp forests and uncharted reefs. Nearshore transects were selected systematically to sample 20% of the shoreline. Beginning at a random start point, the coastline was segmented into potential transects of 5 km, with the first segment selected for sampling, followed by two unsampled potential transects. Transects were stratified by habitat type (exposed vs. protected coastline) such that the proportion of each habitat type surveyed reflected the actual proportions of each habitat type in the Kodiak Archipelago. One offshore transect was conducted at the end of every second nearshore transect, with start point beginning 300 m offshore from the end of the nearshore transect. I attempted to sample each transect twice in June and twice in August (usually on consecutive days).

Surveys were conducted from a 6-m aluminum skiff at speeds of 5-8 knots (9-15 km h^{-1}) , with four crew members: two observers (Evans Mack et al. 2002, Hoekman et al. 2011), one person entering observations into a computer program (dLOG3; Dean & Bodkin 2006), and one person navigating the skiff. Observers positioned at the bow scanned a 90° arc from directly ahead to 90° abeam, out to 300 m from the transect line (observer eye height 1.5 m, transect width of 600 m). Distance sampling protocols (Buckland et al. 2001) were used to record birds on the water, including the estimated perpendicular distance of birds from the transect line (distance estimated using laser rangefinder when possible), and the number of birds in a cluster (individual or group of the same species). *Brachyramphus* murrelets were identified to species ~99% of the time, although occasionally the bird dove before identification could be confirmed, in which case the bird was recorded as “unknown *Brachyramphus*”. Surveys were conducted only in Beaufort sea states 0-3.

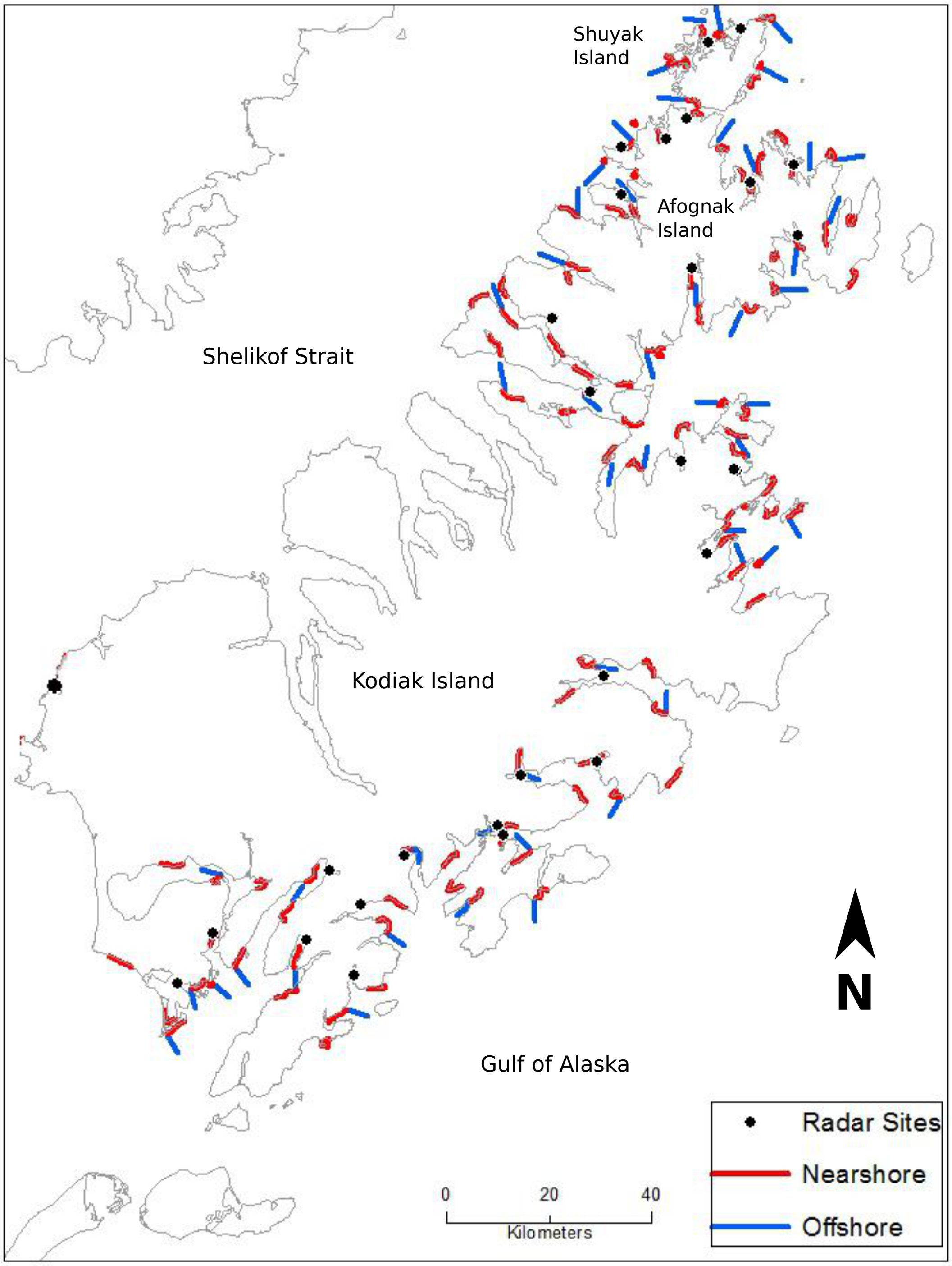

Figure 25: Radar sites and at-sea transects (nearshore and offshore) surveyed within 15 km of radar sites in the Kodiak Archipelago, 2011-2012.

Calculating densities from transects

Murrelet densities were calculated for each transect using standard distance sampling procedures (Buckland et al. 2001). The basic concept of distance sampling is that individuals closer to the transect line have a higher probability of detection (Buckland et al. 2001). By estimating the perpendicular distance to each individual or group, the probability of detection with respect to distance from the boat can be calculated in the form of a detection function. The detection function is used to produce a correction factor that accounts for missed objects (individuals or groups) when calculating abundance. This detection probability correction factor can be visualized as the area under the curve of the detection function, or the ratio of the "effective strip width" to the truncation distance in the detection function. The effective strip width is the distance from the boat at which the number of birds missed within that distance is the same as the number of birds seen beyond that point. Distance sampling methodology has been widely used and validated for estimating at-sea densities of marbled murrelets (Becker et al. 1997, Evans Mack et al. 2002, Peery et al. 2004b, 2006, 2007, Ronconi & Burger 2009) and Kittlitz's murrelets (Kissling et al. 2007, 2011, Lukacs et al. 2010, Piatt et al. 2011).

To estimate murrelet abundance in offshore transects, I fitted a detection function to all offshore murrelet detections using the Distance package (v. 0.7.1) in the statistical program R (v. 3.0.0; R Core Development Team 2013) which uses the mark-recapture distance sampling (MRDS) engine (Miller 2012). Following standard distance sampling methods, approximately 5% of the data were truncated at 275 m before fitting the detection function (Buckland et al. 2001). Several models (key functions and expansion series) were fitted to the data and compared using Akaike's Information Criterion values (Burnham & Anderson 2002) to select the best model. The half-normal key function with cosine series expansions provided the best fit to the data. This produced an effective strip width of 172 m with a probability of detection of 0.62, which was slightly higher than other marbled murrelet studies (e.g., 0.39-0.59 in southern British Columbia, Ronconi & Burger 2009). There were insufficient data to test other covariates (weather, sea state, observer) in the model; these covariates are known to affect murrelet detection probabilities to varying degrees in other studies. Ronconi & Burger (2009) found that increasing sea state significantly reduced detection probabilities of murrelets, and also found significant observer effects, as did other studies (Evans Mack et al. 2002). Kissling et al. (2007) found that increasing cloud cover increased the detection probability of murrelets, most likely due to reduced glare on the water.

