PROSPECTING DECISIONS AND HABITAT SELECTION BY A NOCTURNAL BURROW-NESTING SEABIRD

by

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ABSTRACT

Introduced predators have caused declines and extirpations of many populations of insular avifauna, especially nocturnal burrow-nesting seabirds. The successful eradication of these introduced predators has resulted in recovery of some species but not others, the reasons why are not understood. The objectives of my study were to understand the recovery of seabird populations after the removal of an introduced predator by studying the processes underlying the formation of new colonies and the expansions of colonies after establishment. Specifically I asked: 1) how nocturnal seabird colony area and population size change with time and across a metapopulation; and 2) how prospectors choose suitable breeding habitat by looking at habitat selection and use of public information. Using an information theoretic approach I found 1) regional differences in both colony area and population density over time and between island groups; 2a) Ancient Murrelets breeding in Haida Gwaii exhibit a high degree of flexibility in their use of available breeding habitats and the amount of suitable habitat at Langara Island has not changed between 1981-2007; 2b) differences in colony attendance decisions between sites, and life history stages; and 2c) Ancient Murrelet prospector activity increased during playback of conspecific vocalizations, but no preference for burrows with olfactory and/or visual cues over those left empty was found. Overall, I conclude that although Ancient Murrelet life history may prolong recovery times, both

recovery and recolonization of restored breeding sites are plausible and using

playbacks of conspecific vocalizations is an effective method to attract

prospecting individuals to those sites.

DEDICATION

For Ethel O. Dorey

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Introduction

Introduced predators continue to cause declines and extirpations of many populations of insular avifauna. The removal of introduced species from islands is often considered one of the most powerful tools in conservation biology. To date there have been at least 787 successful animal eradications from 582 islands, including at least 120 with goats, 284 with rodents, and 75 with cats (Nogales et al. 2004, Campbell and Donlan 2005, Howald et al. 2007, Donlan and Wilcox 2008, Island Conservation 2010). Improving techniques and experience have led to the successful eradications at sequentially larger islands, the largest being Campbell Island, New Zealand at 11,300 ha (McClelland and Tyree 2002). However, ecosystem restoration is not achieved by solely eradicating an introduced predator.

All species within an ecosystem work in concert with each other providing ecosystem function. The loss of species can result in decreased ecological resilience, or a loss in the ability to maintain a particular state (Peterson et al. 1998, Scheffer et al. 2001). Introduced predators on islands have been shown to alter the flow of nutrients by decimating seabird populations and therefore eliminating marine nutrient inputs (Martin and Joron 2003, Croll et al. 2005). Thus, the shift from a 'seabird' island to a 'non-seabird' island can drive a change between ecosystem states. However, the successful eradication of introduced

predators from important seabird breeding islands may not be sufficient to facilitate ecosystem recovery as these systems may become locked into this 'non-seabird' state (Jones 2010). Assisted seabird recovery (i.e., translocations and the use of decoys and playbacks to attract immigrants) has therefore become an important strategy to mitigate the long-term impacts of introduced species (Kress 1978, 1983, 1997, Parker et al. 2007), while the propensity for many species to recover naturally remains relatively unknown.

Many introduced predator eradication attempts are either not published or are published in the grey literature and even fewer papers are published concerning natural recovery of seabird populations after predator eradication. In fact, a concise review of the literature found only 33 papers detailing post-eradication seabird trends (Appendix A). Of those, there were 64 individual species accounts across 26 islands accounting for 42 seabird species. Thirty-five accounts described increases in either reproductive success or population size for individual seabird species, and 15 documented recolonizations (plus three possible recolonizations) by individual species, whereas 10 accounts (i.e., 16% of the individual species accounts) documented seabird trends with no change. Yet, cases where recovery has been observed cannot be solely attributed to introduced predator eradication, as it is not always apparent whether the eradicated predator caused or was the sole cause of population declines and extirpations. Population declines associated with the eradication of introduced predators were not found; most accounts were focused on recovery or life history of a specific seabird. Based on this small analysis, published accounts of

recovery and recolonization are likely biased towards positive outcomes. The
reasons why some populations are quick to recolonize post-predator eradication,
while other sites remain seabird-free remains largely unanswered. Clearly,
proximity to a source population, metapopulation dynamics, life-history
characteristics, and site fidelity/philopatry are all determining factors associated
with recovery and recolonization of a population post-predator eradiation (Buxton
2010). As well, the ability to predict the response of a seabird population,
especially a threatened or endangered population, is of the utmost importance.
Therefore, understanding how individuals evaluate and choose a nesting site is
of great conservation concern and can be used to enhance recovery and
recolonization programs.

Colonization/re-establishment and colony expansion imply the movement
of individuals across space, which is a key process in metapopulations (Ims and
Yoccoz 1997). Local dynamics and life history play important roles determining
movement, where immigration from a colony may be driven by temporal
heterogeneity in the relative quality of different colonies, while site fidelity
increases when the predictability of a breeding site increases (Oro and Ruxton
2001). Colonizing new habitat can be risky, aggregations at occupied sites that
leave high quality habitat unoccupied occur because of the tendency of
individuals to base settlement decisions upon factors associated with conspecific
attraction and public information (Forbes and Kaiser 1994, Alonso et al. 2004).
Yet many factors outside of the behaviour of an individual species may affect the
ability of that species to colonize a new area. For example, large-scale factors

such as limited food resources and availability, disease, competition, and age bias within a population, can impact populations by preventing growth within a population. However, the scale of these factors means they would likely not impact one local population and would therefore be visible from the perspective of larger population dynamics and potentially the metapopulation. On the other hand, small-scale factors that operate at a local population level, such as habitat availability, density dependence, and predator abundance, will impact the success of settlement, probability of immigration/emigration, and whether a site is successfully colonized.

Objectives

The objectives of this study were to understand the recovery of seabird populations after the removal of an introduced predator by studying the processes underlying the formation of new colonies and the expansions of colonies after establishment. I placed special focus on habitat selection by prospecting individuals (i.e., pre-breeding individuals that are searching for a location within which to settle and breed) and how to promote prospecting at abandoned colony sites. Specifically I asked: 1) how nocturnal seabird colony area and population size change with time and across a metapopulation; and 2) how prospectors choose suitable breeding habitat by looking at habitat selection and use of public information.

Study species

Ancient Murrelets (*Synthliboramphus antiquus*) are a nocturnal burrow-nesting seabird whose North American breeding range extends from Haida Gwaii, British Columbia through the western Aleutian Islands, Alaska (Gaston 1992). Ancient Murrelets will breed both under forest cover and in more open landscapes, where in forested areas breeding burrows are tunnelled under the base of trees, stumps, fallen logs, and may penetrate fissures in underlying rocks; outside of forested areas they use either rock crevices or burrows made among the roots of grass tussocks (Gaston 1994). Ancient Murrelets have relatively low annual adult survival (between 0.67-0.84) but high reproductive output with a clutch size of two and approximate annual productivity of 1.2 chicks per pair (Gaston 1990). Chicks are precocial and leave their natal colony approximately two days after hatching, where they are provisioned and raised completely at sea (Gaston 1992). Ancient Murrelets do not show philopatry (i.e., fidelity to their natal site) and are believed to disperse from their natal colony (Gaston and Adkins 1998, Pearce et al. 2002), visiting and assessing a number of breeding colonies prior to settling in one location, known as a prospecting phase. This prospecting phase may begin in the first summer but typically begins in the second, with some individuals beginning to breed in their third summer with most breeding in their fourth (Gaston 1994). Once an individual begins breeding they will often do so every year, showing high breeding site fidelity (Gaston 1990, 1992). Prospecting activity peaks during the peak of chick departures, when chicks and adults are calling back and forth during the first half of the evening, once all family groups

have left the breeding colony, all activity at the colony site (including that of prospectors) ceases (Gaston 1992). Thus, there are two main times of high activity at Ancient Murrelet colonies, the first occurring when adults first arrive at the colony site and the second during chick departures when family groups depart the island and prospecting activity peaks (Gaston 1992). During this second phase of activity the majority of non-breeders (i.e., prospectors) attending colony sites are two year olds (Gaston 1990).

Throughout their North American breeding range, Ancient Murrelet populations have been declining due to introduced foxes (*Alopex* sp.), raccoons (*Procyon* sp.), and rats (*Rattus* sp.). Norway rats (*R. norvegicus*) introduced to Langara Island, Haida Gwaii, British Columbia, decimated one of the world's largest Ancient Murrelet breeding colonies (Bertram and Nagorsen 1995). The successful eradication of introduced rats from Langara Island has resulted in a gradual increase in Ancient Murrelet burrow occupancy, but large areas of the island remain unoccupied (Regehr et al. 2005, Regehr et al. 2007). Similarly in Alaska, introduced Arctic foxes (*A. lagopus*) and Norway rats have caused extirpations and population declines of many species of seabirds, including Ancient Murrelets (Atkinson 1985). Arctic foxes have been removed from nearly a million acres of refuge land in the Aleutian Islands, benefiting many species including nocturnal burrow-nesting seabirds (Williams et al. 2003). Ancient Murrelets are at times the most abundant seabird seen on spring surveys around Adak Island as they stage on the water and their populations are believed to be increasing (J Williams, U.S.F.W.S., Homer, AK, personal communication), yet

surveys aimed to assess this increase have not been completed nor have surveys of recolonization at abandoned colony sites. The concurrent eradication of introduced predators from Ancient Murrelet breeding colonies in both Haida Gwaii and the Aleutian Islands provided a unique opportunity to explore habitat selection and recolonization of this species throughout it's North Pacific breeding range.

Spatiotemporal changes in seabird populations

Many species of seabirds have recovered after the removal of an introduced predator (see Appendix A). While others, such as Ancient Murrelets, are slow to recover. The reasons behind this lay within the life-history of the species and how it chooses habitat (Lack 1968, Weimerskirch 2002, Gaston 2004). Yet, when assessing populations it is also important to understand the dynamics of the entire population (Tilman and Kareiva 1997) and how they might influence recovery. Seabird colonies are often dynamic in space and time and all areas once occupied will not likely be occupied again. Thus, assessing population recovery in relation to large-scale population dynamics that contribute to overall increasing/decreasing populations can be more informative than occupied breeding sites. Where overall decreasing populations due to the availability of forage fish, for example, could limit any one local population from recovering.

The Ancient Murrelet population in Haida Gwaii is believed to be increasing overall (Gaston et al. 2009). Therefore, if Langara Island is recovering after the eradication of Norway rats as suggested by Regehr et al. (2007) Ancient

Murrelet population density and the extent of the colony should: a) remain the same in the presence/absence of introduced rats, if population threats are large-scale (e.g., climate); b) converge with those at other sites, even though rat removal may be insufficient to alter population declines associated with other factors, if population threats are many (e.g., climatic and rats); or c) allow a redistribution of Ancient Murrelets within Haida Gwaii and faster growth at Langara Island than all other populations in Haida Gwaii, if rats are the only threat at Langara Island.

In an analysis of six pristine islands and within a 436-hectare region of Langara Island (i.e., McPherson Point, the one location Ancient Murrelets were not extirpated by introduced rats) I found regional differences in both colony area and population density over time and between island groups (Chapter 1). These results suggest local population dynamics are not strongly correlated, a requirement for metapopulation models (Hanski and Gilpin 1997). Thus, metapopulation dynamics are occurring within the Haida Gwaii Ancient Murrelet population and the observed increases in population size at Langara Island are not different than any other island (Chapter 1). Where the eradication of introduced rats has stopped the decline of Ancient Murrelets but was not sufficient to allow faster growth at Langara (i.e., definitive recovery), suggesting population threats are many and factors outside of introduced predators are limiting the recovery of Ancient Murrelets at Langara Island.

It is important to note that this result only suggests that the McPherson Point colony at Langara Island, the only site that remained occupied by Ancient

Murrelets throughout rat presence on the island and the only site surveyed consistently between 1980-2004, has not changed and says nothing of the numerous other areas on Langara Island where Ancient Murrelets were completely extirpated. Yet, if recruitment to restored areas at Langara Island is not occurring, over ten years after Norway rats were eradicated, questions regarding habitat suitability and the importance of conspecifics in settlement decisions remain.

Habitat selection

To preserve and manage populations it is necessary to understand how and why animals choose different habitats (Manly et al. 1993). In theoretical studies, these issues are addressed in terms of Allee effects, settlement costs, and ideal distributions (Brown 1969, Fretwell and Lucas 1970, Pulliam and Danielson 1991, Greene and Stamps 2001), all of which assume that individuals select the highest quality habitat available. Occupying alternative habitats will maximize overall fitness only when all high quality habitats are already occupied. Thus, when high quality habitats are abandoned, or a population is extirpated because of introduced predators, relatively quick recolonization should occur, assuming site quality has not changed. Therefore, rapid recolonization post-predator eradication will only occur when high quality habitat remains.

At Langara Island, Haida Gwaii, I asked whether the apparent lack of recovery and little to no expansion of the current active Ancient Murrelet colony could be attributed to diminished habitat quality outside of the currently occupied colony area. A comprehensive assessment of habitat preferences of Ancient

Murrelets in Haida Gwaii found no statistical preference for large-scale physical

habitat features, or a change in habitat at Langara Island between 1981-2007

(i.e., both during and after rat presence; Chapter 2). Thus, recovery of Ancient

Murrelets is not limited by suitable habitat and other factors such as the presence

of conspecifics are likely important to attract individuals into a breeding site.

Use of public information

Methods used to restore seabird colonies are tailored to the biology of the

species in question. Two fundamental and commonly occurring features of these

restoration programs are social facilitation and philopatry (i.e., natal site fidelity;

Kress 1997). Ancient Murrelets do not show philopatry (Gaston and Adkins

1998, Pearce et al. 2002), thus translocations are unlikely to be a valuable tactic

as Ancient Murrelet chicks do not imprint on the colony site they depart and

return there to breed. Additionally, the use of decoys will not aid in luring

nocturnal individuals, such as Ancient Murrelets, to a site as it does with diurnal

species such as Atlantic Puffins (*Fratercula arctical*) (Kress 1997) and Common

Murres (*Uria aalge*) (Parker et al. 2007), because nocturnal species presumably

do not rely upon visual cues when flying into colony sites. Alternative methods

are therefore required for these non-philopatric nocturnal species.

As it is prospectors that will respond strongly to conservation actions,

understanding their behaviour (e.g., how they decide to attend a colony, what

high quality habitat is, how far they wander while prospecting, etc.) is extremely

important. Yet, little is known about this life-history stage. Here, I investigated

the different colony attendance trade-offs being made by breeding and

prospecting Ancient Murrelets and found that prospectors appear to make colony attendance decisions based upon factors different from those of breeders. In particular, physical habitat features at the colony site are important factors determining how a prospector decides when to visit a colony (Chapter 3). Specifically, I found that in Haida Gwaii prospector attendance was three times lower when waves were high and two times lower during very bright light conditions, while in the Aleutian Islands prospector attendance was over 34 times lower during the full moon than the new moon (Chapter 3).

In many cases the presence of nocturnal burrow-nesting seabirds at breeding colonies is evident by the cacophony of calls and/or a distinctive odour. For example, in a study of the vocal behaviour of Ancient Murrelets, nine distinct vocal displays were found (Jones et al. 1989). One, referred to as a song, attracted other Ancient Murrelets, was presumably only sung by males, and late in the breeding season was sung only by male non-breeders. Jones et al. (1989) suggested that Ancient Murrelet vocalizations show unusually locatable and individually distinctive characteristics, and that this may be an adaptation to their nocturnal lifestyle. Thus, audio cues are likely important when finding a mate, locating a colony, and for communication. In addition, Nevitt and Haberman (2003) found that Leach's Storm-petrels (*Oceanogroma leucorhoa*) approached artificial presentations of dimethyl sulfide more often in a colony setting than either cod liver oil (which they are attracted to at sea) and a control. This suggests that birds are not only attracted to the odour but to behaviours associated with that odour as well. While Podolsky and Kress (1989) found that

Leach's Storm-petrels were more likely to utilize burrows close to speakers when call playback was performed.

Here I aimed to understand the role of different modes of social information in habitat selection by prospecting Ancient Murrelets and to test the efficacy of using artificial cues as a means of restoring their colonies. Using playback of conspecific vocalizations I experimentally tested a conspecific attraction hypothesis for Ancient Murrelets in both Haida Gwaii and the Aleutian Islands and found that Ancient Murrelets used conspecific vocalizations to locate and orient to potential colony sites (Chapter 4). This implies that areas lacking audio cues are unlikely to be recolonized, as they lack the primary signal used to locate potential colony sites. However, experiments testing the efficacy of visual and olfactory cues in breeding burrows did not reveal any preference for those cues (Chapter 4).

Conclusions

Ecosystem recovery resulting from the eradication of an introduced predator is a long process and is often assisted by reintroducing extirpated species with the hope that the system will regain some of its lost function. In addition, from the perspective of a manager, the recovery and recolonization of threatened species is often of the utmost importance. Yet, it is also important to understand the functional roles of these species within an ecosystem, and how their populations are changing within a larger spatial scale (i.e., over the larger metapopulation). For example, keystone species are those that the composition of a community depends (Paine 1969). Removing a keystone species results in

a compositional change of the community and may drive that community (i.e., local population) towards and into a new ecosystem state. By examining and comparing a metapopulation of seabirds breeding in pristine, impacted, and recovering ecosystems, I found support for a metapopulation hypothesis resulting in spatiotemporal dynamics across a metapopulation. Here individuals presumably emigrate from a disturbed site, resulting in population increases at undisturbed sites. Furthermore, a remnant population is not definitively recovering when population increases are noted, as these may be due to the larger-scale metapopulation dynamics and recovery must be judged in terms of the disturbance and resulting changes due to mitigation of that disturbance.

Overall, the impacts of an introduced predator are dependent upon the species affected and the role they play within the ecosystem. Yet, these ecosystem roles are often overlooked as restoration efforts are generally focused on mitigating the impacts to specific species, opposed to mitigating impacts on ecosystem function. Without identifying the role of a native species within an ecosystem, how their presence/absence changes the ecosystem, and whether prolonged absence and related trophic changes will limit the ability for species to re-establish themselves, it is premature to attempt meaningful restoration activities. My results do not support a prediction that Ancient Murrelets act as a keystone species, and their extirpation from many areas at Langara Island has not led to a change in ecosystem state. This is likely due to the fact that Ancient Murrelets spend very little time on land compared to other seabird species. For example, Ancient Murrelets are one of only a few alcid species with precocial

young. Thus, Ancient Murrelet chicks are never fed or defecate at the breeding colony and depart the colony just two days after hatching (Gaston 1992). In comparison, Cassin's Auklet (*Ptychoramphus aleuticus*) chicks spend approximately 41 days in the nest before leaving the colony, throughout which they are fed and defecate within the breeding burrow (Manuwal 1974, Vermeer 1981). Although the marine nutrient impact of one chick, or one family group is likely not significant, the additions of marine nutrients from a large colony of Cassin's Auklets will be much greater than that of a similar sized colony of Ancient Murrelets. Furthermore, it is thought that Ancient Murrelets do not actively dig their breeding burrows like many burrow nesting species, but instead compact the ground (Gaston 1992). Together these two examples illustrate how minimal the impacts of Ancient Murrelets likely are when compared to similar seabird species and the loss of Ancient Murrelets from a site is unlikely to instigate a change in ecosystem state.

The tendency of individuals to disperse has been linked with individual personalities, where differences in aggression may lead to differences in dispersal (Cote et al. 2010). In seabirds generally, individuals are most likely to settle within an established area, while few will colonize new areas and this may be due to different personality types and life history stages. While young individuals need to learn what constitutes suitable habitat and may use public information as both a method to assess habitat quality and locate potential sites; older experienced individuals may use public information only as an indication to the location of colonies. Therefore, unassisted recolonization may be the result

of older dispersers leaving a colony due to overcrowding or a disturbance, while young individuals may be more likely to settle within established colonies. Therefore, to enhance recolonization at abandoned colony sites presenting artificial public information will help attract young prospecting individuals and some older experienced individuals. However, this method may attract individuals to dangerous sites and should therefore only be used after careful analysis of habitat requirements and site suitability.

Overall this project reveals that colony formation or re-establishment and expansion are dependent upon metapopulation dynamics, disturbance, and dispersal probabilities. Where the level of disturbance is dependent upon the species disturbed and their role within the ecosystem. While recovery and the time-scale associated with recovery depends upon the life history of a species and how settlement decisions are made. Where prospecting behaviour can trap island ecosystems into a 'non-seabird' state, and large-scale population dynamics are important to understand and may relate directly to the propensity and timeframe associated with a species expected recovery. Specifically, I found that the observed increase in population size at Langara Island within the last 10 years is encouraging (Regehr et al. 2007), and is positive evidence that rat eradication successfully prevented this colony from complete extirpation, but recovery is not definitively occurring. While the recolonization of Amatignak Island in the Aleutian Islands is strong evidence that both recovery of a remnant population and recolonization are both plausible events under the correct circumstances.

DATA CHAPTERS

CHAPTER 1: SPATIOTEMPORAL VARIATION IN COLONY AREA AND POPULATION DENSITY FOR A NOCTURNALLY BREEDING COLONIAL SEABIRD

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1.1 Abstract

Population dynamics are an important aspect of species management plans, and understanding how local populations fluctuate through time and how this impacts a metapopulation are of the utmost importance. Yet, in many cases metapopulation dynamics are not fully considered, especially when assessing population recovery and recolonization following the mitigation of an anthropogenic disturbance. Here I investigated how populations change through space and time and how these changes differ between local populations within one metapopulation using nocturnally breeding Ancient Murrelets in Haida Gwaii as a case study. I asked whether differences between colony area and population density occur through space and time and whether recovery is occurring at Langara Island by examining regional changes within local populations (i.e., 10 ha regions within each island). Using an information theoretic approach I found regional differences in both colony area and population density over time and between island groups. These results suggest metapopulation dynamics are occurring within the Haida Gwaii Ancient Murrelet population and that the observed increases in population size at Langara Island are not associated with definitive population recovery but factors outside of the presence/absence of introduced rats are limiting the recovery of this colony. However, this analysis does not consider any regions outside of the current McPherson Point colony at Langara Island, the only colony site that persisted while rats were present on the island. This study emphasizes the need of consistent long-term monitoring and the importance of considering population recovery in terms of metapopulation dynamics.

1.2 Introduction

Understanding both large and small –scale (i.e., local and whole population) spatiotemporal fluctuations of populations is an important topic in population biology (Tilman and Kareiva 1997). Annual fluctuations in local population size can be attributed to both environmental stochasticity and anthropogenic influences (e.g., habitat degradation, and introduced predators), while metapopulations enable the persistence of both a species when a local population is lost, and a local population through immigration (Levins 1970, Hanski and Simberloff 1997). Monitoring local populations is important when factors operating at the local (small) scale influence population dynamics and may benefit the metapopulation, and can be especially important when managing commercially important species by protecting specific local populations (e.g., Hu and Wroblewski 2009). However, understanding how factors operating at a larger metapopulation scale influence local populations is also of high conservation importance.

