BREEDING ECOLOGY OF RADIO-MARKED MARBLED MURRELETS

(*BRACHYRAMPHUS MARMORATUS*) IN DESOLATION SOUND,

BRITISH COLUMBIA

by

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ABSTRACT

Understanding the population biology of a species requires thorough study of its breeding behaviour and success. The Marbled Murrelet is a small alcid seabird which cryptically nests at inland sites in old-growth trees. Concern for murrelet populations, primarily from breeding habitat loss, has led to listing of the species as threatened or endangered over most of its range. However, because of its elusive breeding, reproductive ecology of Marbled Murrelets is still poorly understood. I investigated the breeding ecology of radio marked Marbled Murrelets in Desolation Sound, British Columbia. Movement patterns of radioed birds showed that breeding state and success can be accurately inferred with radio telemetry. Male breeding birds visited their nests, and likely provisioned young, more than females during chick rearing. The male bias was primarily due to a reduction in female visitation during late chick rearing. These findings offer a behavioral explanation for the annual male bias of birds flying inland during the chick rearing period at Theodosia Inlet in Desolation Sound from 1994–1999. Early breeding birds commuted further from foraging areas to nests, and nested at sites of steeper slopes than later breeding birds. Earlier breeding birds were more successful, while higher nest site elevation, steeper nest site slope, and longer commuting distance were all associated with greater success. Data from radio marked birds showed no evidence to suggest that nesting near forest edges, particularly natural edges, reduces reproductive success in Marbled Murrelets. Advantages of steeper nest site slopes and close proximity to edges, like nest site access, may outweigh the potential costs of nest predation in our study location, which is free of human habitation in murrelet breeding areas.

ACKNOWLEDGEMENTS

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GENERAL INTRODUCTION

Marbled Murrelets (*Brachyramphus marmoratus*) are small seabirds of the family Alcidae that occur along the Pacific coast of North America from central California to western Alaska (Nelson 1997). This species is normally found close to shore and is the most common alcid in the sheltered oceans of its range (Gaston and Jones 1998). Marbled Murrelets forage primarily on small schooling fishes during the breeding season, and also on invertebrates during the winter (Burkett 1995). This species, and the closely related Long Billed Murrelet (*Brachyramphus perdix*) of the Russian far east, are unique among the Alcidae because they nest solitarily on the mossy limbs of old-growth trees in coastal forests (Nelson 1997). Birds are active at nests primarily at dusk and dawn, and their breeding habits have been extremely difficult to study (Cooke 1999). Because of this cryptic behaviour, much of the breeding ecology and demography of Marbled Murrelets remains poorly known (Nelson 1997, Cooke 1999, Cam et al., in review). Not only is the biology of the species poorly understood, but there are many potential threats to both its nesting and marine habitats. As a consequence, it was listed as threatened south of Alaska and endangered in California (Nelson 1997).

Because of management concerns and lack of knowledge regarding breeding biology, there was a strong need to conduct an intensive study of Marbled Murrelet demography (Ralph et al. 1995). A large scale capture-mark-recapture study of murrelets was initiated in Desolation Sound, British Columbia in 1994 (Cooke 1999). Desolation Sound is located ~150 km NW of Vancouver and is characterized by deep glacial fjords. The surrounding coniferous temperate rainforests are primarily in steep sided glacial river valleys. Commercial forestry has operated in the area for over a century and the majority of low elevation old-growth stands have been removed. An early goal of the study was to use radio telemetry to locate murrelet nests and study

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breeding ecology in a large sample of individually marked birds. However, early attempts were largely unsuccessful due to incorrect assumptions about timing of breeding in murrelets. In 1998, after changes were made to capture techniques and timing, new efforts yielded 23 nests from 40 radios (Lougheed and Boyd, unpublished data), showing that the method could be useful in investigating the breeding biology of individually marked birds. Thus, telemetry research was increased in the following years, to produce the largest sample of Marbled Murrelets with known nest sites and breeding success ever studied.

My goal in this thesis was to investigate Marbled Murrelet breeding ecology from a large sample of radio-marked birds in Desolation Sound from 1998 to 2001. Chapter 1 describes our telemetry methodology used to infer breeding state and success, as visual observation of all nests was logistically impossible. I address the reproductive success estimates, and the biases and reliability associated with those inferred estimates. In Chapter 2, I address how telemetry methodology allowed us to investigate the behavioural ecology of chick rearing Marbled Murrelets. I examine the sex ratio of nest visitation in chick rearing birds to test the hypothesis that a 1.8:1 male sex bias in birds flying inland in our study area (Vanderkist et al. 1999) may have been caused by male biased provisioning. In Chapter 3, I examine our results for breeding success in relation to marine and terrestrial habitat use by the birds.

CHAPTER 1. INFERRING BREEDING SUCCESS THROUGH RADIO TELEMETRY IN THE MARBLED MURRELET

1.1 INTRODUCTION

When studying the population ecology of a given species, it is essential to assess reproductive success. This assessment is relatively straightforward for many species: investigators locate large numbers of breeding individuals and identify breeding state and success by direct observation (Clutton-Brock et al. 1982, Cooke et al.1995). However, some species cannot be studied in this way. They may be too cryptic, use breeding habitats inaccessible to humans, or be too sensitive to disturbance. Few studies assess reproductive status indirectly using physiological (Vanderkist et al. 2000) or behavioural (Green et al. 1997) approaches.

Radio telemetry allows remote monitoring of free-ranging animals (White and Garrott 1990). Radio and satellite telemetry has permitted extensive study of habitat use (Aebischer et al.1993, Ganey et al. 1998, Polovina et al. 2000), movement (Thompson et al. 1996, Hughes et al. 1998), survival (Bunck and Pollock 1993, Hellgren et al. 2000), and population estimation (Ries et al.1998, Landa et al.1998). However, few studies have used telemetry to directly estimate breeding success. One example is that of Green et al. (1997), who described timing of breeding, duration of breeding stages, and mortality rates of clutches and broods of the cryptic corncrake (*Crex crex*) using telemetry data.

Cryptically breeding species often have poorly understood reproductive ecologies. This makes management decisions difficult due to uncertainty about the status of populations and their habitat preferences. Without such information, it is virtually impossible to develop an unbiased understanding of population demographics. While demographics are most sensitive to rates of adult survival in long lived animals, for threatened or endangered species, a conservation

strategy developed without knowledge of breeding propensity and reproductive success might not fully address management needs (Ralph et al. 1995, Meretsky et al. 2000, Sutherland 2001).

In this paper, we describe a methodology to assess breeding status and success indirectly based on presence and absence of radio marked birds in marine (foraging) and forest (nesting) habitats. The Marbled Murrelet (*Brachyramphus marmoratus*) is a small Pacific seabird in the family Alcidae which is difficult to study because it nests cryptically. Nests are located in relatively inaccessible habitats, primarily large trees in coastal old-growth forest (Nelson 1997). Concern for the Marbled Murrelet has grown in recent years due to suspected population declines over much of the species' range, the near-shore waters of Alaska to central California. These suspected declines have been associated with loss of nesting habitats by forestry activities (Nelson 1997). However, a lack of basic information on population and breeding biology for this species has hampered our knowledge of the status of populations and the development of management and conservation policy (Ralph et al. 1995).

Based on the knowledge that Marbled Murrelets' incubation shifts last 24 hours (Nelson 1997, this study), we predict that individuals alternate between nest sites and marine foraging habitat daily during the incubation stage. If we detect a bird at its nest site on day i, we expect to find it on the ocean on day $i + 1$, and vice versa. We used patterns of presence of marked individuals in foraging or nesting habitats and their movement between locations to determine reproductive status. The time period during which an individual alternates daily between locations provides evidence of incubation and its success. After hatching, the pattern of presence of adult birds at their nest sites for feeding trips can be used to infer chick rearing and its success. The objectives of this paper are to assess Marbled Murrelet reproductive success through radio telemetry and possible biases in this indirect approach.

1.2 METHODS

Breeding Biology

This study was conducted at Desolation Sound, British Columbia, Canada (50 05'N, 124 40'W) (Figure 1.1). Birds on the ocean in our study area prior to nesting include breeders and non-breeders (Vanderkist et al. 2000). Birds feed in the ocean, primarily on pacific sandlance (*Ammodytes hexapterus*), for self-maintenance and chick provisioning (Carter and Sealy 1990, Lougheed 2000). Most birds start nesting in April and May (Lougheed 2000, McFarlane Tranquilla 2001). They lay one egg and incubate for approximately 30 days, with males and females taking equal 24 hour incubation shifts, switching duties at dawn (Sealy 1975, Nelson 1997, this study). Unlike most alcids, breeding is asynchronous, both in our study area (Lougheed 2000) and across the range of the species (Nelson 1997). After incubation failure, adults return to the sea but may continue some inland activity (R. Golightly, pers. comm.).

During the chick rearing period, adults are generally absent from nest sites during the day, and provision young primarily at dawn and to a lesser extent at dusk (Nelson 1997, Bradley et al. 2002). Some non-breeding birds visit inland sites possibly prospecting for future nest sites (Nelson 1997, Bradley et al. 2002). Breeding birds in our area often commute long distances from foraging to nesting sites, sometimes greater than 100 km each way (Hull et al. 2001). Chick rearing lasts approximately 30 days (Bradley et al. 2002) but periods up to 40 days have been reported for the species (Nelson 1997). Upon fledging, chicks fly to sea (Nelson 1997).

Capture and Radio-Marking of Birds

One hundred and ninety adult Marbled Murrelets were captured in Desolation Sound from April to early June from 1998-2000 (n=40 in 1998, 100 in 1999, and 50 in 2000). A further 25 birds were captured in 2000 in Toba Inlet (50 25'N,124 37'W), located ~35km NW of Desolation

Sound. Birds were captured from small boats at night using a "dip-netting" technique

(Whitworth et al. 1997, Vanderkist et al. 1999) and fitted with radio transmitters attached to a

subcutaneous anchor (Advanced Telemetry Systems, Isanti MN – Model 394 in 1998 and Model

386 in 1999 and 2000) following methods of Newman et al. (1999). However, we attached radios

without anesthetic and used a small amount of epoxy (Bird Adhesive, Titan Corporation, USA)

to secure the transmitter to body feathers. Model 394 radios weighed 2.2 grams and had an

insured life of 45 days while Model 386 radios weighed 3.0 grams and had an insured life of 80

days. The actual transmitter lifespan was often well in excess of the insured lifespan. Most

radioed birds were captured prior to breeding (McFarlane Tranquilla 2001), though 8% of known

nesters had already begun incubation at the time of capture.

Aerial Telemetry Tracking

Once radios were attached, each bird was located as often as possible until the transmitter failed,

the radio fell off, or the bird died or left the area. Marine and inland locations were determined

by over 350 hours of helicopter telemetry from early May until early August from 1998 to 2000

(see Hull et al. 2001 for methodology in 1998). A Robinson 44 piston engine helicopter, with H

antennas mounted at 45° on brackets at the anterior ends of the helicopter struts, was used in

1999 and 2000. Two types of helicopter search flights were conducted.

"Water flights" obtained general marine locations of individuals and determined whether

radioed birds were present in a standardized marine search area (Figure 1.1). These flights were

conducted daily for the majority of the breeding season, and were reduced in frequency when all

known nesting radioed birds were well advanced in chick rearing. These flights ranged in

altitude from 300m in poor conditions to 1500m in good conditions. Field trials indicated

detection distance in good conditions was a minimum of 5km. These "water flights" were

supplemented by stationary telemetry from a mountain peak (elevation ~4200ft) using a

handheld Yagi 3D antennae (Advanced Telemetry Systems, Isanti, MN) over open stretches of

ocean. Marine detections from the entire breeding season verified whether radios of nesting birds

continued to function properly. Therefore, telemetry data from chick rearing birds visiting their

nests could be accurately assessed.

"Nest search flights" searched inland for nesting sites of birds not present on the ocean.

Flights ranged from 1500-3000 m in altitude, and detection distances in good weather exceeded

10km. When an inland signal was detected, the location of the signal was determined to an area

~100m x 100m in size. This range was determined from blind trials of aerial locations of test

radios with known position. Ground based telemetry was then used to locate the nest tree in

which the radio-marked bird was incubating. Not all nests stands could be reached with ground

telemetry, since many were located in or adjacent to exceptionally steep or dangerous terrain, or

were remote from suitable helicopter landing locations.

Land Based Telemetry Tracking

In order to detect birds flying between nests and their feeding areas, we conducted ground-based

telemetry observations along likely inland travel routes, often close to nest sites. In this way we

could monitor adult nest visitation during chick rearing. It was logistically impossible to monitor

each nest at the end of chick rearing due to equipment and personnel restrictions, and the

breeding asynchrony of the birds. Therefore, our monitoring activities, lasting 2 –15 days at each

nest site, took place between 10 days after estimated hatch and the end of chick rearing. We

define breeding success estimated from this activity as "Mid-Chick" rearing success and examine

the potential biases of this method in comparative analyses between nests we could only monitor

remotely and those accessible nests which we could examine at the end of the breeding season. Detailed methodology for this nest site monitoring is described in Bradley et al. (2002).

Tree Climbing at Accessible Nest Sites

To confirm the fate of nests, accessible nest trees were climbed after the breeding season (Hamer et al. 1994). Nests assumed to have fledged a chick show a pronounced fecal and down ring around the nest cup (Nelson 1997, Manley 1999). Nests assumed to have failed in chick rearing showed signs of hatch, egg shell fragments with albumen, and usually signs of chick activity - a small amount of feces or presence of a dead chick, but no large fecal ring and down. Nests which failed during incubation showed no murrelet feces or down, no evidence of hatch, and usually the presence of a predated or unhatched egg.

Statistical Analyses

All analyses were conducted within a framework designed to start with nesting birds for which we had the most data and extrapolate backwards to assess certainty in our behaviour based inferences. Therefore, all radioed birds used in these analyses fall into one of three categories: 1), breeding birds for which we obtained good marine detection data, located the nest site from helicopter telemetry, conducted telemetry observations of nest visits during chick rearing, and climbed the tree to assess nesting success. 2), breeding birds for which we have all the data from the first category, excluding tree climbing results as the sites were inaccessible to ground based telemetry, and 3) birds for which we had no inland nest detections but only marine detection data. Eight birds were excluded from the analyses because they had very few (< ten) marine detections throughout the monitoring period.

Initiation of Breeding.--We assessed behavioural data from radio-marked birds in the early stages of breeding to 1) infer breeding birds and the initiation of incubation, 2) differentiate

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breeders from non-breeders, and 3) investigate bias in our methodology. We observed an attendance pattern in breeding birds associated with a 24 hour incubation shift of each breeding bird. This pattern is a consecutive 2 day presence – absence pattern of detection on the ocean, referred to here as an "On-Off pattern" (OP) (Figure 1.2). For example, an OP value of 4 would correspond to a consecutive 8 day presence – absence pattern of a bird on the ocean. We wanted to quantify this pattern, and its value as an indicator of the start of breeding and of success through incubation.

In breeding birds for which we had fledging success data from climbed trees, and unquestionable proof of a nesting attempt, we examined OP duration during incubation. We then compared the distribution of this behaviour with results from suspected breeding birds with ground inaccessible nests (using SAS Proc Freq with Fisher's 2-tailed exact test). Our goal was to determine whether both samples showed similar OP values. To address the differences in OP between breeders and non-breeders we combined datasets of the two samples of breeding birds. We then compared this combined dataset to OP duration in suspected non-breeding birds.

To assess potential bias in OP values from failing to detect birds on the ocean, we calculated our probability of detecting individuals in our marine survey area from 1999 and 2000 telemetry data. We assumed the only time birds were not in our survey area was when they were incubating. We also developed curves to illustrate the probability of detecting OP by chance under different detection rate scenarios – simulating detection probabilities of 90%, 75%, and 50%. In addition, the day and coverage area of nest search flights affected our likelihood of finding a nest. In many bird species, nests which fail early are less likely to be located (Mayfield 1975). To quantify the length of time needed to locate nests, we developed a logistic probability curve (SAS Proc GENMOD) to determine the probability of locating the nest of a breeding bird

based on the frequency distribution of the OP duration for breeders compared to suspected non-breeders. We also investigated the degree to which each individual was faithful to the OP and whether anomalous incubation shifts were common.

Incubation Success.--We tested for statistical differences between the mean (Mann-Whitney Test, Minitab) and distribution (SAS Proc Freq with Fisher's 2-tailed exact test) of OP in climbed nests of birds which successfully completed incubation and those that failed.

Chick Rearing Success.--We compared the mean dawn (AM), dusk (PM), and total visitation rates of adults per 4 hour monitoring session (Bradley et al. 2002) at their nest sites during the chick rearing period. This was done to investigate the relative rates of visitation for nests assumed to be successful and those assumed to have failed. Since preliminary analyses showed an equal sex ratio in the sample (24 females, 25 males) and no significant effects of year, we pooled data from all sexes and years. Comparisons were made between the following three groups of chick rearing birds (Mann-Whitney tests, Minitab): 1) "Confirmed successful" birds successfully fledged a chick, as inferred by tree climbing observations, 2) "Suspected successful" birds visited their nests regularly during chick rearing, as documented from telemetry results, but had nest sites inaccessible to tree climbing, and 3) "Suspected failed" breeders had nests inaccessible to tree climbing, were assumed to have succeeded through incubation, and visited their nest sites very sporadically or not at all during chick rearing. Nests which were confirmed failures in chick rearing were not included in these analyses due to extremely low sample size (n=4).

1.3 RESULTS

Telemetry results yielded over 8000 detections of Marbled Murrelets on the water and at, or traveling to, their inland breeding areas. Of the 207 radio marked birds used in these analyses, 84

were identified as breeders with their inland nest sites located. Twenty five of these breeders were confirmed based on tree climbing, while the remainder were suspected with unclimbed nest sites. All confirmed nesting trees from ground based telemetry contained one active nest from that year. At all sites where a chick was fledged, the radio-marked adults were detected visiting the nest regularly during the "Mid-Chick" rearing stage. Our cumulative estimated success probabilities for all breeding birds were as follows: incubation success: 82%, "Mid-Chick" Rearing success: 62%, Fledging success: 46%. We also report the annual proportion of radio marked individuals reaching successive stages of reproduction (Table 1.1). Note that the fledging success data were only available from nests in climbed trees. Further discussion of our nesting success and fecundity results for 1998 – 2000 data can be found in Appendix 1.

Initiation of Breeding

For radio-marked birds with confirmed nest sites, where a breeding attempt was certain, we observed extended OP associated with incubation (Figure 1.3). We detected no difference in the OP frequency distributions (Fisher's 2-tailed Exact Test, p=0.535) or means between confirmed and suspected breeders (Mean (SE) Confirmed = 12.24 (0.855), Suspected = 11.097 (0.579), 2-tailed Mann-Whitney test, p=0.172). The OP distribution of birds assumed to be non-breeders, in this analysis defined as birds with no detected nest site, showed most individuals with a maximal OP value of 1, followed by a rapid frequency decrease with increasing OP (Figure 1.4). Conversely, the pooled sample of breeders showed an increase in frequency with greater OP (Figure 1.5). The mean OP for pooled breeders of 11.726 (0.465 SE) was 6.5x greater than the mean of presumed non-breeders of 1.813 (0.215) (2-tailed Mann-Whitney test, p= 0.00001).

