POPULATION ECOLOGY OF THE ENDANGERED VANCOUVER ISLAND MARMOT: DECLINE AND POTENTIAL FOR RECOVERY

By

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To Jack White (and Meg too)

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Abstract of Thesis Presented to the Graduate School
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By

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Recovery of the endangered Vancouver Island marmot is contingent upon releases of captive-born marmots into natural habitats. Success of such reintroduction programs largely depends on the ability of released animals to survive in the wild. We used radio-telemetry (1992-2007) and mark-resight (1987-2007) data to estimate seasonal and annual survival rates of the Vancouver Island marmot, to compare survival and cause-specific mortality rates of captive-born marmots that have been released into the natural habitat with those of wild-born marmots, and to test for the effect of age at release on survival of the released marmots. However, annual survival of captive-born marmots released into the wild was low compared to wild-born marmots. Marmots released as two-year-olds or older survived more successfully than those released as yearlings. Predation by golden eagles was the most important cause of mortality for captive-born marmots, whereas predation by wolves and cougars was more important for wild-born marmots. These results suggest that delaying release of captive-born marmots until two years of age may enhance their probability of survival in the wild, and will likely improve the success of the release program.

In order to formally test the effects of survival and reproduction on population growth rate, we constructed population projection models and performed elasticity analysis. We estimated

age-specific reproductive parameters and used various age-specific survival rates spanning different periods of time and/or representing various subsets of the population. We found that population growth rate in recent years (2003-2008) was only slightly higher than in the past (1987-2002), and currently the population is still declining by at least 12% annually. The population growth rate estimated for a hypothetical population of captive-born marmots corresponds with a 28% decline annually, indicating released individuals alone will not result in a persistent population. However, population growth rate for a population of wild-born individuals in recent years was greater than one, indicating a 3% annual increase in population size. Elasticity analysis confirmed the relative importance of survival for the population, especially adult survival. Our results provide insight into the potential for recovery of the species through reintroductions.

CHAPTER 1
POPULATION ECOLOGY, REINTRODUCTION BIOLOGY, AND THE ENDANGERED VANCOUVER ISLAND MARMOT: AN INTRODUCTION

Understanding causes of population decline is an important first step towards recovery of endangered species (Caughley 1994; Caughley & Gunn 1996). Change in population size is the consequence of changes in one or more vital demographic rates (Caswell 2001; Mills 2007; Oli & Armitage 2004); effects of the environment and management actions on the dynamics of populations are mediated through their influences on demographic variables. Furthermore, reduction in survival can lead to decline of wildlife populations whose growth rate is very sensitive to changes in survival rates (Heppell et al. 2000; Oli & Dobson 2003; Stahl & Oli 2006). Therefore, rigorous estimates of survival and knowledge about how various factors influence this key demographic rate are necessary for conservation of species at risk and specifically reintroduction planning (Le Gouar et al. 2008).

Captive-breeding and reintroduction are frequently used for the conservation of rare or endangered species (Caughley & Gunn 1996; Sarrazin & Legendre 2000). However, few reintroduction programs have achieved success, due in part to poor understanding of the population-level effects of alternative release strategies (Armstrong & Seddon 2008; Grenier et al. 2007; Sarrazin & Legendre 2000; Seddon et al. 2007). Furthermore, the reintroduction literature largely consists of descriptive accounts of success or failure of reintroduction programs; progress in this branch of conservation biology has been slow due to the lack of quantitatively rigorous analysis of data generated from well-designed comparative or experimental studies (Armstrong & Seddon 2008). Demographic models can provide valuable insights into likely results of conservation efforts, and allow for evaluation of the population-level impacts of release strategies; however, few reintroduction programs have benefitted from such models (Caswell 2001; Meretsky et al. 2000; Sarrazin & Legendre 2000).