Many conservation biologists and managers have been attempting to restore island ecosystems by removing introduced species (Flint and Rehkemper 2002, Williams et al. 2003, Nogales et al. 2004, Carrion et al. 2007, Jones et al. 2008, Zino et al. 2008). Yet the time-scale associated with recovery and recolonization may be extended by long-lived species with low reproductive and recruitment rates, and high site fidelity, such as seabirds (Gaston 2004). To reduce these long recovery times, managers have used translocations, decoys, and playbacks to enhance natural recovery with many successes (Kress 1978,

1997, Parker et al. 2007). However, populations of non-threatened species are often over-looked and studies aimed at assessing natural recolonization are lacking, especially in relation to nocturnal species that are generally difficult to census.

When a local population is completely eradicated the chances of recolonization may be decreased and recovery times increased over those when a remnant population remains (Buxton 2010). Yet, measuring recovery of a remnant population can be difficult and ought to be judged in terms of the population dynamics of the entire metapopulation as the apparent success or failure of a restoration program may reflect factors operating at a larger scale. For example, recovery might be slow or non-existent if factors operating at a large spatial scale (e.g., climate events, oceanographic conditions) cause declines across the metapopulation. Furthermore, recovery of a highly mobile species could also reflect a redistribution of individuals across the metapopulation rather than an overall increase in metapopulation size.

Greater understanding of how metapopulation dynamics influence local populations and apparent recovery of restored islands would be achieved through a comparison of population dynamics on islands following conservation efforts with population dynamics on islands where introduced predators are present, or have been eradicated. The success of conservation efforts could be the end of population declines within a local population, where population dynamics return to match those of the metapopulation; or the end of population declines and a subsequent population increase resulting in an overall increase in

metapopulation size. However, the success must match the impact of the disturbance (e.g., introduced predators). For example, if one impacted local population resulted in metapopulation declines, recovery would be subsequent local- and metapopulation increases.

Environment Canada has been monitoring local populations of Ancient Murrelets (*Synthliboramphus antiquus*) within Haida Gwaii, British Columbia for over 30 years (with repeated visits to many colony sites), including populations impacted by introduced predators, populations recovering after predator eradiation, and those occurring at unimpacted sites. I used the Haida Gwaii metapopulation of Ancient Murrelets as a study population and investigated how this metapopulation changes through space and time and specifically whether recovery is occurring at Langara Island, where introduced rats decimated what was historically the largest Ancient Murrelet breeding colony in the world (Bertram and Nagorsen 1995), by comparing regional changes within local populations (i.e., 10 ha regions within each island) between 1981-2005. I used the classic definition of a metapopulation; a population of populations connected by migration (Levins 1970, Hanski and Simberloff 1997) and local populations as island colony sites. Where movement among Ancient Murrelet colonies is known to occur within Haida Gwaii but also within the entire global population (Gaston and Adkins 1998, Pearce et al. 2002). It is likely that one metapopulation of Ancient Murrelets occurs globally, but data concerning population trends are only available for the Haida Gwaii population, thus, I have limited this analysis to the Haida Gwaii population and describe this as the Haida Gwaii metapopulation.

I hypothesized that Ancient Murrelet populations are dynamic and differences occur within each local population, while temporal changes in colony area and population density are different at Langara Island than non-impacted islands in Haida Gwaii because introduced rats (*Rattus* spp.) were the major driver of change at Langara Island. I predicted if population threats are large-scale (e.g., climate), than population dynamics at Langara Island would remain the same in the presence/absence of introduced rats; while if population threats are many (e.g., climatic and rats), than population dynamics at Langara Island may converge with those at other sites, even though rat removal may be insufficient to alter population declines associated with other factors; but if rats are the only threat at Langara Island, than their removal would allow a redistribution of Ancient Murrelets within Haida Gwaii and faster growth at Langara Island.

1.3 Methods

1.3.1 Colony surveys

Line transects from six pristine islands (i.e., islands without introduced predators; East Copper, Frederick, George, Helgesen, Lihou, and Little Helgesen islands) and one impacted island (Langara Island where introduced Norway rats *Rattus norvegicus* were eradicated in 1997) were completed during 1980-2005 by the Canadian Wildlife Service (CWS) branch of Environment Canada, where quadrats at predefined distances along transects were investigated for evidence of breeding Ancient Murrelets (Rodway et al. 1988, 1994). The years surveyed, number of transects, distance between transects, quadrat size, and distances

between quadrats varied among islands and are listed in Appendix B, while the specific methodology of counting burrows and determining occupancy remained fixed during all years surveyed (Rodway et al. 1988, 1994). I analyzed the quadrat data for all seven islands and estimated Ancient Murrelet colony area in hectares (ha), location, population size (number of breeding pairs), and change between years using inverse distance weighted interpolations in ArcGIS 9.3 (ESRI, Redlands, CA), using methods outlined in Major and Chubaty (Unpublished data).

1.3.2 Interpolations

A total of 20 interpolations were completed, one for each year and island surveyed, where I divided each study island into 10 ha landscapes (hereafter referred to as regions). Because of the differences in quadrat size among islands, I used the density of burrows (burrows/m^2) as the interpolated metric with a cell size of 25 m^2 (this includes all burrows discovered, those empty and occupied). The results of the interpolation were then used to compute the total area (in hectares) of the colony and the population size (number of breeding pairs).

Regions covered all potentially occupied areas and were distributed as evenly as possible over each island. Using the spatial analyst mask function, I obtained an estimate of the total area, the area occupied, and population size of Ancient Murrelets within each region for each time period. On large islands, such as Frederick and Langara, a polygon was first drawn to encompass the total area of a potential colony; from the vegetation edge to approximately 400 m inland

(Figure 1.1 a & b), as this is the breeding extent of Ancient Murrelets (Sealy

1976, Vermeer and Lemon 1986), and was used as a spatial analyst mask for

interpolations. I then applied the regions as a spatial analyst mask to obtain

estimates of colony area and population density within the potential colony area

for each region. In addition, Langara and Helgesen islands had different areas

surveyed among years. To be consistent, only areas surveyed in all years were

used in the interpolations, resulting in colony area and population size estimates

for a portion of the island. At Langara Island the portion of the island used was

436 hectares located at the northwestern point and at Helgesen Island the

portion of the island used excludes a large section in the north (Figure 1.1 a & c).

Additionally, when the number of transects surveyed changed among years, I

used only those transects surveyed from similar locations in every year, resulting

in colony area and population size estimates from the lowest number of transects

surveyed among years. This means that I used the least amount of data

available and therefore the results are less accurate estimates, but conclusions

are not biased towards increased survey efforts. I grouped the islands and years

into categories depending upon 1) their location and proximity to other islands in

the analysis (North =Frederick; Southeast =East Copper & George; Southwest

=Lihou, Helgesen & Little Helgesen; and Impacted =Langara); and 2) the time

period surveys were completed (1=1980-1988; 2=1989-1997; and 3=1998-2005).

Langara Island was the only island to have more than one survey completed

within each time period. Although I present all of this data in a summary table, I

used only one survey for each time period in the analyses, and these were the

years that corresponded best with those surveyed at the other islands (i.e., 1981, 1997, and 2004).

1.3.3 Statistical analysis

To evaluate recovery at Langara Island and regional changes among local Ancient Murrelet populations in Haida Gwaii, I considered six *a priori* candidate models, in two analyses of colony area and population density, composed of biologically plausible combinations of four explanatory variables of interest (time period, island nested within island group, the interaction between time period and island group, and region). In all analyses, I used a mixed general linear model with a restricted maximum likelihood estimation method using PASW 18 (SPSS Inc., Chicago, IL), where island was nested within group and was included as a fixed factor, and region was included in all models as a random factor. Both colony area and population density were standardized to account for large differences in island size. Colony area was therefore analyzed as the proportion of area occupied by Ancient Murrelets (area occupied/total area), and population size was analyzed as density (burrows/m^2). I used an information theoretic approach where models were ranked using Akaike's information criterion for small sample sizes (AIC$_c$), and AIC$_c$ weights (w_i) were used to evaluate model likelihood (Burnham and Anderson 2002). When the best supported model received a weight less than 0.9, I used model averaging to generate parameter estimates and unconditional standard errors, which were used with parameter likelihoods to draw inference from the data set (Johnson and Omland 2004).

1.4 Results

1.4.1 Spatiotemporal changes in colony area and population density

During 1980-2005, 20 surveys were completed among seven islands resulting in a total of 1856 quadrats, or 51,488 m^2 surveyed. A total of 792 quadrats (43% of all quadrats surveyed) contained at least one active Ancient Murrelet burrow; of these occupied quadrats the mean density of burrows/m^2 ($\pm$ 95% confidence intervals) was 0.11 ($\pm$ 0.01). I delineated a total of 154 regions; all regions contained data for time period 1, 146 for time period 2, and 144 for time period 3. In general, I found a large amount of change in colony and population size among islands over time (Table 1.1) and a large amount of variation in the proportion of regions with no, positive, and negative change among island groups within the three time period comparisons (Table 1.2, Figure 1.2). However, proportional changes between regions suggested an increase between time periods 1 and 2 and a decrease between time periods 2 and 3 for all island groups except the impacted group (Langara Island) where a slight decrease was noted between time periods 1 and 2 and a possible slight increase between time periods 2 and 3 for colony area. For population density, an increase between time periods 1 and 2, and a decrease between time periods 2 and 3 was noted for all island groups except southwest where a slight decrease was noted between time periods 1 and 2 and an increase between time periods 2 and 3 (Table 1.2).

Statistical analysis revealed differences in Ancient Murrelet colony area and population density between time periods and this difference was not

consistent between island groups. The best-supported model for both Ancient

Murrelet colony area and population density included the terms time and

time*island group (Table 1.3 and 1.5). These top models received 11 times more

support than the second best supported models, which included the nested term

island(group) for colony area (Table 1.3); and the term time period for population

density (Table 1.5). For colony area, the term time period received 92% of the

total weight among models and revealed the highest colony area occurred in time

period 2, while the term time*island group received 91% of the total weight

among models and revealed differences in colony area among island groups

over time (Table 1.4). For population density, the term time period received

100% of the total weight among models and revealed the highest population

density occurred in time period 2, while the term time*island group received 91%

of the total weight among models and revealed variability between population

density over time among island groups (Table 1.6).

1.5 Discussion

Ancient Murrelets do not show philopatry and are believed to prospect

widely when making settlement decisions (Gaston and Adkins 1998, Pearce et

al. 2002). Thus, a dramatic increase in population size at any colony location

would indicate increased recruitment to that site. Generally, seabirds are

relatively long-lived species with low reproductive output (Lack 1968, Gaston

2004), as a result Ancient Murrelets are not be expected to recover quickly from

anthropogenic population decreases. However, if Ancient Murrelets respond to a

decrease in changes in perceived habitat quality by abandoning low-quality sites

(such as rat infested islands) and moving to high-quality sites, one would expect that when high-quality habitat becomes available (through rat eradication, for example) individuals should return to that site. Thus, the overall metapopulation size may not change despite changes in local populations. Gaston et al. (2009) found that Ancient Murrelet populations in Haida Gwaii have increased in all monitored colonies except those impacted by introduced predators. These data suggest there may be movement between colony sites and higher recruitment at non-impacted sites, but not necessarily an increase in the overall metapopulation size. My data support this assertion as I found that all island groups except one (impacted for colony area and southwest for population density) showed similar trends in colony area and population density (i.e., an increase between time periods 1 and 2 and a decrease between time periods 2 and 3).

Furthermore, my analysis examining spatial changes in colony area and population density among island regions, found variation between the interaction of time period and island group for both colony area and population density. Overall, this analysis suggests that colony area and population density were highest in the second time period and that the impacted island group (i.e., Langara) had consistently lower colony areas and population density than all other island groups, even after introduced rats were eradicated. This suggests that individuals may have emigrated from this colony, possibly increasing density at pristine colonies, revealing support for metapopulation dynamics within the Haida Gwaii Ancient Murrelet population.

The only area with continuous monitoring between 1981-2004 was the 436-hectare area located along the northwestern shore of Langara Island (i.e., McPherson Point). This area is also the only location within which Ancient Murrelets remained active throughout rat presence. There are two possible explanations for the observed population dynamics at McPherson Point. First, the observed increase in Ancient Murrelet population between 1981 and 1993 may be due to individuals emigrating from other areas of Langara Island where rat predation was stronger and establishing at McPherson Point masking rat impacts at this site. The subsequent decrease in population size in 1999 could then be due to emigration from McPherson Point to other islands within Haida Gwaii, as McPherson Point became the focus of rat predation until their eradication in 1997. After rats were eradicated in 1997, this remnant colony began attracting new individuals leading to the observed population increase between 1999 and 2004. A second possible explanation is that for an unknown reason McPherson Point was not exposed to a large amount of rat predation, introduced rats therefore did not impact this local population and population dynamics followed those of the larger metapopulation. Although this second explanation seems unlikely, the fact that this remnant population was the only one to survive rat presence on Langara Island does suggest something unique to this site. Therefore, although this analysis does not suggest recovery at McPherson Point, interpretations could be that recovery is occurring and will be apparent with time, or that because rats were never an issue at this location, recovery is not occurring because a disturbance never occurred. Outside of

McPherson Point, surveys have not been completed since 1981, thus conclusions concerning the larger-scale dynamics and possible recovery/recolonization cannot be drawn. However, some circumstantial information suggests recolonzations along the outside boarders of McPherson Point (HLM personal observation).

Contrary to my results, Regehr et al. (2007) found that Ancient Murrelet colony area and population size at McPherson Point had more than doubled since rat eradication, and these increases are the result of recovery. However, data were not standardized between years, i.e., the number of transects and quadrat data used in the estimates of colony and population size were not kept consistent, resulting in some years with much more data than others. As changes in the frequency, intensity, and timing of surveys can lead to biases in data, it is important to keep survey effort and parameters consistent over time (Laudenslayer 1988, Aguirre and Vergara 2009). I do acknowledge that the methods I employed use the least amount of data available and likely result in the least accurate estimates. However, between-year comparisons are not valid when data accuracy differs. Thus, analyzing trends using the less accurate data, results in conclusions that are not biased towards increased survey effort.

Furthermore, year to year variation in the proportion of birds breeding and the success of those breeders may lead to some of the within colony differences observed in this analysis (Wrege et al. 2006). For example, it has been found that large-scale climate indices (e.g., North Pacific Oscillation, Pacific Decadal Oscillation, etc.) are linked with seabird demographic rates (Kitaysky and

Golubova 2000, Jones et al. 2007, Byrd et al. 2008, Hipfner 2008, Sandvik et al. 2008). Similarly, Ancient Murrelet breeding success and the regression of chick departure mass on date were correlated with May Sea Surface Temperature (Gaston and Smith 2001). If climate also affects the proportion of birds breeding, the anomalous atmospheric blocking event of 2005 could be related to the perceived population decline at Frederick Island in that year, as it was related to unprecedented reproductive failures of Cassin's Auklets (*Ptychoramphus aleuticus*) in both California and British Columbia (Sydeman et al. 2006). If this is the case, the decline is not a decline in total population size but likely an indication of poor reproductive effort in that year. Contrary to this hypothesis, Ancient Murrelet chick departures at East Limestone Island in 2005 were not drastically lower than other years, suggesting the 2005 atmospheric blocking did not have an impact in southern Haida Gwaii (Rock 2005, Pattison and Brown 2009). This emphasizes the need for continued monitoring of these colonies in order to understand true population trends and whether this large colony has undergone a drastic population decline.

Overall this analysis shows spatiotemporal variability and the occurrence of metapopulation dynamics in the Haida Gwaii Ancient Murrelet population. Where the observed increases in population size at Langara Island are not different than any other island so that the eradication of introduced rats has stopped the decline of Ancient Murrelets at Langara Island but was not sufficient to allow faster growth at Langara (i.e., definitive recovery), suggesting population threats are many and factors outside of introduced predators are limiting the

recovery of Ancient Murrelets at Langara Island. Definitive evidence of

population recovery would be the recolonization of abandoned colony sites and

the resulting increase in the local Langara Island population size and the overall

Haida Gwaii metapopulation. My results emphasize the need to consistently

monitor populations over the long-term. Changing the number of transects and

quadrats surveyed between years results in inconsistent data and potentially

limits the amount of inference that can be drawn. Expanding the transects run at

Langara Island to encompass all those surveyed in 1981 (the last year surveys

were run completely around the island) will benefit the overall projections of this

island, as there is circumstantial evidence of recolonization at some sites outside

of McPherson Point (HLM personal observation).

Table 1.1 Summary of the islands surveyed and interpolated estimates of colony and population size.

Island	Year	Colony Size in hectares	Population Size # breeding pairs	Total Number of Burrows Found per m^2
East Copper	1985	20.61	3627	1.20
	2003	22.09	5225	1.49
Frederick	1980	217.40	82621	14.84
	1998	239.31	96192	14.24
	2005	222.34	39463	10.28
George	1985	30.72	8527	3.18
	1996	31.19	16236	4.37
Helgesen	1986	14.24	4533	3.04
	1993	20.48	2498	1.68
	2004	17.82	6912	3.80
Langara	1981	279.03	41614	2.36
	1988	63.62	19427	4.20
	1993	230.48	52369	4.04
	1999	184.48	24842	1.84
	2004	179.38	35155	1.64
Lihou	1986	31.41	5464	2.21
	1993	45.32	19359	7.40
	2004	35.06	11428	3.08
Little Helgesen	1986	1.32	462	0.89
	2004	0.93	90	0.16

Table 1.2 Summary of the total proportion of regions with no changes (NC), increases (↑), and decreases (↓) in colony area and population density among four island groups (North –Frederick, Southeast –East Copper and George, Southwest – Helgesen, Little Helgesen, and Lihou, and Impacted –Langara) in Haida Gwaii between time periods 1 (1980-1988) and 2 (1989-1997); 2 (1989-1997) and 3 (1998-2005); and 1 (1980-1988) and 3 (1998-2005. The time period 2-3 comparison corresponds with rat absence at impacted site Langara Island.

Time Periods	Island Group	Trend					
		Colony Size			Population Size		
		NC	↑	↓	NC	↑	↓
1 (1980-1988) – 2 (1989-1997)	[a]North	0.00	0.59	0.41	0.00	0.69	0.31
	Southeast	0.14	0.79	0.07	0.00	1.00	0.00
	Southwest	0.13	0.56	0.31	0.00	0.44	0.56
	Impacted	0.42	0.18	0.40	0.26	0.43	0.31
2 (1989-1997) – 3 (1998-2005)	[a]North	0.06	0.37	0.57	0.00	0.10	0.90
	Southeast	0.07	0.21	0.72	0.00	0.21	0.79
	Southwest	0.00	0.33	0.67	0.00	1.00	0.00
	Impacted	0.60	0.08	0.32	0.45	0.03	0.52
1 (1980-1988) – 3 (1998-2005)	North	0.00	0.59	0.41	0.00	0.24	0.76
	Southeast	0.09	0.59	0.32	0.00	0.36	0.64
	Southwest	0.00	0.67	0.33	0.00	1.00	0.00
	Impacted	0.52	0.05	0.43	0.36	0.32	0.32

[a] This trend uses data for time period 2 from 1980-1998

Table 1.3 Candidate model set describing changes in Ancient Murrelet colony area estimates in relation to four island groups (included as the nested fixed effect: Island(Group)) around Haida Gwaii and among three time intervals (Time), where region (Region) was included in all models as a random factor (n=444).

Candidate Model	K	AIC_c	ΔAIC_c	w_i
Time+Time*Group	14	303.86	0.00	0.90
Island(Group)	9	308.77	4.91	0.08
Time+Island(Group)	11	312.33	8.47	0.01
Time+Island(Group)+Time*Group	17	314.15	10.29	0.01
Null	3	331.26	27.40	0.00
Time	5	334.19	30.33	0.00

Table 1.4 Summed Akaike weights (w*i*), weighted parameter estimates, and unconditional standard errors (SE*u*) of weighted parameter estimates calculated from all candidate models describing changes in Ancient Murrelet colony area.

Parameter[a]	Summed w_i	Weighted Parameter Estimate	SE$_u$
Intercept	1.00	0.78	0.09
Langara (Impacted)	0.10	0.00	0.06
Frederick (North)	0.10	0.01	0.03
East Copper (SE)	0.10	0.01	0.04
George (SE)	0.10	0.02	0.05
Helgesen (SW)	0.10	0.01	0.03
Lihou (SW)	0.10	0.00	0.02
Time (1980-1988)	0.92	-0.08	0.08
Time (1989-1997)	0.92	0.15	0.08
Time (1980-1988)*Impacted	0.91	-0.65	0.17
Time (1989-1997)*Impacted	0.91	-0.41	0.13
Time (1998-2005)*Impacted	0.91	-0.35	0.12
Time (1980-1988)*North	0.91	0.12	0.10
Time (1989-1997)*North	0.91	-0.04	0.09
Time (1998-2005)*North	0.91	0.06	0.09
Time (1980-1988)*SE	0.91	0.23	0.13
Time (1989-1997)*SE	0.91	0.02	0.13
Time (1998-2005)*SE	0.91	0.19	0.15

[a] We set categorical variables Little Helgesen (SW), Time (1998-2005), Time (1980-1988)*SW, Time (1989-1997)*SW, and Time (1998-2005)*SW to zero in all models.

Table 1.5 Candidate model set describing changes in Ancient Murrelet population density estimates in relation to four island groups (included as the nested fixed effect: Island(Group)) around Haida Gwaii and among three time intervals (Time), where region (Region) was included in all models as a random factor (n=444).

Candidate Model	K	AIC_c	ΔAIC_c	w_i
Time+Time*Group	14	-2393.09	0.00	0.91
Time	5	-2387.48	5.61	0.05
Time+Island(Group)	11	-2386.71	6.38	0.04
Island(Group)	9	-2369.91	23.18	0.00
Time+Island(Group)+Time*Group	17	-2369.11	23.98	0.00
Null	3	-2368.20	24.98	0.00

Table 1.6 Summed Akaike weights (w_i), weighted parameter estimates, and unconditional standard errors (SE_u) of weighted parameter estimates calculated from all candidate models describing changes in Ancient Murrelet population density.