We determined no difference in our probability of detecting birds between the different years tested (t =1.37, p=0.173, df =161). Our mean probability of detecting birds on the ocean

throughout the breeding season, assuming they would only be absent when incubating, was 0.65 (Minimum = 0.14, Maximum = 1, Standard Error = 0.03). Using theoretical detection probabilities of 90%, 75%, and 50%, we determined the likelihood of detecting "false" OP by chance due to missed marine detections when the bird was present in the study area (Figure 1.6).

As expected, the probability of finding the nest of a breeding bird increased logistically with OP duration, and a 95% confidence level corresponded to an OP of ~11.5 (23 days) (Figure 1.7). The OP was consistent throughout the incubation period for 87% of our breeding birds. The remaining 13% showed one skipped incubation shift in their 30 day cycle.

Incubation Success

For confirmed, accessible nest sites where trees were climbed (n=25), birds which failed in incubation showed a significantly lower mean OP than successful incubators (Mean (SE), failed = 9.00 (1.74), successful = 14.59 (0.374), 2-tailed Mann-Whitney U, p=0.005) (Figure 1.3). The distribution of OP frequencies for these two groups were significantly different (Fisher's 2-tailed exact test, p=0.0004). The mean OP for birds which successfully completed incubation approximated the 15 OP value that would represent a 30 day incubation period. The two successful birds with OP values of 11 (22 days) both exhibited OP behaviour immediately after capture, as soon as they were radio-tracked.

Chick Rearing Success

During chick rearing, rates of visitation by radioed birds at confirmed, successful nests did not differ from rates of visitation at suspected successful nest sites (Table 1.2). This pooled sample showed significantly higher rates of nest visitation than suspected failed nests (Table 1.2). These results were consistent in data from AM, PM, and total nest visits (Table 1.2). Of the 4 nests that

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were confirmed chick rearing failures, 2 actively attended early in chick rearing but not in the late rearing period, one never attended, and one bird's radio signal disappeared.

1.4 DISCUSSION

Our results on breeding success are the first estimates of reproductive parameters for a Marbled Murrelet population from observations of individually marked birds. These nesting success estimates are higher than or fall in the upper range of previously published values (Hamer and Nelson 1995, Beissinger and Nur 1997, Nelson and Manley pers. comm.). In contrast to the commonly observed high annual variability in seabird productivity (Bertram et al. 2001), our annual parameter estimates for breeding success were relatively consistent. Using aerial radio telemetry data from a large sample of birds, and ground truthed breeding success data in a smaller sample of individuals, we have shown that the behaviour of birds at confirmed breeding sites does not differ from that at inaccessible suspected breeding sites. In addition, we have shown that the behaviour of successful breeders differs significantly from the behaviour of failed breeders and non-breeders. We detected a strong correlation between OP and incubation behaviour. The observed duration of this behaviour did not vary between confirmed and suspected breeders. But, birds that failed during incubation had OP values significantly less than those of successful breeders. During chick rearing, both confirmed and suspected successful nest sites showed mean visitation rates that were significantly higher than failed nests. Therefore, we believe that radio telemetry is a useful tool for inferring key demographic parameters for the elusive Marbled Murrelet, whose breeding behaviour is difficult to observe. However, before concluding that our results give an accurate measure of breeding success variables, we must examine our methodology for potential sources of bias.

Initiation of Breeding

Detecting Early Breeding Failures.--One difficulty in using OP to assess the initiation of breeding is interpreting an OP which occurs for only a few days and no nest is found. A bird showing a very short OP might be a breeder that failed very early in incubation. However, this OP might also have been generated by chance, due to missed marine detections when the bird was present on the ocean. In addition, locating the nest of a bird as soon as it begins breeding can be difficult (Figure 1.7). Therefore, we may be underestimating the proportion of breeders in our population and overestimating overall nesting success, due to our reduced ability to detect early failures. This problem is a common one in evaluating nesting success (Mayfield 1975). However, these potential early failures misclassified as non-breeders would not affect our estimates of fecundity, which is the number of females produced per adult female.

On-Off Patterns Generated by Chance.--One possible alternative explanation for the OP we observed is that it might be associated with random patterns in the data due to missed marine detections of birds on the ocean when they were actually present. This might occur by failing to detect a bird when it was present in our marine search area or temporary emigration of birds outside the study area on certain days.

It is possible that birds were not detected in the marine survey area when they were actually present. Some radios might periodically produce weak signals, due to inherent qualities of that transmitter or the position of the antennae on the bird, as Boyd et al. (2000) noted in studies of Cassin's Auklets using similar radio transmitters. Submergence of the antennae, when birds dive as they forage, stops transmission of the radio signal and might prevent detection. During "water flights", large numbers of radios (n=100 in 1999, n=75 in 2000) were scanned. Each radio was monitored for 2 seconds in a scanning bank, though frequencies were removed from the bank when they were detected. However, a complete scan of all radio frequencies

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would take 2.5 to 3 minutes, and it is possible that a bird could go undetected because the telemetry observer was scanning other frequencies. In areas of large concentrations of radioed birds, attempts were made to make repeated searches to increase detection. Stationary land based telemetry over areas of open water early in search flights also helped to increase marine detections by scanning each frequency slowly.

An underlying assumption of most capture-mark-recapture methods is that animals will remain local to the study area. However, logistics prevented us from searching all potential marine areas daily for radioed birds. Since Marbled Murrelets have been observed to range over 100km between marine and inland sites during the breeding season (Whitworth et al. 2001, Hull et al. 2001), birds might temporarily emigrate to marine sites outside our core search area during incubation. Therefore, some nesting birds which bred within our inland search area may have frequented marine areas outside of our study area and would show OP's of short duration (Figure 1.5). Hull et al. (2001) noted an expansion in range of Marbled Murrelets out of our central Desolation Sound study area during the chick rearing period in 1998. However, this would likely not affect detection of initiation of breeding events. While Marbled Murrelets are marine birds, there have been observations of individuals loafing and foraging on inland lakes (Carter and Sealy 1986). Therefore, one might suggest that lack of detection of birds on the ocean could indicate that many birds spent time foraging at lake sites. However, we detected lake use by murrelets on only 3 occasions in over 120 hours of inland search flights (Centre for Wildlife Ecology, Simon Fraser University, unpublished data), so we believe the effect of any lake use by murrelets on our OP data is minor.

Despite the potential bias of missed marine detections and temporary emigration on our marine detection data, we believe that these factors cannot explain the extended OP we observed

as random events. For each breeding bird used in these analyses, we obtained up to 80 marine detections and saw strong site fidelity to our core marine survey areas of Desolation Sound, across all three years of study (Appendix 2). Multiple estimates of our detection probability of birds on the water, even overly conservative minimum estimates of 50%, would not randomly produce the OP durations we observed (Figure 1.6). Thus, we conclude that our observed extended OPs are accurate indications of incubation behaviour in Marbled Murrelets.

Confounding Effects on Classifying a Breeder Through Radio Telemetry.--Certain attributes of a bird at capture may cause overestimation of non-breeding in our study population through inferred radio telemetry methods. McFarlane-Tranquilla (2001) used analyses of the egg precursor protein vitellogenin to show that some of the radio-marked females in our sample which did not breed, based on telemetry observations, were producing eggs at the time of capture. Therefore, while any capture effect on breeding success appears to be negligible for radioed birds which do go onto nest, estimates of proportions of non-breeders in our population from telemetry alone may be biased high, and parameter adjustments may be necessary for demographic assessment of the population (Appendix 1). The presence of pre-breeders in our sample might also overestimate our proportion of non-breeders. Age of first breeding in Marbled Murrelets is unknown, but most alcids first breed in their third year (Gaston and Jones 1998, Pyle et al. 2001). There are no known age birds in our sample, and juvenile murrelets take on adult appearance after their first basic feather molt (Carter and Stein 1995). Finally, capturing birds much later in the breeding season, after they might have already failed, could also inflate estimates of non-breeding. However, the timing of our capture effort in 1999 and 2000 appeared to complement the timing of egg production in our study population (McFarlane-Tranquilla 2001).

In addition, the functionality of using OP to infer breeding is only applicable to incubating birds. As birds do not often visit nest sites during the day during chick rearing (Nelson 1997), birds with radios attached after they had successfully completed incubation would not be classified as breeders. This is because we would detect no prolonged OP and nest search flights during the day, away from prime chick feeding periods, would not locate birds at their nest sites.

Locating Nest Sites.--Our results suggest that it took 75% of the incubation period to achieve a 95% probability of locating the nest of a breeding bird (Figure 1.7). As previously mentioned, nests which failed early would be less likely to be located. Inland search area also affected our ability to locate nests. While we expended great effort to search most potential nesting areas by helicopter, logistical constraints and the commuting ability of the birds did not allow us to consistently cover all of the area available to murrelets for nesting. Therefore, we were unable to locate the nest sites for a small sample of birds which appeared to be successful during incubation (Figure 1.4).

Incubation Success

Temporal variation in initiation of breeding could affect our interpretation of results using OP duration as a measure of incubation success. The strongest behavioural inference in successfully breeding birds appears to be an OP value of 15 (Figure 1.5) relating to the ~30 day incubation period. However, this pattern would only be observed if the radio attachment and telemetry observations began before the bird initiated netting. Some confirmed breeding birds which successfully completed incubation showed OP values well below 15. In all of these cases, the OP began with the first telemetry observations. This suggests that these birds were already incubating at the time of radio attachment.

We used 30 days as an accurate estimate of incubation duration, but there is variation associated with this mean (Figure 1.5). Because of this variation, as well as the logistical difficulties of starting telemetry observations of chick rearing behaviour immediately after hatch, differentiating between late incubation failure and early chick rearing failure is difficult. Thus, results from birds whose radios were attached later in the breeding season and whose lay dates were likely prior to capture, ~8% of our sample, must be carefully interpreted. Assuming that an observed OP value of 15 was necessary for successful incubation in these birds would lead to an overestimation of incubation failure. Preliminary analyses showed no effect of skipped incubation shifts on incubation success.

Chick Rearing Success

Evaluating "Mid-Chick" Rearing Success.--Results from remote telemetry monitoring at nest sites and along flyways show that birds with successful nests visit their breeding sites, presumably to feed chicks, more often than suspected failures. However, "Mid-Chick" rearing success cannot be confused with fledging success. While tree climbing data show that nest visitation appears to indicate that a nest site is active and a chick is being fed, with limited resources to monitor nests, this observation is only valid at that time in chick rearing. A suspected, inaccessible nest could be identified as successful due to the presence of adults feeding young at day 20 of chick rearing, but that nest might still fail before the offspring fledges. Thus, the "Mid-Chick" rearing success measure is only a proxy of fledging success. However, despite its shortcomings, this "Mid-Chick" measure has great utility in that it allows success measures to be calculated for all nest sites, and not just the smaller sample of ground accessible nest trees.

Since successful nests show higher rates of nest visitation than unsuccessful ones, we assume that nest visitations correspond to chick feeding events. However, some birds may be visiting their nest sites for reasons other than provisioning. These might include visiting failed nest sites, prospecting for new nest sites, or defending territories (Bradley et al. 2002).

One other potential bias in evaluating "Mid-Chick" rearing success is radio failure. To ensure that lack of detection of a chick rearing adult at its nest was true absence, we ensured that radios were still functioning properly. This was done by only assessing "Mid-Chick" rearing success in birds which continued to show marine detections and movements from "water flights" during the same time their nests sites were monitored.

Fledging Success.--Our fledging success estimates are based on data from only 30% of our nest sites. Because we could not access the majority of our nest sites for tree climbing, we might assume that rates of success in the final stage of chick rearing are similar in ground accessible and inaccessible sites. However, recent analyses have shown that higher reproductive success is associated with steeper slopes and higher elevations in our radio-marked birds (Huettmann et al., in review, Chapter 3). This would suggest that fledging success estimates presented here may be biased low, as inaccessible sites are often in steep areas at higher elevation.

1.5 MANAGEMENT IMPLICATIONS

Despite the potential biases in our methodology, these methods have allowed for the first estimation of reproductive success parameters for Marbled Murrelets from marked individuals. Our estimates of breeding parameters from telemetry may slightly overestimate incubation success and the proportion of non-breeders in our sample. This may relate to our relatively high incubation success compared to other estimates for the species. However, we also suggest that our higher reproductive success estimates may be due to the majority of sites in inaccessible

habitats, which have higher reproductive success (Chapter 3) and have been previously unsurveyed for murrelet nests. We have shown how our telemetry results illustrate accurate estimates of fecundity for our population. For unbiased estimates of incubation success, adjustments from physiological data (McFarlane Tranquilla 2001) may be necessary. However, unbiased fecundity estimates are more important in assessing the demography of avian populations than are nesting success data (Thompson et al. 2001).

The breeding success data presented here has been incorporated into demographic models to assess population stability and growth in our study population of Marbled Murrelets (Cam et al., in review). We believe this approach has utility for other cryptically breeding species of concern whose behaviour and movement patterns might be used to assess breeding status and success. Our study and the related demographic studies it has facilitated on Marbled Murrelets are examples of the role that behavioural studies can play in conservation biology (Sutherland 1998).

1.6 APPENDIX 1. Breeding Success and Fecundity Estimates for Desolation Sound Marbled Murrelets 1998-2000

METHODS

We used the Kaplan-Meier estimator (1958) to estimate success at different stages, and defined the following intervals: (1) initiated a breeding attempt, (2) hatching, (3) "mid-chick" stage, and (4) fledging. Nesting success is the probability that an individual that initiated a breeding attempt fledges a chick (stages 2 to 4). Breeding success is the probability that an individual fledges a chick (stages 1 to 4). We chose the Kaplan-Meier estimator because transmitters that fail can be censored (White & Garrot 1990).

Based on the entire sample of radio-tagged individuals (160 individuals whose breeding status could be determined), the average proportion of individuals that did not initiate a breeding attempt over the 3 years was equal to 0.375.

Nonbreeding in individuals that previously bred has been observed in many seabirds, but our value seemed inordinately high given that most studies have shown that such high proportions of adult nonbreeders (e.g., 0.40) are observed in exceptional years only (Aebischer & Wanless 1992, Chastel et al. 1995, Cam et al. 1998). This value is unlikely to be representative of typical conditions. There are 3 probable reasons for this; a) our sample includes prebreeders, which should not be included in fecundity estimates and b) there is evidence that our sample has a naturally high rate of renesting which is difficult to detect with telemetry methods (McFarlane-Tranquilla pers. comm.) and c) capturing activities may inhibit birds from breeding in a few cases (McFarlane-Tranquilla 2001). Because of this, we used 2 values (0.05; 0.20) for the proportion of nonbreeders consistent with a large survey of demography in alcids by Hudson (1985).

The measure of productivity required in matrix models is fecundity: the number of females produced per adult female (Caswell 2000). We defined fecundity as the number of females leaving the nest per radio-tagged adult female. We assumed a sex ratio of 1:1 in adults (Vanderkist et al. 1999). Fecundity was thus computed as: [(proportion of adults that initiated a breeding attempt)*(nesting success)] / 2, assuming that sex ratio is the same at fledging.

RESULTS

Based on the telemetry data, if we consider only individuals that initiated a breeding attempt, nesting success was equal to 0.46. Based on the assumption of a proportion of breeders after full recruitment equal to 0.95, the overall breeding success was equal to 0.44. With an assumed proportion of breeders equal to 0.80, breeding success was equal to 0.37. The corresponding fecundity values were 0.22 and 0.18, respectively.

Estimated probability that individuals reach the successive stages of reproduction, based on telemetry data.

Stage	Probability of success at each stage		Cumulative probability (Kaplan-Meier estimates)	
	Estimate	95% CI	Estimate	95% CI
Incubation (2)	0.82	0.74 – 0.90	0.82	0.74 – 0.90
"Mid-chick" (3)	0.76	0.66 – 0.85	0.62	0.53 – 0.72
Fledging (4)	0.73	0.67 – 0.80	0.46	0.37 – 0.54

DISCUSSION

A striking feature of our study is that nesting success estimates are higher than or fall in the upper range of previous published values (Hamer & Nelson 1995, Beissinger & Nur 1997, Nelson & Manley pers. comm.). Several hypotheses can be proposed to explain this. Firstly, we have not considered at-sea juvenile ratios (Beissinger & Nur 1997). These incorporate juvenile mortality after fledging and thus are likely to be lower than other estimates. They also reflect not only the proportion of juveniles observed at sea, but also differences in detection probabilities among age-classes (Lebreton et al. 1992). Juveniles and older individuals may have different behavioral characteristics (Bradley & Wooler 1991; Klomp & Furness 1991). Lougheed (2000) and Parker (pers. comm.) have shown that juvenile and adults have different patterns of behavior after the nesting season; strongly suggesting different detection probabilities.

Secondly some success estimates may be "biased low". It is easier to confirm breeding failure (which occurs earlier in the breeding process) than to confirm success. Individuals that have not been confirmed as having failed cannot be considered as successful. Because of this, "unknown" cases may be more likely to correspond to successful reproduction. Furthermore, our results show that the probability of failure increases as breeders reach later reproductive stages. They show higher success during incubation than previous studies, but similar values during the chick-rearing period. This might reflect the fact that nests found by our approach may be a more random sample in terms of nest location than those from other studies, which depend mainly on nests sighted by observers from accessible locations. The fact that nest sites found in more inaccessible habitats, at steeper slopes and higher elevation, had greater reproductive success (Chapter 3) might also explain our high breeding success values compared to other research in our study area which focused on more accessible nest sites (Manley 1999). Finally, it is possible

that the conditions were particularly favorable for reproduction in the study area between 1998 and 2000.

Table 1.1. Proportion of individuals reaching the successive stages of reproduction, based on telemetry data.

Success (%)	Year		
Stage	1998	1999	2000
Breeding attempt &	70 (33)	64 (79)	54 (48)
Incubation	69 (23) ¥	94 (34)	78 (28)
"Mid-chick"	75 (15)	62 (27)	68 (20)
Fledging	75 (4)	33 (3)	87 (8)

In brackets: sample size

¥ For individual to be included in this total, it must have attempted to first breed. These are probabilities conditional on the fact that the individual reached the previous stage.

Table 1.2. Two tailed Mann Whitney tests comparing visitation rates during the chick rearing of confirmed successful breeders, with climbed nest trees (n =11), suspected successful breeders, without climbed nest trees (n = 29), all successful breeders (confirmed and suspected, n = 40), and suspected failed breeders (n = 9). Comparisons are made for mean nest visitation rates - detections / observation session for AM, PM, and all detections. Standard errors for each sample are reported in parentheses.