For nearshore transects, a detection function could not be fitted to the data since sampling distances were asymmetrical (limited to 100 m on shoreward side vs. 300 m on the seaward side of vessel). Therefore, the detection function for offshore transects was used to estimate the probability of detection for nearshore observations. Nearshore detections were not labelled according to which side of the vessel they came from, and therefore the pooled detections could not be separated and corrected using different detection factors for each side of the vessel. Therefore all data were truncated to 100 m, and the integral of the offshore detection function calculated to 100 m from the vessel, following Kissling et al. (2007). Truncation distance sampling to 100 m resulted in loss of some data, mainly in August transects where marbled murrelets were more often found in large clusters (up to 250 murrelets); these clusters were often > 100 m from the transect line and thus these large concentrations were not included in the analysis. The abundance for nearshore transects was calculated within 100 m on either side of the vessel (200 m transect width) using a Horvitz-Thompson estimator that incorporates cluster size (Thomas et al. 2010):

$$\hat{N} = \sum_{i=1}^{n} \frac{s_i}{\hat{P}_i}$$

where $\hat{P}_i$ is the estimated detection probability for animal i, and s_i is the size of cluster i, $i = 1, \ldots, n$. Because Kittlitz's murrelets and unidentified *Brachyramphus* murrelets accounted for only 0.8% of all murrelets counted at sea, these were pooled with marbled murrelets for each transect to calculate total murrelet abundance. Abundance was then divided by surveyed transect area to calculate density.

The mean at-sea density for total *Brachyramphus* murrelets was calculated separately for transects within 5, 10 and 15 km of each radar station. At each distance, density was calculated for nearshore and offshore transects separately, as well as a combined measure (total density), providing three measures of density for both June and August.

Identification of potential nesting habitat

The area of potential nesting habitat within each spatial scale (5, 10, and 15 km from the radar station) was estimated using ArcGIS v.10.0 from vegetation cover and elevation maps. Vegetation cover came from the Kodiak Archipelago Land Cover Classification v. 1.1 (Fleming & Spencer 2007), which classified 63 vegetation communities from field surveys and digital image analysis (Landsat ETM+). A Digital Elevation Map (30 x 30 m resolution) was used to calculate slope as a variable for potential nesting habitat. Slope was calculated by comparing the elevation of each 30 x 30 m pixel to its nearest neighbour in each direction. Based on these data, three categories of potential nesting habitat were created: shallow slope, steep slope, and dense Sitka spruce forest (details below).

Potential nesting habitat was identified only for marbled murrelets since Kittlitz's murrelets were extremely rare in the survey area. Two types of marbled murrelet nesting habitat were identified: tree-nesting and ground-nesting (Piatt et al. 2007). The proportions of the local populations using each of these habitats was not known. For tree-nesting habitat, detailed forest inventory data were not available, and the best proxy for suitable nesting habitat was the vegetation category labelled "Dense Sitka Spruce Forest" (Figure 26). This forest class includes multi-aged stands ranging from 60-250 years old and crown closure ranging from 60-100%, which falls within the range of "likely" murrelet nesting habitat (Kuletz et al. 1995, CMMRT 2003). Because this forest cover class was not developed using marbled murrelet habitat suitability ranking criteria, it covers a range of likely nesting habitat quality from very low to very high (Burger et al. 2004b).

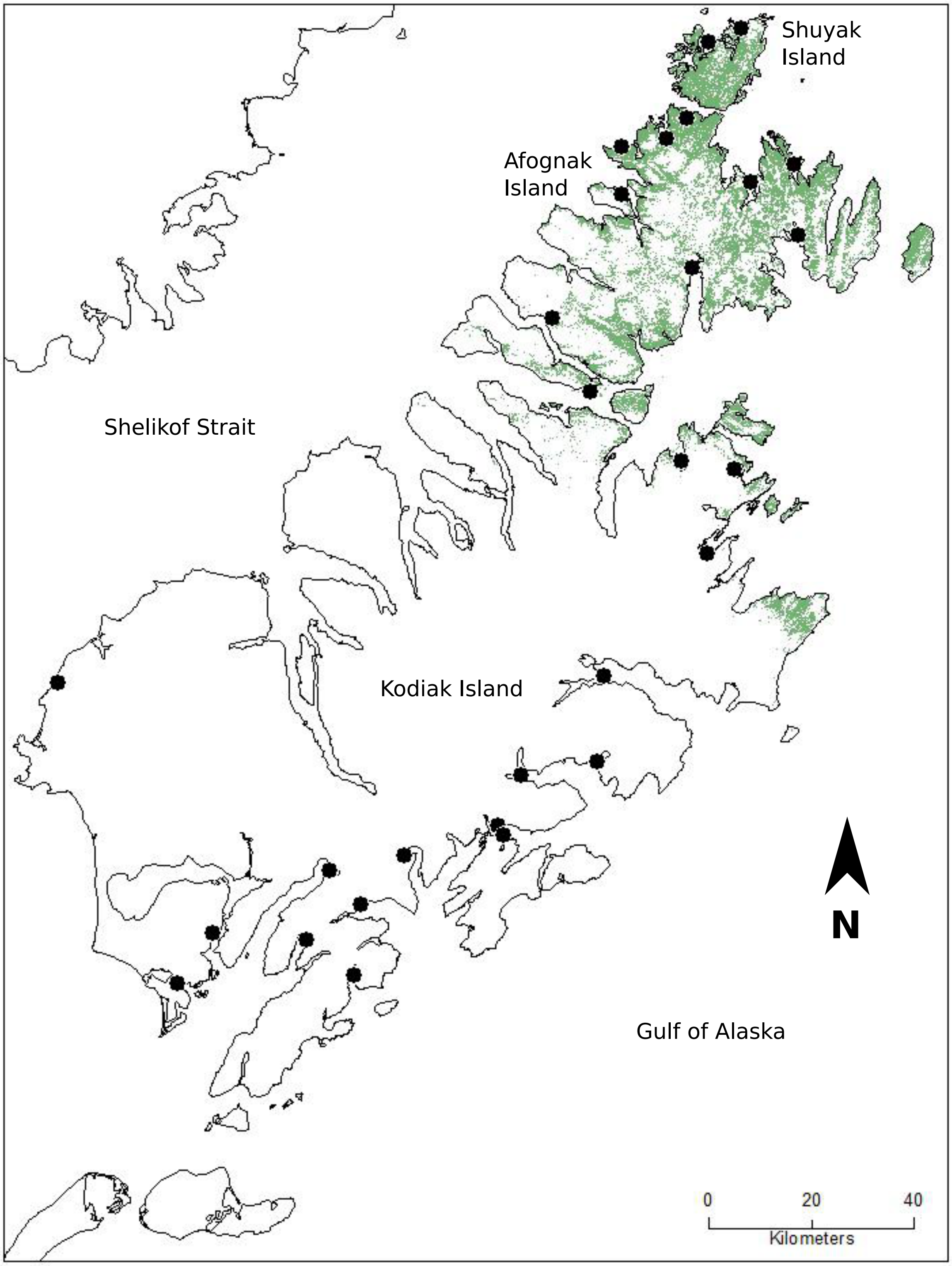

Figure 26: Distribution of "dense Sitka spruce forest" vegetation class in the Kodiak Archipelago, relative to radar sites. The dots show radar stations.