The Vancouver Island marmot (*Marmota vancouverensis*) is an endangered mammal inhabiting subalpine meadows on Vancouver Island, British Columbia (Janz et al. 2000; Nagorsen 1987). The *M. vancouverensis* population went through several range restrictions leaving the population in only two locations on the island by the 1970s. The marmot population increased to 300-350 individuals during the mid-1980s as marmots colonized the openings created by high-altitude logging that resembled marmot habitat (natural meadows, Bryant & Janz 1996). This increase in population size was short-lived, as most marmot colonies in clearcut habitats disappeared by 2000 and the population declined to an estimated 35 individuals by 2003 (Bryant 2005). The disappearance of marmots from clearcut habitat is likely due to forest regeneration reducing the suitability of clearcuts as marmot habitat (Bryant 1998). Changes in landscape structure following logging probably had direct and indirect impacts on the entire marmot population through predator-prey interactions (Aaltonen et al. in review; Bryant & Page 2005).

With the marmot population on the brink of extinction, a captive-breeding program was initiated in 1997 with facilities established both on and off Vancouver Island (Bryant 2005). During 2003-2008, 155 captive-born marmots were released into various sites at both Mt. Washington and Nanaimo Lakes (Kruckenhauser et al. 2009; unpublished minutes, Vancouver Island Marmot Recovery Team, Dec. 2008). The Vancouver Island marmot is an excellent case of an endangered species for which drastic management efforts have been made with little quantitative support. However, we have the long-term monitoring data available to perform quantitative analysis in order to guide the recovery strategy, which is rare for an endangered species. We used 20 years of monitoring data to estimate survival, test hypotheses about factors

affecting survivial, examine population growth rate, and consider the potential for recovery of the species.

CHAPTER 2
REINTRODUCTION, AGE-AT-RELEASE, AND SURVIVAL

Introduction

Understanding causes of population decline is an important first step towards recovery of endangered species (Caughley 1994; Caughley & Gunn 1996). Change in population size is the consequence of changes in one or more vital demographic rates (Caswell 2001; Mills 2007; Oli & Armitage 2004); effects of the environment and management actions on the dynamics of populations are mediated through their influences on demographic variables. Furthermore, reduction in survival can lead to decline of wildlife populations whose growth rate is very sensitive to changes in survival rates (Heppell et al. 2000; Oli & Dobson 2003; Stahl & Oli 2006). Therefore, rigorous estimates of survival and knowledge about how various factors influence this key demographic rate are necessary for formulation of recovery plans and conservation of species at risk (Le Gouar et al. 2008).

The Vancouver Island marmot (*Marmota vancouverensis*) is endemic to Vancouver Island, British Columbia, Canada. Concern brought on by the restricted geographic distribution and low numbers, led to *M. vancouverensis* being listed as endangered in 1978 (Bryant & Page 2005; Shank 1999). Systematic field surveys suggest that the marmot population increased during the early 1980s to a peak of 300-350 individuals during the mid 1980s (Bryant & Janz 1996). However, by 2004 the population had declined to approximately 35 individuals in the wild (Bryant 2005). Landscape changes due to clearcut logging and increases in predation-related mortality are thought to have contributed to the population decline (Bryant & Page 2005; Janz et al. 2000).

Significant conservation accomplishments towards recovery of *M. vancouverensis* have been made through planned captive-breeding and release programs (Janz et al. 2000). Captive

breeding facilities were established both on and off the island beginning in 1997, and captive-bred marmots have been released into their natural habitat since 2003 (Bryant 2005, 2007). There have been both reintroductions of marmots into empty but historically occupied sites and re-enforcement of existing colonies with additional marmots. During 2003-2007, 96 marmots were released and monitored using radio-telemetry. Arguably, the most important conservation measure currently in place is the release of captive-bred marmots into their natural habitat. Although reintroduction programs have been successful in some cases, limitations of captive-breeding and re-introduction programs for species conservation are well documented (e.g., Caughley and Gunn 1996; Snyder et al. 1996; Moorhouse et al. 2009). Success of such programs depends to a large extent on the ability of released animals to survive and reproduce in their natural habitats.