Sample 1	Sample 2	Detection Class	Mann-Whitney p value
Confirmed successful 0.567 (0.0673)	Unconfirmed successful 0.623 (0.0426)	All	0.437
Confirmed successful 0.761 (0.0719)	Unconfirmed successful 0.900 (0.0616)	AM	0.190
Confirmed successful 0.350 (0.0924)	Unconfirmed successful 0.389 (0.0668)	PM	0.938
Confirmed successful 0.567 (0.0673)	Unconfirmed failed 0.197 (0.0821)	All	0.006
Confirmed successful 0.761 (0.0719)	Unconfirmed failed 0.343 (0.1310)	AM	0.019
Confirmed successful 0.350 (0.0924)	Unconfirmed failed 0.0500 (0.0500)	PM	0.007
All successful .608 (0.0358)	Unconfirmed failed 0.197 (0.0821)	All	<0.001
All successful 0.862 (0.0494)	Unconfirmed failed 0.343 (0.131)	AM	0.005
All successful 0.378 (0.0542)	Unconfirmed failed 0.0500 (0.0500)	PM	0.001

Figure 1.1. Core marine telemetry coverage areas for 1998 – 2000. Toba Inlet and Desolation Sound capture areas are marked

Toba Inlet

Desolation Sound

Ds_98_coresurvey areas.shp
Ds_2000_coreflightlines.shp
Ds_1999_coreflightareas.shp
Dempoints
Dempoints

30   0   30   60 Kilometers
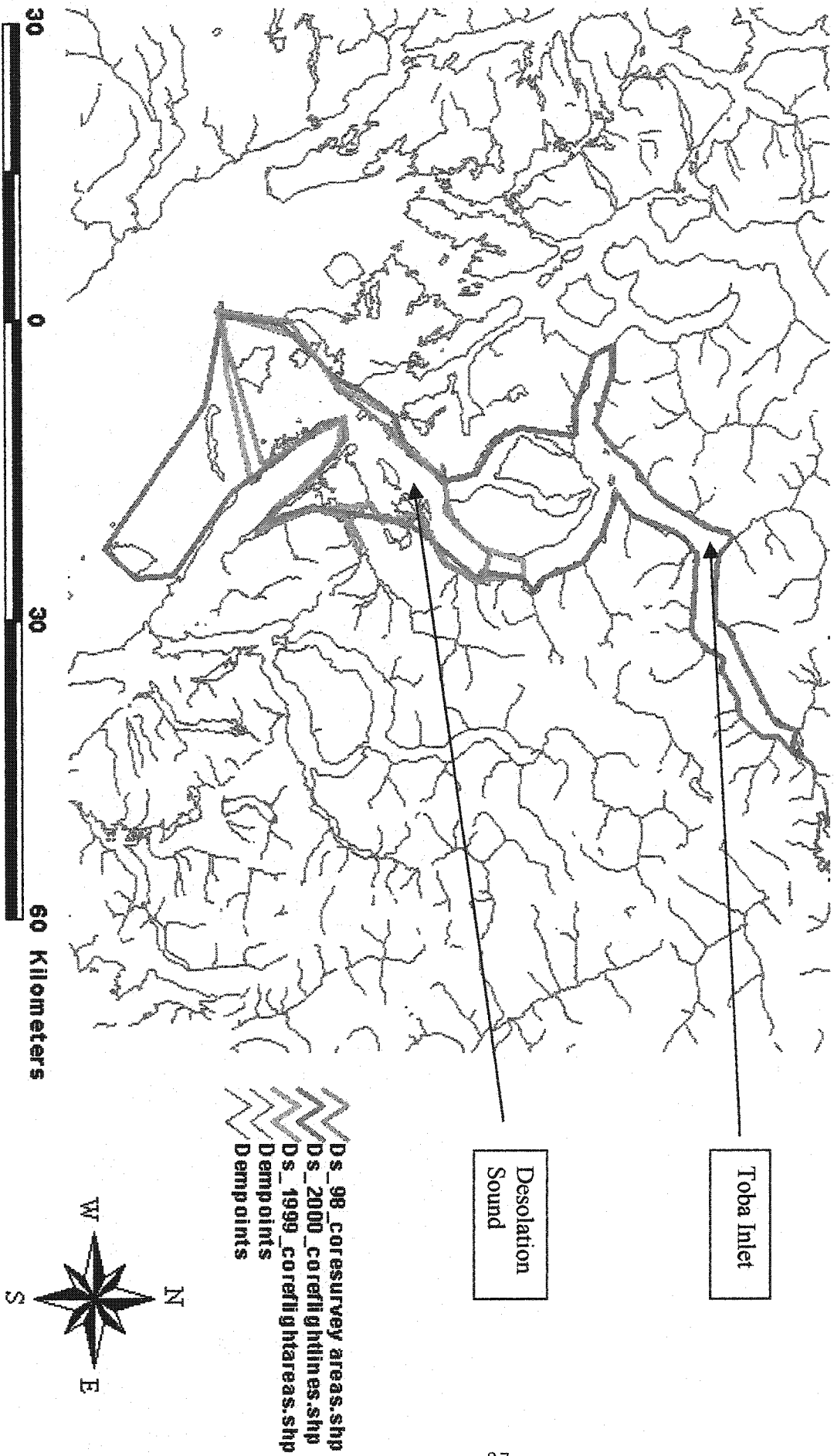
Figure 1.2. Typical On-Off pattern (OP) for Marbled Murrelets during incubation, from 1999

Male 5.254. Unlike most birds, this individual nested close to our camp, so telemetry detections

of the bird on the nest were easy to obtain.
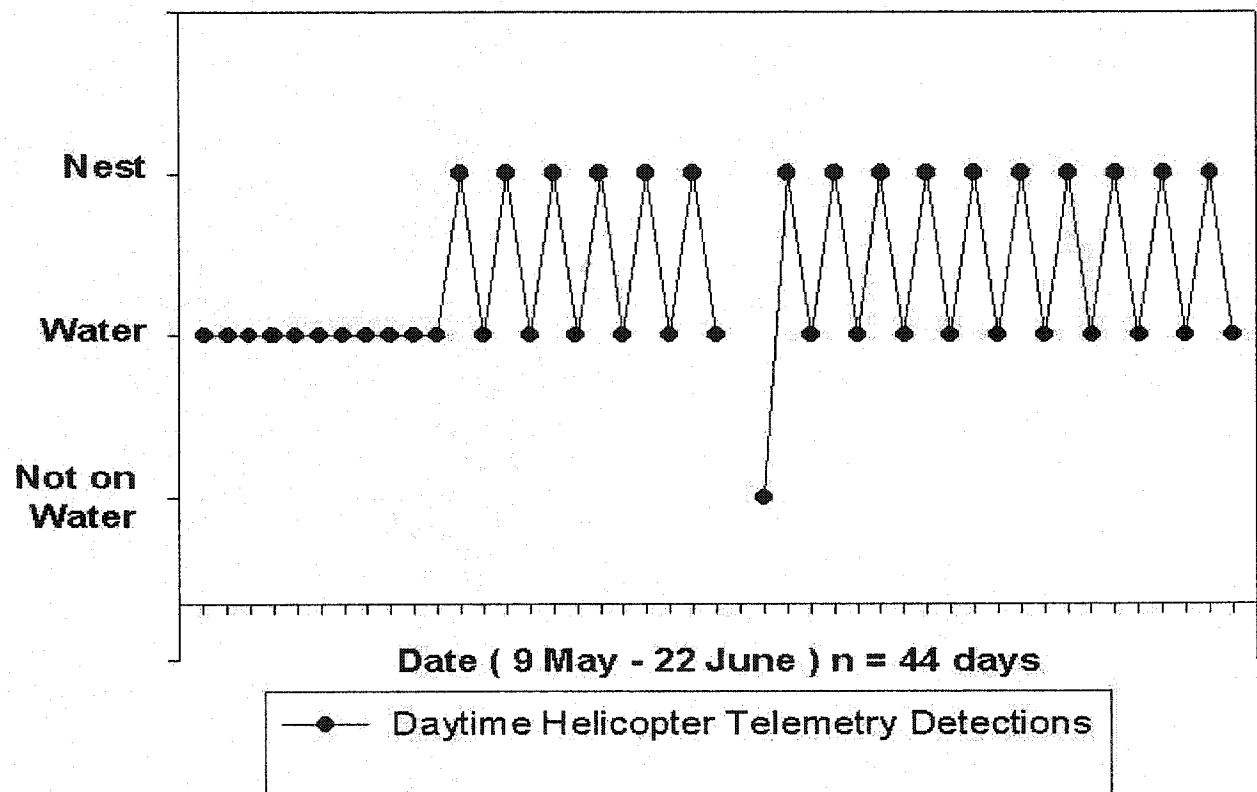
Figure 1.3. On-Off patterns of ocean attendance for failed and successful climbed nests of radio-marked Marbled Murrelets during incubation from 1998 to 2000 (n=25)
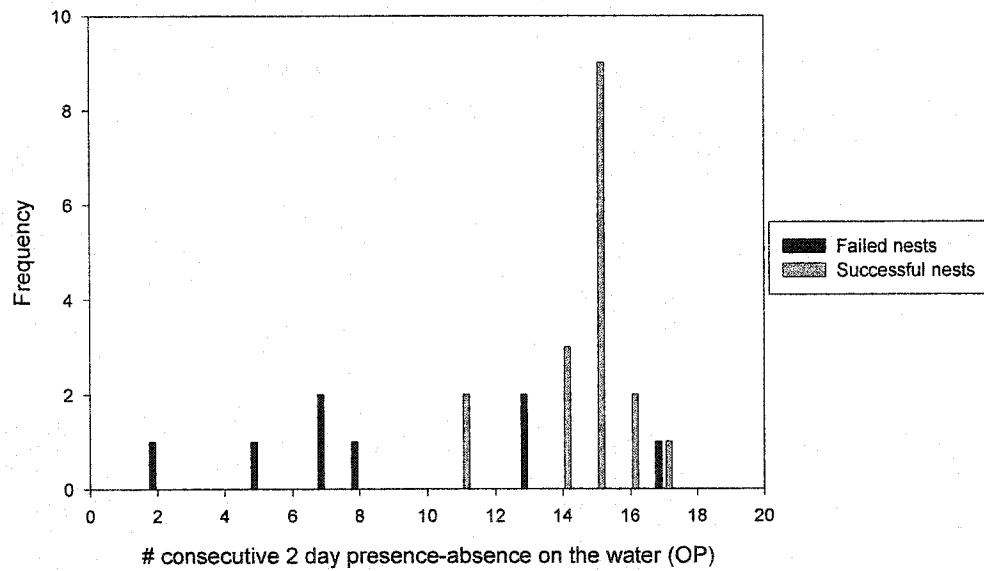
Figure 1.4. Frequency of On-Off patterns (OP) of ocean attendance of Marbled

Murrelets with no nest found (suspected non-breeders) from 1998 to 2000 in

Desolation Sound as % of total sample of breeders and non-breeders (n=207)
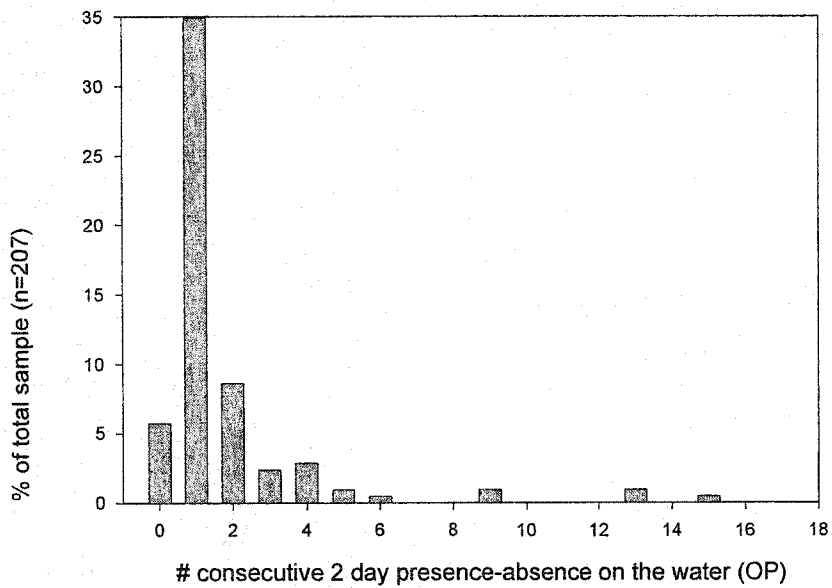
Figure 1.5. Frequency of On-Off patterns (OP) of ocean attendance of breeding

Marbled Murrelets with known nest sites (both confirmed and suspected) from 1998 to

2000 in Desolation Sound as % of total sample of breeders and non-breeders (n=207)
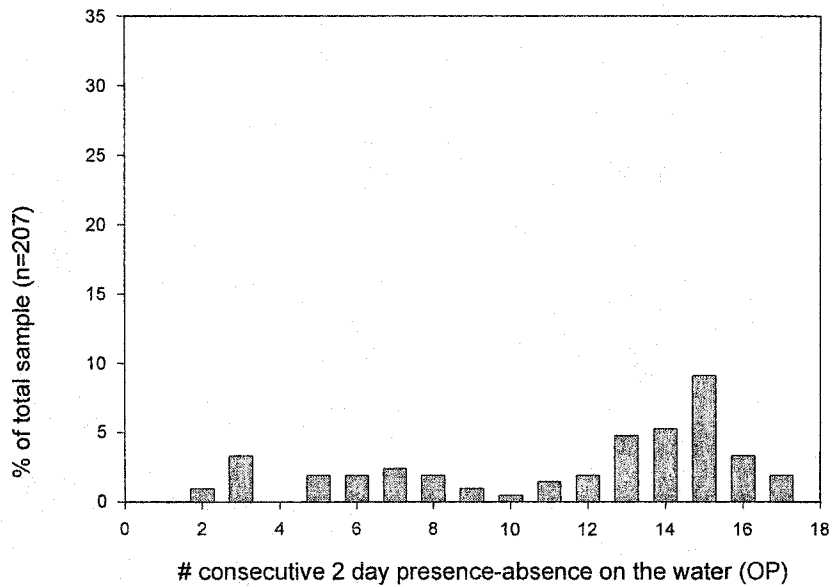
Figure 1.6. Probability (%) of detecting On-Off patterns (OP) by chance, due to

missed detections of birds on the ocean, given the following detection probabilities:

90%, 75%, and 50%.
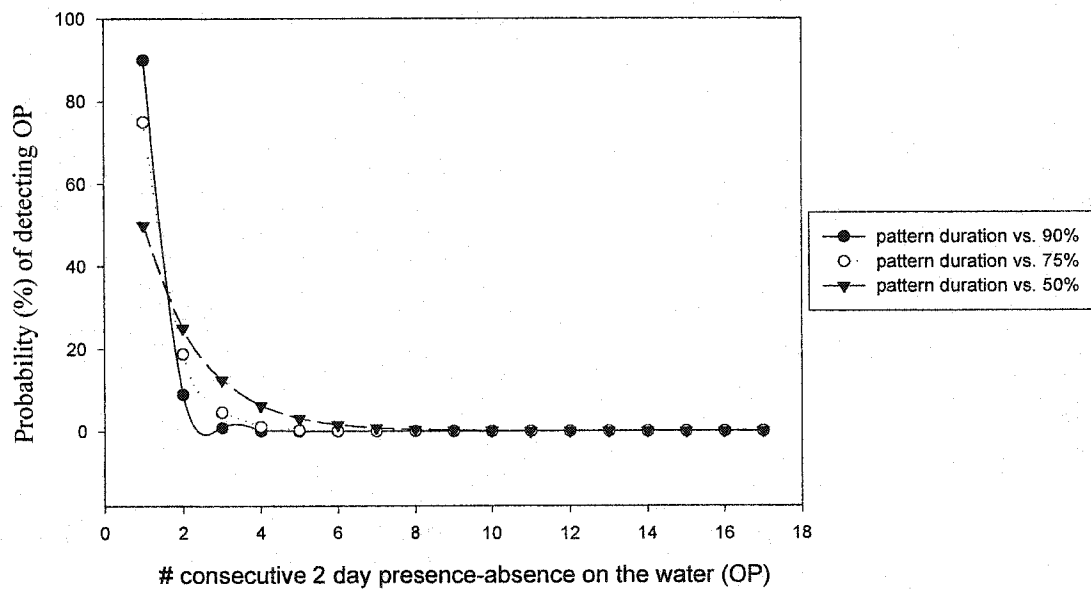
Figure 1.7. Probability of locating the nest of a breeding bird from On-Off pattern duration (OP) in our sample (n=207). Line indicates 95% Confidence Level.
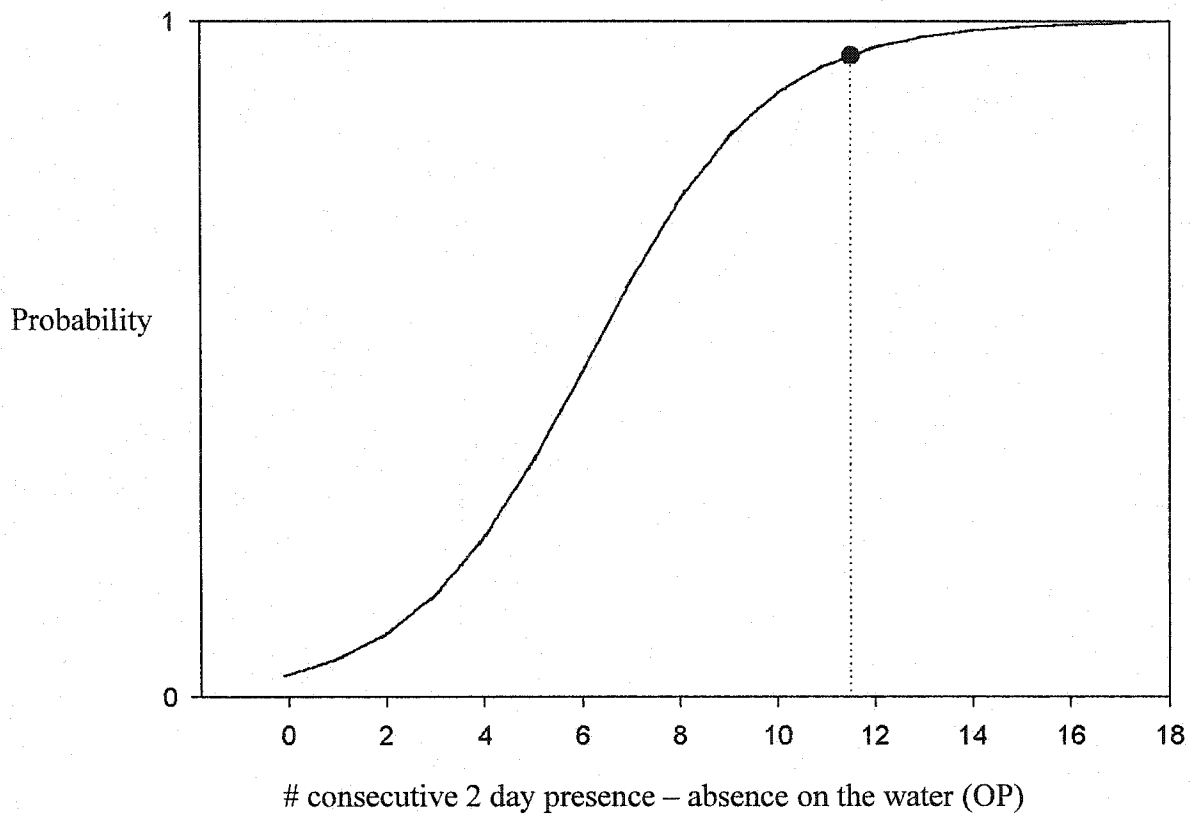
CHAPTER 2. SEX DIFFERENCES IN NEST VISITATION BY CHICK REARING MARBLED MURRELETS[1]

2.1 INTRODUCTION

In altricial birds, biparental care is common. Successful fledging of a chick may often require biparental care where the growth seasons are relatively short, young are usually accessible to predators, and food is widely and unpredictably distributed (Clutton-Brock 1991). However, within biparental bird species, differential provisioning by sex is highly variable. Among passerines, biased provisioning by either sex has been widely documented, as has equal provisioning effort (Pettingill 1970). In monogamous seabirds, total parental investment by males equals and sometimes outweighs that of females (Fasola and Saino 1995). The relative investment by each sex in parental care can reflect trade-offs, energy constraints, and life history strategy for a given species (Roff 1992).