Most of the Kodiak Archipelago (almost all of Kodiak Island) has no coniferous forests, and in these areas it was assumed that marbled murrelets nest on the ground. Two categories of potential ground nesting habitat were developed: shallow slope and steep slope. Categories of slope steepness were developed from known marbled murrelet ground nests in Alaska (DeGange 1996; Piatt et al. 2007; K. Nelson, pers. comm.; unpublished data from M. Kissling, U. S. Fish & Wildlife Service). Slope steepness was considered the most important factor for selecting ground-nesting habitat, since murrelets require a drop-off area to make stall-landings and jump-off departures because of their high wing-loading ratio (Nelson 1997, Burger 2002, Kaiser 2007). The 95% CI for slope steepness of all known ground-nests in Alaska ranged from 6-45° ($n = 12$; K. Nelson, pers. comm.); however these data were presumably biased low because most ground nests were found accidentally rather than through systematic searches, and these data did not include cliff nests. Other search methods (radiotelemetry) have found marbled murrelet nests on much steeper slopes, often on cliff ledges (Bradley & Cooke 2001, Barbaree 2011, unpublished data from M. Kissling, U. S. Fish & Wildlife Service). Two arbitrary categories of slope steepness were developed: shallow slope (18-45°) and steep slope (45-90°; Figure 27). The shallow slope category encompassed the 95% CI for known ground nests in Alaska but was truncated at the low end to 18° to exclude more area from the model and presumably improve its predictive power. This range of slope values is also consistent with Kittlitz's murrelet nests found on Kodiak Island (range 20-37°; Lawonn 2013). The steep slope category reflected maximum slope values for murrelet nests in regions of Alaska outside of the Kodiak/Cook Inlet area (range 70-90°; DeGange 1996, Piatt et al. 2007).

Vegetation cover was not used in selecting ground-nesting habitat for two reasons: the available vegetation categories did not provide adequate information on habitat attributes necessary for nest sites (e.g., openings and spaces between plants allowing access to nests), and ground nest-site selection by marbled murrelets appears to be highly variable. Unlike Kittlitz's murrelets, which select unvegetated bare rock and scree for nest sites (Day et al. 1999, Lawonn 2013, unpublished data from M. Kissling, U. S. Fish & Wildlife Service), marbled murrelet ground nest sites include unvegetated rock, snow-and ice-dominated mountainsides, dense shrubland, and the roots at the base of coniferous trees (Marks & Kuletz 2001, Nelson et al. 2013, unpublished data from M. Kissling, U. S. Fish & Wildlife Service).

Other factors commonly used in mainland habitat selection for marbled murrelets such as elevation and distance from ocean were not used in this study, because the maximum distance from ocean in the Kodiak Archipelago is < 20 km (well within the known inland commuting distance of murrelets; Hull et al. 2001), while maximum elevation (1362 m) is within the range of known marbled murrelet nests in Alaska (unpublished data from M. Kissling, U. S. Fish & Wildlife Service).

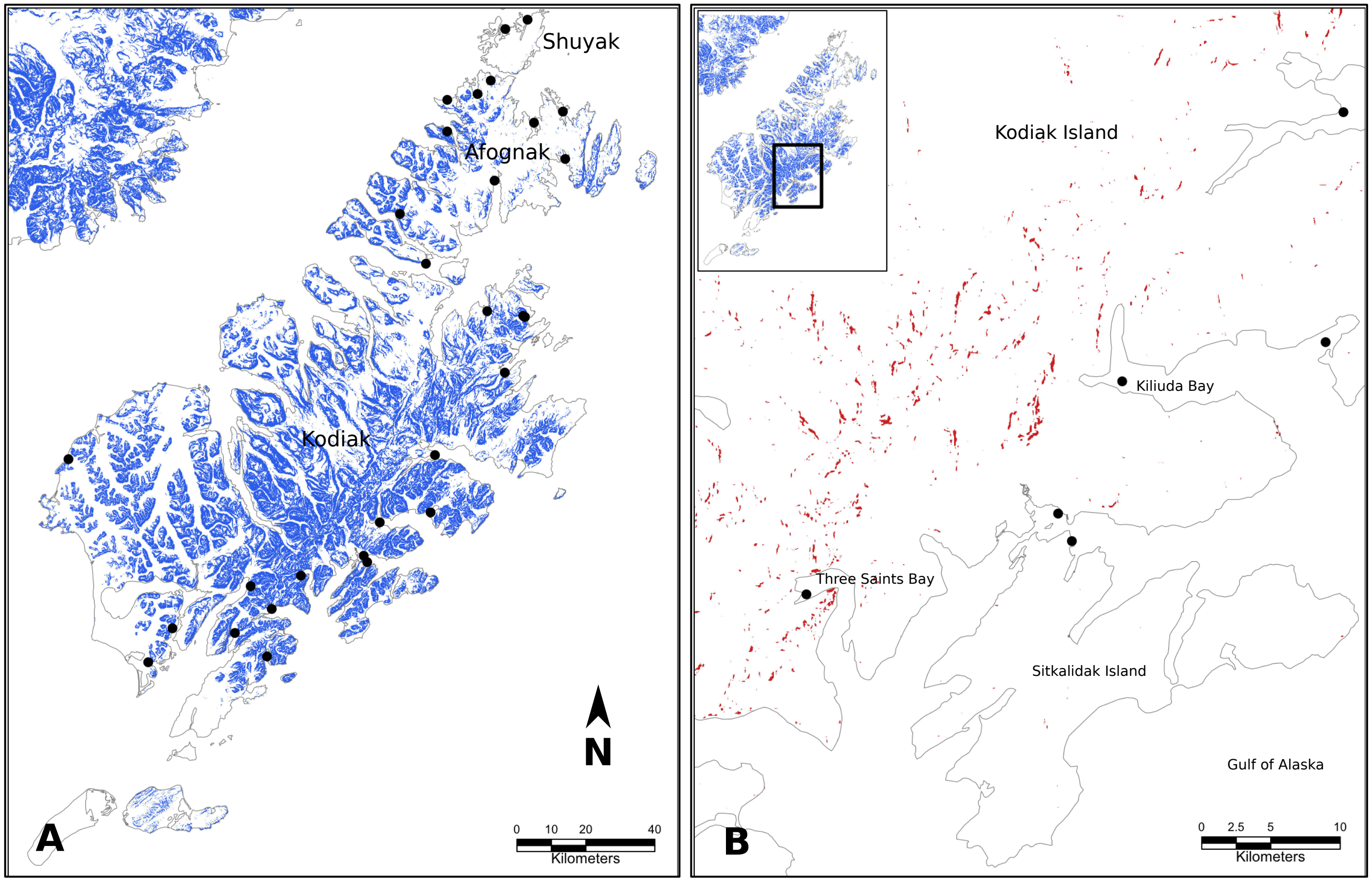

Figure 27: Distributions of slope in the Kodiak Archipelago: A) Shallow slope category (18-45˚), B) smaller-scale map showing distribution of steep slope area (45-90˚) on east Kodiak Island (inset map shows shallow slope and map area). The highest concentration of steep slopes were in this area, where high counts were recorded at radar stations Three Saints Bay and Kiliuda Bay. Radar sites are shown in black.

Statistical methods

As a first step, I tested the linearity of relationships between each of the variables using Pearson correlations. At each spatial scale, correlation coefficients were calculated for radar counts and each of the marine and terrestrial explanatory variables to be used in multiple regression models; no evidence of non-linearity was detected and therefore no data transformations were performed. Correlation tests between nesting habitat and radar counts were performed on subsets of the data to test each habitat type independently (forested habitat tested only for sites with forest, unforested sites used to test slope variables). One site (Salonie Creek) was included in both analyses, because it had only a small area of forest (1063 ha) at the largest spatial scale.