Parameter[a]	Summed w_i	Weighted Parameter Estimate	SE_u
Intercept	1.00	0.03	0.00
Langara (Impacted)	0.04	0.00	0.00
Frederick (North)	0.04	0.00	0.00
East Copper (SE)	0.04	0.00	0.00
George (SE)	0.04	0.00	0.00
Helgesen (SW)	0.04	0.00	0.00
Lihou (SW)	0.04	0.00	0.00
Time (1980-1988)	1.00	-0.01	0.00
Time (1989-1997)	1.00	0.00	0.00
Time (1980-1988)*Impacted	0.91	-0.01	0.00
Time (1989-1997)*Impacted	0.91	-0.16	0.03
Time (1998-2005)*Impacted	0.91	-0.02	0.01
Time (1980-1988)*North	0.91	0.01	0.00
Time (1989-1997)*North	0.91	0.00	0.00
Time (1998-2005)*North	0.91	-0.01	0.01
Time (1980-1988)*SE	0.91	0.01	0.01
Time (1989-1997)*SE	0.91	0.02	0.01
Time (1998-2005)*SE	0.91	0.00	0.01

[a] We set categorical variables Little Helgesen (SW), Time (1998-2005), Time (1980-1988)*SW, Time (1989-1997)*SW, and Time (1998-2005)*SW to zero in all models.
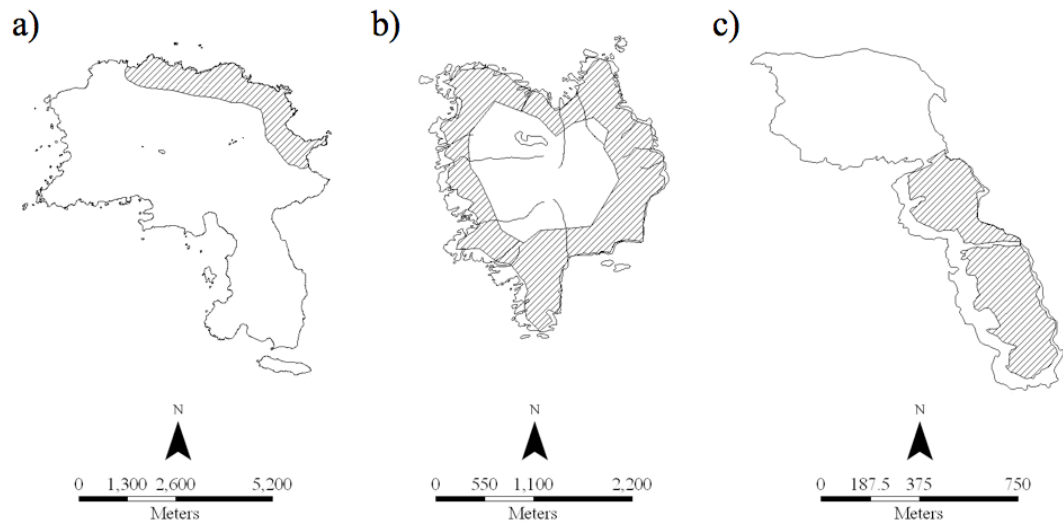
Figure 1.1 Polygon areas (hatched) used as spatial analyst masks during interpolations to estimate colony and population size at a) Langara, b) Frederick, and c) Helgesen islands.
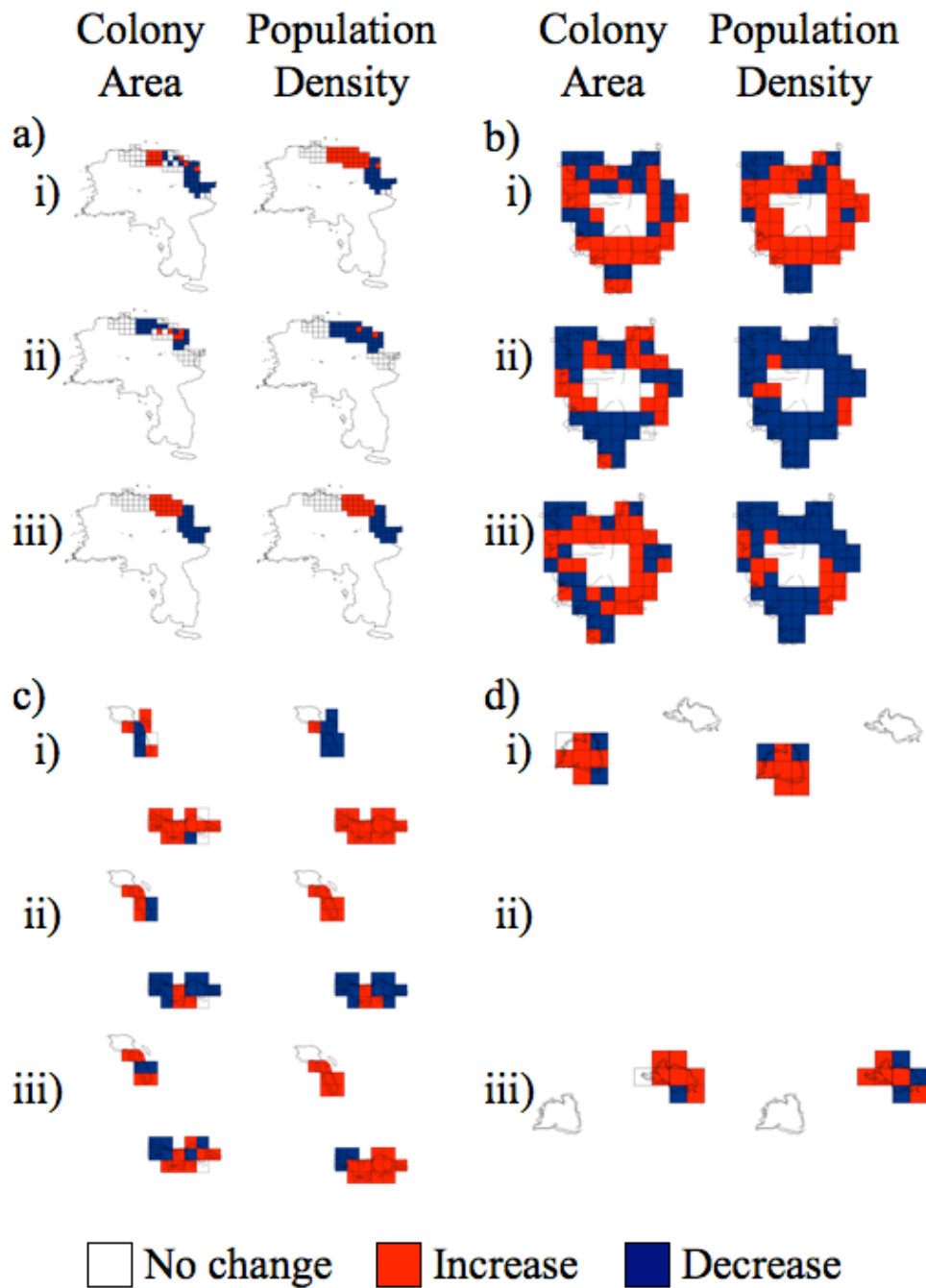
Figure 1.2 Summary and comparison of change per 10 ha region in occupied colony area and population density among seven islands split into four island groups: a) Impacted (Langara Island); b) North (Frederick Island); c) Southwest (Helgesen, Little Helgesen, and Lihou Islands); and d) Southeast (East Copper and George Islands) and three time periods: i) 1980-1988 and 1989-1997; ii) 1989-1997 and 1998-2005; and iii) 1980-1988 and 1998-2005; all regions are 10 ha.

CHAPTER 2: HABITAT SUITABILITY AS A POTENTIAL FACTOR LIMITING THE RECOVERY OF A POPULATION OF NOCTURNAL SEABIRDS

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2.1 Abstract

Understanding how and why animals choose specific habitat is of the utmost importance in developing effective conservation plans. Programs to eradicate introduced predators from breeding colonies are widely employed to restore seabird populations, yet sometimes result in little or no recovery. Rats (*Rattus* spp.) were removed from Langara Island, British Columbia, in the mid-1990s to restore breeding habitat for Ancient Murrelets (*Synthliboramphus antiquus*) at what was at one time the species' largest breeding colony. Fifteen years later, the vast majority of formerly occupied habitat remains unused, and the population has been slow to recover. We asked whether this could be due to a change in habitat resulting in a lack of suitable habitat outside the currently occupied area. To answer this question, we 1) quantified Ancient Murrelet habitat associations on 12 islands free of introduced predators and 2) assessed how changes in habitat at Langara Island over 26 years (1981-2007) might affect their expected recovery distribution. Using an information theoretic approach, we found that Ancient Murrelets breeding in Haida Gwaii exhibit a high degree of flexibility in their use of available breeding habitats, as none of a suite of six variables previously predicted to influence breeding distribution had strong effects. In addition, we did not find any changes in available habitat at Langara Island between 1981 and 2007. Given these results we conclude that recovery of Ancient Murrelets at Langara Island is unlikely to be limited by habitat; settlement decisions may instead be based on the presence of conspecifics, rather than physical habitat. We propose artificial attraction as a method to speed recovery at Langara Island.

2.2 Introduction

Understanding how and why animals choose different habitats is a necessary step to preserve and manage populations (Manly et al. 1993). In many theoretical studies, habitat or resource selection is addressed in terms of Allee effects, settlement costs, and ideal distributions (Brown 1969, Fretwell and Lucas 1970, Pulliam and Danielson 1991, Greene and Stamps 2001), all of which assume that individuals select the highest quality habitat available. How individuals, especially those that are young and inexperienced, recognize high quality habitat has been the focus of much research (Parejo et al. 2006, Betts et al. 2008, Harrison et al. 2009).

Understanding how individuals assess potential breeding sites is vitally important, as recruitment requires that young individuals (i.e., prospectors) decide to settle in that location. The introductions of non-native species to islands have caused declines and extirpations of many native populations, altered the flow of nutrients from sea to land and changed vegetative structure (Martin and Joron 2003, Croll et al. 2005, Fukami et al. 2006, Grant-Hoffman et al. 2009). Populations of burrow-nesting seabirds, which are mainly species with high adult survival and low fecundity (Weimerskirch 2002, Gaston 2004) have been heavily impacted (Harris 1970, Bertram 1995, McChesney and Tershy 1998). Yet, while sometimes effective (Williams et al. 2003, Whitworth et al. 2005, Samways et al. 2010), the removal of invasive mammals from seabird colonies does not always result in recovery (Gaze 2000, Ratcliffe et al. 2009). Over the past 30 years there have been many successful assisted-recovery

programs (Kress 1978, 1997, Miskelly and Taylor 2004, Parker et al. 2007) but little attention has been paid to natural population recovery and the probability of its occurrence at restored sites.

Norway rats (*R. norvegicus*) introduced to Langara Island, Haida Gwaii, British Columbia (Figure 1), decimated one of the world's largest Ancient Murrelet breeding colonies (Bertram and Nagorsen 1995). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) lists Ancient Murrelets as a species of Special Concern. The eradication of rats from this island in the mid-1990s (Taylor et al. 2000) has resulted in a gradual increase in Ancient Murrelet burrow occupancy but only within a relatively small area, while large areas of the island remain unoccupied (Taylor et al. 2000, Regehr et al. 2007).

There are two possible explanations for this. First, some animals use conspecifics as cues to habitat selection (Stamps 1988, Doligez et al. 2003), which results in clustering of individuals within occupied habitat (Danchin and Wagner 1997, Greene and Stamps 2001). Experiments have shown that prospecting Ancient Murrelets are more likely to visit areas where conspecifics are vocalizing (Chapter 4) suggesting that public information is important when locating potential nesting sites. Therefore, abandoned colony sites may remain unused irrespective of habitat quality. On the other hand, rats have been shown to act as ecosystem engineers, altering the flow of nutrients through island systems and changing vegetative structure (Fukami et al. 2006, Grant-Hoffman et al. 2009). During the 20-30 years Ancient Murrelets have been absent from much of Langara Island, vegetation may have changed and there may be a lack

of high quality habitat outside of the currently occupied area. Thus, prospectors might avoid these peripheral areas until the core sites are saturated.

To test whether suitable habitat is limiting recovery at Langara Island we: 1) quantified Ancient Murrelet breeding habitat suitability on 12 islands in Haida Gwaii free of introduced predators and used this information to; 2) estimate the extent of suitable habitat at Langara Island; and 3) assess how changes in habitat at Langara Island over 26 years (1981-2007) might affect their expected recovery distribution. Taken together these analyses will allow managers to focus their efforts in the most cost-effective manner.

We used previously published information to develop a suite of variables that could predict habitat suitability for Ancient Murrelets based on unique features of their breeding biology; –notably their habit of precocial nest departure (Gaston 1992). Specifically, we hypothesized that Ancient Murrelets will nest where the easiest land-to-ocean travel route and cover from predation occur. If true, then we can predict that Ancient Murrelets will: 1) select habitat close to the sea, as this will minimize the travel distance for the two precocial chicks (Sealy 1976, Vermeer and Lemon 1986, Duncan and Gaston 1990); 2) nest on moderate slopes, as adults must accompany chicks further towards the sea on flat ground increasing their susceptibility to predators (Jones et al. 1987); 3) nest in locations with moderate canopy cover, balancing the antipredator benefits of increasing canopy cover against the increased danger in having more obstacles (i.e., branches and trunks) to avoid when flying into colony sites; 4) avoid dense shrub cover, as increasing shrub cover increases the risk of colliding with

obstacles while flying through the area to attend the colony; and 5) favour areas

with mossy ground over other ground cover types (Vermeer and Lemon 1986).

Finally, as there is an effect of island size, with larger islands in Haida Gwaii

having larger colonies (Gaston 1992), we predicted that Ancient Murrelets will: 6)

be more likely to breed on islands with greater shoreline perimeters.

2.3 Methods

2.3.1 Habitat surveys

Habitat on 12 introduced predator-free islands ranging in size between 7.3

and 1622.8 ha in Haida Gwaii was quantified by the Canadian Wildlife Service

(CWS) branch of Environment Canada using distance sampling with transects

and quadrats between 1980 and 1986 (Figure 2.1). Island area, number of

transects, transect lengths, distance between transects, quadrat size, and

distances between quadrats varied among islands and are listed in Appendix C,

while specific details of sampling methods are available elsewhere (Rodway et

al. 1988, 1990, 1994). Within each quadrat, measures of habitat (including

slope, ground cover species, and shrub and canopy cover percent) were noted.

For this analysis we simplified the habitat data to reflect dominant ground cover

species (i.e., species with >50% cover and classified them as either: moss,

grass, or other), and percents total shrub and canopy cover. Distance to nearest

shoreline was calculated using a map with plotted transect lines, while shoreline

perimeter was estimated using a Geographic Information System (GIS), where

shoreline was modelled using Terrain Resource Information Management (TRIM

– 1:20,000) digital data set, which delineates coastal island boundaries as "the

apparent high water mark", and was digitized from ortho-photographs.

Perimeters of the study islands were then calculated in GIS using the Universal

Transverse Mercator (UTM) projection - Zones 8 and 9 based on the 1983 North

American Datum.

Presence of breeding birds within each quadrat surveyed was based on

the presence of adults, eggs, hatched eggshells, eggshell membranes, and/or

chicks in burrows. All burrows found within a quadrat were searched by hand

and the contents noted, including bird sign at the entrance (i.e., worn tunnels,

feathers, and droppings). We controlled for differences in quadrat size by

assigning each quadrat as either occupied by Ancient Murrelets or not, as

opposed to using the number of occupied burrows within each quadrat.

Habitat surveys at Langara Island were conducted in 1981 by CWS

personnel using the same methods (Rodway et al. 1994), we repeated these

surveys and quantified habitat along 28 transects, excluding those on the

northwestern coast, which was inaccessible, during May and June 2007. For

consistency between years we did not include the 1981 transect surveys located

in this northwestern region in this analysis. Specific details concerning transect

and quadrat data are listed in Appendix C.

2.3.2 Statistical analysis

To test Ancient Murrelet habitat suitability and habitat change at Langara

Island between 1981 and 2007, we used an information theoretic approach

where models were ranked using Akaike's information criterion for small sample

sizes correcting for overdispersion by including an estimate of model deviance

(c-hat=model deviance/df) for the global model, and QAIC$_c$ weights (w$_i$) were used to evaluate model likelihood (Burnham and Anderson 2002). When the best supported model received a weight less than 0.9 we used model averaging to generate parameter estimates and unconditional standard errors, which were used with parameter likelihoods to draw inference from our data set (Johnson and Omland 2004). We used a repeated measures logistic regression with a maximum pseudo-likelihood fitting method (allowing for inter-model comparisons), a binomial distribution, and a log link function in SAS 9.1 (proc GLIMMIX; SAS Institute, Cary, NC) for both analyses, where quadrat was nested within transect and included as a random factor in all models, including the null.

We considered 70 *a priori* candidate models composed of biologically plausible combinations of six explanatory variables of interest (dominant ground cover, percent shrub cover, percent canopy cover, slope, shoreline perimeter, and distance to nearest shore) including a null model to assess Ancient Murrelet habitat suitability. We then considered 10 *a priori* candidate models composed of biological plausible combinations of three explanatory variables of interest (dominant ground cover, percent shrub cover, and percent canopy cover) including a null model to assess change in habitat at Langara Island between 1981 and 2007. Dominant ground cover, shrub cover, and canopy cover were included in this analysis while all others were excluded (i.e., slope, distance to nearest shoreline, and shoreline perimeter) as they are the only habitat variables measured that could change with time.

2.4 Results

2.4.1 Habitat suitability on 12 introduced predator-free islands

During 1980-1986, 1118 quadrats were surveyed along 121 transects on 12 islands free of introduced predators. Quadrats ranged in size from 25-49 m^2 for a total of 45,854 m^2 surveyed, of which 18% (8,463 m^2) was occupied by Ancient Murrelets. Our analysis did not reveal selection for any of the habitat variables used in this analysis: the top-ranked model was the null model. This model received 1.53 times more support than the second ranked model, which included the term slope*slope^2 (Table 2.1, Figure 2.2). Further, the parameter estimate and standard error for the term slope*slope^2 (-4.77e-7 ± 2.34e-6) suggests that Ancient Murrelet habitat suitability decreases with increasing slope, but the estimate is very small and bounds zero, suggesting this effect is weak.

2.4.2 Change in habitat on Langara Island

Between 1981 and 2007, 160 (1981) and 134 (2007) quadrats were surveyed along 58 (29 in each year) transects on Langara Island. All quadrats were 25 m^2 in area for a total of 4,000 m^2 and 3,350 m^2 surveyed in 1981 and 2007. No differences in habitat cover of any type were noted between 1981 and 2007 as the null model was the best supported model in the candidate set receiving three times more support than the second best supported model which included the term canopy cover (Table 2.2, Figure 2.3). The parameter estimate and standard error for the term canopy cover (3.33e-4 ± 1.24e-3) suggests that canopy cover increased between 1981 and 2007, but the estimate is very small and bounds zero, suggesting this effect is weak.

Discussion

We found that Ancient Murrelets exhibit considerable flexibility in their choice of nesting habitat, as none of the habitat variables we tested appeared to strongly influenced habitat suitability. Given this flexibility and lack of long-term change in habitat at Langara Island, we conclude that habitat is not likely to be limiting recovery and that breeding site selection is based upon factors other than physical habitat features, such as social cues. Our results run counter to published accounts suggesting that Ancient Murrelets preferred to nest in mossy habitat between 40-450 m inland when Cassin's Auklets (*Ptychoramphus aleuticus*) were present (Vermeer and Lemon 1986). However, the suggestion that Ancient Murrelets will nest closer to shore in the absence of Cassin's Auklets (Vermeer and Lemon 1986) further hints at flexibility in habitat use.

In comparison with other *Synthliboramphus* species, Ancient Murrelets have a relatively vast geographical breeding distribution, ranging from Haida Gwaii through the Aleutian chain and into Southeast Asia (Gaston 1992, 1994). Their populations on three introduced predator-free islands in Haida Gwaii (Frederick, East Copper, and George islands) are estimated to be stable or increasing (Regehr et al. 2007, Gaston et al. 2009), and among pelagic seabirds, Ancient Murrelets have relatively low adult survival and high reproductive output (Gaston 1990). Given all of this, their proximity to a stable/increasing source population (Frederick Island), the presence of a residual colony, a presumed stable prey base, and apparent high inter-colony dispersal (Gaston 1990, 1992, Pearce et al. 2002), Ancient Murrelet recovery at Langara Island is highly

plausible. The observed flexibility in suitable habitat types for nesting only lends more support to the notion that Ancient Murrelets are highly likely to recover and recolonize abandoned areas. Therefore, management actions to restore Ancient Murrelets at Langara Island are expected to be highly effective.

In addition to population trends, recolonization may depend upon behavioural aspects relating to breeding site selection. Ancient Murrelets congregate at offshore 'gathering grounds' before sunset, flying into colony sites one to two hours after sunset (Gaston 1992). Prospectors may cue into these gathering grounds, using them as a first indication to the locations of suitable breeding sites, as other species use similar congregations as a compass when searching for foraging patches (Weimerskirch et al. 2010). Distance to the nearest gathering ground therefore, may be an important factor related to prospecting and later settlement decisions. Furthermore, there is evidence that Ancient Murrelets in Haida Gwaii do not necessarily dig burrows but rather compact the ground (Gaston 1992). We did not have access to data on soil properties, but believe this could be an important factor related to breeding site selection and merits further study. Another variable we could not measure but merits further study were differences in reproductive success among different habitat types. Our inference is limited to quantifying what habitat Ancient Murrelets utilize but does not investigate whether some individuals are present in inferior habitats where reproductive success is low.

Campomizzi et al. (2008) assert that models of habitat selection should account for the use of conspecific cues in breeding site selection. In this context,

public information is a beneficial aspect of sociality and obtaining information from others allows an individual to gain and use this information, increasing their fitness (Valone 2007). Ancient Murrelet prospectors are highly attracted to the vocalizations of conspecifics, and may use vocalizations as a locator cue when searching for potential breeding colony sites (Chapter 4). Therefore the presence of conspecifics might outweigh the benefits of specific physical habitat types.

A fundamental question in ecology and wildlife population management is habitat preferences of animal species. Understanding why certain species select for a particular habitat and what fitness benefits that habitat conveys are important when evaluating species management plans and predicting recovery after large anthropogenic disturbances. Overall this study has shown that nocturnally breeding Ancient Murrelets do not select for any of the large-scale habitat features we tested and therefore display considerable flexibility in the habitats they can inhabit. In addition, Ancient Murrelet demography and local population trends suggest recovery is highly plausible. But, the lack of public information at abandoned colony sites suggests we can expect these sites to remain abandoned. Therefore, management actions could target artificial cues to induce recolonization and enhance the recovery of Ancient Murrelet populations.