Marbled Murrelets (*Brachyramphus marmoratus*) are nearly unique among alcids and other seabirds in that they nest predominantly at cryptic sites in large, old-growth coniferous trees (Nelson 1997). This species shows no sexual dimorphism and is impossible to sex visually in the field (Hull, Vanderkist, et al. 2001). Thus, there is little information on relative provisioning of young by males and females in this species. However, Vanderkist et al. (1999) suggested that provisioning in Marbled Murrelets may not be equally distributed between male and female parents. They reported a significant male bias in birds captured while flying between

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marine foraging areas and inland nesting areas during July and August, when most breeding birds are feeding young (Lougheed 2000). However, birds captured in marine areas showed no bias in sex ratio (Vanderkist et al. 1999). Analyses of the egg precursor protein vitellogenin indicated only 2% of females ($n = 100$ birds) from the male-biased sample were producing eggs at the time of capture (Vanderkist et al. 2000, L. Tranquilla, unpubl. data). Vanderkist et al. (1999) also reported an increase in the male bias of their capture sample as the breeding season progressed. In this paper we report on relative nest site visits of male and female radio-marked Marbled Murrelets during the chick rearing period in Desolation Sound from 1998–2000. Our aim was to test the hypothesis that the male bias of birds flying inland reported by Vanderkist et al. (1999) was due to an increased level of nest visits by male Marbled Murrelets relative to females. Vanderkist et al. (1999) also suggested an alternative hypothesis that additional males flying inland were nonbreeders prospecting for breeding sites or defending territories.

2.2 METHODS

Adult Marbled Murrelets were captured in Desolation Sound, British Columbia, Canada (50°05′N, 124°40′W) prior to nesting in April and May 1998–2000. Birds were captured from small boats at night using dip nets (Whitworth et al. 1997, Vanderkist et al. 1999) and fitted with subcutaneous anchor radio-transmitters (model 386, Advanced Telemetry Systems, Isanti, Minnesota), following methods of Newman et al. (1999) but without the use of anesthetic. Trace blood samples (<0.1 mL) were taken and birds were sexed after the field season using genomic DNA subjected to PCR amplification (Griffiths et al. 1996, Vanderkist et al. 1999).

Radio-Tracking

Nest locations and incubation status of Marbled Murrelets were determined by aerial helicopter telemetry (Hull, Kaiser, et al. 2001). Daily marine detections of birds from early May to early

August were used to determine the breeding status of each bird and to determine initiation of breeding, as incubating Marbled Murrelet pairs alternate regular 24-hr incubation shifts and exchange duties at dawn (Nelson 1997). Therefore, an incubating bird shows a regular pattern of marine detections every second day. Behavioural inferences from these attendance patterns at marine and nest locations, and analysis of the egg precursor protein vitellogenin in blood-sampled individuals, suggested that all radio-marked birds used in these analyses were captured prior to or during incubation.

We estimated hatch date as the date when parents switched from being present at nest sites during the day to visiting their nests mainly at dawn and dusk to feed their young. The period between suspected laying and hatching was approximately 30 days, consistent with other reports of incubation duration for the species (Nelson 1997). Radio-marked birds were monitored inland at nest sites and along flyways adjacent to nest sites. Nests were classified as active during chick rearing if they were visited at least once every 48 hr by radio-marked parents. We ensured that radios of all birds used in our nest visitation analyses were functioning properly by only including data from birds with regular daytime marine detections throughout their chick rearing period.

Nest-site monitoring was conducted by human observers in all years and also by remote data loggers (model DCC II, Advanced Telemetry Systems) in 2000. Observers conducted AM (03:30–7:30 PDT) and PM (20:00–24:00 PDT) radio-monitoring sessions coinciding with the peak times of chick-provisioning trips (Nelson 1997, Manley 1999). Both methods relied on an antenna (Advanced Telemetry Systems, four-element and H antennae) and a radio receiver (model R4000, Advanced Telemetry Systems). Static radio-monitoring was conducted at locations near nest sites (~0.5 km from the nest) or along flyways downstream from target nest

sites. Both methods recorded the time a radio-marked bird was first and last detected, and counted detections of birds flying in and then out of a valley as one nest visit. To maximize the probability of detecting birds traveling up watersheds, flyway monitoring stations were often positioned at the height of land along ridgelines and subalpine plateaus. Human observers recorded the direction and signal strength of a detection every few minutes. This information was used to determine the location and movement direction of a radio-marked bird. Data loggers recorded similar data, except for movement direction. Due to the reduced directionality in the data-logger results, antennae were oriented to target specific watersheds. To further reduce bias in the data-logger data, "dummy frequencies" were used to ensure that data were not corrupted by interference. Data loggers were not used in coastal areas or on ridges within 5 km of the ocean to avoid falsely classifying a bird flying over the ocean as traveling inland. Coastal nests were monitored by human observers stationed in a location where they could distinguish presence of birds on the ocean or at the nest.

At the completion of each breeding season, 15 accessible nest trees (of 46 total) were climbed to investigate nest sites and determine true fledging success (Hamer et. al. 1994, Manley 1999).

Statistical Analyses

A total of 48 birds (23 females, 25 males) were used in these analyses. For each adult at each nest, we determined a rate of AM, PM, and overall detections relative to the number of observation sessions for that individual. Results across years were pooled to test three predictions about nest visitation. First, that overall rates of nest visits by males during the chick rearing period were greater than females (Vanderkist et al. 1999). Second, that PM rates of nest visits by males were greater than those of females, and by a greater margin than in AM visits. Third, that

male-biased nest visitation by males increased over the breeding season (Vanderkist et al. 1999).

To test the third hypothesis, we divided observations into early or late chick rearing for each bird. Preliminary analyses which partitioned data into more than 2 time periods during chick rearing seemed to lack statistical power due to small sample sizes. Early chick rearing was defined as the first 15 days post-incubation, given that murrelets usually have a 30-day chick rearing period (Nelson 1997). We examined these seasonal, within-sex differences both within and among individuals. Individuals with known visitation rates in both early and late chick rearing were compared in a paired analysis, separate from within-sex comparisons of different individuals in the two stages of chick rearing.

We used t-tests when data were normally distributed (Anderson Darling test) and nonparametric Mann-Whitney-Wilcoxon tests when data were not normally distributed. When testing the hypotheses that females visited nest sites less often than males, we used one-tailed tests. A chi-square test was used to test for increased male bias in evening captures of birds flying inland during chick rearing relative to morning captures. A significance level of 5% was used for statistical tests. Results are presented as means $\pm$ SE. All analyses were done with Minitab release 13.1 (2000)

2.3 RESULTS

On average we conducted 11.0 ± 2.0 observation sessions per male and 12.1 ± 1.7 per female per year over three years of study. Thirty-three percent of sample birds were monitored throughout early and late chick rearing, while the remainder were observed only during one-half of their chick rearing period. The mean total observation period was 11.6 days per bird. Males visited their nests 1.3 times as often as females ($t_{45} = 2.4$, $P = 0.01$). The discrepancy between male and female visitation rates was even greater (1.8 times) during evening visits ($W = 710.5$, $P = 0.02$, n

= 23 females, 25 males). Both within and among individuals, male visitation rates did not significantly differ between early and late chick rearing, while female visitation rates significantly decreased between these two periods (Table 2.1). In addition, male and female visitation rates did not significantly differ in early chick rearing, but female rates were significantly lower than those of males during late chick rearing (Table 2.1). All 15 of the nest trees we climbed showed evidence of a nest, including chick feces and down.

We had continuous late-chick rearing monitoring data on only one of the two nests where both parents were radio-marked. In the final eight days of chick rearing at this successful nest, the male visited the nest 2.3 times as often as the female ($n = 23$ total visits by both parents). Eighty-six percent (6 of 7) of the female's visits were AM feedings compared to 63% (10 of 16) for the male.

Although Vanderkist et al. (1999) found no significant difference in male bias between the morning and evening captures of birds flying inland at Theodosia Inlet, we reanalyzed the capture data with an additional two years of results. Pooling capture data (1994–1999, $n = 680$), male bias in birds flying inland during the likely chick rearing period was greater in the PM (2.29:1) than in the AM (1.64:1; $\chi^2_1 = 9.1$, $P < 0.01$).

2.4 DISCUSSION

Male Marbled Murrelets were detected visiting or traveling toward active nests during the chick rearing period significantly more often than females. This trend was greater during trips made at dusk. During the late chick rearing period, females significantly reduced their rate of nest visitation, both within and between individuals. These results support the hypothesis that previous findings of male bias in birds flying inland were at least partly due to male-biased provisioning in this population of Marbled Murrelets (Vanderkist et al. 1999).

Most sightings of adult birds at active nests during the chick rearing period are associated with provisioning (P. Jones 1993, Nelson and Hamer 1995, Nelson 1997), with the only noted exception involving disturbance from predator calls played by human observers (T. Hamer, pers. comm.). Therefore, we assume the nest visits we have recorded indicate chick-provisioning trips. Tree-climbing observations of evidence of chicks and chick-feeding at all our accessible active nests support this assumption. Still, some nest visits by breeding birds may not involve provisioning and may involve activities like territory defense, as observed in other alcids (Wanless and Harris 1986). The role of breeding territory defense in the noncolonial Marbled Murrelet is unknown (Nelson 1997). However, even if some male visits to nest sites are not provisioning trips, these males still expend more energy than females for this aspect of reproductive effort.

Sex-biased provisioning in altricial birds takes many forms. Male-biased provisioning is observed in several seabird species, including many larids (Fasola and Saino 1995) and albatrosses (Huin et al. 2000, Weimerskirch et al. 2000). However, this pattern is reversed in most studies of the Alcidae. Creelman and Storey (1991) found female Atlantic Puffins (*Fratercula arctica*) making more chick-provisioning visits than males. A similar trend has been observed in Common Murres (*Uria aalge*; Wanless and Harris 1986) and Crested Auklets (*Aethia cristatella*; I. Jones 1993). However, male puffins and murres are involved in much more territory defense during the breeding season than females (Creelman and Storey 1991, Wanless and Harris 1986). Increased territory defense by males was observed throughout the breeding period, primarily pre-egg-laying in murres and during chick rearing in puffins (Creelman and Storey 1991, Wanless and Harris 1986). Thus, contrasting sex biases are observed in allocation of resources for different aspects of reproductive effort. If male Marbled Murrelets do not invest

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in territorial behaviour to the same extent as male alcids of colonial species, perhaps they have more energetic resources to devote to provisioning.

While our results on overall feeding bias are opposite to findings for most other alcids, a study of Dovekies (*Alle alle*) showed male provisioning bias late in chick rearing. While female Dovekies provide the majority of chick provisioning until late chick rearing, they cease provisioning about five days before the chick fledges, after which the male does all feeding (Taylor and Konarzewski 1992).

The overall male bias of inland trips by confirmed breeders reported here (1.3 times) is markedly less than the 1.8 times male bias reported by Vanderkist et al. (1999). Our result may be due to our limited sample of birds of known sex and breeding status. As suggested by Vanderkist et al. (1999), there may also be a male bias in nonbreeding birds flying inland to prospect for breeding sites or defend territories. Our radio-telemetry surveys have focused on breeding birds, but there is a need for future study to quantify the inland behaviour of known nonbreeders.

The decrease in female effort during the late chick rearing period is similar to trends observed in other birds outside the Alcidae, such as Pacific Loons (*Gavia pacifica*; Petersen 1989) and Merlins (*Falco columbarius*; Sodhi 1993). The behavioural change observed in Marbled Murrelets may be due to the likely high cost of egg production in this species. Marbled Murrelet eggs are approximately 20% of adult body mass (Nelson 1997), in addition to the mass increase and energetic cost of ovary development to females for their one-egg clutch. Monaghan et al. (1998) showed that parental effort is mediated through the negative influence of egg production on female condition. Therefore, the decrease in female investment during the chick-rearing period may result from more female self-feeding to recover egg production costs.

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However, there is little empirical evidence that supports an immediate "egg cost" hypothesis in murrelets. After egg laying, female Marbled Murrelets show no mass declines throughout the breeding season (Sealy 1975). In addition, females share incubation duties equally with males (Nelson 1997) and appear to decrease their investment in provisioning only during the latter half of the 30-day chick rearing period. Therefore, females apparently invest in reproduction as much as males do for approximately 45 days post-laying. This suggests two hypotheses. First, that egg production is energetically costly to females but that payment of this cost can be deferred. Under this scenario, female energetic reserves for reproduction are not depleted until the late chick rearing stage, leaving males as primary provisioners. Alternatively, there may be an advantage to females in decreasing their reproductive effort late in chick rearing which is independent of breeding. Other costly activities, such as post-breeding molt, may be adversely affected by prolonged breeding effort (Dawson et al. 2000). In addition, a change in food availability or accessibility for Marbled Murrelets late in the breeding season, as observed in Prince William Sound, Alaska (K. Kuletz, pers. comm.), could make foraging more costly, with females reaching a threshold at which their energetic deficit must be addressed. However, a reduction in prey availability appears to be unlikely in Desolation Sound, as birds remain in the area after the breeding season to molt in the same marine areas they occupy during the summer (N. Parker, pers. comm.).

On a broader scale, these results may help to explain common behaviour patterns observed in inland monitoring of Marbled Murrelets. In most observations of chick feedings and murrelet activity in potential breeding habitat during the chick rearing period, there are fewer detections at dusk than at dawn from standard surveys (Nelson 1997, Manley 1999) and radar monitoring (Burger 1997, Cooper et al. 2001). Assuming that parents provide equal feeding

loads throughout the chick rearing period, and that there is no mean increase in prey size, the reduction in female nest visitation we observed may correspond to the marked drop in feeding rate by Marbled Murrelet parents just prior to fledging (P. Jones 1993, Nelson and Hamer 1995). This phenomenon is seen in many alcids and other seabird species (Gaston and Jones 1998).

A general increase in inland audiovisual detections of murrelets in July has been widely reported throughout most of the species' range (O'Donnell 1993, Rodway et al. 1993, Manley 1999, Jodice and Collopy 2000). Most of our study birds were in the late chick rearing phase during the month of July. Therefore, our findings of reduced overall nest visitation in late-chick rearing support the hypothesis that this increase in Marbled Murrelet inland detections during July is due to the influx of nonbreeding or prospecting birds and not chick rearing breeders. Our study demonstrates the interpretive advantage gained when we can follow individuals over extended periods. In a species of such strong management concerns (Nelson 1997), it is imperative that basic breeding ecology is well understood, in order to develop the most informed, progressive management policy possible.

Table 2.1. Male and female Marbled Murrelet nest visitation rates during early and late chick rearing. Visitation rates are mean ± SE number of detections per 4-hr observation session. Tests for differences in visitation rates between sexes and among individuals were conducted with all available independent data points. Reported sample sizes are subsets of the total number of birds tracked (23 females, 25 males). Unless noted, all tests are one-tailed. Early = nestling days 1-15; late = nestling days 16-30.

	Female (n)	Male (n)	P
Female vs. male[a]			
Early	0.62 ± 0.05 (16)	0.73 ± 0.06 (17)	>0.09
Late	0.43 ± 0.05 (16)	0.59 ± 0.08 (15)	0.05
	Early	**Late**	
Within sex, among individuals			
Female[a]	0.67 ± 0.08 (7)	0.41 ± 0.07 (7)	<0.02
Male[b, d]	0.83 ± 0.08 (10)	0.62 ± 0.09 (8)	0.11
Within individuals[c]			
Female	0.59 ± 0.06 (9)	0.45 ± 0.08 (9)	<0.04
Male[d]	0.58 ± 0.07 (7)	0.55 ± 0.13 (7)	0.87

[a] Two-sample t-tests.

[b] Mann-Whitney-Wilcoxon test.

[c] Paired t-tests.

[d] Two-tailed test.

CHAPTER 3. THE EFFECTS OF MARINE AND TERRESTRIAL HABITAT USE ON REPRODUCTIVE SUCCESS IN RADIO-MARKED MARBLED MURRELETS

3.1 INTRODUCTION

The expansion of human activity and resource consumption has created major potential threats to wild animal populations. Among birds, approximately one fourth of the world's species have been driven to extinction by humans in the last two thousand years (Steadman 1995). Thus, there is concern for avian populations which are perceived to be currently threatened. This concern has generated strong interest in ecological research on perceived "species-at-risk" to guide appropriate management action. Data on behaviour, habitat use, and demography for a given species are crucial to ensure that informed and appropriate conservation action is taken (Sutherland 1998, Collins 2001). However, generating these data is not easy in species that are logistically difficult to study. The situation is further complicated by political constraints of management policy, which tends to operate on a timeline far shorter than that of ecological research. This conundrum is well demonstrated in the science and management of Marbled Murrelet populations.