Often, released animals have a lower probability of survival in the wild than their wild-born counterparts, reflecting some cost associated with being raised or held in captivity (Beck et al. 1994; Mathews et al. 2005; Sarrazin and Legendre 2000; Snyder et al. 1996). Any additional mortality may only apply for a period immediately post-release after which survival of released individuals increases to a rate near that of wild-born individuals (Bar-David et al. 2005; Sarrazin et al. 1994; Maran et al. 2009). Age at which animals are released can also influence their subsequent survival and the success of a reintroduction program (Green et al. 2005; Le Gouar et al. 2008; Sarrazin and Legendre 2000). Understanding differences between captive-born and wild-born marmots in survival and causes of death can provide information to potentially improve success of the recovery program. However, whether and to what extent survival and causes of mortality of captive-born marmots differs from those of wild-born marmots, or if age at release influences survival of captive-born marmots, remained unknown until this study.

To provide demographic information needed for effective recovery of *M. vancouverensis*, Bryant and Page (2005) analyzed radio-telemetry data collected through 2004. These authors provided estimates of survival and also examined causes of mortality and seasonal variations in survival. Field study has continued since this work was completed, and many more marmots have been monitored via radio-telemetry. Consequently, sample sizes and our ability to test hypotheses regarding factors influencing survival of marmots have increased substantially in recent years.

Our goals were to build upon previous work, provide more rigorous estimates of survival, and test hypotheses about factors influencing survival of marmots using radio-telemetry data. Using a subset of radio-telemetry data collected since the first releases of captive-born marmots in 2003, we also tested the hypotheses that wild-born marmots would have a higher probability of survival than their captive-born counterparts, and that captive-born marmots released at an older age would survive better than those released as yearlings.

Predation is the most important cause of mortality of wild Vancouver Island marmots (Bryant & Page 2005). Given that captive-born marmots are not exposed to predators during early, possibly important developmental stages as wild-born marmots are, their behavioral responses to the risk of predation may differ (Blumstein et al. 2001). Alternatively, their ability to escape various predators may differ due to disparities in experience or body condition. Thus, we also estimated cause-specific mortality rates, and tested for differences in mortality rates between captive-born and wild-born marmots for each cause.

Pups were seldom implanted with radio-transmitters. Consequently, radio-telemetry data were sparse and it was not possible to estimate survival rates for this age-class. We combined the radio-telemetry and long-term capture-mark-resighting (CMR) data and analyzed the

combined dataset within a multi-state CMR modeling framework (Williams et al. 2002). Combining the data from two sources allowed us to estimate age-specific survival rates, and to test hypotheses regarding the influence of age, sex, habitat type, and geographic location on survival of marmots.

Methods

Study Species

The distribution of *M. vancouverensis* is restricted to the interior mountainous zones of Vancouver Island (Nagorsen 1987). Marmots live in open, subalpine meadows characterized by colluvial soils, diverse vegetation, and lookout spots (Heard 1977; Milko & Bell 1986). These small patches of suitable habitat were historically interspersed within much larger areas of dense old-growth forest, creating a pronounced metapopulation structure (Bryant 1998).

Vancouver Island marmots are generalist herbivores (Martell & Milko 1986) living in social colonies consisting of one or more family groups (Bryant 1998). They exhibit slow maturation, delayed dispersal, and large body size relative to most marmots, but similar to other members of the *M. caligata* group (Armitage 1999; Barash 1989; Griffin et al. 2008). The annual cycle of Vancouver Island marmots consists of an active season (approximately, early May through early October) and hibernation during the winter in underground burrows for an average of 210 days (SE ± 7.6 days`, Bryant & McAdie 2003).