Table 2.1 Top ten candidate models describing Ancient Murrelet presence at 12 islands without introduced predators located in Haida Gwaii, British Columbia in relation to distance to nearest shore (Sdist), slope (Slope*Slope^2), percent canopy cover (CC*CC^2), percent shrub cover (SC*SC^2), dominant ground cover (DGC – grass, moss and other), and shoreline perimeter (Shore; n=1118; c-hat=1.00).

Candidate Model	K	QAIC$_c$	$\triangle$QAIC$_c$	w$_i$
null	3	5566.45	0.00	0.55
Slope*Slope^2	4	5567.29	0.84	0.36
CC*CC^2	4	5571.69	5.23	0.04
Slope*Slope^2+CC*CC^2	5	5572.08	5.63	0.03
SC*SC^2	4	5576.20	9.75	0.00
Slope*Slope^2+SC*SC^2	5	5576.95	10.50	0.00
SC*SC^2+CC*CC^2	5	5580.35	13.89	0.00
SC*SC^2+CC*CC^2+SC*SC^2*CC*CC^2	6	5585.35	18.90	0.00
Sdist	4	5588.64	22.19	0.00
Sdist+ Slope*Slope^2	5	5592.89	26.43	0.00

Table 2.2 Candidate model set describing change in habitat at Langara Island between 1981 and 2007 in relation to percent canopy cover (CC), percent shrub cover (SC), and dominant ground cover (DGC – grass, moss and other; n=294; c-hat=0.48).

Candidate Model	K	$QAIC_c$	$\Delta QAIC_c$	w_i
null	3	2598.19	0.00	0.68
CC	4	2600.47	2.28	0.22
SC	4	2602.49	4.31	0.08
SC+CC	5	2605.58	7.40	0.02
SC+CC+SC*CC	6	2607.92	9.73	0.01
DGC	5	2612.98	14.79	0.00
DGC+SC	6	2615.11	16.92	0.00
DGC+CC	6	2615.33	17.15	0.00
DGC+SC+CC	7	2617.62	19.43	0.00
DGC+SC+CC+SC*CC	8	2620.48	22.30	0.00
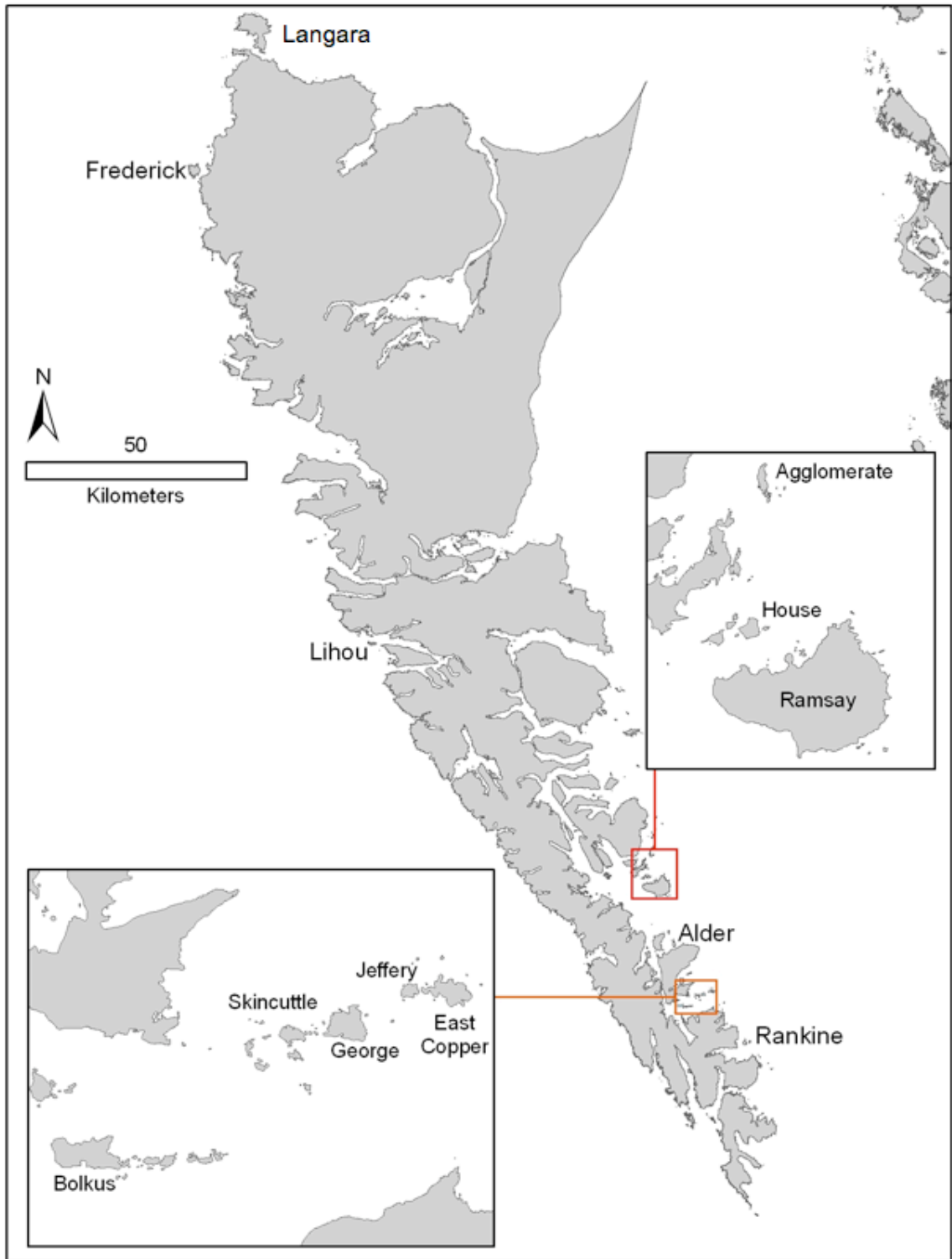
Figure 2.1 Map of Haida Gwaii showing locations of each of the 12 introduced predator-free islands used in this analysis and Langara Island.
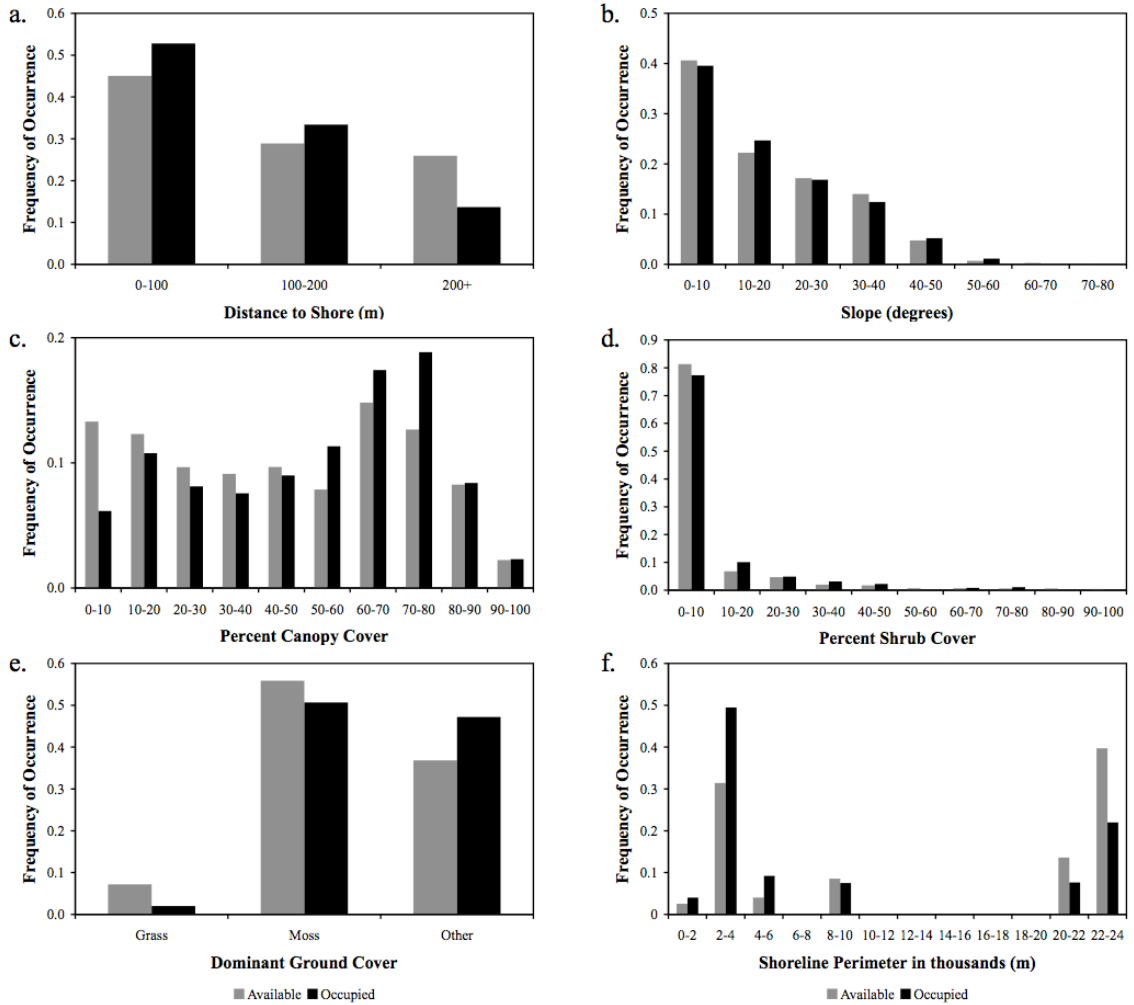
Figure 2.2 Ancient Murrelet use (black bars) and availability (grey bars) of a) distance to shore, b) slope, c) percent canopy cover, d) percent shrub cover, e) dominant ground cover, and f) shoreline perimeter at 12 introduced predator-free islands in Haida Gwaii, British Columbia.

55
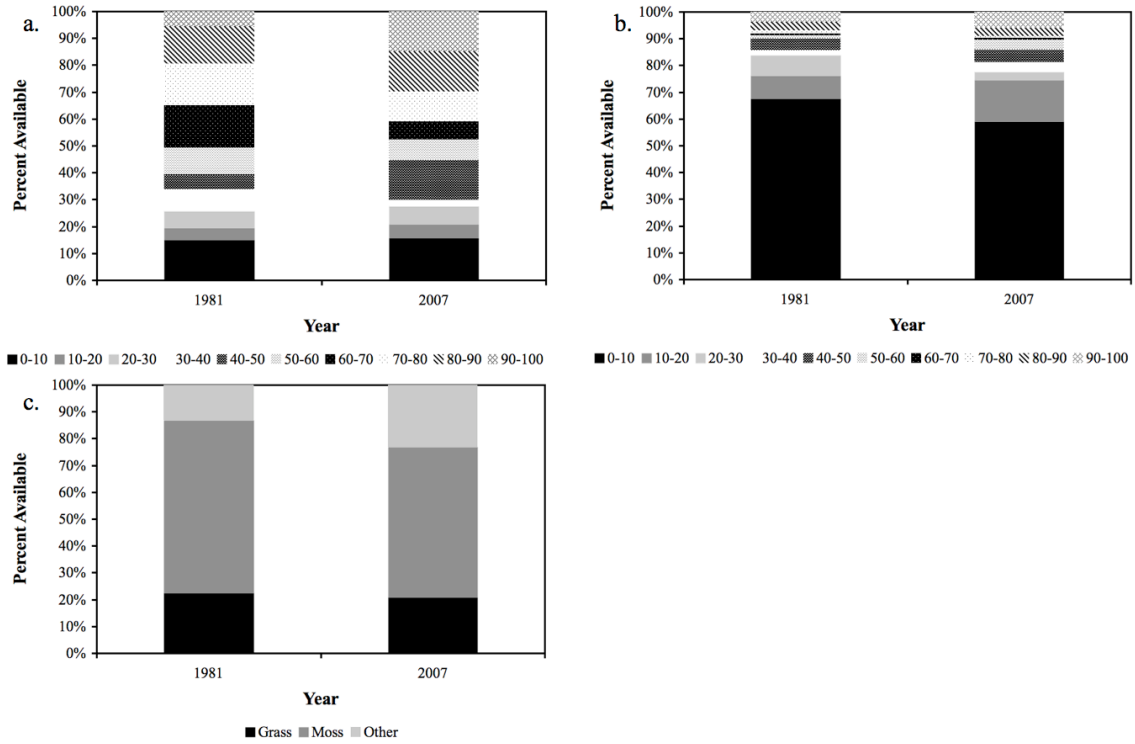
Figure 2.3 Summary of the percent available a) canopy cover, b) shrub cover, and c) dominant ground cover at Langara Island in 1981 and 2007.

CHAPTER 3: VARIABILITY IN COLONY ATTENDANCE DECISIONS BY A COLONIAL SEABIRD

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3.1 Abstract

Day-to-day decisions to attend and care for young by breeding individuals can be viewed as a trade-off between survival and current reproductive success. Pre-breeding prospecting individuals, make colony attendance decisions based on survival (i.e., overall lifetime reproductive success), where colony attendance may lead to a successful future-breeding attempt but death eliminates all offspring. Thus, prospectors have proportionally more to lose than breeders when attending colonies during risky environmental conditions and therefore should be more risk averse than breeders. Additionally, differences in habitat between colonies may lead to differences in mortality resulting in different attendance patterns. By comparing patterns of colony attendance in nocturnal burrow-nesting Ancient Murrelets (*Synthliboramphus antiquus*) between Haida Gwaii (forested colony site) and the Aleutian Islands (open, grassy colony site), we evaluated whether prospectors are more risk averse than breeders and whether colony attendance decisions change depending upon local physical habitat attributes. Using an information theoretic approach we found that in Haida Gwaii, breeder colony attendance was at least two times lower when wave heights were high and during very bright light conditions; prospector attendance was three times lower when waves were high and two times lower during very bright light conditions. In the Aleutian Islands, breeder colony attendance was five times lower during very bright light conditions; prospector attendance was over 34 times lower during the full moon than the new moon. Thus, differences in colony attendance decisions occurred between sites, but prospectors were not conclusively more risk averse than breeders.

3.2 Introduction

Trade-offs between reproductive investment and survival are central to theories of animal behaviour (Drent and Daan 1980, Stearns 1989). Most studies focus on when animals breed, how many offspring to produce, and how long to care for young (e.g., Blomquist 2009). The decision of whether or not to breed in a given year is argued to be a strategy to increase overall lifetime reproductive success (Schaffer 1974, Aebischer and Wanless 1992). Similarly, the daily decision to attend a colony may be fixed for breeders, who need to attend the colony to ensure their current reproductive effort is successful (Rice and Kenyon 1962, Weimerskirch 1998, Calvert and Robertson 2002); whereas prospectors (i.e., young individuals that have not bred and are searching for a nesting location and mate) can be more flexible in their colony attendance, exhibiting behaviours aimed at minimizing the risk of colony attendance (Watanuki 1986, Mougeot and Bretagnolle 2000). Thus, colony attendance by breeders can be argued as a trade-off between survival (i.e., overall lifetime reproductive success) and current reproductive success, where colony attendance and a successful breeding attempt increase overall lifetime fitness and death eliminates both current and future offspring. Prospecting individuals, on the other hand, make colony attendance decisions based on survival (i.e., overall lifetime reproductive success), where colony attendance may lead to a successful future-breeding attempt but death eliminates all offspring.

Many colonial burrow-nesting seabirds attend their colonies nocturnally, which is widely accepted as a strategy to avoid avian predators that require at

least moderate ambient light levels for successful hunting (Cody 1973, Watanuki 1986, Brooke and Prince 1990, Jones et al. 1990, Mougeot and Bretagnolle 2000, Keitt et al. 2004). However, nocturnal activity does not eliminate the risk of predation completely (Stenhouse and Montevecchi 1999, Mougeot and Bretagnolle 2000). Therefore, many nocturnal seabirds decrease colony attendance during bright and anticipated bright (i.e., anticipated moon phase) light conditions, when they are most vulnerable (Watanuki 1986, Bretagnolle 1990, Mougeot and Bretagnolle 2000, Bourgeois et al. 2008). Furthermore, adverse weather conditions may decrease forage efficiency, leaving individuals under increased energetic stress and less likely to attend colony sites (Gaston and Nettleship 1982, Finney et al. 1999), and may also decrease the amount of ambient light at the colony site, which can increase the risk of colliding with conspecifics and with trees in forested landscapes, decreasing colony attendance during very dark conditions (Jones et al. 1990). Sound levels may also be an important factor affecting colony attendance of nocturnal seabirds. While attending a colony site both breeders and prospectors use vocalizations to communicate; increasing ambient noise due to increased wind speeds, wave heights, and anticipated wind speeds and wave heights (i.e., atmospheric pressure) may decrease the efficiency of communication leading to decreased colony attendance. Light and sound attenuate faster in forested landscapes than in open landscapes (Wiley and Richards 1982, Brown and Parker 1994), while the level of masking ambient noise, auditory sensitivity, amplitude of the sound at the source, and the specific attenuation rate of the sound are all factors

contributing to attenuation rate (Morton 1975). Furthermore, the canopy in a forest may act as a ceiling, bouncing sound back towards the forest floor, while wind and the rustling of leaves may increase attenuation (Morton 1975). In open landscapes, attenuation increases with distance above the ground and wind can limit the distance of effective communication (Morton 1975). Therefore, individuals in open landscapes might be predicted to preferentially attend colonies during a different range of environmental conditions than those attending colonies in forested landscapes.

The nocturnal colony behaviour of Ancient Murrelets (*Synthliboramphus antiquus*) is believed to be a strategy to avoid diurnal predators. Their large vocal repertoire is an adaptation to this nocturnal lifestyle and may replace visual cues as a social signal (Brooke 1978, Jones et al. 1989, Jones et al. 1990). Ancient Murrelet's North American breeding range stretches from Haida Gwaii, British Columbia westwards through the Aleutian Islands, Alaska (Gaston 1994). Ancient Murrelets limit their breeding season to approximately three months, which is likely a strategy to avoid predation (Gaston 1992, Ydenberg 2001). Additionally, Ancient Murrelets do not show strong philopatry (Gaston and Adkins 1998, Pearce et al. 2002), meaning that young individuals are free to search for the 'safest' location to settle, where they will maximize their overall lifetime reproductive success. Ancient Murrelets attend their colonies in Haida Gwaii from March until the end of June with egg laying in April and the peak of chick departures and prospecting occurring in late May (Gaston 1992). In the Aleutian Islands, the Ancient Murrelet breeding cycle is completed much later with egg

laying in June and the peak of chick departures and prospecting occurring in early July, even though colonies in Haida Gwaii and the central and western Aleutian Islands are at the same latitude (Byrd and Day 1986, Gaston 1992, 1994). Chick departure timing for Ancient Murrelets in both Haida Gwaii and the Aleutian Islands avoids the period when nights in the northern hemisphere are at their shortest (mid-June). Cover and shade are provided by dense grass tussocks in the Aleutian Islands and by coniferous trees in Haida Gwaii. Trees provide more protection from predators, but add risk during very dark nights when collisions and related injuries may occur (Jones et al. 1990). Coastal breeding colony sites such as those in Haida Gwaii are exposed to avian predators (e.g., crows) that are absent from oceanic Aleutian Island breeding sites. Avian predators such as gulls, eagles, ravens, and falcons are present in both locations, but differences in predation pressure have not been quantified.

Here we investigated the different colony attendance trade-offs being made by breeding and prospecting Ancient Murrelets. By limiting our study to the four-week time-frame encompassing the peak of family group departures and prospecting, we were able to differentiate colony attendance behaviour of breeders, that arrive and vocalize at the colony site early in the evening, while leading their chicks to the ocean (Jones et al. 1987); and prospectors, who arrive and vocalize at the colony site later in the evening (Gaston 1992). We hypothesized that prospectors are more risk averse than breeders and because of the differing physical habitat features (light and sound environments) experienced between Haida Gwaii and the Aleutian Islands, individuals in the

Aleutian Islands will attend their colonies during a broader range of environmental conditions than those in Haida Gwaii. This hypothesis makes a series of predictions about how attendance patterns differ between breeders and prospectors, and between Ancient Murrelet populations in Haida Gwaii and the Aleutian Islands. Specifically, we predicted that because breeders are constrained by their incubation and chick care duties, prospectors would be more sensitive to 1) light conditions, due to predation risk, attending colonies in higher numbers during very dark conditions (relationship to be more pronounced in the Aleutian Islands as flying into the colony sites does not include the risk of collision with trees); 2) weather at the colony site, due to decreased audibility of acoustic cues during foul weather (wind and surf noise -relationship to be stronger in Haida Gwaii due to increased sound attenuation in the forest); and 3) weather at the foraging site, due to costs associated with flying to colony sites.

3.3 Methods

3.3.1 Langara Island

Langara Island (54°12′N, 133°01′W) is located at the northern tip of Haida Gwaii, British Columbia. The densely forested Ancient Murrelet breeding colony site is situated on the northeastern tip of Langara Island (McPherson Point) and is used by approximately 24 000 breeding pairs (Gaston 1992, Regehr et al. 2007). In Haida Gwaii the peak of chick departures and prospector activity occurs during late May and early June (Gaston 1992), thus colony attendance was monitored from May 18- June 18 2006 and May 12- June 11 2007 by counting the number of arriving individuals (identified by noting the presence of

wing beats entering the colony site from the ocean) in 60-minute intervals between 2230-0330h PDT (Pacific Daylight Time) each night. We present these data as arrivals per minute in one hour-long intervals. Gaston (1992) found that at Reef Island, Haida Gwaii during May 21- June 10 prospectors (identified by the lack of a brood patch) made up at least 70% of the individuals arriving between 0000-0400h, whereas breeders made up approximately 80% of the individuals arriving between 2300-0000h. We therefore split our hour-long observation intervals into two groups: breeders (2230-0030h PDT) and prospectors (0030-0330h PDT).