Over the last two decades, the Marbled Murrelet has become the focus of much controversy in western North America. This small auk ranges along the eastern coast of the Pacific Ocean from central California to Alaska. Along with the Long-billed Murrelet, Marbled Murrelets are unique among alcids in that they do not breed on remote island colonies, but nest inland, primarily on mossy platforms of canopy branches of old growth trees (Nelson 1997). The cryptic nesting behaviour of this species has made study of its breeding ecology extremely difficult. By 1997, only 150 nests had been found in all of North America (Nelson 1997). Most study of Marbled Murrelets during the breeding season has consisted of at sea and inland surveys

of birds of unknown breeding status and success (Ralph et al. 1995). Not only is the biology of the Marbled Murrelet poorly understood, but there are many potential threats to both its nesting and marine habitats. As a consequence, it was listed as threatened south of Alaska, and endangered in California (Nelson 1997). Therefore, great amounts of time and effort have been expended by scientists and managers to develop conservation plans for this species, such as the Northwest Forest Plan and the Identified Wildlife Management Strategy for British Columbia. These conservation plans primarily involve habitat protection in areas believed to be of the highest quality to breeding murrelets; however, there are few data on marine and terrestrial habitat use from individually monitored birds of known breeding status and success.

The at-sea distributions and foraging ranges of seabirds have been well studied (review in Shealer 2001). In many avian species, there are often significant differences among individual lifetime reproductive success, resulting in a small proportion of individuals producing most of the new recruits into a population (review in Partridge 1989). Thus, higher quality parents might be more efficient foragers and the spatial foraging distribution of successful breeders may be different from failed breeders (Eberl and Picman 1993, Obst et al.1995, Moore 1999). The distance that birds travel between nest sites and foraging areas is an important component of time-energy budgets during the breeding period (Ricklefs et al. 1986). While alcids have a high rate of energy expenditure during flight due to their flapping, nongliding technique (Pennycuick 1987), Marbled Murrelets have been shown to travel up to 124km each way from foraging locations to inland sites during the breeding season (Whitworth et al. 2000a) and nest up to 50km inland (Nelson 1997). Hull et al. (2001) reported no differences in breeding success with varying commuting distance in a small sample of marked Marbled Murrelets in southwestern British Columbia. However, further investigations into the inland breeding range of the species

and implications of commuting for reproductive success are important for management decisions regarding the geographic limitations of areas considered to be available nesting habitat for murrelets (Ralph et al. 1995).

Loss of potential nesting habitat has been the driving force behind conservation concerns for the Marbled Murrelet. Most murrelet nest sites have traditionally been found in low elevation coniferous old growth forests, on the lower two thirds of forested slopes (Hamer and Nelson 1995). However, landscape level analyses of nesting habitat selection of a large sample of individual murrelets have only recently been conducted (Huettmann et al, in review). Radar surveys have shown positive relationships between amount of old-growth forest habitat and numbers of birds visiting a watershed (Burger 2002, Raphael et al., in press), but the breeding status and success of these birds is unknown. Studies of reproductive success and habitat selection in a large sample of birds are needed to identify whether certain habitat variables are associated with increased reproductive success. One major suspected cause of Marbled Murrelet nest failure has been nest site predation on eggs and chicks, which has been linked to the proximity of nest sites to forest edges (Nelson and Hamer 1995, Manley 1999, Marzluff et al. 2000). Many studies, primarily from the forests of the eastern United States, have documented increases in avian nest predation, usually within 50 to 200 m of a forest boundary, from these "edge effects" (Martin 1993, review in Paton 1994). However, there is substantial discrepancy among recent studies about the relative intensity and biological significance of edge effects (review in Murcia 1995). Documenting the effects of edge on nesting success in a large sample of Marbled Murrelets has value in evaluating the size and spatial structure of breeding habitat reserves.

In this paper we will attempt to address some of these gaps in present knowledge of how marine and terrestrial habitat use by Marbled Murrelets relates to annual reproductive success, with implications for management of populations. We report on the largest sample of breeding Marbled Murrelets with known nesting locations, reproductive success, and marine distributions from a long term study of radio marked individuals in Desolation Sound, British Columbia. We integrated behavioural data with information on marine and terrestrial habitat use to examine the effects of timing of breeding, commuting distance from foraging zones to nests, and nest site slope and elevation on reproductive success. We also investigated the effects of nest proximity to forest edges on reproductive success. We discuss our findings in the context of the Marbled Murrelet's unique life history and breeding ecology.

3.2 METHODS

Radio Telemetry

Field work was conducted at Desolation Sound, British Columbia, Canada (50°05'N, 124°40'W) during the 1998 – 2001 breeding seasons. Our approach was to capture and mark a sample of birds prior to nesting, find their nests, and record their breeding status and movements using radio telemetry. In 4 years of study, 290 Marbled Murrelets were marked with radio transmitters (1998 n=40, 1999 n =100, 2000 n=75, 2001 n=75). Detailed accounts of our methodology for capturing, radio-marking, tracking, and assessing reproductive status of birds can be found in Hull et al. (2001), Bradley and Cooke (2001), Bradley et al. (2002), and Cam et al. (in review). For some analyses, certain data from some study years were not available. Therefore, data and sample sizes used for each analysis are clearly stated.

Except for one analysis of fledging success from ground accessible nests, our measure of reproductive success in all analyses was that of "mid-chick rearing" success from radio

telemetry data. This is a measure of success based on adult visitation to the nest up to at least the mid-chick rearing period (Cam et al., in review). Bradley et al. (2002) discuss the assumptions and justification of this measure as evidence of chick feeding visits at an active nest. "Mid-chick rearing" success was used because it could be determined at all active nest sites as many nests were physically inaccessible and we were unable to determine final fledging success.

Core Marine Foraging Areas of Marbled Murrelets

We used daily marine detections of birds in 1998-2000 to examine the marine distributions of individual murrelets with known breeding success. Marine location data for 2001 was unavailable at the time of writing. We used daytime detections of birds collected by daily helicopter and boat (1998 only) surveys throughout the breeding season. These were primarily conducted to determine presence or absence of birds on the ocean to make inferences about the bird's breeding state (Hull et al. 2001, Bradley et al. 2002). Primary marine telemetry coverage areas for different study years are shown in Figure 3.1. Telemetry locations were georeferenced to landmarks and digitized in a Geographic Information System (GIS). These surveys were designed to maximize our ability to determine general marine locations for all radioed birds, so we were not always able to pinpoint exact locations of individuals. However, the strength of our data is the number of detections per individual, minimum 20 and maximum 80 per bird. Therefore, we confined our analysis and interpretation to a large scale investigation of an individual murrelet's core area of marine habitat use during the breeding season to limit the effects of potential spatial inaccuracy in our data. We used one detection per bird per day, and assumed that individual murrelet locations were independent of previous or subsequent locations because the time between locations was sufficient for a murrelet to cross the range of our study area (White and Garrott 1990). We imported daily marine locations into ARCVIEW GIS 3.2

(Environmental Systems Research Institute Inc.). We developed 50% fixed kernel home-range estimators from ARCVIEW's ANIMAL MOVEMENT extension v 3.1. These 50% contours represent the core area of animal activity and are preferred for statistical comparisons between individuals as they are not strongly affected by deviations from the assumptions of the home-range models and from outlier locations (Hooge 1999, Kenward 2001). Our number of detections for each bird was well in excess of the sample size needed for home-range size to stabilize using this methodology (Kenward 2001). No post breeding detections, based on the predicted end of chick rearing or date of failure from telemetry data, were included to limit the effects of change in marine habitat use after completion of breeding or breeding failure (Hull et al. 2001, Fernandez et al. 2001).

Commuting Distance

We investigated the effect of commuting distance on "mid-chick" reproductive success. We calculated nest distance to the centre of 50% kernel home-ranges of breeding season marine habitat use for each individual. If multiple density centres were created in the 50% homerange estimation (Kenward 2001), the size corrected mean distance to all centres was used. Two distance measures were calculated. The first was direct distance from foraging centre to the nest, which served as a minimum estimate of commuting distance. Another distance measure, flyway distance, took into account flight path of individual birds obtained from telemetry observations of transit corridors used by chick rearing birds (Bradley et al. 2002).

Timing of Breeding

We investigated the role of timing of breeding in "mid-chick" reproductive success. Initiation of breeding was determined by behavioural changes associated with the presence and absence of

radio marked birds on the ocean and inland as described in Hull et al. (2001), Bradley and Cooke (2001), Bradley et al. (2002), and Cam et al. (in review).

Terrestrial Habitat Use

All nests sites were found by helicopter telemetry, and locations were determined to an accuracy of approximately 100m from the air (Cam et al. in review, Huettmann et al., in review, Bradley and Cooke 2001). Thus, all locations were available for landscape level GIS habitat analyses. Data used from GIS in analyses in this paper included elevation and slope from a digital elevation model and habitat type measures for edge analyses. At 38% of our sites we could access suspected nest sites on the ground. Suspected nest trees were located by ground based radio telemetry, and presence of nests was confirmed by tree climbing (Bradley and Cooke 2001). Fledging success was also determined through tree climbing and inspection of nest contents after the breeding season (Hamer et al. 1994). The inaccessibility of the majority of our nest sites from the ground creates a potential bias when assessing fledging success for our sample.

Edge effects

We examined large and small scale patterns in the potential effects of forest edges or high contrast changes in habitat type on Marbled Murrelet breeding success, as nests closer to edges are hypothesized to have lower success due to increased predation. At the small scale, we examined forest edges in relation to fledging success at 37 accessible nest trees climbed after the breeding season from 1999 - 2001. For these sites, edges were classified as natural or artificial. Natural edges included rivers, avalanche chutes, and large natural openings, but not small canopy gaps. Artificial edges were forest clearcuts and logging roads. Chi Square tests were used to compare fledging success between sites adjacent and not adjacent to edge, and sites near

artificial versus natural edges. Fisher's exact probabilities are reported due to small sample sizes. Two sets of analyses were conducted, one with adjacent edges 50m from the nest tree and another with edges up to 100m away.

At a larger, coarser scale, we used GIS to determine the edge type adjacent to 98 nests with known "mid-chick" rearing success from 1998-2001. Edge type was taken from a 1:250,000 LUP data layer from the British Columbia Ministry of Environment. Nearest edge within 200m was classified by edge type. 200m was chosen as a measure to allow for GIS error and give a general classification for each nest as edge or interior. Adjacent edge types included natural edges and artificial edges. For these analyses, natural edges were classed as: alpine, barren surfaces, avalanche chutes, wetlands, and ocean. Unnatural edges were clearcuts and transitions between old and second growth forest. Sites with no edge within 200m were classified within old forest or within second growth forest. Edge classifications were coarse and high resolution landscape classification maps were not available.

Univariate and Multivariate Analysis of the Effects of Timing of Breeding, Commuting Distance, Slope, and Elevation of Nesting Sites on Reproductive Success

We examined the effects of timing of breeding, commuting distance (both direct and estimated flyway), slope, and elevation of nest sites on "mid-chick rearing" success. First we developed a correlation matrix and examined Pearson correlation coefficients and p values of relationships between all variables. We conducted logistic regression in SAS, in both univariate and multivariate approaches, with "mid-chick" rearing success as the response variable. We examined for year effects by testing year as a categorical variable in all models.

We attempted to use all available data, which made comparisons difficult as commuting distance information was not available for the 2001 season. Therefore we present correlation

matrices and analyses for 2 datasets. The first contains information from 1998-2000, which includes data on all tested variables (n=68). Analyses which included the 2001 data only contain new information on nest slope, elevation, and timing of breeding (n=98).

3.3 RESULTS

Correlation Between Timing of Breeding, Commuting Distance, Slope, and Elevation of Nesting Sites

Our two measures of commuting distance, direct and flyway distances from core foraging sites to nesting sites, were highly positively correlated (Table 3.1). Timing of breeding was negatively correlated with both commuting distance measures and correlations were moderate (Table 3.1). Nest site slope was negatively correlated at a moderate level with timing of breeding and positively correlated with both commuting distance measures (Tables 3.1, 3.2). In summary, early breeding birds tended to travel further from foraging areas to nesting areas, and nest at sites which had steeper slopes than later breeding birds.

In both data sets examined, nest site elevation was not significantly correlated with either measure of commuting distance or with timing of breeding (Tables 3.1, 3.2). In data from 1998 to 2000, nest site slope was not significantly correlated with elevation (Table 3.1). However, several nests sites from 2001 were in very steep areas of high elevation, and slope and elevation were highly significantly correlated in that year (Table 3.2).

Univariate Analysis of the Effects of Timing of Breeding, Commuting Distance, Slope, and Elevation of Nesting Sites on Reproductive Success

Since both measures of commuting distance were highly correlated, we used estimated flyway distance as our commuting measure, as it seemed more biologically relevant. In univariate logistic regression, timing of breeding, commuting distance, nest site slope, and nest site

elevation were all significant predictors of reproductive success (Tables 3.3, 3.4). Results were similar for the two datasets (Tables 3.3, 3.4). Maximum Likelihood parameter estimates were all positive except for laying date (Tables 3.3, 3.4). So earlier breeding birds were more successful, while higher elevation, steeper slope, and longer commuting distance were associated with higher reproductive success (Tables 3.3, 3.4).

Addition of year as a categorical variable to all univariate models showed no apparent "year effects" on any relationships. As a predictor of nesting success, year never produced a p value of less than 0.2 for any of the models tested.

Multivariate Analysis of the Effects of Timing of Breeding, Commuting Distance, Slope, and Elevation of Nesting Sites on Reproductive Success

All combinations of multivariate logistic regression were run with all five variables for the 1998-2000 dataset and for all variables excluding distance for the 1998-2001 dataset (Tables 3.5, 3.6). Most of the highest ranked models (with lowest AIC values – Akaike 1974) contained several or all of the variables with predictors having similar significance levels (Table 3.5, 3.6). Stepwise modeling of all potential interactions revealed no significant effects, so none are reported.

Nesting Success and Forest edges

In our analysis of fledging success relative to distance to edge in ground accessible nests, we observed no significant differences in nest success of sites adjacent to or far from forest edges (Table 3.7). Many more nests were within 100m of an edge than were within 50m (Table 3.7). Though the focus of ground based habitat plots was measurements within 100m of a nest tree, no sites with edges detected had those edges fall greater than 100m but less than 200m from the nest tree. Most nest trees were located adjacent to natural edges rather than artificial ones (Table 3.7). Interpreting the results of nest success differences between natural and artificial edges is

difficult, as very few nests were located near artificial edges, especially at the 50m scale, making the power of these analyses very low (Table 3.7).

In the larger scale GIS analysis, similar proportions of sites adjacent to edges were observed compared to the ground based analyses (Table 3.8). Like the ground based analyses, the majority of nesting sites were adjacent to natural edges (Table 3.8). The dominant edge types in these GIS analyses were avalanche chutes, with the overwhelming majority of these sites being successful (Table 3.8). Nesting success differed significantly between sites adjacent to natural, artificial, and no edges (Table 3.8). The primary source of this difference appears to be the significantly higher "mid-chick" rearing success of nests adjacent to natural edges compared to nests in more interior forest conditions (Table 3.8). In paired comparisons, we found no differences in success between nests adjacent to artificial and natural edges and artificial edges and interior conditions (Table 3.8).

3.4 DISCUSSION

Our results suggest that earlier breeding birds nest further away from their foraging sites and nest on steeper slopes than those nesting later. These early birds have higher reproductive success, as do birds that nest at higher elevations. While higher success of birds nesting in steeper slopes has been previously documented for our study area (Huettmann et al., in review), our results of longer commuting distance associated with higher reproductive success differ from Hull et al.'s (2001) finding of no detected effect between these two variables from the 1998 data.

Our results suggest that natural edges do not have a negative effect on breeding success and that most of our sample birds breed near natural edges, despite a high level of forest fragmentation from logging in our study area (Huettmann et al., in review). In our analysis of edge distance in relation to fledging success from ground accessible nest trees, we observed no

differences in success between birds nesting at edges and those nesting in more interior forest locations. In analyses of ground collected data, we could not confidently assess differences in success among edge types due to the very low sample size of nests near artificial edges. Using GIS data, with its lower spatial accuracy but larger sample size of both accessible and inaccessible nests, we found higher nesting success adjacent to natural edges, especially avalanche chutes, compared to nests in interior forest conditions.

Marine Habitat Use and Commuting Distance

The ultimate factors in determining seabird breeding location are availability of food and shelter from predators (Lack 1968, Nelson 1980, Warham 1996, Forbes et al. 2000). Seabirds generally settle in predator free breeding locations that are as close to their feeding areas as possible, so that the benefits of feeding are not outweighed by the costs of commuting between breeding and foraging sites (Lack 1968, Buckley and Buckley 1980). In some seabirds (Red-Throated Loons, Least Auklets, and Yellow-Eyed Penguins), increased foraging distance from the nest site has been associated with lower reproductive success (Eberl and Picman 1993, Obst et al. 1995, Moore 1999). It appears that this relationship does not hold for Marbled Murrelets in our study area.

There is no evidence to suggest that long commuting distance, up to ~100km each way, carries an excessive energetic cost for Marbled Murrelets. Regular long distance flights (>100km) from feeding to inland areas have been well documented (Hamer and Nelson 1995, Whitworth et al. 2000, Hull et al. 2001, this study) as have 100km commuting trips in similar sized alcids, Cassin's Auklets (Boyd et al. 2000, Ryder et al. 2001). Hull et al. (2001) estimated the flight costs of commuting murrelets as 11x BMR at maximum power and a mean increase in 16% energetic cost during the breeding season. Empirical studies have shown flight costs in

birds vary between 4.8 to 11.6x BMR (Roby and Ricklefs 1986, and references therein). Hull et al. (2001) found no differences in reproductive success with varying commuting distance in our sample, using only the 1998 season of data. We suspect this finding may have been due to a lack of statistical power. Hull et al. (2001) hypothesized that murrelets may have enough plasticity in their energy budgets to absorb commuting costs, and that there may be other advantages of nesting further inland, namely higher quality nesting habitat (DeSanto and Nelson 1995).

Our results suggest that foraging areas of successfully breeding Marbled Murrelets are often not the nearest ocean to their inland breeding sites. In other seabirds, both colony location and presence of prey have been shown to have a significant effect on the fine scale distribution and abundance of breeding individuals (Parrish et al. 1998). Many of our nesting birds had breeding sites which were directly adjacent to marine areas in Toba Inlet (Figure 3.1), but most chose to forage much further south in Desolation Sound.

Further investigations into distributions and abundance of murrelet prey need to be conducted to assess the relative impact of prey on marine murrelet distribution and breeding success. Information on prey populations of seabirds are rarely available but crucial knowledge to obtain, as changes in prey populations are often inferred from predator data - making a critical evaluation impossible (Monaghan 1996). Migratory prey which arrive at certain periods of the breeding season can heavily impact the reproductive performance of seabirds (Takahashi et al. 2001), as can variation in the timing of prey availability (Bertram et al. 2001). More consistent availability of sandlance prey for coastal murrelets in the Strait of Georgia may contribute to the more consistent productivity of the birds (Chapter 1) compared to colonial alcids relying on more pelagic prey resources (Bertram et al. 2001). Foraging ecology of Marbled Murrelets has not been well studied and we suggest this is a key topic for future research.