Correlation tests revealed two extreme outliers from the 21 radar sites, both of which were at the northern tip of Shuyak Island. These sites had low radar counts, but had large areas of forest habitat identified in the forest cover layer, as well as high offshore transect counts. Both of these potential predictors of murrelet population size were misleading. Despite being considered “Dense Sitka Spruce Forest,” trees in this area were stunted with small branches; moss platforms were extremely rare, making them poor habitat for tree-nesting by murrelets (ranked very low quality nesting habitat; Burger et al. 2004b). Offshore transects at the northern tip of Shuyak Island had some of the highest at-sea densities of marbled murrelets in the archipelago, and had the highest overall seabird densities of any transects in the northern archipelago. This indicates a highly productive foraging area that most likely drew murrelets and other seabirds from a wide area and was not necessarily related to the size of nearby breeding populations. For these reasons, the two sites at the northern end of Shuyak Island were removed from further analyses. The remaining 19 sites were used in model selection to investigate factors predicting population size (radar counts). Each radar site was treated as one datum, averaging repeated radar counts and at-sea counts to provide one estimate per location.

Spatial patterns of abundance were tested using multiple linear regression models to determine which factors (at-sea densities, terrestrial nesting habitat) best predicted murrelet radar counts. Candidate models were constructed at each scale (5, 10, 15 km) to test the predictive power of three types of at-sea density measures (nearshore, offshore, and total density; one for each of June and August), and three measures of potential nesting habitat (area of forest, shallow slope, and steep slope). Based on the top models across all spatial scales, combinations of the best predictors were tested in mixed scale models. Initially, all variables were tested for collinearity before being included in the model; if collinearity was detected, the parameter with greater explanatory power was selected for inclusion in the model. The total number of variables were limited in the candidate models to prevent overfitting the model (Burnham & Anderson 2002). Candidate models were compared, refined and evaluated using Akaike's Information Criterion (AICc; corrected for small sample size, Burnham & Anderson 2002). Akaike weights (*w*) were calculated to represent the weight of evidence in favour of a particular model, relative to other models being considered (Burnham & Anderson 2002). All data analyses were performed in the statistical program R (v. 3.0.0, R Core Development Team 2013).

Limitations of the data

Variables used to predict murrelet population size were simplified representations of marine and terrestrial habitat. At-sea density estimates represent the distribution of murrelets in response to multiple underlying and dynamic marine processes that were not accounted for in models (e.g., prey densities, areas of upwelling, tidal currents, etc.), and these underlying processes, coupled with the highly mobile nature of murrelets, generated variation in the data. Estimates of terrestrial nesting habitat area were relatively crude due to the lack of detailed vegetation inventory mapping relevant to murrelet habitat suitability, as well as the lack of data on ground-nesting habitat selection by marbled murrelets. Furthermore, forest cover data were produced from aerial photos taken in 1999-2000, and there has since been considerable logging of old growth Sitka spruce forest in the Kodiak Archipelago, which is ongoing in both Chiniak Bay (Kodiak Island)

and across large areas of Afognak Island. Therefore, inferences from differences in the relative strengths of marine and terrestrial predictors of abundance should be limited.

Sampling design limited the ability to make inferences about the relative predictive strengths of June vs. August and nearshore vs. offshore at-sea density variables. The greater sampling effort in the nearshore stratum likely reduced variation in at-sea densities compared to the offshore stratum, potentially increasing the predictive power of nearshore transects. Radar surveys were conducted for most sites within 1-2 days of June surveys, potentially increasing the likelihood of better correlations between June at-sea densities and radar counts compared with August densities.

Results

Survey effort

In 2011-2012, radar surveys were conducted at 21 sites in the eastern and northern regions of the Kodiak Archipelago respectively, yielding a total of 16,118 murrelet detections (Table 7). At-sea surveys sampled 161 transects (73 in 2011, 88 in 2012), which were repeated up to 4 times in each year yielding a total of 8,695 *Brachyramphus* murrelet records.

Table 7: Survey effort for at-sea vessel counts and radar counts in the Kodiak Archipelago, 2011-2012. Murrelet species counted include marbled murrelet (MAMU), Kittlitz's murrelet (KIMU), and unidentified *Brachyramphus* (UNBR). Radar counts were conducted only in June-early July, while at-sea counts were also conducted in August.

Region	East Kodiak		North Kodiak Archipelago		
Year	2011	2011	2012	2012	Totals
Dates	13 Jun-2 Jul	9 Aug-1 Sep	4 Jun-1 Jul	31 Jul-6 Sep	
No. transects	73 (39)	68 (36)	87 (63)	88 (46)	161
Area (km^2)	249	228	341	304	1,122
No. birds per species:					
Marbled Murrelet	838	1,460	1,809	4,511	8,618
Kittlitz's Murrelet	1	6	1	16	24
Unidentified murrelet	23	5	0	25	53
Total	862	1,471	1,810	4,552	8,695
Radar sampling:					
No. radar sites	8	NA	13	NA	21
Number of murrelets	5,710	NA	10,408	NA	16,118

Correlations among radar, at-sea density and nesting habitat area

There were significant correlations between radar counts and at-sea densities, as well as terrestrial habitat variables (Table 8, Table 9). For at-sea densities, correlations with radar counts were generally stronger at larger spatial scales. This trend may have been due to a sampling effect: at larger scales, a greater number of transects were averaged to calculate each type of density, potentially reducing variation. Despite this, nearshore densities in June were more strongly correlated with radar counts at the smallest spatial scale (r = 0.602 at 5 km), indicating that murrelets may be more clustered near nesting flyways in nearshore waters in the early breeding season.

Table 8: Pearson correlation coefficients (*r*) between radar counts (June and July) and at-sea densities made in June and August (by transect type and month) of murrelets in the Kodiak Archipelago. Transect types include nearshore, offshore and total density (the combined average of nearshore and offshore transects) within the spatial scale selected. Significant correlations are shown in bold type.

Sampling radius (km)	Month of at-sea surveys	Nearshore			Offshore			Total		
		r	p-value	df	*r*	p-value	df	*r*	p-value	df
5	June	**0.602**	**0.006**	17	0.175	0.568	11	0.416	0.076	17
	August	**0.484**	**0.036**	17	0.209	0.493	11	0.438	0.061	17
10	June	0.307	0.201	17	0.384	0.102	17	**0.625**	**0.004**	17
	August	**0.481**	**0.037**	17	**0.549**	**0.018**	16	**0.592**	**0.008**	17
15	June	0.247	0.308	17	**0.518**	**0.023**	17	**0.608**	**0.006**	17
	August	**0.588**	**0.008**	17	**0.577**	**0.012**	16	**0.643**	**0.003**	17

Correlations between forest cover and radar counts were strongest at the 5 km scale (Table 9) with decreasing correlation coefficients at larger scales. For both shallow and steep slope, correlations with radar were not significant at 5 km but grew increasingly stronger at 10 and 15 km. Steep slope area was more strongly correlated with radar counts than shallow slope at all spatial scales. At the 15 km scale, steep slope was more strongly correlated with radar counts than any other variable across all spatial scales ($r = 0.917$).

Table 9: Pearson correlation coefficients (*r*) between radar counts and area of habitat by habitat type (dense Sitka spruce forest, shallow slope: 18-45°, and steep slope: 45-90°). Only sites with coniferous forests were considered in analyses of forested habitat, while only unforested sites were considered in analyses of slope. Significant correlations are shown in bold type.

Sampling radius (km)	Forest			Shallow slope			Steep slope		
	r	p-value	df	*r*	p-value	df	*r*	p-value	df
5	**0.672**	**0.017**	10	0.409	0.275	7	0.623	0.071	7
10	**0.660**	**0.020**	10	**0.723**	**0.029**	7	**0.909**	**0.001**	7
15	**0.611**	**0.035**	10	**0.763**	**0.019**	7	**0.917**	**0.001**	7

Spatial patterns of abundance

Model selection revealed different factors predicting murrelet abundance at different spatial scales. Within 5 km of the radar, the best model to predict population size included June nearshore densities, forest area, and steep slopes (Akaike weight [*w*] = 0.857). The explanatory power of this model relative to the null model (model with no predictor variables, just the intercept) was high (ΔAICc of 11.850), and the coefficient of determination for the best model indicated good fit ($R^2 = 0.71$, $F_{3,14} = 11.22$, $p < 0.001$).