3.3.2 Amatigank Island

Amatignak Island (51º15´N, 179º04´W) is part of the Alaska Maritime National Wildlife Refuge (AMNWR) located in the western Aleutian Islands, Alaska. Prior to our study, Amatignak Island was not known as a breeding site of Ancient Murrelets, which were presumably extirpated from the island by introduced Arctic foxes (*Alopex lagopus*) in the 19th or 20th centuries (Byrd et al. 2005). However, Ancient Murrelet family group departures (Jones et al. 1987) were recorded by automated recording devices (Song Meters model SM-1, Wildlife Acoustics Inc.) situated at four locations around Amatignak Island during June 18- August 6 2008 and May 28- August 5 2009, indicating a breeding population (Buxton 2010). Gain on both left and right channel microphones was set to +42.0 dB with a sensitivity of -35 dBV/pa. Detection of calls depended largely on background noise levels, but in ideal conditions, Song Meters can detect chirrup calls up to 50 m away, all Song Meters were placed more than 50

m from the shoreline (Buxton 2010). This colony is presumably recovering

following the eradication of Arctic foxes in 1991. The peak of Ancient Murrelet

chick departures and prospecting activity occurs in the western Aleutian Islands

during late June and early July (Gaston 1992), a full month later than in Haida

Gwaii. Activity at Amatignak was thus assessed using the number of chirrup and

song calls recorded by the Song Meters in 15-minute intervals at each half hour

between 0100-0500h HADT (Hawaii-Aleutian Daylight Time) each night between

June 18- July 22 2008 and May 28- July 22 2009. We present these data as the

total number of vocalizations (summed chirrup and song calls) recorded per

minute in one hour-long intervals. We used vocalization activity as an indication

of colony attendance, as low colony attendance is reflected in a low number of

calls recorded and vice versa (Gaston et al. 1988, Jones et al. 1990). We again

split our observations into two groups: breeders (0100-0300h HADT) and

prospectors (0300-0500h HADT) under the assumption that a similar trend

among arriving breeders and prospectors was occurring as in Haida Gwaii.

3.3.3 Light conditions and weather variables

We examined colony attendance in relation to nine variables (see Table

3.1), where three weather variables (wind speed, wave height, and atmospheric

pressure) were included as three separate variables but were included or

excluded from candidate models as a group as they are likely correlated and we

were interested in how each one might affect colony attendance. 1) Moon phase

(MP); 2) Cloud Cover (CC): recorded by visual estimation as the proportion of the

sky that was covered by clouds at the end of each one hour-long interval at

Langara Island and was noted once during an evening at Amatignak Island

unless significant changes occurred which were noted along with the time of the

change; 3) Light intensity (LI): where precipitation was recorded by visual

estimation at the end of each one hour-long interval at Langara Island, and noted

once during an evening at Amatignak Island unless significant changes occurred

which were noted along with the time of the change; Colony weather (CW;

marine weather representative of weather at the colony site during arrivals):

includes 4) wind speed in meters per second, 5) wave height in meters, and 6)

atmospheric pressure in kilopascals; and Foraging weather (FW; marine weather

representative of weather at the offshore foraging grounds during the day, 12

hours prior to arrivals) again included 7) wind speed in meters per second, 8)

wave height in meters, and 9) atmospheric pressure in kilopascals.

3.3.4 Statistical analysis

All analyses were completed using a nested general linear model with a

maximum likelihood fitting method and a Satterthwaite approximation in SAS 9.1

(proc MIXED; SAS Institute, Cary, NC), where hour was nested within day and

included as a random variable in all models. We assume that the 2006-2007

breeding seasons at Langara Island and the 2008-2009 breeding seasons at

Amatignak Island were typical, so a direct comparison of factors affecting

attendance/activity at the two sites could be made. We further believe that our

sample of nights monitored at each site was sufficient to detect such patterns (55

at Langara Island and 75 at Amatignak Island). We used an information theoretic

approach to evaluate the relationship between Ancient Murrelet colony

attendance and environmental variables, where models were ranked using Akaike's information criterion for small sample sizes (AIC_c) and AIC_c weights (w_i) were used to evaluate model likelihood (Burnham and Anderson 2002). When the best supported model received a weight less than 0.9 we used model averaging to generate parameter estimates and unconditional standard errors, which were used with parameter likelihoods to draw inference from our data set (Johnson and Omland 2004).

We considered 17 *a priori* candidate models in four separate analyses composed of biologically plausible combinations of the nine explanatory variables of interest including a null model to assess factors determining Ancient Murrelet 1) breeder arrivals at Langara Island in 2006 and 2007; 2) prospector arrivals at Langara Island in 2006 and 2007; 3) breeder activity at Amatignak Island in 2008-2009; and 4) prospector activity at Amatignak Island in 2008-2009.

3.4 Results

3.4.1 Langara Island

During 2006 and 2007 at Langara Island we sampled Ancient Murrelet colony arrivals during 251, one hour-long intervals over 55 days. Of these 135 intervals over 34 days had complete weather, moon, cloud cover, and light intensity information. The West Dixon Entrance weather buoy was out of service during May 2007, resulting in 93% of the missing data points. Ancient Murrelet colony arrivals at Langara Island ranged between 0.00-0.63 breeders per minute (mean 0.15 ± 0.06 birds/minute), and 0.00-0.87 prospectors per minute (mean

0.27 ± 0.04 birds/minute) with most birds arriving during 0030-0130h (Figure 3.1a).

Ancient Murrelet breeder colony arrivals at Langara Island increased with increasing darkness and decreased with increasing wave height. The best-supported model from our candidate set explaining Ancient Murrelet breeder colony arrivals at Langara Island included the terms light intensity and weather at the colony site, this model received more than four times more support than any other model in the candidate set (Table 3.2). Models that included the terms weather at the colony site received 85% of the total weight among models, while those that included the term light intensity received 62%, and moon phase received 23% of the total weight among models (Table 3.3). Ancient Murrelet breeder colony arrivals decreased with increasing wind speed, wave height, and atmospheric pressure, decreased as the moon phase approached full, and increased with increasing darkness (Table 3.3, Figures 3.2 & 3.3a). However, parameter estimates and standard errors for all parameters other than wave height and light intensity bound zero suggesting those effects are weak (Table 3.3).

Ancient Murrelet prospector colony arrivals at Langara Island decreased with increasing wave height. The best-supported model from our candidate set explaining Ancient Murrelet prospector colony arrivals at Langara Island included the terms light intensity and colony weather, this model received almost two times more support than the second best supported model in the candidate set (Table 3.4). Models that included the term colony weather received 100% of the

total weight among models, while those that included the term light intensity received 44%, and moon phase received 37% of the total weight among models (Table 3.5). Ancient Murrelet prospector colony arrivals decreased with increasing wave height, were not affected by either wind speed or atmospheric pressure, increased with increasing darkness and as the moon approached full (Table 3.5; Figure 3.2). However, parameter estimates and standard errors for all parameters other than wave height bound zero suggesting those effects are weak.

3.4.2 Amatignak Island

During 2008 and 2009 at Amatignak Island we sampled Ancient Murrelet colony activity (summed hourly chirrup and song calls during 15 minute intervals every half hour) during 295, one hour-long intervals over 75 days. Because Ancient Murrelet colony activity dropped to virtually nil after July 21st, we used only colony activity recorded during May 28th -July 21st which encompassed 229 intervals over 59 days. Ancient Murrelet breeder colony activity at Amatignak Island ranged between 0.00-5.40 calls per minute (mean 0.92 ± 0.19 calls/minute), and Ancient Murrelet prospector colony activity at Amatignak Island ranged between 0.00-5.57 calls per minute (mean 0.99 ± 0.19 calls/minute), with most colony activity occurring between 0200-0400h (Figure 3.1b).

Ancient Murrelet breeder colony activity at Amatignak Island was influenced by light intensity, with activity increasing with increasing darkness. The best-supported model from our candidate set explaining Ancient Murrelet breeder colony activity at Amatignak Island included the terms light intensity and

weather at the foraging site (Table 3.6). This model received over two times more support than the second best supported model, which included the single variable light intensity. Models that included light intensity received 87% of the total weight among models, while weather at the foraging site received 58% (Table 3.7). Ancient Murrelet breeder colony activity increased with increasing darkness, decreased with increasing wind speeds, increased with increasing wave height, but showed no change with atmospheric pressure (Table 3.7; Figure 3.3b). However, parameter estimates and standard errors for weather at the foraging site all bound zero suggesting these effects are weak.

Ancient Murrelet prospector colony activity at Amatignak Island was influenced by moon phase, with activity decreasing as the full moon approached. The best-supported model from our candidate set explaining Ancient Murrelet prospector colony activity at Amatignak Island included the terms moon phase and weather at the foraging site (Table 3.8). This model received over two times more support than the second best supported model, which included the single term moon phase. Models that included moon phase received 78% of the total weight among models; while weather at the foraging site received 64%, light intensity 22%, cloud cover 21%, and colony weather 15% (Table 3.9). Ancient Murrelet prospector colony activity decreased as the moon approached full and with increasing wind speed and wave heights at the foraging site and wind speed at the colony, but increased with increasing cloud cover, increasing darkness, atmospheric pressure at the foraging site, and both wave heights and atmospheric pressure at the colony (Table 3.9; Figure 3.4). However, parameter

estimates and standard errors for all variables except moon phase bound zero suggesting those effects are weak.

3.5 Discussion

The decision to attend a colony given the risk of being depredated on any given day or night is arguably a trade-off between survival and overall lifetime reproductive success. We evaluated the hypothesis that variability in colony attendance exists between breeders and prospectors and between locations with different physical environmental features. We predicted that Ancient Murrelet prospectors would be more risk averse than breeders (i.e., more sensitive to light and weather conditions) because breeders have a much more fixed pattern of colony attendance (Sealy 1976, Jones et al. 1990); and Ancient Murrelets attending colonies in Haida Gwaii would show different colony attendance patterns based upon different factors than those in the Aleutian Islands. Overall our results revealed no consistent factor that influenced attendance patterns of Ancient Murrelets, but differences between breeders, prospectors, and locations were evident.

Jones, Gaston & Falls (1990) suggested that Ancient Murrelets in Haida Gwaii require some light to navigate the forest while also requiring darkness to avoid predation. Additionally they suggested that inclement weather (i.e., heavy cloud cover, rainy and windy conditions) decreases visibility in the densely forested colony sites in Haida Gwaii discouraging Ancient Murrelets from attending colony sites by making breeding sites more difficult to find and increasing the risk of injury due to collision with tree branches. This would not be

the case in the Aleutian Islands as the colony sites are not forested and have little obstructing cover. Additionally, it has been found that activity by non-breeding petrels and shearwaters is influenced by light intensity, anticipated lunar cycle and weather conditions (Watanuki 1986, Bretagnolle 1990, Mougeot and Bretagnolle 2000, Bourgeois et al. 2008). Consequently, we predicted that Ancient Murrelet prospectors would be more sensitive to light conditions than breeders and this relationship would be stronger in the Aleutian Islands. Our results show a strong connection between light intensity and breeder colony attendance behaviour in both locations but a weak connection for prospectors. However, we did find a strong connection between moon phase and prospector colony attendance behaviour in the Aleutian Islands, consistent with our prediction.

Light attenuation and therefore ambient light levels vary between Haida Gwaii and the Aleutian Islands, with the Aleutian Islands being overall brighter due to the lack of a forest canopy. Therefore, breeders in the Aleutian Islands may limit colony attendance during very bright conditions, as light levels at the colony are relatively brighter than in Haida Gwaii and risk of predation therefore higher. Prospectors, on the other hand, arrive later in the night (Gaston 1992), as a result they do not experience the same bright light levels as breeders and therefore are not influenced by light conditions but instead by moon phase as this will have the most impact on light levels late in the night.

The auditory environment at Langara Island is very different than that at Amatignak Island as sound attenuation rates differ between forested and open

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landscapes (Wiley and Richards 1982). Increased ambient noise and sound attenuation in Haida Gwaii could contribute to different colony attendance decisions being made in Haida Gwaii than in the Aleutian Islands by limiting communication between conspecifics, and between adults and chicks during family group departures, and decreasing the locatable signal originating from the colony site. Our predictions that prospectors should be more sensitive to weather than breeders and that this relationship would be stronger in Haida Gwaii than in the Aleutian Islands are both supported by our data. Breeder and prospector colony attendance in Haida Gwaii decreased with increasing wave height, suggesting that in Haida Gwaii Ancient Murrelets decease colony attendance due to decreased ability to locate and communicate at the colony site, whereas colony attendance in the Aleutian Islands did not change in response to any colony weather variable. However, it is important to note that differences in breeding density occur between the two sites, with density at Amatignak Island likely lower than that at Langara Island. This could affect colony attendance during poor acoustic conditions by limiting attendance at the less dense site (i.e., Amatignak Island). This is opposite of our result, lending more support to the notion that increased wave height and the associated increase in ambient noise and decreased acoustic cue originating from the site are related to the decrease in colony attendance at Langara Island.

Imber (1975) suggested non-breeding petrels only attend colony sites if they are well fed. Thus, we predicted that prospectors in both locations should be more sensitive than breeders to weather at the foraging sites. Our results do

not support this prediction, even though a weak effect was observed between both breeders and prospectors and weather at the foraging grounds in the Aleutian Islands. This result suggested that foraging success and the energetic stresses associated with flying to the colony during poor weather were not important factors determining Ancient Murrelet colony attendance.

Overall this study suggests that there are no consistent factors determining colony attendance and activity but decisions differ between breeders and prospectors, and between Haida Gwaii and the Aleutian Islands. Specifically we found that Ancient Murrelet colony attendance in Haida Gwaii decreased with increasing wave height, while breeder colony attendance also decreased during bright light conditions. While in the Aleutian Islands, breeders limit colony attendance during bright light conditions, while prospectors limit colony attendance in response to the moon phase. The differences in colony attendance decisions in Haida Gwaii and the Aleutian Islands supports our prediction that different physical habitat features will alter the importance of environmental factors associated with colony attendance, but does not support our prediction that prospectors are more risk averse than breeders.

It is important to understand how and why individuals make colony attendance decisions in order to effectively monitor and manage populations. Understanding prospector behaviour is particularly important, as they are the individuals that colonize and recolonize sites and are thus the individuals most likely to respond to many conservation actions. However, little is known about this stage of a seabirds' life. In order to fully appreciate the decisions being

made during the prospecting stage, future studies should focus on factors

determining prospector colony attendance, intra-annual change (e.g., do they

become less risk averse over time), what implications age has on prospecting,

how far an individual will travel during one season, and how many potential sites

an individual visits before making a settlement decision.

Table 3.1 Summary of all variables and their construction used to evaluate Ancient Murrelet breeder and prospector colony activity at Langara and Amatignak islands.

Variable	Explanation	Categories
Moon Phase (MP)[a]	Proportion of moon visible regardless of moonrise and set times	
Cloud Cover (CC)	Proportion of sky covered by clouds	
Precipitation (Precip)	Type of precipitation present	None = 0.00 Light Rain = 0.25 Heavy Rain = 0.50 Drizzle = 0.75 Fog = 1.00
Twilight (TW)[a]	Proportion of light remaining/appearing from sunset/rise	
Light Intensity (LI)	Sum of the inverse of MP, inverse of TW, Precip, and CC; divided by 4, where 0=very bright and 1=very dark	
Colony Weather (CW)[b,c]	Wind Speed (m/s) Wave Height (m) Atmospheric Pressure (kPa)	
Foraging Weather (FW)[c,d]	Wind Speed (m/s) Wave Height (m) Atmospheric Pressure (kPa)	

[a]Astronomical Applications Department of the U.S. Naval Department website (http://aa.usno.navy.mil/idex.php)

[b]Central Dixon Entrance weather buoy (buoy 46145) located at 54º22´N, 132º27´W was downloaded from the Fisheries and Oceans Canada website

(http://www.dfo-mpo.gc.ca/science/data-donnees/index-eng.html?sub=climWeath#result)

[c]Western Aleutians weather buoy (buoy 46071) located at 51º09´N, 179º00´E was downloaded from the National Data Buoy Center, National Oceanographic and Atmospheric Administration (NOAA) website (http://www.ndbc.noaa.gov/).

[d]West Dixon Entrance weather buoy (buoy 46205) located at 54º10´N, 134º16´W) was downloaded from the Fisheries and Oceans Canada website (http://www.dfo-mpo.gc.ca/science/data-donnees/index-eng.html?sub=climWeath#result)

Table 3.2 Candidate model set describing Ancient Murrelet breeder colony arrivals at Langara Island in relation to moon phase (MP), cloud cover (CC), light intensity (LI), colony weather (CW), and foraging ground weather (FW) in 2006 and 2007 (n=34).

Candidate Model	K	AIC_c	ΔAIC_c	w_i
LI+CW	7	-25.39	0.00	0.55
MP+CW	7	-22.59	2.80	0.13
CW	6	-22.49	2.90	0.13
LI	4	-21.22	4.17	0.07
MP	4	-20.12	5.27	0.04
MP+CC+CW	8	-19.94	5.45	0.04
MP+CC	5	-18.16	7.24	0.01
Null	3	-17.40	7.99	0.01
LI+FW	7	-16.49	8.90	0.01
MP+FW	7	-15.99	9.40	0.00
CC	4	-15.62	9.77	0.00
FW	6	-15.19	10.20	0.00
LI+CW+FW	10	-14.73	10.66	0.00
CW+FW	9	-13.40	11.99	0.00
MP+CC+FW	8	-12.94	12.45	0.00
MP+CW+FW	10	-12.53	12.86	0.00
MP+CC+CW+FW	11	-8.80	16.59	0.00

Table 3.3 Summed Akaike weights (w_i), weighted parameter estimates, and unconditional standard errors (SE_u) of weighted parameter estimates calculated from the top candidate model of Ancient Murrelet breeder colony arrivals at Langara Island, British Columbia in 2006 and 2007.

Parameter[a]	Summed w_i	Weighted Parameter Estimate	SE_u
Intercept	1.00	9.20	4.90
Moon Phase	0.23	-0.03	0.06
Light Intensity	0.62	0.20	0.19
Colony Weather			
Wind Speed	0.85	-0.01	0.01
Wave Height	0.85	-0.17	0.09
Atmospheric Pressure	0.85	-0.01	0.01

Table 3.4 Candidate model set describing Ancient Murrelet prospector colony arrivals at Langara Island in relation to moon phase (MP), cloud cover (CC), light intensity (LI), colony weather (CW), and foraging ground weather (FW) in 2006 and 2007 (n=101).

Candidate Model	K	AIC$_c$	ΔAIC$_c$	w$_i$
LI+CW	7	-23.50	0.00	0.41
MP+CW	7	-22.40	1.10	0.24
CW	6	-21.81	1.69	0.18
MP+CC+CW	8	-20.43	3.06	0.09
MP+CW+FW	10	-18.56	4.94	0.03
LI+CW+FW	10	-18.06	5.44	0.03
CW+FW	9	-16.82	6.67	0.01
MP+CC+CW+FW	11	-16.53	6.96	0.01
Null	3	-6.35	17.14	0.00
LI	4	-6.28	17.21	0.00
CC	4	-4.58	18.91	0.00
MP	4	-4.38	19.11	0.00
LI+FW	7	-3.40	20.10	0.00
FW	6	-2.91	20.59	0.00
MP+CC	5	-2.67	20.83	0.00
MP+FW	7	-1.20	22.30	0.00
MP+CC+FW	8	0.87	24.36	0.00

Table 3.5 Summed Akaike weights (w$_i$), weighted parameter estimates, and unconditional standard errors (SE$_u$) of weighted parameter estimates calculated from the top candidate model of Ancient Murrelet prospector colony arrivals at Langara Island, British Columbia in 2006 and 2007.

Parameter[a]	Summed w$_i$	Weighted Parameter Estimate	SE$_u$
Intercept	1.00	1.22	4.43
Moon Phase	0.37	0.04	0.06
Light Intensity	0.44	0.11	0.14
Colony Weather			
Wind Speed	1.00	0.00	0.01
Wave Height	1.00	-0.26	0.06
Atmospheric Pressure	1.00	0.00	0.00

Table 3.6 Candidate model set describing Ancient Murrelet breeder colony activity at Amatignak Island in relation to moon phase (MP), cloud cover (CC), light intensity (LI), colony weather (CW), and foraging ground weather (FW) during 2008 and 2009 (n=116).

Candidate Model	K	AIC_c	ΔAIC_c	w_i
LI+FW	7	338.24	0.00	0.46
LI	4	339.36	1.12	0.26
LI+CW	7	341.24	3.00	0.10
LI+CW+FW	10	342.60	4.36	0.05
MP+FW	7	342.84	4.60	0.05
MP	4	343.96	5.72	0.03
MP+CC+FW	8	344.65	6.41	0.02
MP+CW	7	345.74	7.50	0.01
MP+CC	5	345.75	7.51	0.01
FW	6	346.87	8.63	0.01
MP+CC+CW	8	347.65	9.41	0.00
MP+CW+FW	10	348.20	9.96	0.00
Null	3	348.41	10.18	0.00
MP+CC+CW+FW	11	350.24	12.00	0.00
CC	4	350.56	12.32	0.00
CW	6	351.27	13.03	0.00
CW+FW	9	352.60	14.36	0.00

Table 3.7 Summed Akaike weights (w_i), weighted parameter estimates, and unconditional standard errors (SE_u) of weighted parameter estimates calculated from the top candidate model of Ancient Murrelet breeder colony activity at Amatignak Island, Alaska during 2008 and 2009.

Parameter[a]	Summed w_i	Weighted Parameter Estimate	SE_u
Intercept	1.00	-5.81	12.23
Light Intensity	0.87	1.57	0.71
Foraging Weather			
Wind Speed	0.58	-0.07	0.06
Wave Height	0.58	0.11	0.17
Atmospheric Pressure	0.58	0.00	0.01

Table 3.8 Candidate model set describing Ancient Murrelet prospector colony activity at Amatignak Island in relation to moon phase (MP), cloud cover (CC), light intensity (LI), colony weather (CW), and foraging ground weather (FW) during 2008 and 2009 (n=115).

Candidate Model	K	AIC_c	ΔAIC_c	w_i
MP+FW	7	333.65	0.00	0.35
MP	4	335.45	1.82	0.14
MP+CC+FW	8	335.66	2.02	0.13
LI	4	335.96	2.32	0.11
LI+FW	7	337.15	3.50	0.06
MP+CC	5	337.55	3.90	0.05
MP+CW+FW	10	337.62	3.97	0.05
LI+CW+FW	10	338.52	4.87	0.03
MP+CW	7	338.85	5.20	0.03
MP+CC+CW+FW	11	339.46	5.82	0.02
LI+CW	7	339.75	6.10	0.02
MP+CC+CW	8	340.86	7.21	0.01
Null	3	344.72	11.07	0.00
FW	6	345.28	11.63	0.00
CC	4	346.76	13.12	0.00
CW	6	348.58	14.93	0.00
CW+FW	9	349.01	15.37	0.00

Table 3.9 Summed Akaike weights (w_i), weighted parameter estimates, and unconditional standard errors (SE_u) of weighted parameter estimates calculated from the top candidate models of Ancient Murrelet prospector colony activity at Amatignak Island, Alaska during 2008 and 2009.