We acknowledge that our descriptions of murrelet foraging ranges are large scale, coarse measures of marine habitat use over the breeding season. Studies of at sea transect surveys of Marbled Murrelets have shown how survey type, temporal, and tidal effects can influence detected murrelet abundance and distribution (Speckman et al. 2000, Day and Nigro 2000). However, radio telemetry estimates of seabird foraging ranges have been shown to be more representative than those obtained by transect surveys, due to greater survey coverage and detection probability (Ostrand et al. 1998). Wood et al. (2000) used similar Kernel home-range criteria to the ones we describe here to quantify core areas of habitat use within the enormous foraging range of breeding South Georgia albatrosses. Future analyses of our data will provide more in-depth analyses of seasonal changes in foraging distributions of our breeding murrelets, and compare marine distributions of breeders and non-breeders.

Slope and Elevation

Our results of higher reproductive success in nests at greater slope concur with the findings of preference for steeper slopes for our sample of birds (Huettmann et al., in review). Most interpretations of nest preferences in Marbled Murrelets relate to the availability of suitable nesting platforms (moss covered tree branches), but it appears unlikely that steeper slopes have trees with more platforms than trees at shallower slopes in our study area (Falk Huettmann, unpublished data). Here we present two potential explanations for the nest preferences and higher success on steeper slopes, 1) a morphological hypothesis involving habitat selection to facilitate murrelets easily and safely accessing their breeding sites, and 2) the possibility that greater success at these sites may be more closely linked to a covariate of slope, rather than slope itself.

Marbled Murrelets are alcids, whose shortened wings and reduced surface area improves underwater propulsion immensely, but restricts aerial flight due to high wing loading (Nettleship 1996). Therefore, flight is direct, rapid, and energetically expensive with limited maneuverability once birds are airborne (Nettleship 1996). This makes take off and landings difficult (Nettleship 1996). Most alcids breed in colonies with few trees and very open sky, allowing them to conduct clumsy takeoffs and landings. Many alcid colony islands have burrow nesting species breeding on steep slopes and surface nesting species breeding on cliffs (Gaston and Jones 1998). Kittlitz's Murrelets are the most related species to Marbled Murrelets (Friesen et al. 1996) and are the only other alcids to breed several kilometers inland. This species breeds on unvegetated steep scree and talus, and all known nests have been found on slopes of 15-45 degrees (Day et al. 1999). Ancient Murrelets and some Rhinoceros Auklets breed in forested habitat, but usually within 300m of shore (Gaston and Jones 1998).

Marbled Murrelets are the only alcids that breed far inland in areas of thick vegetation cover under the forest canopy, where a miscalculated landing and fall to the ground could seriously threaten a bird's survival. Because of their difficulty in taking off, landing, and maneuvering during flight, taking off from the forest floor with significant canopy cover would be extremely difficult. Grounded individuals that have fallen from nests or crashed on inland flights may walk hundreds of meters on the ground in search of suitable launching areas (Nelson 1997). Numerous fledging birds appear to become grounded during flights from the nest to the ocean (Carter and Sealy 1987, Nelson and Hamer 1995a, Nelson and Hamer 1995b). A study of aerial photography interpretation of forest habitat from our nests sites showed the major forest stand variable associated with increased "mid-chick" reproductive success was vertical complexity (Waterhouse et al. 2002). Vertical complexity is a measure of the "openness" of a forest canopy, based on the configuration of the canopy and the spatial arrangement of the trees, taking landscape variables into account. One would assume that a more vertically complex canopy would be easier for a murrelet to access and depart from than a more uniform canopy structure.

Therefore, we hypothesize that murrelets in the forest may incur a moderate risk to their own survival by flying into dense forest. Birds might not be able to take off from the ground and starve, be killed by a predator, or become grounded on their fledging flight. We believe that our signal for increased slope as a predictor of nesting success may relate to this phenomenon. A forest patch on a slope would allow much easier access for a bird to visit and depart from its nest site, or for a chick to fledge successfully, with less danger of crashing and falling to the ground. One would suspect that natural selection would favour this strategy in a long lived seabird, as

benefits to adult survival probably outweigh the potential fitness consequences of having a nest site which might be slightly more exposed to predators.

An alternative explanation to this morphological hypothesis is that increased reproductive success at nest sites of increased slope may be due to some covariate of slope. Nest site elevation was also a significant predictor of reproductive success in our sample, though there is no strong preference for increased nest site elevation in our radioed birds (Huettmann et al. in review). Within our study landscape, slope and elevation are positively correlated (Huettmann et al., in review). Thus, some attributes of sites which have steep slopes, perhaps a potential lower predator abundance, may be more linked to increasing elevation. However, when examining correlations between slope and elevation, we must note that slope does not necessarily increase linearly in our landscape. Our study area consists of many U shaped valleys, where slope initially increases with elevation to a maximum but then declines at the highest elevations in the valley. So the highest elevations may not have the greatest slopes. But, the great majority of our nest sites do not fall into this upper category of reduced slopes, where alpine conditions prevail and trees are often stunted or absent.

In addition, we found no correlation between nest site elevation and timing of breeding. This would suggest that birds are not restricted from initiating higher elevation nests early in the breeding season when cold temperatures and moderate snow levels are still present. Perhaps murrelets which choose to breed under these conditions are exposed to reduced nest predation risk. In areas of cold temperature and late summer snow pack, small birds and mammals which would potentially prey on murrelet nests should still be primarily at lower elevations, where food would be more abundant (Badgley and Fox 2000). In contrast, murrelets gain all of their energy

from the marine environment and are not restricted to breeding in snow-free areas. Also, small mammals at higher elevations might still be hibernating when murrelets initiate nesting.

It is also possible that some other covariate of slope might be influencing this relationship. Detailed information on forest and landscape attributes of potential Marbled Murrelet habitat in very steep areas is extremely difficult to obtain. Many of these sites are physically inaccessible to collect ground based measurements and most of the GIS data produced on forests does not intensely inventory these regions, as they often have less commercial value than larger, contiguous forest patches.

Timing of Breeding

We found commuting distance and nest site slope to be negatively correlated with timing of breeding. Among most avian species, older birds are often the first to return to breeding grounds, nest early, and have higher nesting success than other birds – suggesting that experience may have an important influence on the timing of breeding (Cooke et al. 1995, Hamer et al. 2001 and references therein). We hypothesize that these early breeding birds, that are commuting further distances and nesting at greater slopes than late breeding birds are older, more experienced breeders. Harris et al. (1997) demonstrated how certain Common Murre breeding sites were associated with consistently high annual breeding success far longer than any individual pair duration – suggesting that these high quality breeding sites were occupied by a succession of high quality birds. Therefore, we suggest that in our study area, these early breeders are commuting further distances to gain access to steeper breeding sites which are potentially of higher quality than sites closer to marine foraging habitats occupied by later breeders.

Multivariate Modeling

Our results from multivariate modeling of the effects of timing of breeding, commuting distance, nest site slope, and nest site elevation did not provide any strong evidence on the relative impact of each of these variables on reproductive success. The highest ranked models often contained all of the possible input variables. The significance levels of predictors in these models were comparable. The moderate correlation between these variables may have influenced the results of this modeling to some extent. Therefore, we cannot conclusively determine the relative importance of each of these variables to Marbled Murrelet nesting success in our study area.

Edge effects

As previously stated, the negative effects of fragmentation on avian reproductive success have been well documented from the midwestern and eastern United States (Hartley and Hunter 1998). However, new synthesis of research on the negative implications of "edge effects" from the more naturally fragmented forests of the Pacific Northwest, with their extreme elevation gradients and glacial topography, have produced unexpected contrasting results. These results suggest that there may be strong geographic differences between the response of species to forest habitat fragmentation in the two areas (Scott 1999). In their recent review of edge effects, Kremsater and Bunnell (1999) detail how in the east and midwest many studies document increased predation and parasitism near edges; while in the Pacific Northwest researchers have found little effect of patch area or negative edge effects. In regards to avian nest predation, negative edge effects have been shown to be more common in forests with urban or agricultural matrices than in regenerating forest (Marzluff and Restani 1999). Unlike urban and agricultural expansion, few new predators accompany the creation of clearcuts and young forest, except Steller's Jays (Marzluff and Restani 1999). Even within "high effect areas", negative edge

effects were only found in half of the studies surveyed by Marzluff and Restani (1999). These reviewers suggest that avian population viability in fragmented western forested landscapes will be regulated by more absolute habitat loss or habitat isolation, whose effects will be determined by species-specific dispersal activities, rather than by inflated rates of nest predation. Nest predation rates are high regardless of fragmentation and edge effects are unlikely to increase these rates (Marzluff and Restani 1999).

These recent findings of less negative effects of forest edges on avian nesting success in northwestern forests of the United States, which have more natural fragmentation and less human activity than eastern forests, may affect interpretation of the role of edge habitat on Marbled Murrelet nest predation. Marzluff et al. (2000) and Luginbuhl et al. (2001) conducted intensive investigation into the effects of timber harvest and forest edges on the success of artificial Marbled Murrelet nests in Washington State. Their study area, like ours, has many areas of commercial forest development. However, unlike Desolation Sound, many areas of western Washington State where Marzluff et al. conducted their study have heavy human activity (i.e. campers, park visitors) in addition to timber harvest. Marzluff et al. (2000) found higher predator abundance and rates of nest predation less than 1km from regular human activity; however, stands >5km from human activity had equal rates of nest predation at the edge of forest habitats compared to the interior. In contrast to expectation, Marzluff et al. (2000) also found stands of mature forest with uniform ("simple") structure had significantly lower rates of predation than stands of complex or very complex structure, which are associated with the oldest late seral forest. In coastal edges, negative edge effects may be stronger, as few murrelet nests have been found in suitable Murrelet habitat within 1km of the coast (Hamer et al. 1995). Burger et al. (2000) documented an increased level of potential murrelet nest predators along coastal edges.

Nest predation is a major factor in Marbled Murrelet nesting success. However, we have no evidence that forest edges negatively affect Marbled Murrelet nesting success in most of our study area, likely due to a high level of natural forest fragmentation and reduced influence of human induced nest predators at most remote murrelet nest sites.

Our data suggest that forest edges, especially natural forest edges, play a role in providing adequate access for murrelets to easily leave and depart their nest sites, as increased slope appears to do. Our findings of increased reproductive success at natural edges compared to interior forest conditions, and the high successful use of forest adjacent to natural openings like avalanche chutes suggests that these edges may have value to the birds as access points which exceeds the risk of potential nest site predation.

Implications

In interpreting our results regarding habitat use and reproductive success, we need to acknowledge that all of our data were obtained from radio marked animals, and that the effect of carrying a radio transmitter may influence an animal's behaviour (Hill et al. 1999). While we have evidence that handling and radio attachment may cause some of our birds to abort a breeding attempt (McFarlane Tranquilla 2001), our annual reproductive success estimates from the radioed birds which did breed are the highest ever reported for the species (Cam et al., in review). Therefore, while carrying a radio may affect individual birds, we believe that these effects do not strongly influence the large scale patterns of habitat use and reproductive success of breeding murrelets.

Our analyses of forest edges suggest that in terms of Marbled Murrelet reproductive success, direct loss of forest habitat may be more important than forest fragmentation, as appears to be the case for many other species (Fahrig 1999). Birds will commute extremely long

distances from their nest to marine sites, presumably because of good foraging conditions, and preservation of these important marine areas should be given a similar level of attention as the conservation of breeding habitat.

Annual reproductive success plays a crucial role in the fitness of individual Marbled Murrelets and the health of murrelet populations. However, as a species with a lifespan of at least ten years (Centre for Wildlife Ecology, Simon Fraser University, unpublished data), and the potential to breed in the majority of those years, the effects of annual reproductive success on fitness are minor compared to adult survival (Cam et al. in review). Annual reproductive success in long lived seabirds is often low and highly variable, making high adult survival the key life history trait for maintaining populations (Chastel et al. 1993).

In conclusion, our study investigated the effects of Marbled Murrelet habitat use on reproductive success in the largest sample of individually marked birds ever documented. Our use of radio telemetry has allowed us to investigate murrelet demography and habitat use with less bias than is associated with conventional methods of studying this elusive species. Few studies of endangered or threatened species have been able to address both reproductive success and habitat use in a study population (Clark and Shutler 1999, Sallabanks et al. 2000). These types of studies on elusive species are extremely difficult and costly, but necessary in terms of developing a thorough understanding of the ecology of a species at risk, in order to formulate the most appropriate management action.

3.5 APPENDIX 2. Marine Distribution and Density of Radio-Marked Marbled Murrelets in Desolation Sound

In addition to using 50% Kernel home-range estimators to determine commuting distance, we also examined the spatial distribution and overlap of core marine areas used by radio-marked birds. The following sample sizes of birds with enough marine detections and known breeding success were used in analyses (1998 n=19, 1999 n=25, 2000 n=19). To assess annual variation and account for slight differences in survey area coverage between years (Figure 3.1), results are presented on an annual basis. For each year, areas of overlap between individual home ranges were calculated. Low, medium, and high areas of home-range overlap were determined by placing each map pixel where home-range overlap occurred into one of the three categories created by assigning quantitative outputs of overlap (ARCVIEW Map Calculator) into one of three qualitative bins representing 1/3 of the actual values. We tested for effects of habitat use on reproductive success between birds which used low home range overlap areas versus ones which had high overlap zones in their core marine areas. Chi Square tests were conducted and Fisher's exact probabilities are reported in annual comparisons due to low sample size. Five birds from 2000 were excluded from these home range overlap analyses because the birds were captured at a site in Toba Inlet, 30km north of our primary capture site in Desolation Sound.

We observed a high annual overlap in core marine foraging habitats (high and medium areas – Figures 3.2, 3.3, 3.4) used by radio marked Marbled Murrelets during the breeding season in our study area from 1998-2000 (Figures 3.2, 3.3, 3.4). These areas of use were centered in Desolation Sound, our capture area. Regions of lower murrelet density covered more spatial area (Figures 3.2, 3.3, 3.4), were more variable between years (Figures 3.2, 3.3, 3.4) birds using

these areas showed no differences in reproductive success compared to birds that had their core area of activity confined to the higher density areas (Table 3.9).

Our results suggest that, across 3 years, most radio-marked Marbled Murrelets in our study area used a relatively small core area of marine foraging habitat during the day. Even when examining the year with the widest marine survey coverage and greatest detection area (2000), birds in our sample had core areas of marine activity (~404km^2) that were 6.8x smaller than the overall area they nested in (~2767km^2). In addition, if you consider that the majority of core marine areas for most birds (in the high and medium density classes) were focused in a very small spatial unit in Desolation Sound (~63km^2), then the discrepancy between the size of marine areas frequented compared to the total nesting area increases to 43.9x. This pattern of "reverse coloniality", with widely disparate nest sites and a relatively localized foraging radius is unusual in comparison to the normal seabird breeding paradigm of limited breeding sites and a wide pelagic foraging range.

In addition, 4 out of 5 breeding birds captured in Toba Inlet in 2000 showed home range overlap with "high density" use areas of birds captured in Desolation Sound (Centre for Wildlife Ecology, Simon Fraser University, unpublished data). These cumulative data suggest that our capture area of Desolation Sound, the high density area of marine habitat use, may represent a "marine hotspot" for our sample of birds in our study area. Use of centralized, abundant food sources for seabird foraging has normally been associated with pelagic feeders responding to prey concentrations generated by large scale variable oceanographic processes (Hunt 1990, Hunt 1997, Whitworth et al. 2000b, Bertram et al. 2001). While inshore feeding alcids have been recorded foraging in consistent areas through a breeding season (Gaston and Jones 1998), no studies have examined these patterns in individual birds.

This hypothesis supports the view that preferred marine habitat for Marbled Murrelets is not ubiquitous and equal, and that certain areas may be of more value to the birds. Management of these types of marine habitats may be of equal importance to the management of terrestrial environments to maintain nesting habitats (Ralph et al. 1995).

We will conduct further analyses to test this "hotspot" hypothesis by incorporating more data from birds captured in Toba Inlet, to determine the degree to which these birds used Desolation Sound in their core areas of marine activity. In addition, we will also examine spatial marine patterns from non-breeding birds and from data at our other field site, Clayoquot Sound on the west coast of Vancouver Island.

3.6 APPENDIX 3. Nest Predator Densities and Elevation

Ground based habitat plots were conducted at accessible sites around nest trees, and also at random sites along an elevation gradient. In addition to information on forest edges collected from these plots, potential murrelet predators observed were also recorded. We investigated whether the distribution of Marbled Murrelet nest predators varied with major landscape features, namely elevation. We used predator counts from random habitat plots conducted in 100m elevation classes (Table 3.10 shows sample sizes by class) in our study landscape in a 50km circle from the central capture location as an index of available habitat. All potential murrelet adult and nest predators (raptors, corvids, and small mammals) (Nelson and Hamer 1995b) were counted and the time taken to complete each plot was recorded. As these habitat plots were not primarily predator surveys, we interpreted them as an index of predator presence and absence. Therefore, we used presence of a particular predator species, corrected for one hour of observation, as a value for analysis. We conducted linear regressions of predator densities, as % of plots within a class, against elevation classes. We examined all potential Marbled Murrelet nest predators (corvids, raptors, and small mammals) for linear changes in predator density with elevation.

Our predator data show a significant linear decrease in potential murrelet nest predators with increasing elevation in our study area (Figures 3.5, 3.6). This overall trend held when examining all potential predators, and potential avian predators only (Figures 3.5 – 3.8). Both these relationships had a strong outlier of high predator presence in the first elevation class, but these negative trends were still significant when outliers were removed (Figures 3.6, 3.8). The Stellers Jay, thought to be one of the most likely species to prey on murrelet nests (Nelson 1997) showed no such linear trend (Figure 3.9), and appears to have high numbers at the mean nest

elevation of Marbled Murrelets at our study site, approximately 700m. There were no apparent trends in the small mammal data.

As previously described in our discussion of "edge effects" on murrelet nests, it appears that nest predation is common across many varied forest habitats. However, our data suggest that potential predators are much more likely at very low elevations, and reduced at very high elevations. Most of our nests in the lowest elevation class are near coastal sites, where high numbers of potential murrelet nest predators have been previously documented (Burger et al. 2000). The mean predator density at our random plots within 1 km of the ocean (n=24) was 3.1x greater than those plots greater than 1km from the ocean (n=94) (Mann Whitney test, W=1841.5, p=0.001). At extremely high elevations, the food resources for birds and small mammals which might prey on murrelet nestlings is likely scarce, as distributions of these potential predator species have elevation limits (Badgley and Fox 2000). Therefore, low elevation coastal sites are likely to contain many potential murrelet nest predators, while sites in the higher elevation classes are likely to support fewer potential predators. However, in extreme elevations the availability of suitable nesting habitat also appears to decrease dramatically.