Study Area

This study was conducted on Vancouver Island, British Columbia, Canada. The regional vegetation is dominated by western hemlock and mountain hemlock, with interspersed meadows. The landscape of Vancouver Island has undergone extensive change since the late 1950s when forestry companies began harvesting at progressively higher elevations. Clearcuts created open habitats resembling meadows, and marmots began to colonize them extensively during the

1980s. By the mid-1980s, more than half of the marmot population was living in clearcut habitats; however, few marmots have inhabited clearcut habitats since 2000.

The present distribution of marmots on Vancouver Island consists of two main populations (Bryant 1998). The larger metapopulation, Nanaimo Lakes, is on the southern part of the island, and is characterized by mountains of lower elevation and less rugged terrain than the central and northern regions. All colonies within the Nanaimo Lakes metapopulation are concentrated in an area encompassing 840 km^2 within 5 adjacent watersheds (Bryant 1998). The smaller population on Mt. Washington is in central Vancouver Island, 80-95 km north of Nanaimo (Figure 2-1). Based on DNA evidence, dispersal between the two metapopulations is unlikely (Kruckenhauser et al. 2009).

Releases of captive-born individuals have taken place at both Nanaimo Lakes and Mt. Washington. Within the past two years, there have also been re-introductions to Strathcona Provincial Park and Mt. Cain, to the west and north of Mt. Washington respectively.

Field Methods

Marmots were captured using single door Havahart traps baited with peanut butter; transferred to a tapered handling bag to restrict marmot movement, and sedated using procedures described in Bryant (1996). Each marmot received a pair of numbered metal ear tags. Individuals were classified into one of four age-classes: pup (0-1 years); yearling (1-2 years); two-year-old (2-3 years old); or adult ($\geq$3 years old). Age was accurately known for marmots captured for the first time as pups or yearlings; it was estimated for marmots captured for the first time as two-year-olds or adults (Bryant 1998). The majority of trapping occurred during the months of July and August. Marmot resightings were made throughout the active season using 60x spotting scopes, usually before 1100 hours when marmots were most active. Resightings were considered visual recaptures, and were included in CMR analysis.

Radio-telemetry of marmots began in 1992, with an increasing proportion of the marmot population radio-tagged since (Figure 2-2). Types of transmitters and methods used for surgical implant of transmitters are described in detail by Bryant and Page (2005). Radio-tagged marmots were tracked from the ground or from a helicopter. Non-dispersing marmots typically remained close (100-1000 m) to home burrows in most cases, and thus could be tracked from the ground. However, helicopter flights were necessary to reach remote colonies and to track dispersing marmots. The frequency of tracking varied depending on funding, weather, road access problems, and research priorities in various years of the study (Bryant and Page 2005).

Data Analysis

Analysis of radio-telemetry data

We used known fate models implemented in Program MARK (White & Burnham 1999; Williams et al. 2002) to estimate and model survival of marmots. Based on radio-telemetry data, we constructed encounter histories for each marmot for each year with 13 time intervals: 12 active season intervals, each 2 weeks long; and one winter season (hibernation) interval, approximately 28 weeks long (Bryant & Page 2005). The differences in time interval length between the active and the winter seasons were accounted for during data analysis. A marmot can survive and be radio-tracked for more than one year, each of which was considered a separate encounter history; therefore, sample sizes are reported as "marmot-years".

We developed and tested an *a priori* set of candidate models investigating the effects of several factors on survival. First, we tested for the additive and interactive effects of sex and age on survival. For age effect, we considered a 2-age-class model (yearlings versus older animals) and a 3-age-class model (yearlings, two-year-olds, and adults). Limited sample sizes did not permit consideration of pup survival or additional adult classes. Using the most parsimonious model from the preceding analyses, we tested for seasonal variation in survival using 2-season

(active season, early May-early Oct.; and winter, hibernation), 3-season (spring/early summer, emergence-31 Jul; August/fall, 1 Aug-immergence, and winter) and 4-season models (spring/early summer, emergence-31 Jul; August, 1 Aug-28 Aug; fall, 29 Aug-immergence; and winter). Finally, we tested for the additive and interactive effects of habitat type (natural versus clearcut) and location (Nanaimo versus Washington) using the most parsimonious seasonal model as the base model.