Table 10: Candidate multiple regression models predicting marbled murrelet radar counts relative to at-sea densities and areas of potential nesting habitat types within 5 km of radar sites. Model parameters include: NearshoreJune (nearshore density in June), Forest (forest area), SteepSlope (area of slope 45-90°), TotalAugust (total density in August), TotalJune (total density in June).

Model	*K*	AICc	ΔAICc	*w*
NearshoreJune+Forest+SteepSlope	5	216.882	0.000	0.857
NearshoreJune+TotalAugust+Forest+SteepSlope	6	220.823	3.941	0.119
NearshoreJune+TotalJune+TotalAugust+Forest+SteepSlope	7	224.264	7.382	0.024
Null Model	2	228.732	11.850	0.002

Best fit equation: RadarCount = 27.38 + 30.59(NearshoreJune) + 0.05(Forest) + 1.09(SteepSlope)

At the 10 km spatial scale, the best model included only forest and steep slope area as predictors of radar counts (*w* = 0.557); however, weight of evidence in favour of the second model (*w* = 0.321) was also high, indicating that total at-sea density in June was also an important but weaker predictor (Table 11). The best model at 10 km had a lower coefficient of determination than the best models at 5 km, but it was still a good fit ($R^2 = 0.62$, $F_{2,15} = 12.14$, $p < 0.001$).

Table 11: Candidate multiple regression models predicting radar counts relative to at-sea densities and areas of potential nesting habitat types within 10 km of radar sites. Model parameters include: Forest (forest area), SteepSlope (area of slope 45-90°), TotalJune (total density in June), NearshoreJune (nearshore density in June), OffshoreJune (offshore density in June), and NearshoreAug (nearshore density in August).

Model	*K*	AICc	ΔAICc	*w*
Forest+SteepSlope	4	217.676	0.000	0.557
TotalJune+Forest+SteepSlope	5	218.775	1.099	0.321
TotalJune+Forest+SteepSlope+NearshoreJune+OffshoreJune	7	220.902	3.226	0.111
TotalJune+Forest+SteepSlope+NearshoreJune+OffshoreJune +NearshoreAug	8	226.037	8.361	0.009
Null Model	2	228.732	11.056	0.002

Best fit equation: RadarCount = 38.78 + 0.018(Forest) + 0.69(SteepSlope)

At the largest spatial scale, 15 km, the best model had the same predictors of radar counts as the best model from the 10-km scale: areas of forest and steep slope (w = 0.676; Table 12). The second model also had moderate support (w = 0.272) indicating that shallow slope area was a weaker but important predictor of radar counts. The only candidate model containing at-sea densities had very low support (w = 0.004). The best model for 15 km radius had the lowest fit among the best models for all spatial scales (R^2 = 0.57, $F_{2,15}$ = 10.07, p = 0.002).

Table 12: Candidate multiple regression models predicting radar counts relative to at-sea densities and areas of potential nesting habitat types within 15 km of radar sites. Model parameters include: Forest (area of forest), SteepSlope (area of slope 45-90°), ShallowSlope (area of slope 18-45°), and TotalAugust (total density in August).

Model	*K*	AICc	ΔAICc	*w*
Forest+SteepSlope	4	219.683	0.000	0.676
Forest+SteepSlope+ShallowSlope	5	221.505	1.822	0.272
Forest+SteepSlope+ShallowSlope+TotalAugust	6	225.118	5.435	0.045
Null Model	2	228.732	9.049	0.001

Best fit equation: RadarCount = 24.95 + 0.010(Forest) + 0.42(SteepSlope)

The predictive power and fit of the best models at each scale declined with increasing spatial scale, and the best model across all scales was at 5 km. This model outperformed mixed-scale models constructed from the best predictors at each scale. This provides strong support for this combination of predictors (area of forest and steep slope, and at-sea densities in June) as the best overall predictors of radar counts. Forest and steep slope area were among the top predictors of radar counts across all spatial scales, while shallow slope was only a weak predictor of radar counts at the largest spatial scale (15 km). At-sea densities were included in only one top model (at the 5 km scale) and were a weak predictor at the 10 km scale, and not included in any top models at 15 km.

Discussion

Correlations between radar counts and at-sea density

The range of significant correlation strengths between radar and at-sea counts in this study (0.484-0.643) was similar to the range observed in a comparison of radar and at-sea counts in Oregon (0.395-0.680; Cooper et al. 2000). Correlation strengths in the Kodiak data generally increased at larger spatial scales, particularly for offshore and total densities. In contrast, in Oregon Cooper et al. (2000) found no consistent trend in correlation strength across spatial scales ranging from 12-32 km, but correlation strength decreased dramatically at the 40-km scale. These two studies indicate that a spatial signal of local abundance can be detected in at-sea distributions relative to inland flyways over a range of distances, which may depend on local factors.

The only at-sea density measure that did not follow the trend of increasing correlation strength with increasing spatial scale was nearshore density in June. Despite increasing sample sizes (more transects averaged) across larger spatial scales, the strongest correlation of nearshore density with radar counts was at 5 km. This provides strong evidence that in the early-mid breeding season, active breeders cluster near nesting flyways in nearshore water. Peery et al. (2009) found that breeding murrelets in California foraged closer to nesting flyways during active nesting than during pre- or post-breeding phases. The mean distance of breeders from flyways during nesting in

California was approximately 6 km, which corresponds well with the apparent clustering observed at the 5-km scale off Kodiak.

The contrasting pattern of increasing correlation strength at larger spatial scales in August surveys, along with offshore and total densities (for both June and August) can be attributed to larger sample sizes. At larger scales a greater number of transects were averaged in each comparison of at-sea density with radar, increasing power to detect a signal. Biological factors could also contribute to correlations between at-sea patterns of abundance and radar counts. First, the proportion of breeding murrelets in a given area could affect spatial patterns of abundance, since active breeders appear to aggregate closer to nesting flyways than non-breeders (Peery et al. 2009). Second, the seasonal progression of breeding phases is also likely to play a role in spatial distribution; later in the breeding season (August), murrelets may aggregate more loosely around nesting flyways when they have finished breeding (post-breeders, failed breeders) or while prospecting. This could explain the general spatial and temporal trend observed in at-sea correlations with radar counts, shifting from a strong correlation at the smallest spatial scale in June (mainly active breeders clustered near flyways) to stronger correlations at larger spatial scales in August (driven by greater contributions of non-breeding and post-breeding murrelets to spatial patterns of abundance).

Terrestrial habitat associations

Terrestrial habitat parameters were among the best predictors of population size across all spatial scales. Area of forest and steep slope were in all of the top models at each spatial scale, indicating that these terrestrial habitat types were likely nesting habitat for murrelets. The strongest correlation between radar counts and forest area was within 5 km, while the strongest correlation with steep slope area was at 15 km. This most likely reflects the spatial distribution of these habitat types, since forest occurs at low elevation near the coast, while steep slopes are more patchily distributed inland. Shallow slope was only a weak predictor at the 15 km spatial scale, despite its significant correlation with radar counts at both 10 and 15 km. It is likely that shallow slope habitat is more variable in quality than forest or steep slopes, and this habitat classification needs to be further refined using vegetation cover or elevation levels to determine its potential importance as nesting habitat. Additionally, shallow slope habitat may be inferior compared to steep slopes and forest because nests may be more accessible to terrestrial predators such as the red fox (*Vulpes vulpes*), which was responsible for 47% of Kittlitz's murrelet nest failures on Kodiak Island (Lawonn 2013), and might similarly impact ground-nesting marbled murrelets.