While studies of artificial murrelet nest predation in Washington State have shown that point counts of corvid abundance were strongly correlated with predation on artificial murrelet nests in a landscape similar to our study area, none of these trials were conducted at elevations greater than 600m (Luginbuhl et al. 2001). In addition, weather conditions significantly affected the results of corvid surveys (Luginbuhl et al. 2001). Therefore, we recommend that more rigorous, replicated data needs to be collected on murrelet predators and potential predation rates at higher elevations, and slopes – as the two variables are positively correlated in many landscapes, to empirically test if birds may be exposed to reduced predation risk in these areas.

Table 3.1. Correlation matrix for the following characteristics of nesting Marbled Murrelets: laying date (julian date), nest elevation (metres), direct distance from nest to centre of core marine foraging area (km), estimated flyway distance from nest to centre of core marine foraging area (km), nest slope (Classes of 10 degree blocks). Sample includes data from 1998-2000 (n=68).

	Lay Date	Elevation	Direct Distance	Flyway Distance
Elevation	-0.063			
	0.610			
Direct Distance	-0.370	-0.092		
	0.002	0.453		
Flyway Distance	-0.414	-0.074	0.955	
	0.0004	0.548	<0.0001	
Slope	-0.282	0.137	0.250	0.246
	0.020	0.266	0.040	0.043

Table 3.2. Correlation matrix for the following characteristics of nesting Marbled Murrelets: laying date (julian date), nest elevation (metres), direct distance from nest to centre of core marine foraging area (km), estimated flyway distance from nest to centre of core marine foraging area (km), nest slope (Classes of 10 degree blocks). Sample includes data from 1998-2001 (n=98). Data from 2001 does not include distance so only marked correlations differ from Table 3.

	Lay Date	Elevation	Direct Distance	Flyway Distance
Elevation	-0.065			
	0.541			
Direct Distance	-0.370	-0.092		
	0.002	0.453		
Flyway Distance	-0.414	-0.074	0.955	
	0.0004	0.548	<0.0001	
Slope	-0.298	0.410	0.250	0.246
	0.003	0.0001	0.040	0.043

Table 3.3. Univariate binary logistic regression results for the following characteristics of nesting Marbled Murrelets as predictors of "Mid-Chick" rearing success: laying date (julian date), nest elevation (metres), Flight Distance - Estimated flyway distance from nest to centre of core foraging area (km), nest slope (classes of 10 degree blocks). Sample includes data from 1998-2000 (n=68). Intercept coefficients and p values are not included.

Parameter	Coefficient	St. Error	Chi-Square (df=2)	p
Laying Date	-0.055	0.023	5.669	0.017
Flight Distance	0.037	0.015	6.585	0.010
Slope	0.500	0.193	6.713	0.010
Elevation	0.002	0.001	5.249	0.022

Table 3.4. Univariate binary logistic regression results for the following characteristics of nesting Marbled Murrelets as predictors of "Mid-Chick" rearing success: laying date (julian date), nest elevation (metres), nest slope (classes of 10 degree blocks). Sample includes data from 1998-2000 (n=98). Intercept coefficients and p values are not included. Distance information was not available for 2001 data, so a univariate model using distance as a predictor of success was not run.

Parameter	Coefficient	St. Error	Chi-Square (df=2)	p
Laying Date	-0.060	0.019	9.935	0.002
Slope	0.402	0.141	8.119	0.004
Elevation	0.001	0.001	4.638	0.031

Table 3.5. Akaike's Information Criterion (AIC) values for all possible logistic regression model combinations using Laying Date, Flight Distance, Slope, and Elevation as predictors of "mid-chick" rearing success. Model ranks (lowest AIC = best fit) and parameters included in the model are indicated. Data is from 1998-2000 (n=68). Equations and associated predictor p values of best fit models for each dataset are listed.

Model Rank	Date	Distance	Slope	Elevation	AIC
1		x	x	x	79.162
2	x	x	x	x	80.065
4	x	x		x	80.847
3		x		x	80.909
5		x	x		83.568
6	x	x	x		84.031
7			x	x	84.060
8	x			x	84.290
9	x		x		84.755
10	x	x			86.229
12			x		86.748
11		x			86.977
13	x				87.801
14				x	88.734

Best Model Selection

Parameter	DF	Coefficient	St. Error	Chi-Square	p
Intercept	1	-4.251	1.330	10.210	0.001
Distance	1	0.043	0.018	5.940	0.015
Elevation	1	0.003	0.001	5.417	0.020
Slope	1	0.388	0.207	3.510	0.061

Table 3.6. Akaike's Information Criterion (AIC) values for all possible logistic regression model combinations using Laying Date, Slope, and Elevation as predictors of "mid-chick" rearing success. Model ranks (lowest AIC = best fit) and parameters included in the model are indicated. Data is from 1998-2001 (n=98). Equations and associated predictor pvalues of best fit models for each dataset are listed.

Model Rank	Date	Slope	Elevation	AIC
1	x	x		115.334
2	x	x	x	115.767
3	x		x	116.000
4	x			118.125
5		x		121.434
6		x	x	122.052
7			x	125.624

Best Model Selection

Parameter	DF	Coefficient	St. Error	Chi-Square	p
Intercept	1	7.410	3.083	5.776	0.016
Date	1	-0.052	0.020	6.873	0.009
Slope	1	0.309	0.146	4.516	0.034

Table 3.7. Fledging success by presence or absence of forest edge within 50m and within 100m of accessible Marbled Murrelet nests located by radio telemetry from 1999-2001, n=37. Nests adjacent to edges were further tested to assess differences in fledging success between nests located adjacent to natural edges (rivers, avalanche chutes, large natural disturbances) vs artificial edges (clearcuts and logging roads). Chi Square statistics and Fisher's exact probabilities are reported.

50 m edges		Edge	No Edge	chi-square (1df)	p
	Fail	11	10	0.055	1
	Fledge	9	7		
		Natural Edge	Artificial Edge	chi-square (1df)	p
	Fail	11	0	2.716	0.189
	Fledge	7	2		

100m edges		Edge	No Edge	chi-square (1df)	p
	Fail	14	7	2.141	0.248
	Fledge	14	2		
		Natural Edge	Artificial Edge	chi-square (1df)	p
	Fail	11	3	0.7	0.677
	Fledge	9	5		

Table 3.8. "Mid-Chick" Rearing Success of 98 Marbled Murrelet nests located from radio telemetry (1998-2001) by edge type within 200m from 1:250,000 GIS LUP. Chi Square tests perform all possible comparisons between nests adjacent to natural edge, artificial edge, or no edge.

Natural Edges	Successful	Not Successful
Alpine	4	0
Barren Surfaces	9	4
Avalanche Chutes	17	2
Wetlands	2	3
Ocean	1	0

Artificial Edges		
Clearcuts	6	4
Old growth / second growth transition	8	5

No Edges		
In Old Growth	14	11
In Young Forest	2	6

	Successful	Not Successful	Success Rate
Natural Edge	33	9	0.786
Artificial Edge	14	9	0.609
No Edge	16	17	0.485

Chi Square Tests

Groups compared	Chi-Square	df	p
All	7.439	2	0.024
natural and artificial	2.326	1	0.127
natural and no edge	7.386	1	0.007
artificial and no edge	0.836	1	0.361

Table 3.9. "Mid-Chick" rearing success of Marbled Murrelets using "Low Density" marine areas in their core marine foraging zones compared to those birds foraging only in core areas of higher density of radio-marked breeding birds. Annual and pooled data are shown from 1998 to 2000. Values represented numbers of Murrelets with known breeding success. Chi Square statistics are reported for each test. Fisher's exact p values are reported for annual comparisons due to low sample sizes in some cells.

Year	Success	No "Low Density" Use	"Low Density" Use	Chi - square (1 df)	p
1998	Yes	4	8	1.028139802	0.3765
	No	4	3		
1999	Yes	8	8	0.071225074	1
	No	4	5		
2000	Yes	5	7	0.325822098	0.6561
	No	2	5		
Pooled	Yes	17	23	0.005706559	0.939784
	No	10	13		

Table 3.10. Sample size of accessible random habitat plots in each 100m elevation class used for analysis of predator surveys

Elevation Class	Sample size
1	13
2	13
3	14
4	12
5	10
6	8
7	7
8	12
9	10
10	6
11	5
12	8

Figure 3.1. Core marine telemetry coverage areas for 1998 – 2000. Toba Inlet and Desolation Sound capture areas are marked

Toba Inlet

Desolation Sound

Ds_98_coresurvey areas.shp
Ds_2000_coreflightlines.shp
Ds_1999_coreflightareas.shp
Dempoints
Dempoints

30   0   30   60 Kilometers

Figure 3.2. Overlap of core marine areas of 1998 radio-marked Marbled Murrelets (50% Kernel Homeranges)

Dempoints
Dempoints
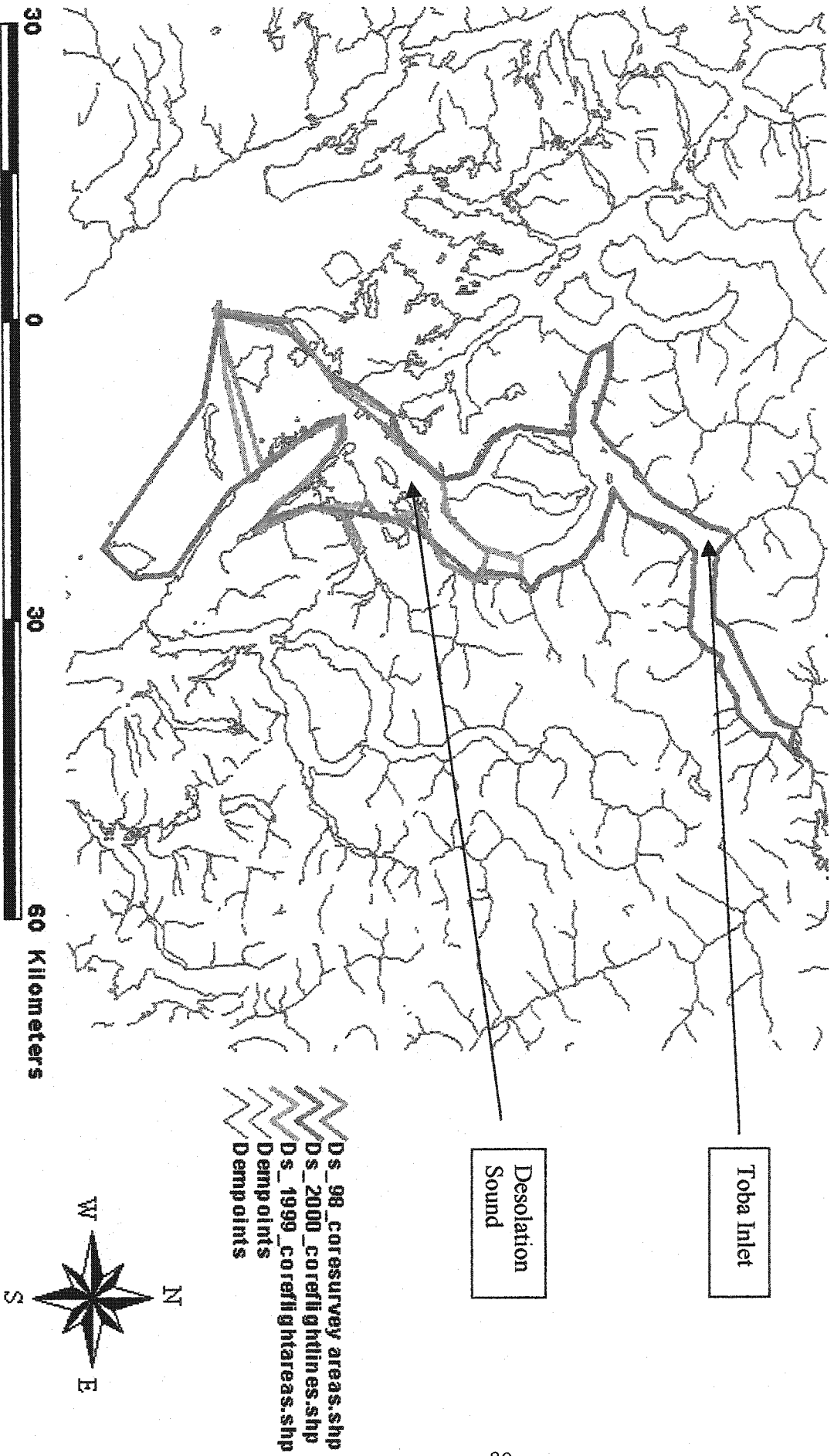Densityclasses1998.shp
Low
Medium
High

81
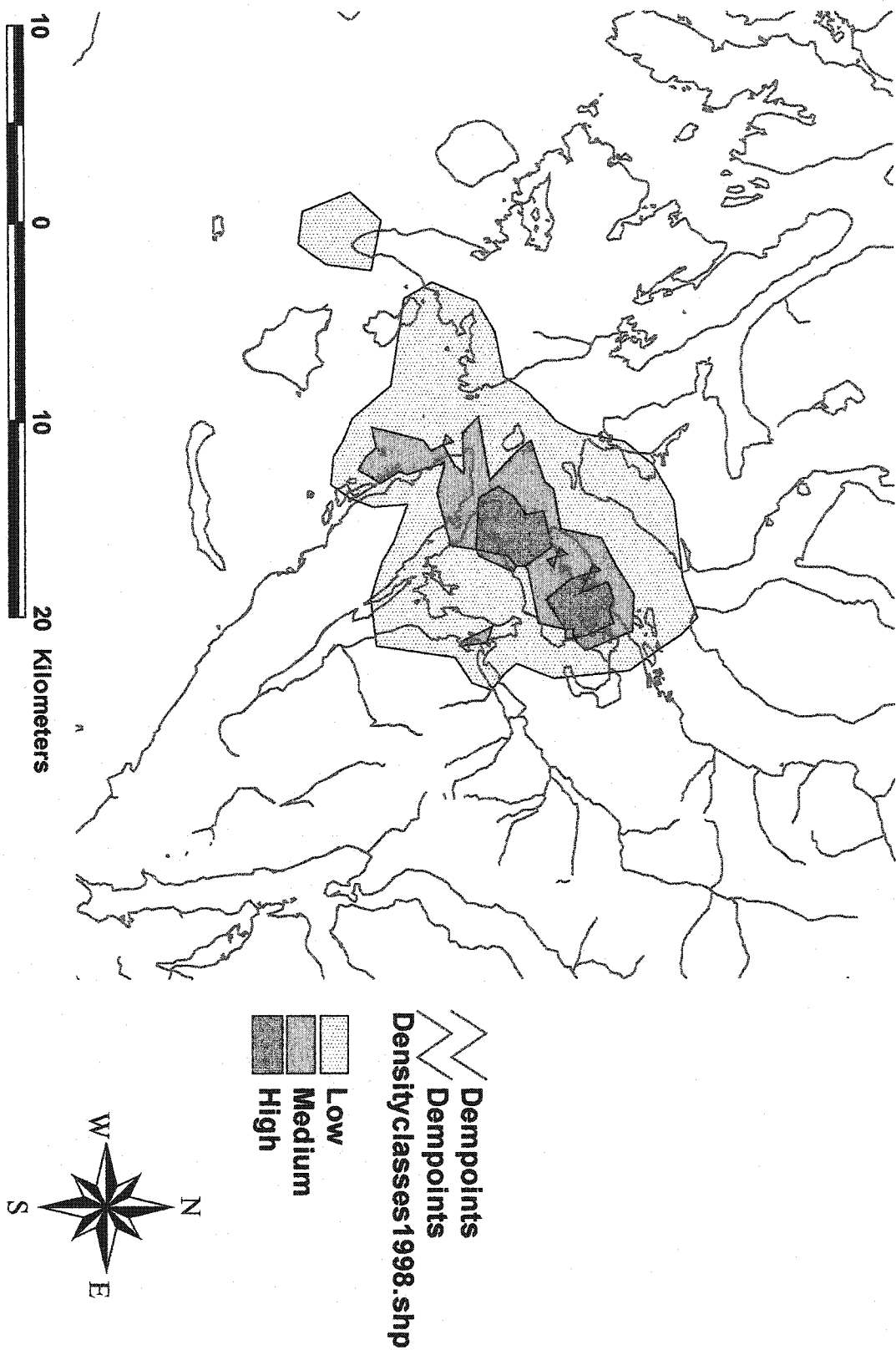
Figure 3.3. Overlap of core marine areas of 1999 radio-marked Marbled Murrelets (50% Kernel Homeranges)
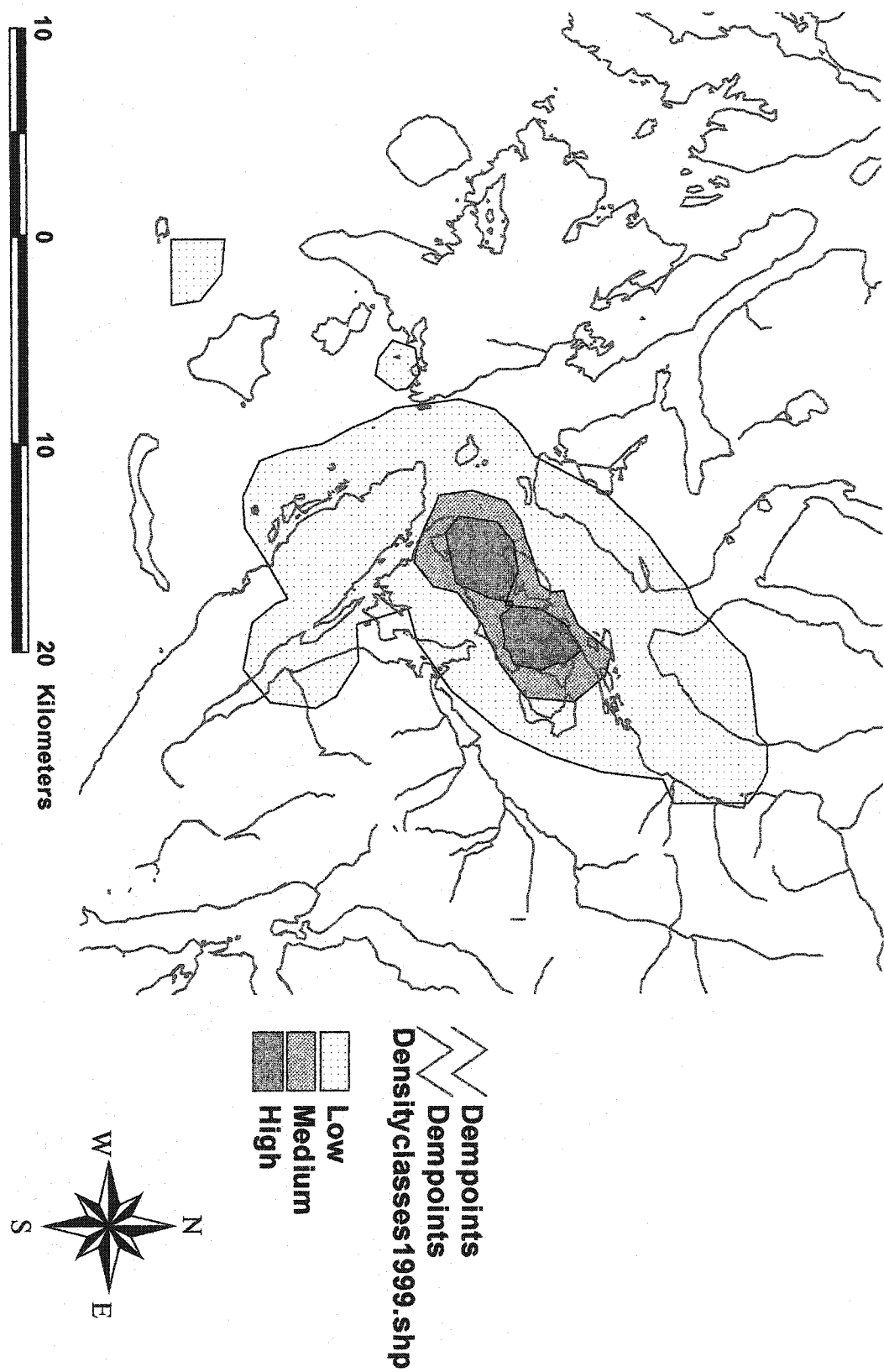
Figure 3.4. Overlap of core marine areas of 2000 radio-marked Marbled Murrelets (50% Kernel Homeranges)