A subset of radio-telemetry data collected from 2003-2007 contained both wild-born and captive-born individuals that were released into natural marmot habitat. Analyses proceeded as described previously, except that we also tested for the effect of origin (captive-born versus wild-born) on survival. Additionally, we tested for the effect of "release cost", where survival of released individuals was allowed to differ from that of wild-born individuals for one year post-release but not thereafter (represented by the covariate, "first"). Small sample sizes precluded testing for the effect of year or influence of temporal covariates. To test if survival of released marmots was influenced by the age at which a marmot was released, we used a subset of data including captive-born individuals only.

When a radio-tagged marmot died, cause of mortality was determined based on clues left by predators on and around the recovered transmitter (Bryant and Page 2005). Winter mortalities were occasionally confirmed by excavation of hibernacula, although the specific cause of winter mortality could not be determined. We attributed each mortality event to one of five causes: 1) eagle, 2) cougar, 3) wolf, 4) winter, and 5) unknown (includes unknown predator). We estimated cause-specific cumulative mortality rates from radio-telemetry data using the nonparametric cumulative incidence function estimator (NPCIFE; Heisey & Patterson 2006). The NPCIFE is a generalization of the staggered-entry Kaplan-Meier method of survival

estimation (Pollock et al. 1989), and uses information on the number and timing of deaths from each cause and the number of radio-collared animals at risk at the time to estimate cause-specific mortality rate. We tested for differences in cause-specific mortality rates between captive-born and wild marmots using the Cox proportional hazard model stratified by cause of mortality (Heisey & Patterson 2006).

Analysis of combined CMR and radio-telemetry data

From 1987-1992 the *M. vancouverensis* population was monitored by capture-mark-recapture (CMR) only. From 1992-1999 ≤10% of the known population was radio-telemetered; from 2000-2006, > 60% of the known population was radio-telemetered, with an estimated maximum of 95% radio-tagged in 2006 (Figure 2-2). Analysis of radio-telemetry data is the method of choice for the estimation and modeling of survival because they provide estimates of true survival rates and also allow determination of cause of death (Williams et al. 2002). However, radio-telemetry data were sparse or non-existent until about a decade ago. Also, only a few pups were radio-tagged, so survival could not be estimated using the same methods. Thus, we merged radio-telemetry and CMR data because the combined dataset (1) spanned a longer period of time (1987-2007), (2) allowed estimation and modeling of survival of pup survival, and (3) had larger sample sizes which would increase the precision of estimates of survival.

To merge the two data sets, the radio-telemetry data were converted into capture histories with annual intervals between capture occasions. A marmot was considered detected if it was radio-tracked any time during July/August of a given year. A marmot was excluded from the dataset if it was only tracked for a portion of a year which did not overlap the trapping season (July/August); however, this was uncommon as most marmots were monitored during some portion of that two month interval. Merging the two datasets inevitably leads to a loss of

temporal resolution and other information contained in the radio-telemetry data, but we gain a cohesive data set over the entire duration of the study (1987-2007).

We analyzed the combined dataset using multi-state Cormack-Jolly-Seber models implemented in Program MARK (White & Burnham 1999; Williams et al. 2002). The states used were four age classes chosen based on the biology of the species, as described previously. Vancouver Island marmots disperse as two-year-olds, and females reproduce for the first time as three or four-year-olds (average age of first reproduction = 3.6 yrs; Bryant 2005). Probability of transition from younger to subsequent older age classes was fixed to 1.0, and probability of transition from older to younger age classes was fixed to zero because those transitions are impossible.