The strongest correlation between radar counts and area of forest (5 km; r = 0.672), was lower than correlations between radar counts and core area areas of old growth forest in Washington (r = 0.81; Raphael et al. 2002), and radar counts and low-elevation old growth forest in British Columbia (r = 0.85; Burger 2001). However, these studies used more refined techniques to identify likely nesting habitat and compared radar counts to area of habitat within discrete watershed units, which was likely a more accurate estimate of potential available nesting habitat. The explanatory power of the best multiple regression model ($R^2 = 0.71$) in this study, which included marine and terrestrial variables, was equal to the best model from a study in British Columbia that compared measures of old growth habitat to predict population size from 98 watersheds (Burger et al. 2004).

Predictive models of population size identified steep slope as an important parameter across all spatial scales, and at the largest scale (15 km) the correlation coefficient between radar counts and steep slopes was higher than any other terrestrial habitat type ($r = 0.912$). The use of steep slopes for nesting by marbled murrelets in Alaska may be more important and widespread than previously thought. Recent radiotelemetry studies in Alaska at Port Snettisham (Barbaree 2011) and Icy Bay (unpublished data from M. Kissling, U.S. Fish & Wildlife Service) have found that 49-53% of marbled murrelets nest on the ground, even when forested habitat is available. In the Kodiak Archipelago, some of the largest marbled murrelet populations sampled by radar in this study were in unforested areas surrounded by steep slopes (e.g., pre-sunrise counts for Kiliuda Bay: 296 murrelets, Three Saints Bay: 318 murrelets; Figure 27).

Linking marine and terrestrial habitat

Comparisons of the best models to predict radar counts across spatial scales revealed that the best predictive model included both marine and terrestrial parameters, emphasizing the link between marine and terrestrial habitat. The strongest predictors of murrelet population estimates were forest area, steep slope area, and at-sea density within the smallest spatial scale (5 km), indicating that breeding murrelets cluster near nesting flyways. Alternatively, the smallest scale may have been the best model because at larger scales, it is more likely that murrelets could be using flyways other than the one sampled by radar to commute between nest and ocean.

The importance of high-quality marine habitats adjacent to nesting habitat has been identified in numerous studies (Piatt & Ford 1993, Day et al. 1999, Meyer et al. 2002, Miller et al. 2002, Becker & Beissinger 2003, Ronconi 2008, Hazlitt et al. 2010). Reducing the distance between nest and foraging sites lowers energetic expenditures through flight and reduces risk of predation to parents. Recent energetic modeling of Kittlitz's murrelets revealed that energy expenditure under conditions of low prey or long commuting distances to nest sites may exceed the rate at which food energy can be assimilated by breeding murrelets, resulting in nutritional stress and potentially contributing to low reproductive success (Hatch 2011). In the Kodiak Archipelago, murrelet commuting distances (by default < 20 km from nest to ocean) appear to be relatively short or comparable to distances identified by radiotelemetry from other regions (mean distance 78 km in southeast Alaska, Whitworth et al. 2000; 39 km in British Columbia, Hull et al. 2001; 16 km in Prince William Sound, Kuletz 2005). The proximity of suitable nesting habitat to productive marine foraging areas in the Kodiak Archipelago may be an important factor in the archipelago's overall suitability as a population centre for marbled murrelets in Alaska (Piatt & Ford 1993).

Implications for radar studies of murrelets in Alaska

In this study I compared radar counts to areas of potential nesting habitat at three spatial scales, rather than delineated watershed boundaries as has been done in previous comparisons of radar counts with habitat area (Burger 2001, Burger et al. 2004, Raphael et al. 2002). Despite the lack of defined catchment areas, comparisons of radar with areas of potential nesting habitat were significantly correlated, indicating that this method can be used to make inferences about murrelet habitat associations even in the absence of clearly defined watershed boundaries. Furthermore, habitat variables within a range of spatial scales can be compared to identify which spatial scale is most likely to reflect the habitat being used by commuting murrelets.

Correlations between radar and at-sea counts were weaker than correlations between radar counts and areas of potential nesting habitat. Although murrelets were clustered at sea near nesting flyways, at-sea densities were variable because murrelets are highly mobile and their spatial distribution also reflects dynamic processes governing prey densities. Thus, by taking advantage of predictable daily movement patterns, radar studies are a more reliable tool than at-sea vessel counts for making inferences about use of terrestrial habitats by breeding murrelets.

Synthesis

The goal of this study was to test new remote-sensing methods for monitoring populations of *Brachyramphus* murrelets in Alaska: marine radar and autonomous acoustic sensors. Secondary goals were to compare the strengths and limitations of these and other standard population monitoring methods, to investigate spatial and temporal patterns of abundance, and to develop methods to differentiate between marbled and Kittlitz's murrelets on radar. This chapter summarizes insights into *Brachyramphus* murrelet ecology, and recommendations for integrating remote-sensing methods into population monitoring and research.

Brachyramphus murrelet behaviour at high latitude

Commuting flight behaviour

Murrelets responded to the longer twilight period at high latitude by lengthening the duration of predawn commuting activity relative to more southerly latitudes. This suggests that murrelets commute during an optimal range of light levels to maximize crypsis: populations dominated by marbled murrelets appeared to avoid commuting in total darkness, perhaps to reduce collision risks, while all populations reduced commuting during daylight when murrelets would be more visible to predators. Seasonal trends in activity, increasing from June to late July, were recorded in all four survey methods. The seasonal increase in commuting and social flight behaviour detected by radar, audio-visual and Song Meter counts peaked in late July, while at-sea survey counts increased significantly from June to August. This clear trend in seasonal activity may be the result of the shorter breeding season at high latitude promoting a greater degree of breeding synchrony compared to populations at lower latitudes.

It was not possible to differentiate marbled and Kittlitz's murrelet targets on radar. However, comparisons between Grant Lagoon (near known concentration of Kittlitz's murrelet nests) and other radar sites (presumed to have negligible numbers of Kittlitz's murrelets) indicated that Kittlitz's murrelets might engage more frequently in commuting flight inland during darkness compared to marbled murrelets. This may be a consequence of nesting in barren, open habitat where murrelets can navigate more easily in darkness, while predation pressure at higher light levels may be more extreme than in vegetated habitat. This behaviour should be investigated more closely in areas with high abundances of Kittlitz's murrelets.

Habitat associations

Comparisons between radar counts and terrestrial habitat variables revealed strong associations of marbled murrelets with old-growth forest and steep slopes (45-90˚). The largest populations across the Kodiak Archipelago were recorded at sites with old-growth forest, and also at completely unforested sites with steep topography. These results suggest that unforested habitat can support large populations of marbled murrelets and that this habitat may be of greater importance to marbled murrelets in Alaska than previously recognized. In their range south of Alaska where suitable trees are more abundant, ground and cliff nesting by marbled murrelets is rare (Nelson 1997, Burger 2002, Piatt et al. 2007). Models predicting suitable nesting habitat for marbled murrelets in Alaska clearly need to incorporate parameters important for both ground-nesting (i.e., steep slopes) and tree-nesting (i.e., large trees with suitable canopy platforms).

Correlations between radar and at-sea densities were significant across all spatial scales tested (5, 10, 15 km), but significance and strength of correlations differed by month (June vs. August) and at-sea density measure (nearshore, offshore, or total density). In June, nearshore densities (< 200 m from shore) were significantly correlated with radar counts only at the 5 km spatial scale, potentially indicative of a clustered distribution of active breeders relative to flyways. Combined models of at-sea densities and terrestrial habitat variables revealed that the strongest predictors of radar counts were at-sea density for June nearshore surveys, area of old-growth forest, and area of steep slopes, all within 5 km of radar stations. These data indicate that murrelets sampled by radar in the Kodiak Archipelago are likely to be using both marine and terrestrial habitat within short distances of coastal flyways. The availability of coastal nesting habitat near a highly productive marine environment (Piatt 2011) has made this an area of high importance to the Alaskan marbled murrelet population (Piatt & Ford 1993). Ultimately, *Brachyramphus* murrelets have evolved as non-colonial seabirds to take advantage of widely available coastal habitats (forests and steep slopes) near productive marine environments. Colonial seabirds depend on mammal-free islands and sea cliffs as nesting sites, which limits their breeding distribution through much of Alaska and the Pacific Northwest. By maintaining low population densities across large areas, murrelets avoid density-dependent inter- and intra-specific competition experienced by colonial seabirds, such as resource depletion near the colony ("fishing down the foodweb"; Elliott et al. 2009) during reproduction, an energetically demanding and resource-limiting period.