Parameter[a]	Summed w_i	Weighted Parameter Estimate	SE_u
Intercept	1.00	-10.83	14.66
Moon Phase	0.78	-0.74	0.42
Cloud Cover	0.21	0.03	0.09
Light Intensity	0.22	0.39	0.63
Colony Weather			
Wind Speed	0.15	-0.01	0.02
Wave Height	0.15	0.04	0.09
Atmospheric Pressure	0.15	0.01	0.01
Foraging Weather			
Wind Speed	0.64	-0.05	0.06
Wave Height	0.64	-0.08	0.17
Atmospheric Pressure	0.64	0.01	0.02
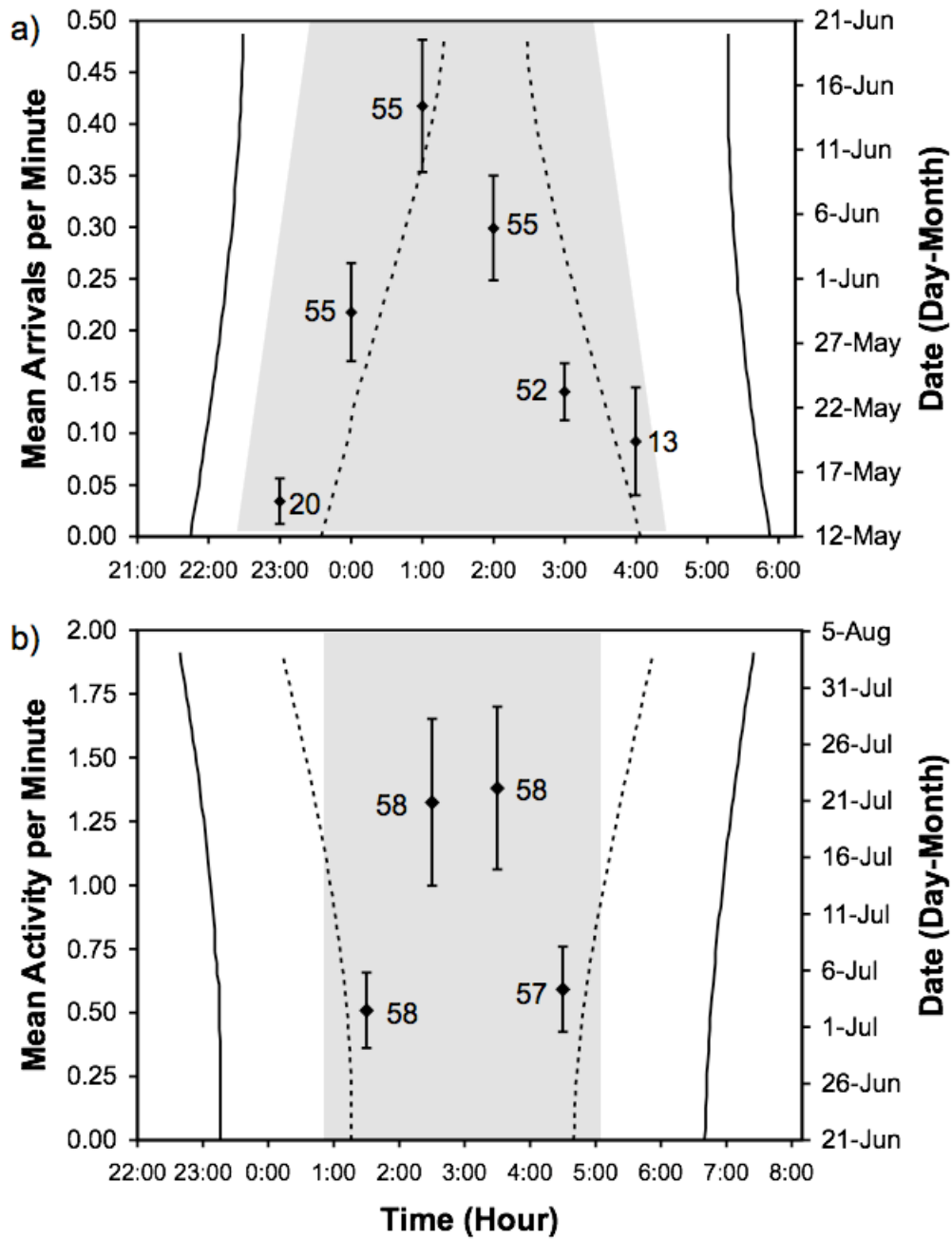
Figure 3.1 Summary of the sunrise/set (solid black lines) and the beginning/end of nautical twilight (dashed black lines), and a) mean number of arriving Ancient Murrelets per hour at Langara Island in 2006 and 2007; and b) mean amount of Ancient Murrelet activity per hour at Amatignak Island in 2008 and 2009. Grey boxes outline our continuous observation times and our counts are shown as means ± 95% CI with sample sizes.
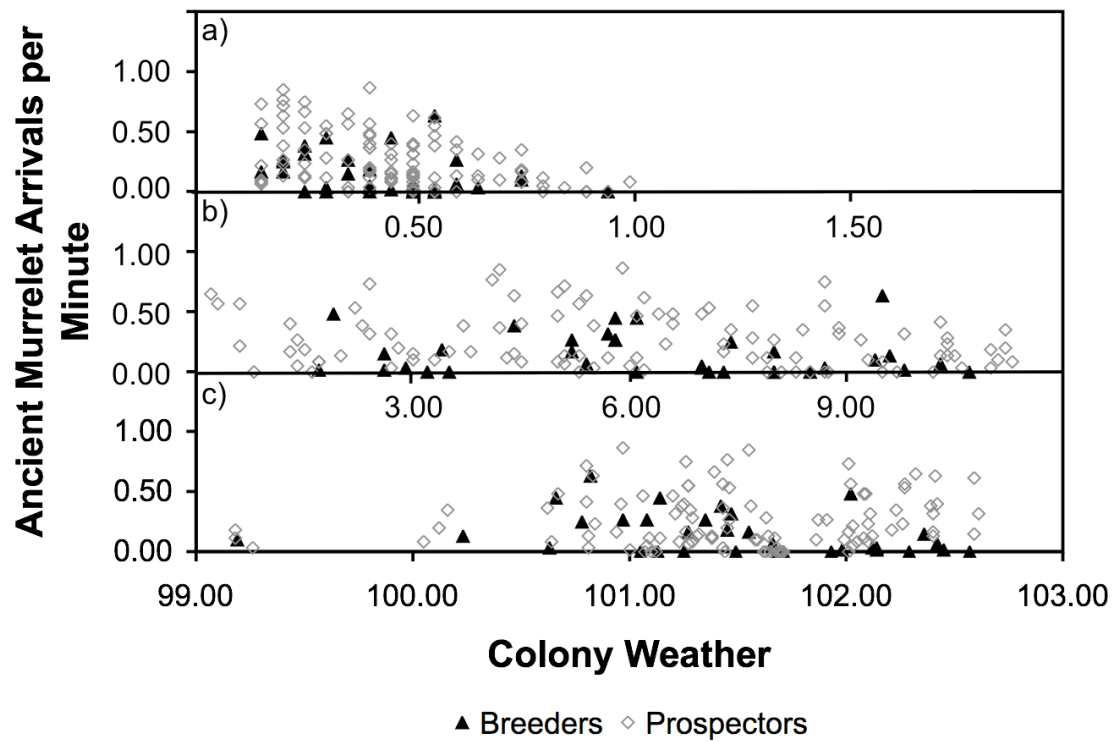
Figure 3.2 Summary of the per minute colony arrivals of breeders (solid black triangles) and prospectors (open grey diamonds) at Langara Island in 2006 and 2007 during one-hour long intervals and a) wave height in meters, b) wind speed in meters per second, and c) atmospheric pressure in kilopascals.
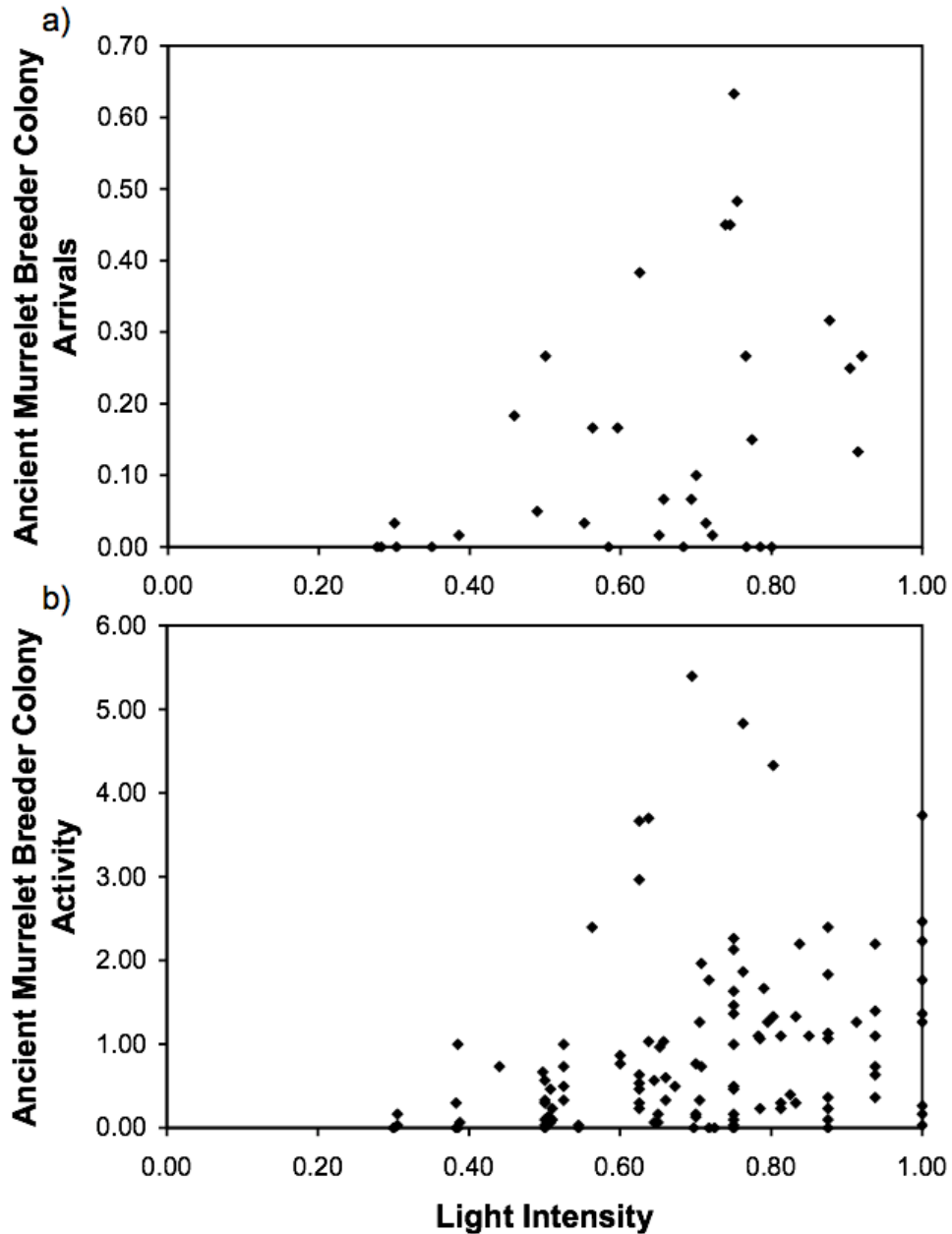
Figure 3.3 Summary of Ancient Murrelet a) breeder colony arrivals at Langara Island in 2006 and 2007 and b) breeder colony activity at Amatignak Island in 2008 and 2009 during one hour-long intervals; and light intensity where a value of zero indicates very bright conditions and a value of one indicates very dark conditions.
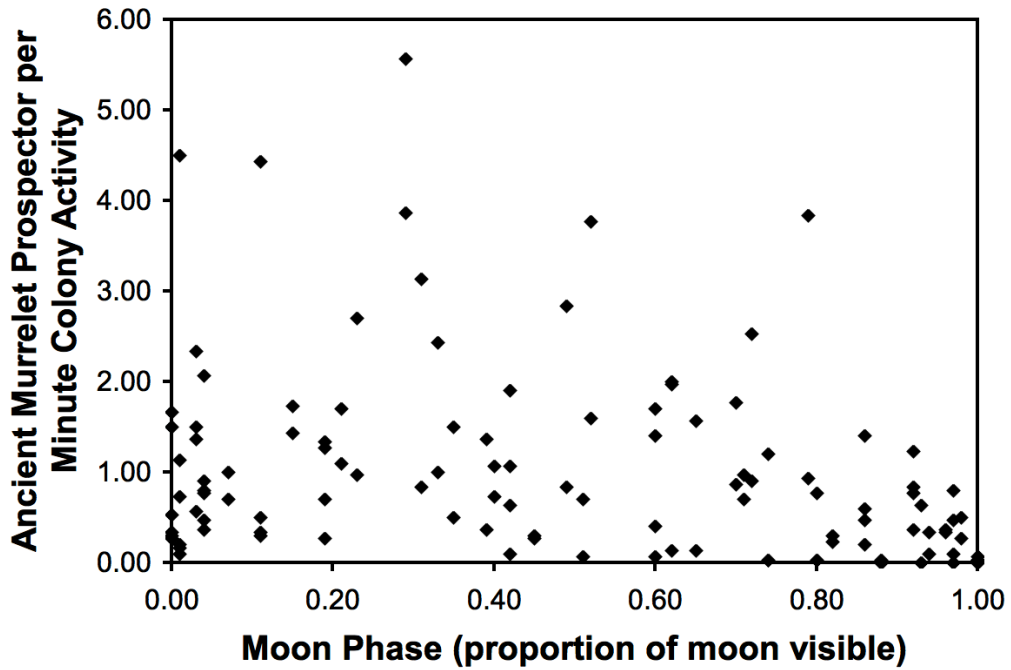
Figure 3.4 Summary of Ancient Murrelet prospector colony activity at Amatignak Island in 2008 and 2009 during one hour-long intervals and moon phase, where a value of zero indicates a new moon and a value of one indicates a full moon.

CHAPTER 4: AN EXPERIMENTAL STUDY OF THE USE OF SOCIAL INFORMATION BY NOCTURNAL BURROW-NESTING SEABIRD PROSPECTORS

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4.1 Abstract

Cue use and social information are important in settlement decisions by many animal species. In colonial seabirds, settlement decisions are based upon information gathered during a prospecting phase, where social information from conspecifics is a key aspect of these settlement decisions. Yet, the specific cues that prospectors use and why, remain debated questions. We used an experimental approach to evaluate a conspecific attraction hypothesis, predicting that nocturnal Ancient Murrelets use social information in the form of audio, visual and olfactory cues during prospecting. Specifically, we used (1) call playback experiments to test whether prospectors use conspecific vocalizations to locate potential colony sites; and (2) burrow trials to test whether prospectors use visual (presence of hatched eggshell fragments) and olfactory (presence of feather odour) cues in breeding burrows as indicators of site suitability. As predicted, Ancient Murrelet prospector activity increased by 271% at Langara Island and 458% in the Aleutian Islands over background levels during playback trials, supporting a conspecific attraction hypothesis. In addition, Ancient Murrelet activity decreased with increasing wave height, as moon phase approached full, and with increased distance to the nearest occupied colony site. Counter to predictions, prospectors showed no preference for burrows with visual or olfactory cues, however our inference is weak and further study is required. We conclude that prospectors use conspecific vocalizations to locate potential colony sites and playbacks may be used as a first step towards speeding the process of recolonization in areas with historical anthropogenic extirpations.

4.2 Introduction

Most animals, at some point in their life history, show site fidelity. For example, breeding and natal site fidelity have been found in many species of elasmobranches and fish (Ridgway et al. 1991, Feldheim et al. 2002, King and Withler 2005, Carlisle and Starr 2009), birds (Williams and Rodwell 1992, Illera and Diaz 2008), and marine mammals (Chittleborough 1965, Carr and Carr 1972). Species with philopatry return to their colony of birth, some breeding meters from their natal site, such as the Thick-billed Murre *Uria lomvia* (Steiner and Gaston 2005). Other species show allopatry, evaluating a number of colonies before choosing one (e.g., Henaux et al. 2007). Once a colony site is chosen, individuals often show high site fidelity by returning to the same location year after year and base decisions to remain or move on reproductive success and timing of reproductive failure (Danchin et al. 1998, Schmidt 2004, Naves et al. 2006).

Generally colonial individuals prefer settling amidst conspecifics (e.g., Podolsky and Kress 1989) and this is likely due to the risks associated with pioneering new habitat (Forbes and Kaiser 1994) and the advantages of acquiring high-quality habitat and choice among a selection of mates (Schjorring et al. 1999). Conspecific attraction increases an individual's ability to access social information used in settlement decisions by acting as an indication of general area suitability (Shields et al. 1988), a way to assess site quality (Stamps 1988, Doligez et al. 2003), and as the first step in identifying seemingly suitable breeding sites (Danchin et al. 1991). The use of conspecific cues as a proxy of

habitat quality reinforces coloniality, with areas of suitable habitat remaining unoccupied (Danchin and Wagner 1997, Greene and Stamps 2001). Studies aimed at testing a conspecific attraction hypothesis have successfully used bird decoys and call playbacks to attract conspecifics to areas of researcher interest (Kotliar and Burger 1984, Podolsky and Kress 1989, Crozier and Gawlik 2003, Harrison et al. 2009) and to induce group displays and nesting behavior (O'Connell-Rodwell et al. 2004). Social information in the form of conspecific cues have also been found to be more important than structural cues about vegetation in some species of passerine birds (Betts et al. 2008, Harrison et al. 2009) and are effective methods used to enhance recolonization of many species (e.g., Parker et al. 2007).

In seabirds, conspecific attraction techniques have been relatively widely studied and are an effective means of luring individuals to potential colony sites and facilitating breeding (Kress 1978, 1983, 1997, Sato et al. 1998, Parker et al. 2007). Many studies have found that nocturnal seabirds (i.e., those that are active at colonies after dark), particularly species of Procellariformes, use vocalizations for individual recognition, location recognition, and nest defense (Grubb 1973, 1979, Aubin et al. 2000, Jouventin and Aubin 2000, Bonadonna et al. 2004, Cure et al. 2009). But, little research has been completed on conspecific attraction in nocturnal seabird species, the roles and hierarchical relationships among audio, visual, and olfactory cues, and how these species make settlement decisions. Prior to making a settlement decision, prospectors (i.e., inexperienced sub-adults searching for a location within which to settle and

breed) visit many colony sites near the end of the breeding season when the most information about reproductive success (i.e., fledglings and/or hatched eggshells) at the site is available (Boulinier et al. 1996). Thus, the use of conspecific cues among prospectors is presumably high. However, whether a hierarchy in cue use by prospecting seabirds occurs has not been experimentally or exhaustively studied. For example, do some cues attract individuals into an area where more precise and localized cues are then used to evaluate that site?

A study of the vocal repertoire of Ancient Murrelets (*Synthliboramphus antiquus*), a nocturnal seabird of the family Alcidae, revealed nine distinct vocal displays that are highly locatable and individually distinctive (Jones et al. 1989). If this is an adaptation to their nocturnal life-style, audio cues may be important for finding a mate, locating a colony, and communicating with conspecifics. Throughout their North American range, Ancient Murrelet populations have been declining predominantly due to introduced foxes (*Alopex* sp.), raccoons (*Procyon* sp.), and rats (*Rattus* sp.), but the successful eradication of these predators from murrelet breeding islands has not reliably resulted in the recolonization of once occupied breeding sites (Regehr et al. 2007). The eradication of introduced predators from Ancient Murrelet breeding colonies in both Haida Gwaii (British Columbia, Canada) and the Aleutian Islands (Alaska, United States of America) provides a unique opportunity to explore habitat selection and recolonization of this species.

Gaston (1992) found that Ancient Murrelets visit colonies for only one or two years before they begin to breed. While the majority of non-breeders visiting

a colony are probably in their second year, there is variation in when individuals begin to breed, most breeding by the time they reach their fourth summer (Gaston 1992). Ancient Murrelets do not show sexual dimorphism and both males and females are thought to prospect for breeding sites (Gaston 1992). The objectives of this study were to understand the role of different modes of social information in habitat selection by prospecting Ancient Murrelets and to test the efficacy of using artificial cues as a means of restoring their colonies. We tested the conspecific attraction hypothesis by examining the response of Ancient Murrelet prospectors to acoustic, visual and olfactory cues. Specifically, we predicted that Ancient Murrelet prospectors would use 1) audio cues to locate potential breeding areas (with prospector activity increased during playback); and 2) both visual and olfactory cues within breeding burrows, where prospectors would enter burrows with visual and/or olfactory cues more often than burrows with no cues. Furthermore, from a management perspective we tested whether distance from an occupied colony would influence prospector activity at our playback sites, and whether prospectors return to sites previously visited leading to a lingering post-experiment effect of playback.

4.3 Methods

4.3.1 Study sites

Our study was conducted at three islands, Langara, Little Sitkin and Amatignak. Langara Island, Haida Gwaii, British Columbia (54°14′N 133°01′W) is 3,105 ha and 160 m a.s.l. at its highest point. Langara Island is predominantly forested, the dominant tree species being Sitka spruce (*Picea sitchensis*) and

Western hemlock (*Tsuga heterophylla*) with Western red cedar (*Thuja plicata*) in the interior, ground cover is predominantly moss and mossy stumps and logs (Rodway et al. 1994). Langara Island was declared free of introduced Norway rats (*R. norvegicus*) in 1997 after a four year eradication campaign (Taylor et al. 2000). Ancient Murrelets attend their colonies in Haida Gwaii from March until the end of June with the peak of chick departures and prospecting occurring in late May (Gaston 1992), thus our playback and burrow trials occurred during May and June 2007-2008. Little Sitkin Island (51°57′N 178°30′E) is 6,354 ha, 1,188 m a.s.l. at its highest point and located in the Rat Islands group, part of the Alaska Maritime National Wildlife Refuge (AMNWR). Also located within AMNWR, Amatignak Island (51°15′N 179°04′W) of the Delarof Islands group is 3,433 ha and 515 m a.s.l. at its highest point. Arctic foxes (*A. lagopus*) were introduced to both islands in 1923 and successfully eradicated from Little Sitkin Island in 2000 and from Amatignak Island in 1991. Both Little Sitkin and Amatignak islands are treeless with mostly low-lying grasses and sedges, leafy plants, and mosses below 450m, above this there is little to no vegetation. In the Aleutian Islands Ancient Murrelets breed much later, attending colonies during May until the end of July with peak chick departures and prospecting occurring in early July (Byrd and Day 1986, Gaston 1992), thus on both Aleutian Islands our playback trials occurred during late June and July 2008. To account for variation between the two playback locations (Langara Island, Haida Gwaii; and Little Sitkin and Amatignak islands, Aleutian Islands) we grouped our experimental sites as independent experimental sites within two locations (Langara Island and

the Aleutian Islands), where an experimental site is a location that is unoccupied by Ancient Murrelets and was used for playback trials.