Dempoints
Dempoints
Newdensityclasses2000ds.shp
Low
Medium
High

30 0 30 60 Kilometers
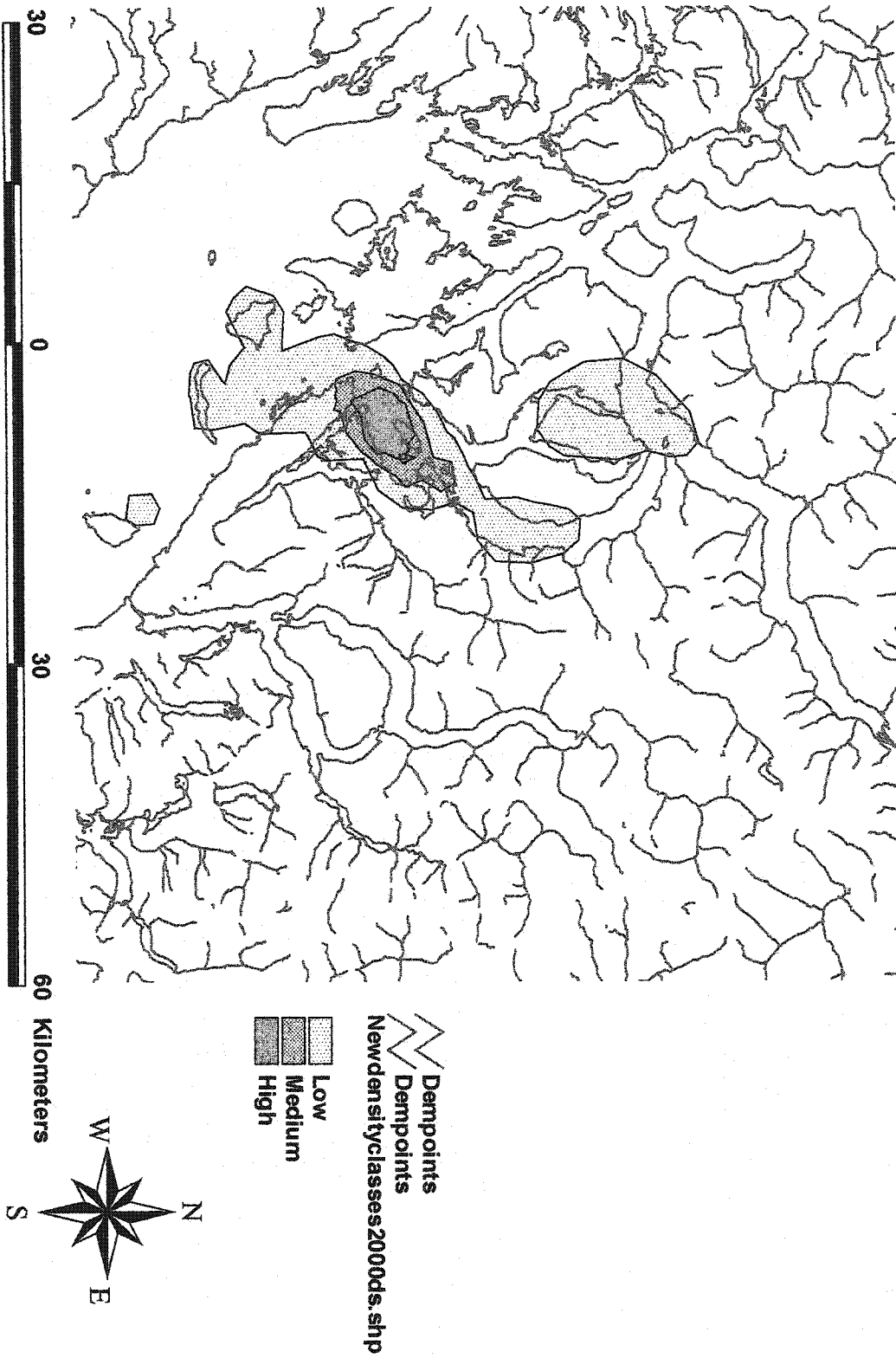
Figure 3.5. Potential Marbled Murrelet nest predators (corvids, raptors, squirrels) vs.

Elevation for random habitat plots (n=118)
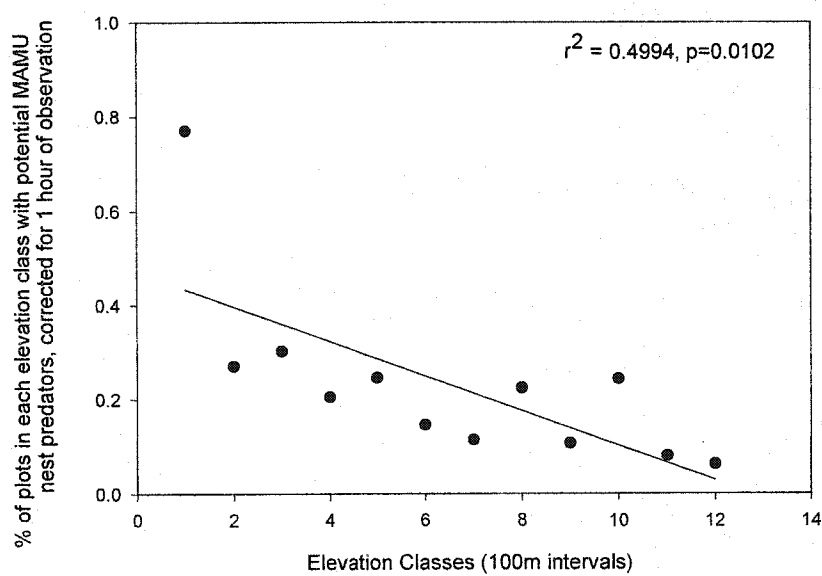
Figure 3.6. Potential Marbled Murrelet nest predators (corvids, raptors, squirrels) vs.

elevation for random habitat plots (n=118), excluding first 100m elevation class
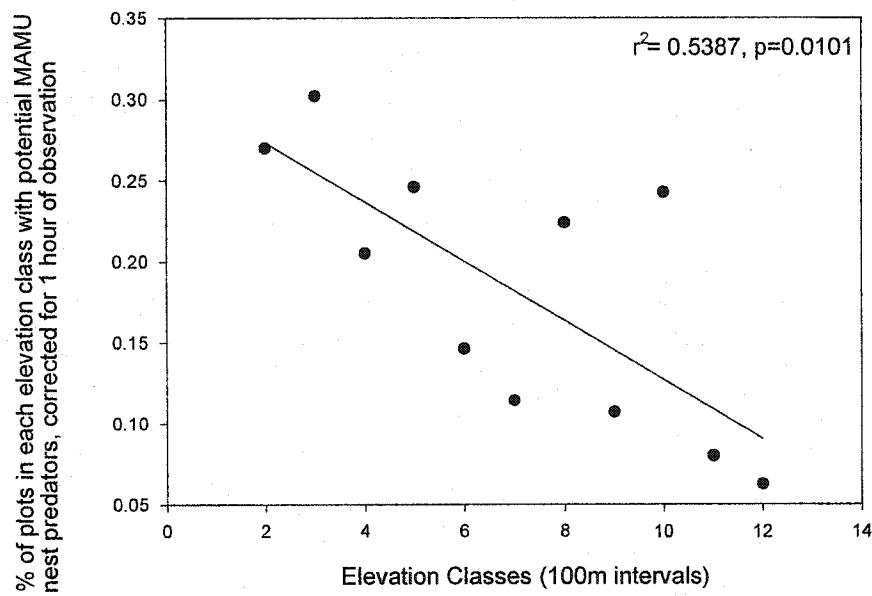
Figure 3.7. Potential avian Marbled Murrelet nest predators vs. elevation for random

habitat plots (n=118)

Figure showing scatter plot with regression line. Y-axis: % of plots in each elevation class with potential avian MAMU nest predators, corrected for 1 hour of observation (range 0.0 to 0.8). X-axis: Elevation Classes (100m intervals), range 0 to 14. Statistics shown: $r^2 = 0.4324$, $p=0.0201$.
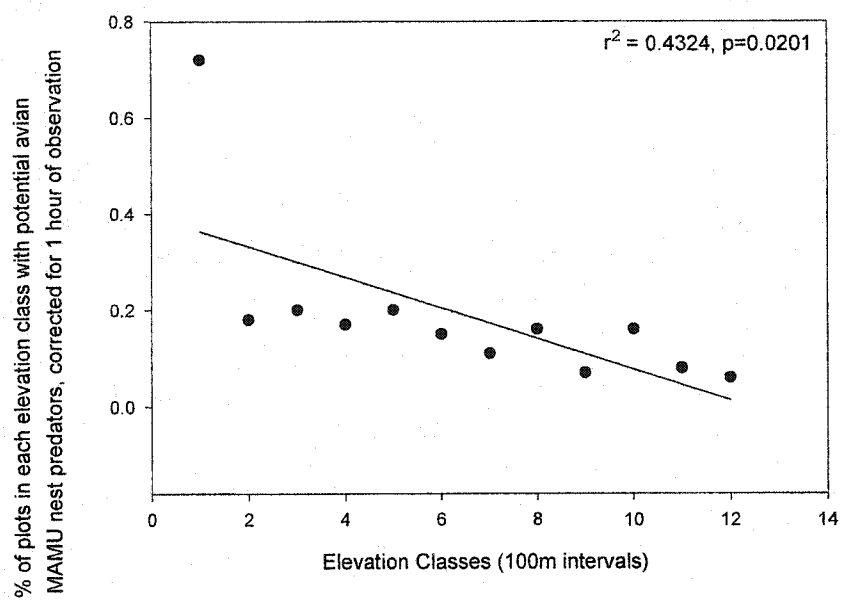
Figure 3.8. Potential avian Marbled Murrelet nest predators vs. elevation for random

habitat plots (n=118), excluding first 100m elevation class

Figure 3.9. Steller's Jays vs. elevation for random habitat plots (n=118)

GENERAL SYNTHESIS

The use of radio telemetry has greatly enhanced our understanding of Marbled Murrelet breeding ecology, providing data thought to be unatt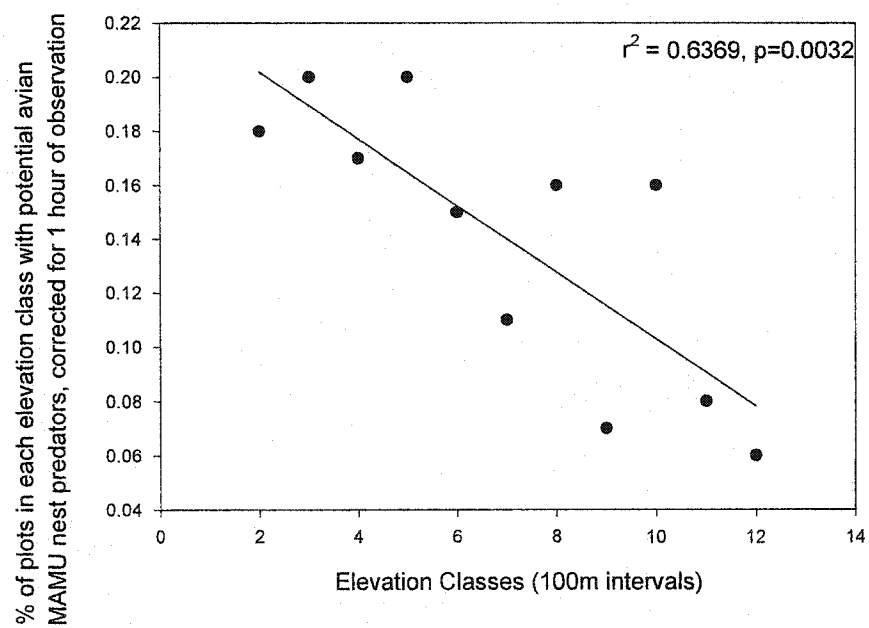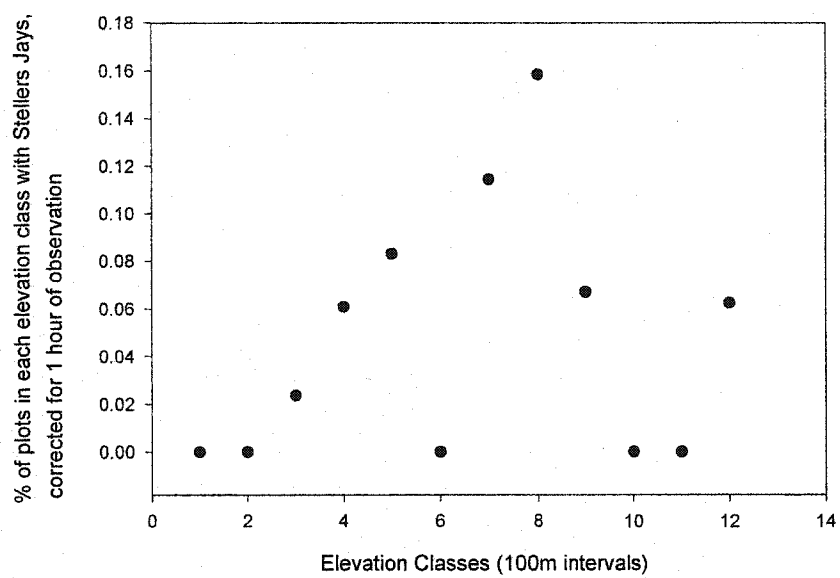ainable only 5 years ago. The primary goal of this thesis was to describe the breeding behaviour and reproductive success of individual radio-marked Marbled Murrelets. The major findings of this study were:

(1) Marbled Murrelet breeding state and success can be accurately inferred with radio telemetry.

(2) Male breeding birds visited their nests, and likely did more provisioning of young, than females during chick rearing. The male bias was primarily due to a reduction of female visitation during late chick rearing.

(3) Early breeding birds commuted further from foraging areas to nest areas, and nested at sites of steeper slopes than later breeding birds. Earlier breeding birds were more successful, while higher nest site elevation, steeper nest site slope, and longer commuting distance were all associated with greater success.

(4) In our study area there is no evidence to suggest that nesting near forest edges, particularly natural edges, reduces reproductive success in Marbled Murrelets.

Demographic parameter estimates are essential for understanding population ecology and developing management plans for species of concern. In cryptic breeding species, these estimates are difficult to obtain. In Chapter 1, I described inferred estimates of breeding success through radio telemetry for Marbled Murrelets. I detailed how behaviour based inferences of activity at different reproductive stages do not differ between confirmed nest sites and suspected ones which were physically inaccessible to us. Initiation of breeding and incubation success were accurately predicted from the duration of repeated daily shifts of adults from the ocean to their

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inland nest sites. Chick rearing success was accurately predicted by visitation rates of adults during provisioning. This method may overestimate early breeding failure but likely provides unbiased fecundity estimates for our population. Accurately inferring breeding status and success through telemetry is costly and labor intensive, but can provide crucial demographic information for cryptic breeding species of concern.

Telemetry methods can also provide insight into murrelet behavioural ecology. Chapter 2 reported a significant male bias in dawn and dusk nest visitations of breeding Marbled Murrelets during the chick rearing period. Overall visitation rates of males during chick rearing were 1.3 times greater than those of females. Dusk visitation rates by males with active nests were 1.8 times greater than those of females. Male visitation rates were similar between early and late chick rearing, both within and among individuals. However, female visitation rates during late chick rearing were significantly lower than female rates early in rearing, both within and between individuals. In addition, between-sex comparisons of nest visitation during early and late chick rearing showed significant reductions in female effort relative to males, only during late chick rearing. These results suggest that male birds may provision chicks more often than females, especially during the last half of chick rearing. These findings offer a behavioural explanation for the annual male bias of birds flying inland during the chick rearing period at Theodosia Inlet in Desolation Sound from 1994–1999. Although female-biased provisioning has been documented in several species, male-biased provisioning has not been widely reported in other alcids. Findings of reduced overall nest visitation in late chick rearing support the hypothesis that the increase in forest detections of murrelets in July across the species range is due to an influx of non-breeders, and not increased visitation by active breeders.

Chapter 3 details investigations into the effects of marine and terrestrial habitat use on

reproductive success. As expected from many previous avian studies, early breeding birds had higher reproductive success. These early breeders were also nesting more successfully at sites of greater slope, preferred habitat in radioed birds from our study (Huettmann et al., in review). The greater commuting distance of early, more successful breeders contrasts the lack of conclusive findings by Hull et al. (2001) from our 1998 data. Increased commuting distance, up to ~100km from nest to feeding areas, does not appear to be energetically costly for murrelets. My results also suggest that the closest ocean to a nest is often not where birds are foraging. Most murrelet nests we located were adjacent to natural forest edges, despite a high degree of forest fragmentation from logging in our study area. My analyses did not show negative effects of reproductive success from close proximity to forest edges, though ground based analyses of sites near artificial edges had low power. However, it appears that the benefits to murrelets of nesting near edges away from constant human activity, such as increased access – which is also found in sites of steeper slope, may outweigh the negative effects of nest predation.

In conclusion, this study has shown how technology and lots of human effort can produce extremely valuable ecological information for a cryptic breeding species of concern. As always, the more we learn the more questions there are to ask. This study has shown that for elusive species, like the Marbled Murrelet, we cannot assume that good ecological data is impossible to obtain. We must take the hard road, and spend the time and money needed to ensure that our understanding of a species, and our plans for its management, are based on a strong footing of solid science.

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