Recommendations for radar and acoustic monitoring protocols

Radar survey protocols

Standardized radar population monitoring protocols are needed to survey *Brachyramphus* murrelets in Alaska. Protocols designed to survey populations south of Alaska (Evans Mack et al. 2003, Manley 2006) require modifications to address differences in daylight regime, seasonality, and habitat use that affect the temporal and spatial patterns of flight behaviour in Alaskan murrelets.

Timing of surveys Radar surveys should capture the pre-sunrise peak in commuting activity beginning 2 h before sunrise. The peak of landward flight activity occurred 84 ± 3 min (mean ± SE) before sunrise, indicating that local population size (or an index of activity at sites with poorly defined flight paths) could be reliably estimated from counts of landward murrelets occurring during the period 2 h before sunrise. These protocols may need to be modified to accommodate the potentially different diurnal activity patterns of Kittlitz's murrelets. Radar surveys should be conducted in areas of high Kittlitz's murrelet abundance (e.g., Icy Bay, Alaska) to determine whether there is a clear peak of predawn activity that can be used in censuses, and if so, whether the timing and duration of this activity peak differs from that of marbled murrelets.

Seasonally, radar counts increased from June to July, with the highest counts occurring in late July. To measure inter-annual change, sampling should be planned for the same period(s) in the season between years to avoid confounding population change with seasonal changes in abundance. The increase in seasonal activity from June to late July implies that a greater proportion of prospecting murrelets are counted in radar surveys later in the breeding season. If the desired population metric is breeding population size, radar surveys should be conducted early in the season to avoid counting a larger proportion of non-breeders (June-early July).

Survey site characteristics & weather Survey sites with confined, clearly-defined flight paths provided the most reliable counts of commuting murrelets because targets fly along predictable paths, with clear directionality. These sites typically have headlands or steep valleys that confine the flight paths of murrelets. At other sites characterized by low-lying topography, or on peninsulas, a variable proportion of flight paths were ambiguous as to their direction (landward vs. seaward), reducing reliability of landward target counts. Additionally, open, low-lying coastal areas are more often subject to strong winds that can affect the flight speeds of birds. At wind speeds over 18 km h^{-1}, murrelets could no longer be reliably distinguished from other species on radar.

Autonomous acoustic sensor protocols

Timing of surveys In this study, autonomous acoustic sensors recorded for 2 h pre-sunrise to match the peak of murrelet commuting activity recorded by radar. However, the peak of vocal activity began approximately 1 h pre-sunrise and continued after sunrise. Therefore, at sites of similar latitude, the timing of recordings could be shifted later in the morning or expanded to a 3-h sampling period to capture the full peak of vocal activity; alternatively, a shorter period (e.g. 1 h pre-sunrise) could be sampled to reduce processing time for recordings, while still providing a reliable index of abundance. A shorter sampling period would reduce memory and power use, allowing a greater number of samples to be recorded across the season autonomously.

Survey sites Acoustic data are most efficiently collected at sites with low noise interference from other songbirds. Thus, placing sensors as far as possible from perch-sites and brushy vegetation could reduce noise interference.

Integrating monitoring and research methods

Each of the four methods discussed in this study has strengths and weaknesses in terms of censusing and monitoring populations, making inferences about habitat associations, and cost effectiveness. Combinations of monitoring methods can improve cost-efficiency and be targeted to address specific research and management goals.

At-sea vessel counts have been used to monitor population trends and identify terrestrial habitat associations across large spatial scales in Alaska (Piatt & Ford 1993, Piatt et al. 2007, Kissling et al. 2011, Kuletz et al. 2011a,b, Piatt et al. 2011). The advantage of at-sea counts is that the relative proportion of *Brachyramphus* murrelets in a given area can be identified; additionally, at-sea counts include murrelets of all breeding status, providing an estimate of the total population size for a given region. However, these surveys have low power to detect population trends due to inherent variability in marine bird distributions at sea and logistical constraints (Kissling et al. 2007, 2011).

Comparatively, radar monitoring of populations at the watershed scale has high power to detect population trends (Arcese et al. 2005, Bigger et al. 2006b, Cooper et al. 2006). These counts can also be used to make inferences about inland habitat associations at the watershed scale (Burger 2001, Raphael et al. 2002, Burger et al. 2004). However, radar counts detect mainly breeding and prospecting murrelets, excluding an unknown but variable non-breeding proportion of the population from censuses (Peery et al. 2004b). Breeding effort can vary from year to year due to changes in marine conditions, resulting in fluctuations in the proportion of murrelet populations commuting inland (Peery et al. 2004b). Thus, radar counts may reflect changes in breeding effort rather than changes in overall population size. There is evidence that breeding effort in Kittlitz’s murrelet populations is lower and more variable than for marbled murrelets (M. Kissling, unpublished data). However, fluctuations in breeding population size may be offset by the large numbers of non-breeding birds making inland flights (M. Kissling, unpublished data).

Spatial and temporal patterns of abundance within watersheds can be assessed using smaller-scale methods such as autonomous acoustic recording and audio-visual surveys. Autonomous acoustic sensors are particularly useful for sampling remote or poorly accessible areas, such as steep slopes, because unlike radar equipment they can be easily carried and deployed; meanwhile, audio-visual surveys provide more detailed information on murrelet behaviour that can be indicative of nesting. These two methods can be combined to reduce risks and costs for field personnel. For example, acoustic sensors could be used to investigate patterns of habitat use on steep slopes in unforested watersheds by both marbled and Kittlitz's murrelets. Autonomous devices could reduce safety risks to human observers because they can be deployed in daylight, avoiding the need for human observers to negotiate this terrain in dark twilight. Similarly, assessing the nocturnal abundance of Kittlitz's murrelets in inland habitat through autonomous sensors would reduce safety risks to personnel. Audio-visual surveys can be conducted to confirm "occupied" behaviours to indicate nesting in areas that have been identified by autonomous acoustic sensors as likely.

Automated sensors are a cost-effective tool for identifying seasonal trends and for long-term monitoring, because high temporal replication can be achieved without additional field costs. Thus, seasonal activity trends can be used to inform the timing of radar surveys the following season, or to calibrate counts relative to the seasonal activity level in which they were conducted. Long-term monitoring of specific habitat patches can be conducted to monitor environmental change, such as climate change effects, habitat fragmentation, or increases in predator densities (sensors simultaneously record murrelet and potential predator vocalizations).

The remote setting and sympatric distribution of Alaskan *Brachyramphus* murrelets creates unique challenges for population monitoring and research, yet this region supports the majority of global populations for these two threatened seabirds. Given that global climate change disproportionately affects high-latitude ecosystems, it is crucial to develop sound, cost-effective monitoring strategies for these species that encompass a range spatial and temporal scales. I propose specific combinations of monitoring tools for integration into existing monitoring programs.