4.3.2 Call playback trials

4.3.2.1 Playback stimuli

One ten-minute playback track of unaltered Ancient Murrelet vocalizations including chirrup calls, songs, and chick calls recorded from several individuals at McPherson Point, Langara Island during May and June 2006 was constructed using two Sennheiser ME62 omnidirectional microphones connected to a Marantz PMD660 portable solid-state recorder (sample frequency 44.1 kHz and 16-bit resolution). All recordings are deposited in the Macaulay Library, Cornell Lab or Ornithology, Itaca, New York (accession number 1994). Playback tracks were played on an iPod Shuffle (Apple Computer Inc.) set on repeat mode over a TOA ER-2230 wireless megaphone (both iPod and megaphone set to 75% of maximum gain, giving an audible range of approximately 400-600 meters). In all cases, the megaphone was situated at the vegetation edge behind the shoreline, was kept between three and four feet above the ground, and was pointed out to sea.

4.3.2.2 Langara Island

Playback was presented during May and June 2007 and 2008 at two unoccupied locations on Langara Island in each year for a total of four experimental sites with playback trials at varying distances from the current active colony site at McPherson Point on Langara Island (Figure 4.1a).

Experimental sites were chosen as those that were historically occupied by Ancient Murrelets but were unoccupied during the most recent colony surveys at Langara Island in 2004 (Gaston 1992, Regehr et al. 2007).

Observers listened from a location between 5-10 meters behind the playback equipment, where noise from the playback would not hinder counts, each night during a total of 159 one-hour long intervals between 2330-0330h PDT (Pacific Daylight Time) over 34 days and recorded counts of arrivals and departures (using wing beats and landward or seaward direction of flight), and vocalizations; to obtain an indication of the amount of activity at the site. The playback experiment on these four study sites consisted of one replicate of three nights of silent monitoring, followed by three nights of playback monitoring, and finally three nights of silent monitoring (2007: Dibrell Bay – silent on 17-19 and 23-25 May; playback on 20-22 May; Explorer Bay – silent 1-2 and 6-8 June; playback on 3-5 June; 2008: Dadens – silent on 6-8 and 12-14 May; playback on 9-11 May; and South Holland Point – silent on 19-21 and 25-27 May; playback on 22-24 May), allowing us to test for effects of playback on Ancient Murrelet activity. Each of the four study sites were located on the eastern side of the island, and were abandoned by Ancient Murrelets over 26 years ago, longer than the average lifespan of an Ancient Murrelet (Gaston 1992, Regehr et al. 2007). Consequently, our experiments are not confounded by differences in prominent wind and storm directions which are south (average wind and storm directions during our observations), nor are there individuals present within the population with prior experience breeding at these sites. In addition, Ancient Murrelets do

not appear to select for large-scale habitat features in Haida Gwaii (Chapter 2). These factors taken together indicate that the only biologically important difference (in relation to Ancient Murrelets) between the four experimental sites at Langara Island are their distances to the current active colony site. Our experimental design therefore, allows us to test for differences in Ancient Murrelet activity during silent and playback trials and among distances to the current occupied colony site. Ancient Murrelet prospector colony attendance at Langara Island decreases with increasing wave height presumably because increased wave height masks calls originating from the colony site (Chapter 3). Wave height information in meters for Langara Island, was downloaded from the Fisheries and Oceans Canada website (http://www.dfo-mpo.gc.ca/science/data-donnees/index-eng.html?sub=climWeath# result), for a marine weather buoy located off the coast of Langara Island (Central Dixon Entrance weather buoy 46145, located at 54º22´2˝N, 132º27´0˝W) and was included in this analysis. In the Aleutian Islands, Ancient Murrelet prospector colony attendance decreased as the full moon approached, presumably because the increased light from a full moon increased the risk of predation at the colony site (Chapter 3). To keep our data for Langara Island and the Aleutian Islands consistent, moon phase information was downloaded for Langara Island from the Astronomical Applications Department of the U.S. Naval Department website (http://aa.usno.navy.mil/idex.pho), and was included in this analysis.

4.3.2.3 Aleutian Islands

Experimental playback of the same Ancient Murrelet vocalization recordings used at Langara Island occurred during June and July 2008 at one abandoned colony location on each of two islands –Williwaw Cove, Little Sitkin Island (HLM) and Ulva Cove, Amatignak Island (ILJ) for a total of two experimental sites (Figure 4.1b & c). It is unknown when the last Ancient Murrelets bred on each of these islands but the presence of foxes dates to 1923 (S. Ebbert personal communication) and Ancient Murrelets were certainly eradicated from these islands before the 1990s. Similar to our playback sites at Langara Island, there were no individuals present in the population that would have a memory of breeding at either of these Aleutian Island colonies. Furthermore, our experimental sites were located in protected coves on the northern (Little Sitkin Island) and eastern (Amatignak Island) sides of the islands, during the summer prominent wind and storm directions in the Aleutians are southern (average over the course of our observations), thus, our results are not confounded by prominent wind and storm directions. Observers recorded counts of arrivals and departures (using wing beats and landward or seaward direction of flight), and vocalizations during 186 hour-long intervals over 62 days (32 at Little Sitkin Island, and 30 at Amatignak Island) using the same procedures as at Langara Island. The playback experiment at these two study plots consisted of three cycles of five nights of silent monitoring alternating with five nights of playback during 0100-0400h HADT (Hawaii-Aleutian Daylight Time; Amatignak – silent on 22-26 June, 2-6 and 12-16 July, and playback on 27 June– 1 July, and 7-11 and 17-21 July; Little Sitkin – silent on 22-26 June, 5-9 and 16-20 July, and

playback on 30 June- 4 July, 11-15 and 21-25 July). Similar to the Langara

Island data, both wave height in meters and moon phase information were

included in this analysis, even though wave height was not found to be an

important factor determining prospector colony arrivals in the Aleutians Islands

(Chapter 3). Wave height information from the Western Aleutians weather buoy

(buoy 46071) located at 51º09´N, 179º00´E was downloaded from the National

Data Buoy Center, National Oceanographic and Atmospheric Administration

(NOAA) website (http://www.ndbc.noaa.gov/), and moon phase information was

downloaded from the Astronomical Applications Department of the U.S. Naval

Department website (http://aa.usno.navy.mil/idex.pho). Observer impressions of

wind speed and wave height at the two experimental sites and the buoy data are

consistent, thus the buoy data is a reliable indication of marine weather at the

two experimental sites.

We do not believe our use of Ancient Murrelet vocalizations recorded at

Langara Island to conduct playback experiments in the Aleutian Islands to

confound our study as dialect formation depends on vocal learning, which is not

known to occur in the order Charadriiformes, which includes the auks (Kroodsma

1982). Differences in innate vocalizations could nonetheless occur due to

genetic differentiation of isolated populations, but no such differences were

apparent in our general examination of calls recorded in the two regions (ILJ and

HLM personal observations). If such a difference did exist, we might expect to

see reduced response to playback of 'foreign' calls compared to locally recorded

vocalizations - something we considered when interpreting the results of our experiments.

4.3.3 Artificial burrow trials

Burrow use by Ancient Murrelet prospectors at an active Ancient Murrelet colony site, McPherson Point Langara Island, was examined by marking 20 natural burrow entrances on 19 May 2006 and 16 and 19 May 2007 with toothpicks so that birds could not enter the burrows without displacing them (Gaston et al. 1988, Shoji and Gaston 2010). Burrows were checked each morning for displaced toothpicks until 21 June 2006 and 22 June 2007. Any toothpicks that had been displaced the previous evening were noted and replaced. The current active Ancient Murrelet colony is located in an area without other nocturnal seabirds or small mammals, so all knockdowns were assumed to be Ancient Murrelets. In 2006, all 20 burrows were searched by hand on 21 June and the contents noted (empty, eggshell fragments, etc.). If a burrow was empty it was considered part of the no cue treatment, burrows that contained eggshell membranes from previous years (i.e., rubbery membranes that are slightly discolored) were considered part of the visual cue treatment, and those with eggshell fragments from the current year (either hatched eggshells or eggshell fragments that are white with thin membranes) were considered part of the visual and olfactory cue treatment as the presence of the current year's hatched eggshells was used as an indication that adult breeders had occupied that burrow and that feather odor associated with those individuals occupying that site would be present in the burrow. Similar methods were used in 2007 but

on 21 May 2007, all 16 natural burrows were examined by hand; two burrows contained warm eggs, which were removed and replaced with hatched eggshell fragments. These two burrows became part of the visual and olfactory cue treatment and were marked and monitored using toothpicks placed at the entrance (as in 2006) until 22 June when all 26 burrows monitored in 2007 were searched by hand and their contents noted. Monitoring activity at these burrows is not akin to monitoring the departures and arrivals of the breeding pair as that pair would have departed the colony after their eggs were removed. On 21 May 2007 we also dug ten artificial burrows, which were randomly assigned as either empty (no cue) or had hatched eggshell fragments placed within them (visual cue). The ten artificial burrows were therefore split so that five were left empty and five contained eggshell fragments. In an attempt to copy natural burrows, eggshells were placed far enough back in the burrows to not be immediately visible from outside the burrow. Therefore, prospectors would have to enter a burrow to make use of the cues contained within, this design allows us to assess what cues are present inside burrows that entice prospectors to enter and reenter burrows. Gaston (1992) noted that prospectors frequently enter burrows at prospective colony sites, and enter/reenter burrows that successfully hatched chicks more often that those that did not, we assert this experimental design builds on that study and tests the more precise and localized burrow-level cues used during prospecting.

   The peak of chick departures at McPherson Point in 2006 and 2007 was observed to have occurred during the first week of June (based on the relative

number of Ancient Murrelet chick calls heard in the forest; HLM personal observation), consistent with previous accounts (Sealy 1976, Gaston 1992). Using 9 June as the end of peak chick departures, we assumed burrow activity after this date to be the result of prospector activity, as adult colony attendance decreases synchronously with chick departures (Gaston 1992). Therefore, assuming activity at burrows was the result of prospectors after this date, even though the peak of prospecting would have occurred on or before the peak of chick departures (Boulinier et al. 1996), decreases the risk of monitoring adult arrivals and departures from our sample of natural burrows. Using information gathered during burrow searches, each burrow was classified as occupied and successful (containing both visual and olfactory cues), occupied and unsuccessful (cold or broken eggs), not occupied (no cue), or unknown (all burrows whose contents could not be determined). All unsuccessful and unknown burrows were omitted from the analysis as unsuccessful burrows may deter prospectors.

4.3.4 Statistical analyses

4.3.4.1 Call playback trials

To assess whether Ancient Murrelet activity (i.e., summed nightly arrivals, departures, and vocalizations); 1) increased during playback (only the first three trials –off, on, off for each site were used in this analysis) and 2) increased during silent treatments following playback treatments (only silent treatments were included in this dataset), we considered eight and four *a priori* candidate models composed of biologically plausible combinations of six (location, trial, distance,

wave height, moon phase, and day nested within site) and three (trial, site, and day) explanatory variables of interest including a null model. We used 1) a mixed effects nested generalized linear model with maximum pseudo-likelihood estimation method (allowing for inter-model comparisons), a poisson distribution and a log link function, where all models included the term day nested within site as a random factor and location as a fixed effect; and 2) a mixed general linear model with a restricted maximum likelihood estimation method in SAS 9.1 (proc GLIMMIX and proc MIXED; SAS Institute, Cary, NC), where the term day was included in all models as a random factor. We then used an information theoretic approach to rank our candidate models using 1) Akaike's information criterion (Akaike 1974) for small sample sizes correcting for overdispersion by including an estimate of model deviance (c-hat = model deviance/df) for the global model ($QAIC_c$) and $QAIC_c$ weights (w_i) were used to evaluate model likelihood (Burnham and Anderson 2002); and 2) AIC_c and AIC_c weights (w_i) were used to evaluate model likelihood (Burnham and Anderson 2002). All values reported in the results section are means ± 95% CI. When the best supported model received a weight less than 0.9 we used model averaging to generate parameter estimates and unconditional standard errors, which were used with parameter likelihoods to draw inference from our data set (Johnson and Omland 2004).

4.3.4.2 Artificial burrow trials

Using the data collected in 2006 and 2007, the hypothesis that prospectors enter successful burrows (i.e., burrows that contained successfully fledged chicks -containing both visual and olfactory cues) more often than

unsuccessful burrows (with no cue or solely a visual cue) was tested using two *a priori* candidate models composed of one explanatory variable of interest (treatment –empty, visual cue, or visual and olfactory cue) and one null model. Models were assessed using AIC_c and AIC_c weights (w_i) were used to evaluate model likelihood (Burnham and Anderson 2002). We completed this analysis using a general linear model in SAS 9.1 (proc GLM; SAS Institute, Cary, NC). All values reported in the results section are means ± 95% CI. When the best supported model received a weight less than 0.9 we used model averaging to generate parameter estimates and unconditional standard errors, which were used with parameter likelihoods to draw inference from our data set (Johnson and Omland 2004).

4.4 Results

4.4.1 Response to call playback

Overall Ancient Murrelet activity increased during call playback. During 2006 and 2007 at Langara Island, Ancient Murrelet activity ranged between 0-24 wing beats and calls per night (2.09 ± 2.54) during silent observations, and 0-16 wing beats and calls per night (5.67 ± 3.28) during playback (a 271% increase associated with playback; Figure 4.2). Similarly, during 2008 at Williwaw Cove, Little Sitkin Island and Ulva Cove, Amatignak Island, Ancient Murrelet activity ranged between 3-254 calls and wing beats per night (72.26 ± 31.67) during silent observations and 26-559 calls and wing beats per night (331.00 ± 100.00)

during playback observations (a 458% increase associated with playback; Figure 4.3).

The best-supported model from our candidate set explaining Ancient Murrelet activity during one-night long intervals included the terms trial and distance (Table 4.1). This model received 1.5 times more support than the second best supported model, which included the terms trial, distance, and wave height (Table 4.1). Ancient Murrelet activity was highest during trials with playback, at sites closest to a currently occupied site, when wave heights were low, and when moon phase was closest to the new moon (Table 4.2). However, parameter estimates and standard errors bound zero for all terms except trial indicating that those effects were weak.

A lingering post-experiment effect of playback was noted, as Ancient Murrelet activity increased during silent treatments following playback treatments. The best-supported model from our candidate set explaining Ancient Murrelet activity during one-night long intervals included the terms site and trial (Table 4.3). This model received virtually all of the weight among our candidate models. Ancient Murrelet activity was highest during the second silent trail and at Ulva Cove, Amatignak Island (Table 4.4, Figure 4.4).

4.4.2 Response to artificial burrows

During 2006 and 2007 at Langara Island, Ancient Murrelet burrow activity was sampled (proportion of knockdowns per night throughout the sampling period) 432 times at 22 burrows (13 times per burrow in 2006; 28 times per burrow in 2007, and 11 times per dug burrow in 2007). Ancient Murrelet burrow

activity at Langara Island ranged between 0.00-0.15 knockdowns per night (0.04 ± 0.02), with 0.05 ± 0.03 (n=14) knockdowns per night at no cue burrows, 0.01 ± 0.01 (n=5) at visual cue burrows, and 0.09 ± 0.01 (n=3) at visual and olfactory cue burrows. The best-supported model from the candidate set explaining knockdowns at Ancient Murrelet burrows at Langara Island was the null model that included only the intercept but received only 11% more support than the second model that included the term treatment (Table 4.5). Our parameter estimates and standard errors for the term trial bound zero suggesting these effects are weak but show that knockdowns at both the no cue and visual cue treatments were lower than knockdowns at the visual+olfactory cue treatment (Table 4.6). Additionally, power analysis (α= 0.05, f= 0.50, power= 0.46) revealed that this analysis is inadequate to reject the null hypothesis (Cohen 1988), thus our inference is weak and further research is required.

4.5 Discussion

Our experimental data support an important prediction of the conspecific attraction hypothesis: nocturnal Ancient Murrelet prospectors used conspecific vocalizations to locate and orient to potential colony sites. In seabirds generally, including Ancient Murrelets (Gaston 1992), prospecting occurs near the end of the breeding season (i.e., during fledging) when the most reliable information about reproductive success at the site is available (Danchin et al. 1991, Boulinier et al. 1996). Most studies suggest that late-season prospecting is an adaptation that allows prospectors to evaluate conspecific reproductive success at the site (Boulinier et al. 1996, Danchin et al. 1998). We suggest Ancient Murrelets

choose this timing because chick departures (an indicator of reproductive success) coincide with increased calling at colony sites providing a very reliable cue with information about site quality.

Seabird colonies can be loud places (Feare et al. 2003) and in general nocturnal seabirds have highly transmissible calls but constraining environmental conditions at colony sites (wind, vegetation, etc.) may limit communication to short distances (Wiley and Richards 1982, Jouventin and Aubin 2000). Therefore, conspecific vocalizations can be used to locate potential colony sites but communication can sometimes only be achieved close to or within the site. Using vocalizations as a locator cue ensures prospectors focus their efforts evaluating occupied sites (i.e., perceived high quality sites), a reliable method for individuals interested in visiting many potential nesting sites in a relatively short period of time. The first time a seabird arrives at a colony site as a prospector, that individual arrives having previously spent very little time on land. Thus, information concerning places to attempt breeding, and what constitutes 'good' breeding habitat are presumably learned from conspecifics. Once at an already busy site, prospectors can assess habitat, conspecific reproductive success, and interact with potential mates, making later settlement decisions based upon these observations (Danchin et al. 1998, Seppänen et al. 2007). The timing of prospecting and the use of vocalizations to locate colony sites support our conspecific attraction hypothesis, as our results demonstrate that Ancient Murrelets are using audio information from conspecifics when choosing which sites to visit.

Although our results provided no support for the hypothesis that prospectors use visual and olfactory cues in habitat selection, our inference is weak. It is widely accepted that petrels use odor as a foraging cue (Nevitt and Haberman 2003), and it has been suggested that they have individually distinctive odors that could be used in mate and nest site recognition (Bonadonna et al. 2007). If other nocturnal seabirds use odor to locate their nest site, prospectors may use this cue to evaluate colony sites. Olfaction has not been studied in adult Ancient Murrelets, but adults do not remove hatched eggshell fragments from breeding burrows (Gaston 1992), and this visual cue, in addition to associated olfactory cues present in burrows (i.e., feather and eggshell odor), could allow prospectors to evaluate individual nesting burrows, providing more information regarding site and burrow quality. Gaston (1992) suggests that Ancient Murrelet prospectors tend to enter burrows that successfully hatched chicks more often than those that did not. We predicted that this behavior was the result of visual and olfactory cues being present in burrows that successfully hatched chicks but our results did not confirm this prediction. Further study is required to evaluate why successful burrows are attractive to prospectors as our sample sizes are small and inference weak.

Ancient Murrelets gather offshore one to two hours before sunset, flying from 'gathering grounds' to the colony (Gaston 1992). Prospectors may use these grounds as yet another indication of the location of suitable nesting sites, similar to how Guanay Cormorants (*Phalacrocorax bougainvillii*) use rafts situated near their breeding colony as a compass signaling the direction of a

foraging patch (Weimerskirch et al. 2010). Prospector response to playback declined with increasing distance to the nearest occupied site suggesting that this is a factor associated with the locations of offshore gathering grounds. The gathering ground at Langara Island is located just offshore of McPherson Point (Gaston 1992), but locations are poorly known in the Aleutian Islands. Occupied colony sites occur on islands nearby to both Amatignak and Little Sitkin Islands suggesting proximity to gathering grounds. A better description of response to playback and distance would use the location of gathering grounds as opposed to occupied colony sites.

Our playback experiments provide ample evidence that Ancient Murrelet prospectors use audio cues to locate potential nesting sites, this implies that social information is important in future settlement decisions made by nocturnal Ancient Murrelets. Given this, abandoned colony sites lacking audio cues are unlikely to be recolonized, especially if they are far from an occupied site and/or gathering ground. Further study of site-specific settlement decisions are required to assess how prospectors evaluate sites and burrows, whether inter-species vocalizations are used when searching for potential colony sites, and whether a hierarchy of cues are used when assessing potential nesting sites. Additionally, we found a post-experiment lingering effect of call playback suggesting that once activity at a site is initiated, some individuals do repeatedly return to that site.

Table 4.1 Candidate model set describing summed Ancient Murrelet activity during one-night long observation periods at four formerly occupied breeding sites at Langara Island (Dibrell Bay, Explorer Bay, Dadens, and South Holland Point) and two formerly occupied sites in the Aleutian Islands (Ulva Cove Amatignak Island and Williwaw Cove Little Sitkin Island), Alaska in relation to trial (TRL – silent versus playback), distance to the nearest occupied site (Dist), wave height (WH), and moon phase (MP) in 2007 and 2008 (n=64; c-hat=0.94). All models also include location (Loc; Langara Island or the Aleutian Islands) as a fixed effect and day nested within site as a random factor.

Candidate Model	K	$QAIC_c$	$\Delta QAIC_c$	w_i
TRL+Dist+Loc	7	237.19	0.00	0.46
TRL+Dist+WH+Loc	8	238.05	0.86	0.30
TRL+Dist+MP+Loc	8	237.66	2.47	0.13
TRL+Dist+WH+MP+Loc	9	240.65	3.46	0.08
TRL+Loc	6	244.71	7.52	0.01
TRL+WH+Loc	7	244.91	7.72	0.00
TRL+MP+Loc	7	247.35	10.16	0.00
TRL+WH+MP+Loc	8	247.68	10.49	0.00
Dist+Loc	6	250.43	13.24	0.00
Dist+MP+Loc	7	251.11	13.91	0.00
Dist+WH+Loc	7	252.78	15.59	0.00
Dist+WH+MP+Loc	8	253.51	16.32	0.00
Loc	5	256.07	18.87	0.00
MP+Loc	6	257.35	20.15	0.00
WH+Loc	6	257.96	20.77	0.00
WH+MP+Loc	7	259.30	22.11	0.00

Table 4.2 Summed quasi-Akaike weights (w_i), weighted parameter estimates, and unconditional standard errors (SE_u) of weighted parameter estimates calculated from all candidate models of summed Ancient Murrelet activity during one-night long observation periods at four formerly occupied breeding sites at Langara Island (Dibrell Bay, Explorer Bay, Dadens, and South Holland Point), British Columbia during 2007 and 2009, and two formerly occupied sites in the Aleutian Islands (Ulva Cove Amatignak Island and Williwaw Cove Little Sitkin Island), Alaska during 2008.

Parameter[a]	Summed w_i	Weighted Parameter Estimate	SE_u
Intercept	1.00	1.63	0.49
Location (Aleutian Islands)	1.00	5.04	0.36
Trial (off)	1.00	-1.35	0.32
Distance to occupied site	0.97	-0.11	0.03
Wave Height	0.39	-0.21	0.27
Moon Phase	0.22	-0.01	0.21

[a] We set categorical variables Trial (on), and Location (Langara Island) to zero in all models.