Outline of *Brachyramphus* murrelet monitoring design for Alaska

Long-term monitoring of population trends, currently conducted through at-sea counts, should be supplemented by both radar and autonomous acoustic surveys to increase the power and spatial resolution of trend detection. Radar surveys should be conducted at carefully selected stations that have suitable topographic features to confine murrelet flight paths along predictable routes. These counts provide the most reliable estimates of population size, trends, and spatially-defined distribution of breeding birds. A preliminary power analysis from radar surveys in the Kodiak Archipelago (Appendix B) suggests that the power to detect population trends in this area is similar to that of northern California (Bigger et al. 2006b), where annual population declines of 2.5% could be detected with 80% power using a sampling design that included 22 sites with 4 radar surveys per year. At-sea surveys should be conducted adjacent to radar stations to estimate the local relative proportions of the two murrelet species, since they are indistinguishable on radar, and proportions cannot be determined by acoustic methods (Kittlitz's murrelets vocalize infrequently during commuting flight). Fine-scale patterns of habitat use, relative abundance and seasonal trends should be assessed through using automated acoustic sensors, followed by targeted audio-visual surveys to confirm nesting behaviours in areas of interest.

Integrating new remote-sensing approaches into *Brachyramphus* murrelet research and population monitoring in Alaska will provide cost-effective methods to obtain population-level information on spatial and temporal patterns of activity. These tools will complement existing research programs by filling the gap between population monitoring at regional spatial scales (at-sea counts) and within-population scales (tracking individual movements through radio-telemetry and satellite transmitters).

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Appendix A. Song Scope recognizer parameters

Table A-1. Parameter values used to build Song Scope recognizers through feature reduction. Definitions modified from Wildlife Acoustics (2011).

Parameter	Value	Definition
Sample rate (Hz)	16,000	Sample rate (audio samples per second) used to display spectrograms.
FFT size	256	Fast Fourier Transform (FFT) window size: adjusts the resolution of frequency vs. time, e.g., larger FFT values have higher frequency resolution at the expense of temporal resolution.
FFT overlap	1/2	Proportion of overlap between FFT windows; overlap increases frequency and temporal resolution. A combined FFT size of 256 with ½ overlap produces a sampling resolution of 62.5 Hz, time resolution of 0.016 s.
Frequency minimum (FFT bins, equivalent frequency)	36 (2250 Hz)	Lowest frequency displayed on spectrogram and used in comparing vocalizations. Adjusted to match lowest observed frequency of vocalizations.
Frequency range (FFT bins, equivalent frequency)	30 (2250-4125 Hz)	Range of frequencies displayed on the spectrogram and used in comparing vocalizations. Adjusted to match as closely as possible the observed frequency range of vocalizations.
Background filter (s)	1	Reduces background noise, by averaging background noise over a specific time interval (1 second recommended). Reduces smearing effect of echoes.
Maximum syllable (ms)	496	Specifies the largest syllable likely to occur in the vocalization.
Maximum syllable gap (ms)	72	Specifies the largest intersyllable gap likely to occur in the vocalization. If the gap interval between sounds exceeds this gap, the recognizer considers it a separate vocalization.
Maximum song (ms)	1656	Specifies the longest vocalization likely to occur.
Dynamic range (dB)	20	Reduces interference from background noise by cutting off weaker signals in favour of stronger candidates for recognition. The optimal value approximates the signal-to-noise ratio of the field recordings (difference in dB between background noise and calls of interest).
Maximum complexity	20	Limits the number of Hidden Markov Model states in the recognizer; more complex vocalizations (more syllable types) may require higher maximum complexity to model the vocalization accurately.
Maximum resolution	6	Limits the size of spectral vector features; vocalizations with narrow frequency bands and low complexity (e.g., murrelet whistles and keers) require low spectral resolution. A value of 6 is recommended for such calls.

Table A-2. Summary of recognizer training results and model components for “Keer” and “Keheer” recognizers. Definitions modified from Wildlife Acoustics (2011).

Parameter	Value by recognizer		Definition
	Keer	Keheer	
Cross training (%)	68.21 ± 12.84	67.09 ± 5.81	A measure of how well the model is expected to perform; a portion of annotations are withheld from the recognition model and tested against the algorithm. The result (%) is the average and standard deviation of the fit of excluded annotations.
Total training (%)	70.76 ± 9.92	66.45 ± 5.44	The average and standard deviation of the recognition model including all of the training data.
Model states	14	15	Indicates the size of the model (Hidden Markov Model states).
State usage	3 ± 2	6 ± 3	The average and standard deviation of the number of different states traversed by each vocalization.
Feature vector	6	6	The number of dimensions in each FFT window used in feature reduction (comes from the Maximum resolution setting).
Mean symbols	4 ± 4	9 ± 5	The average and standard deviation of the number of symbols contained within each vocalization.
Syllable types	5	3	Number of different syllabic classes used to construct the final model; selected from a sample of models with a maximum of ¼ the maximum complexity value. The model with the highest cross-training result is selected.
Mean duration (s)	0.28 ± 0.07	0.31 ± 0.06	Average and standard deviation of the duration of each vocalization.
Annotations imported for basic recognizer	59	159	The initial number of annotated calls imported to create the basic recognizer.
Annotations used	13	38	The final number of annotations used to generate the recognition model, after unsuitable annotations were removed.

Appendix B. Power analysis of radar surveys in the Kodiak Archipelago, Alaska

(Completed in association with Allan Roberts)

We assessed the power of radar surveys conducted from 2011–2012 in the Kodiak Archipelago, Alaska to detect declines in *Brachyramphus* murrelet populations. We followed analytical methods from Bigger et al. (2006b), but because our study had limited numbers of repeated surveys, we were unable to generate reliable estimates of inter-annual variation. Therefore, rather than producing an independent power analysis, we compared sources of variation in our study area to the values obtained by Bigger et al. (2006b). We compared the values for coefficients of variation rather than variance because coefficients of variation are scaled relative to a mean, and our mean counts were generally higher (mean count of 141.6 murrelets) than those observed by Bigger et al. (2006b; mean count of 13.3 murrelets).

We excluded one site in our analysis (Grant Lagoon, surveyed in 2010), because we considered this site an outlier on account of very low counts and high variability in timing of diurnal activity, which resulted in a relatively high coefficient of variation (0.47). Furthermore, this was the only site sampled in 2010.

Values for within-site variance, among-site variance, inter-annual variance and site * year interaction were estimated using a general linear mixed model based on maximum likelihood estimation, following Bigger et al. (2006b). This mixed effects model was implemented with the package "lme4" (Bates et al. 2013) for the statistics application R (v. 3.0.1; R Development Core Team 2013), with site, year, and the interaction between site and year treated as random effects, and the natural logarithm of radar counts as the dependent variable. For each of the sources of variability, a coefficient of variation was calculated. Confidence intervals on our estimates of coefficients of variation were computed using parametric bootstrapping (10 000 replicates), based on our estimates of variance.

Our estimates of coefficients of variation were lower than those observed by Bigger et al. (2006b; Table B-1). These results suggest that the power of radar surveys to detect population trends in Alaska are likely to be similar, or possibly greater than predicted by Bigger et al. (2006b) in California; however, our study has a lower sample size and these results are preliminary. We sampled a greater number of sites than Bigger et al. (2006b) – 23 compared to 11, but had only 51 surveys compared to 166. Bigger et al. (2006b) found that monitoring programs with 4 visits to each radar site per year at 22 sites had 80% power to detect an annual population decline of 2.5%, while 5% annual declines were detected with almost 100% power.

Table B-1. Estimates of coefficients of variation (CV) and 95% confidence intervals (CI) for radar counts from the Kodiak Archipelago compared with values from Bigger et al. (2006). Confidence intervals for Bigger et al. (2006) were calculated from their reported mean natural logarithm of counts.

	Kodiak Archipelago		Bigger et al. (2006)	
Source of variation	CV	95% CI	CV	95% CI
Site * year interaction	0.01	0–0.16	0.09	0–0.14
Among-site	0.20	0–0.27	0.28	0–0.40
Year	0.03	0–0.14	0.17	0–0.28
Within-site	0.10	0.07–0.13	0.23	0.20–0.26