Table 4.3 Candidate model set describing a post-experiment effect of playback on Ancient Murrelet activity during one-night long observation periods in the Aleutian Islands, Alaska in relation to trial (TRL –pre experiment silent trial versus post-experiment silent trial) and site (Ulva Cove Amatignak Island and Williwaw Cove Little Sitkin Island) in 2008 (n=30). In all models day was included as a random factor.

Candidate Model	K	AIC$_c$	ΔAIC$_c$	w_i
Site+Trial	6	317.55	0.00	0.98
Trial	5	325.60	8.05	0.02
Site	4	332.70	15.15	0.00
Null	3	341.52	23.97	0.00

Table 4.4 Summed Akaike weights (w_i), weighted parameter estimates, and unconditional standard errors (SE_u) of weighted parameter estimates calculated from all candidate models evaluating a post-experiment effect of playback on Ancient Murrelet activity during one night-long observation periods in the Aleutians Islands, Alaska during 2008.

Parameter[a]	Summed w_i	Weighted Parameter Estimate	SE_u
Intercept	1.00	75.06	24.85
Trial(1) -off	1.00	5.63	29.61
Trial(3) -off	1.00	58.20	31.18
Site (Ulva Cove)	0.98	42.67	25.13

[a] We set categorical variables Trial (5) –off and Site (Williwaw Cove) to zero in all models.

Table 4.5 Candidate model set describing nightly prospector burrow activity at Langara Island in 2006 and 2007 in relation to treatment (TRT; no cue, visual cue, or visual and olfactory cue; n=22). This analysis includes both data from natural and artificial burrows.

Candidate Model	K	AIC_c	ΔAIC_c	w_i
null	2	-127.18	0.00	0.53
TRT	4	-126.87	0.23	0.47

Table 4.6 Summed Akaike weights (w_i), weighted parameter estimates, and unconditional standard errors (SE_u) of weighted parameter estimates calculated from all candidate models of burrow activity at Langara Island, British Columbia in 2006 and 2007.

Parameter[a]	Summed w_i	Weighted Parameter Estimate	SE_u
Intercept	1.00	0.06	0.03
Treatment (no cue)	0.47	-0.02	0.03
Treatment (visual cue)	0.47	-0.04	0.05

[a] We set categorical variable Treatment (visual and olfactory cue) to zero in all models.
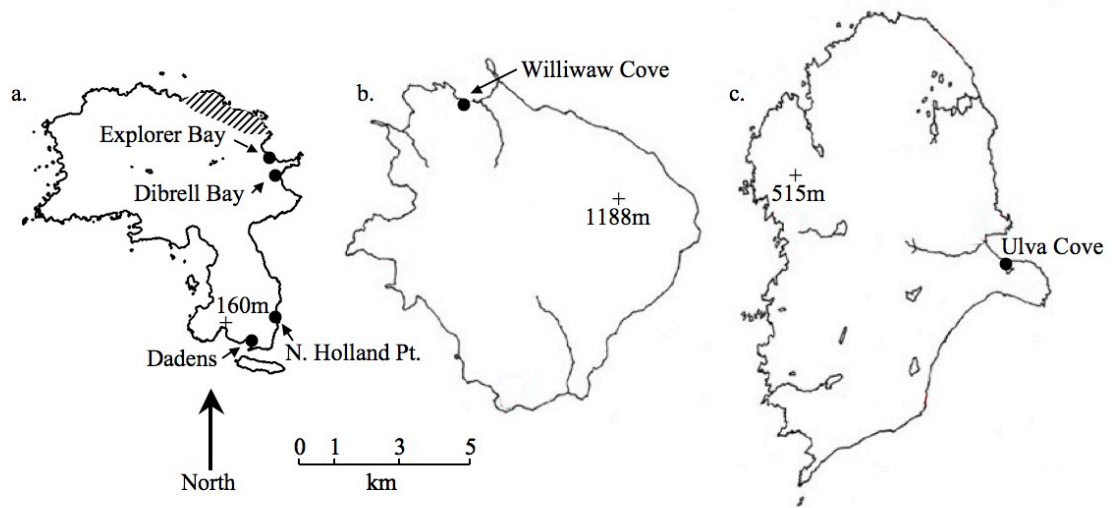
Figure 4.1 Locations of playback sites at a) Langara Island (location of current Ancient Murrelet colony boundaries shaded at McPherson Point), b) Little Sitkin Island; and c) Amatignak Island.
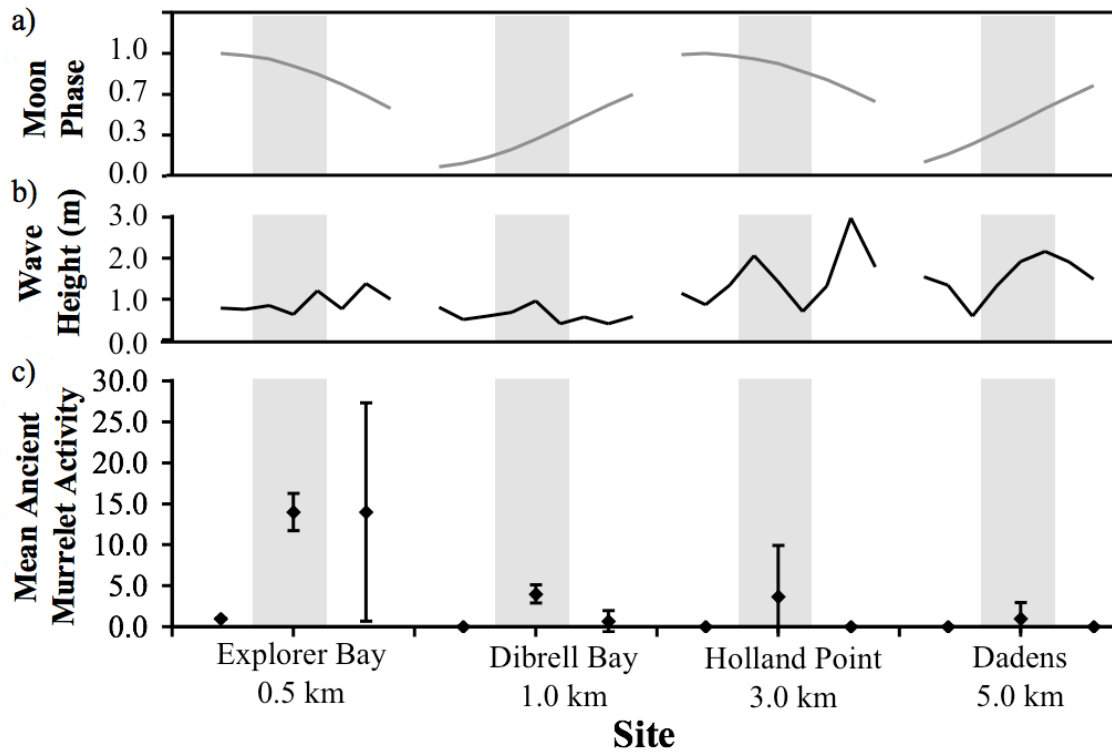
Figure 4.2 Summary of a) moon phase (the proportion of the moon visible), b) wave height in meters, and c) activity (i.e., summed arrivals, departures, and vocalizations in one-night long observation periods, shown as means of three nights of observations ± 95% CI) at four formerly occupied breeding sites (including the distance from the active colony site at McPherson Point) at Langara Island, British Columbia during silent (white areas) and playback (shaded grey areas) observations in 2007 and 2008.
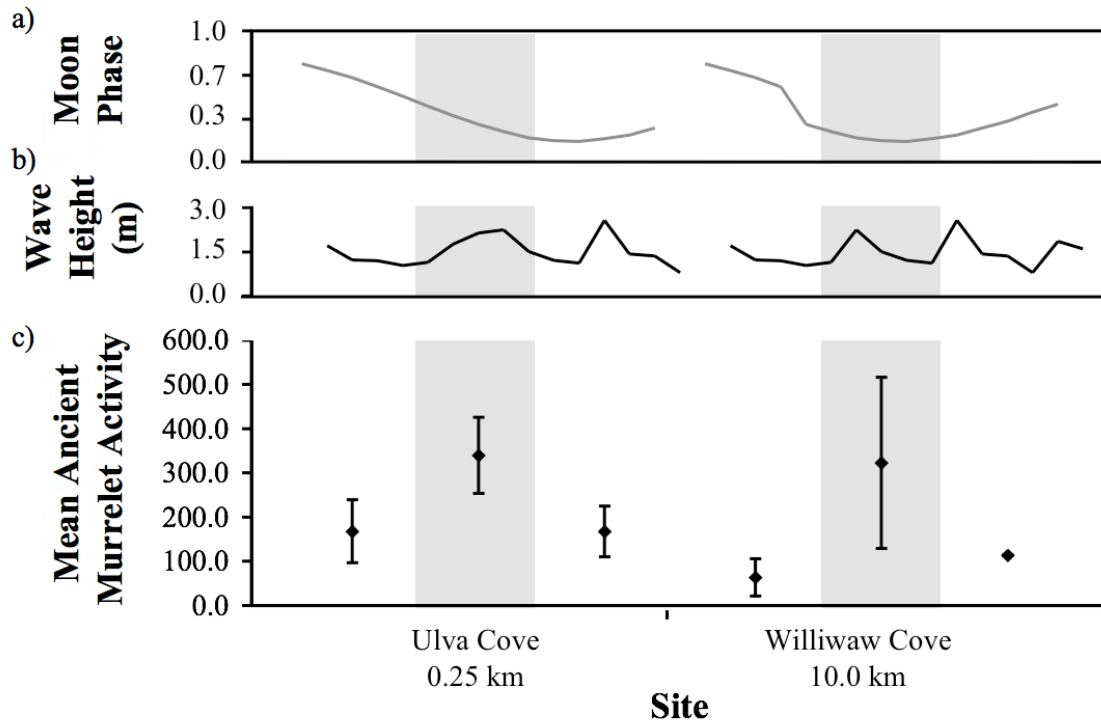
Figure 4.3 Summary of a) moon phase (the proportion of the moon visible), b) wave height in meters, and c) activity (i.e., summed arrivals, departures, and vocalizations in one-night long observation periods, shown as means of five nights of observations ± 95% CI) at two abandoned colony sites in the Aleutian Islands (Ulva Cove, Amatignak Island and Williwaw Cove, Little Sitkin Island); including distance from the nearest active colony site during silent (white areas) and playback (shaded grey areas) observations in 2008.
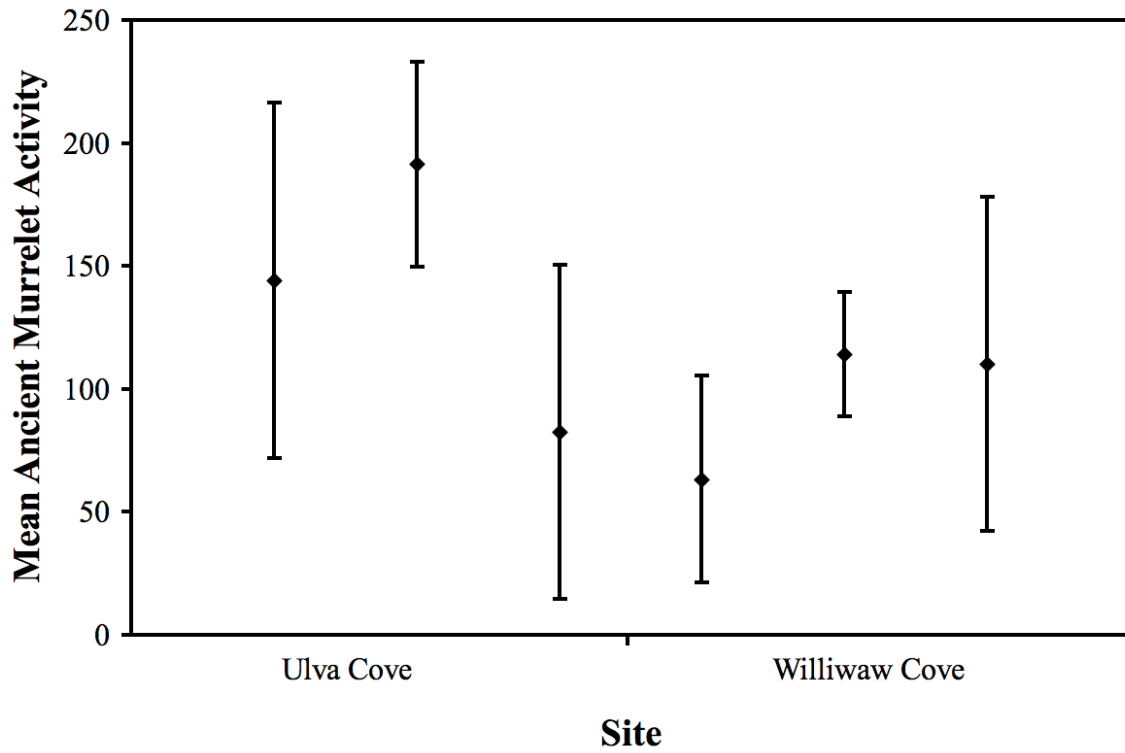
Figure 4.4 Summary of Ancient Murrelet activity (summed arrivals, departures, and vocalizations) in one-night long observation periods, shown as means of five nights of observations ± 95% CI, during three silent observations at two abandoned colony sites in the Aleutian Islands (Ulva Cove, Amatignak Island and Williwaw Cove, Little Sitkin Island) in 2008.

APPENDICES

Appendix A: Summary of documented seabird status and trends post- predator eradication.

Island	Species	Recolonization	Change in:		Source Publication
			Reproductive Success	Population Size	
Ailsa Craig	Atlantic Puffin (*Fratercula arctica*)	Y	-	-	(Zonfrillo and Nogales 1992, Zonfrillo 2002)
	Black Guillemot (*Cepphus grille*)	Y			
Aleutians	Whiskered Auklet (*Aethia pygmaea*)	-	-	↑	(Williams et al. 2003)
Anacapa	Pigeon Guillemot (*Cepphus columba*)	Y (possible)	-	-	(Whitworth et al. 2005, Jones et al. 2006)
	Xantus's Murrelet (*Synthliboramphus hypoleucus*)	-	-	↑	
	Cassin's Auklet (*Ptychoramphus aleuticus*)	Y (possible)	-	-	
Ascension	Maderiran Storm-Petrel (*Oceanodroma castro*)	-	No change	No change	(Hughes et al. 2008, Ratcliffe et al. 2009)
	Ascension Frigatebird (*Fregata aquila*)	-	No change	No change	
	White-tailed Tropicbird	-	-	↑	

	(*Phaethon lepturus*)				
	Red-billed Tropicbird	Y	-	-	
	(*Phaethon aethereus*)				
	Masked Booby	-	-	↑	
	(*Sula dactylatra*)				
	Brown Booby	-	-	↑	
	(*Sula leucogaster*)				
	Red-footed Booby	-	No change	No change	
	(*Sula sula*)				
	Sooty Tern	-	-	↑ (ns)[1]	
	(*Sterna fuscata*)				
	Black Noddy	-	No change	No change	
	(*Anous minutes*)				
	Brown Noddy	-	-	↑	
	(*Anous stolidus*)				
	White Tern	-	No change	No change	
	(*Gygis alba*)				
Baker	Lesser Frigatebird	Y	-	-	(Forsell 1982)
	(*Fregata ariel*)				
	Masked Booby	Y	-	-	
	(*Sula dactylatra*)				
	Sooty Tern	Y	-	-	

	(*Sterna fuscata*)				
	Brown Noddy	-	-	↑	
	(*Anous stolidus*)				
Cabbage Tree	Gould's Petrel (*Pterodroma leucoptera*)	-	↑	↑	(Priddel and Carlile 2009)
Clipperton	Masked Booby (*Sula dactylatra*)	-	-	↑	(Pitman et al. 2005)
	Brown Booby (*Sula leucogaster*)	-	-	↑	
Congreso	Cory's Shearwater (*Calonectris diomedea*)	-	↑	-	(Igual et al. 2006)
Cousine	Sooty Tern (*Sterna fuscata*)	Y	-	-	(Burger and Lawrence 2001, Samways et al. 2010)
	White Tern (*Gygis alba*)	-	-	↑	
Fregate	Sooty Tern (*Sterna fuscata*)	-	↑	↑	(Feare 1999, Merton et al. 2004)
	Brown Noddy (*Anous stolidus*)	-	↑	↑	
Handa	Northern Fulmar (*Fulmarus glacialis*)	-	No change	No change	(Stoneman and Zonfrillo 2005)

	European Storm-Petrel (*Hydrobates pelagicus*)	Y (possible)	-	-	
	Mew Gull (*Larus canus*)	-	-	↑	
	Common Tern (*Sterna hirundo*)	-	↑	-	
	Arctic Tern (*Sterna paradisaea*)	Y	↑	-	
	Black Guillemot (*Cepphus grille*)	-	No Change	No Change	
	Atlantic Puffin (*Fratercula arctica*)	Y	↑	-	
Hardy	Audubon's Shearwater (*Puffinus lherminieri*)	-	↑	-	(Lorvelec and Pascal 2005)
	Bridled Tern (*Sterna anaethetus*)	-	↑	-	
	Brown Noddy (*Anous stolidus*)	-	↑	-	
Ilheu da Priai	Common Tern (*Sterna hirundo*)	-	-	↑	(Groz and Pereira 2005)
	Roseate Tern (*Sterna dougallii*)	-	-	↑	

Island	Species				Reference
Langara	Ancient Murrelet (*Synthliboramphus antiquus*)	-	-	↑	(Regehr et al. 2007)
	Cassin's Auklet (*Ptychoramphus aleuticus*)	Y	-	-	
Lavezzu	Cory's Shearwater (*Calonectris diomedea*)	-	↑	-	(Thibault 1995, Lorvelec and Pascal 2005, Pascal et al. 2008)
Lord Howe	Black-winged Petrel (*Pterodroma nigripennisl*)	Y	-	-	(Hutton and Priddel 2002, Priddel et al. 2003, Hutton et al. 2007)
	Little Shearwater (*Puffinus assimilisl*)	Y	-	-	
	Black Noddy (*Anous minutes*)	Y	-	-	
Malban	European Storm-Petrel (*Hydrobates pelagicus*)	Y	-	-	(Lorvelec and Pascal 2005)
Marion	Blue Petrel (*Halobaena caerulae*)	-	↑	-	(Cooper et al. 1995)
	Great-winged Petrel (*Pterodroma macroptera*)	-	↑	-	
	White-chinned Petrel (*Procellaria aequinoctialis*)	-	No change	No change	
Mokoli'i	Wedge-tailed Shearwater	-	↑	-	(Smith et al. 2006)

	(*Puffinus pacificus*)				
Moutohora	Grey-faced Petrel (*Pterodroma macroptera*)	Y	↑	-	(Imber et al. 2000)
Natividad	Black-vented Shearwater (*Puffinus opisthomelas*)	-	-	↓ mortality	(Keitt and Tershy 2003)
Possession	White-chinned Petrel (*Procellaria aequinoctialis*)	-	↑	-	(Bried and Jouventin 1999, Jouventin et al. 2003)
Raoul	Black-winged Petrel (*Pterodroma nigripennis*)	Y	-	-	(Ismar et al. 2010)
Saint-Paul	MacGillivray's Prion (*Pachyptila macgillivrayi*)	Y	-	-	(Micol and Jouventin 2002)
	Great-winged Petrel (*Pterodroma macroptera*)	Y	-	-	
Selvagem Grande	Cory's Shearwater (*Calonectris diomedea*)	-	↑	-	(Zino et al. 2008)
Titi	Flesh-footed Shearwater (*Puffinus carneipes*)	-	No change	No change	(Gaze 2000)
	Sooty Shearwater (*Puffinus griseus*)	-	No change	No change	

Appendix B: Summary of the islands, years surveyed, and survey metrics used to estimate colony and population size for Ancient Murrelets at six introduced predator-free islands and introduced predator-impacted Langara Island.

Island	Year	Area Interpolated (ha)	Number of Transects Surveyed	Distance between Transects (m)	Number of Quadrats Surveyed	Distance between Quadrats (m)	Quadrat Size (m^2)	Occupancy Rate
East	1985	22.92	4	200	42	30	49	0.63
Copper	2003	22.92	4	200	39	30	49	0.69
Frederick	1980	258.13	28	50-1000	268	45	25	0.54
	1998	258.13	24	200-1000	242	30	25	0.73
	2005	258.13	24	200-1000	244	30	25	0.40
George	1985	31.57	4	200	67	30	49	0.77
	1996	31.57	4	75-300	65	30	49	0.81
Helgesen	1986	39.32	11	75-100	49	15 & 30	9 & 25	0.63
	1993	39.32	11	75-100	62	15	25	*Unknown
	2004	39.32	11	75-100	50	15	25	*Unknown
Langara	1981	436.10	9	50-1000	55	40	25	0.26
	1988	436.10	16	200-700	109	40	25	0.38
	1993	436.10	15	200-700	84	40	25	0.36
	1999	436.10	15	200-700	74	40	25	0.39
	2004	436.10	15	200-700	92	40	25	0.63

Lihou	1986	46.84	14	75-200	106	30	25 & 49	0.63
	1993	46.84	14	75-200	116	30	25	*Unknown
	2004	46.84	7	70-300	61	15 & 30	25	*Unknown
Little	1986	2.02	4	75	18	15	9	0.63
Helgesen	2004	2.02	4	75	13	15	25	*Unknown

[*]Unknown occupancy rates were assumed to be 0.63, as is the mean Ancient Murrelet occupancy rate in British Columbia (Rodway et al. 1988)

Appendix C: Summary of island area and survey parameters for 12 introduced predator-free islands and introduced predator impacted Langara Island.

Island		Area (ha)	Number of Transects	Distance between Transects (m)	Maximum Transect Length (m)	Number of Quadrats	Quadrat Size (m^2)	Distance between Quadrats (m)
Agglomerate		22.9	2	200	200	20	25	20
Alder		56.5	6	200	600	86	49	30
Bolkus		62.1	4	200	510	38	49	30
East Copper		29.9	4	200	420	38	49	30
Frederick		492.1	28	80-500	1170	250	25	45
George		38.5	4	150	660	65	49	30
House		32.9	5	138	560	43	49	40
Jeffrey		7.3	1	*n/a	240	8	49	30
Langara	1981	3105.0	30	600-1000	400	163	25	40
	2007		28	600-1000	400	131	25	50
Lihou		73.3	14	100 & 200	240	80	25 & 49	30
Ramsay		1622.8	44	200	960	372	49	30
Rankine		55.2	6	150	810	102	25	30
Skincuttle		11.9	3	150	180	16	49	30

* only one transect across island

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