The dataset was divided into two groups, based on monitoring method (radio-telemetry and mark-resight). Recapture rate for the radio-telemetry group was fixed to one; this group, therefore, contributed to the estimate of survival rate, but not to recapture rate. Fixing the recapture rate to one in CMR analysis effectively results in a known-fate model. Marmots for which radio transmitters failed were censored. Marmots that were initially monitored by CMR and subsequently radio-tagged were censored from the CMR group and then entered in the radio-tagged group for the appropriate time intervals. Analysis of combined data proceeded as described for the radio-telemetry data; one main difference was that pups were also included as an age class using the combined data.

We used Akaike's Information Criterion, corrected for small sample size (AIC_c), for model comparison and for statistical inferences (Burnham & Anderson 2002). Model comparison was based on the differences in AIC_c values (ΔAIC_c), and relative support for each model in a candidate model set was based on AIC_c weight.

Results

Analysis of Radio-Telemetry Data

One hundred and thirty-two marmots were radio-tracked during 1992-2007 for a total of 367 marmot-years. The number of marmots radio-tracked varied over the study period at each site (Figure 2-2). There were 92 marmot-years of radio-tracking recorded for yearlings, 89 marmot-years for two-year-olds, and 186 marmot-years for adults (Table 2-1).

Although annual survival of females (S=0.750; 95% CI = 0.654-0.826) was slightly higher than that of males (S=0.675; 95% CI = 0.584-0.754), there was no evidence of a sex effect (Table 2-2A). There was also no evidence that survival was age-specific using two age-classes (yearlings and older marmots≥ 2 years) or 3 age -classes (yearlings, two-year-olds, and adults), nor was there any evidence for additive or interactive effects of sex and age. The overall annual survival for the entire population using the most parsimonious model (model 1; Table 2-2A) was 0.709 (95% CI = 0.644-0.766). Therefore, for further analysis we used the model with no sex or age effect as the base model.

Using the most parsimonious model in the preceding analyses (model 1, Table 2-2A), as a base model we tested for the effects of seasons (models 4-6, Table 2-2B). Of the seasonal models, the four season model was the highest ranked; however, the three season model that combined the August and fall seasons, was equally well supported (<ΔAIC$_c$: compare model 4 with model 5 in Table 2-2B). Using the top ranked seasonal model (Model 4, Table 2-2B), two-week estimates of survival were intermediate (S=0.982; 95% CI = 0.973-0.989) during summer, low during August (S=0.963; 95% CI = 0.938-0.978) and fall (S=0.979; 95% CI = 0.963-0.988), and high during the winter (S=0.996; 95% CI = 0.992-0.998).

Using both the most parsimonious seasonal model (model 4, Table 2-2B), we tested for the effects of habitat type (natural or clearcut) and site (Nanaimo or Washington) on survival

(models 1-3, Table 2-2B). There was no evidence for the effect of habitat type on survival. The most parsimonious model (model 1, Table 2-2B) indicated that survival differed between sites during the latter half of the active season (Figure 2-3). Estimated annual survival was higher at the Washington site (S=0.788; 95% CI = 0.710-0.849) than at Nanaimo (S=0.678; 95% CI = 0.606-0.742).

We used a subset of the radio-telemetry data collected during 2003-2007 to test for the effect of origin (captive-born or wild-born) on marmot survival. As in the previous analysis, first we tested for age and sex effect, and found no evidence for either (Table 2-3A). We used model 1 in Table 2-3B as a base model for further analysis because this model differed from the most parsimonious model by $\Delta AIC_c < 2$, and also had fewer parameters. Next, we tested for seasonal variation in survival using the two, three, and four season models as described previously; all of these models were similarly supported (models 5-7, Table 2-3B). Because the two season model (model 6, Table 2-3B) was well supported, and also had fewer parameters, we chose this model for further analysis. Using this model, active season survival (S=0.770; 95% CI = 0.701-0.827; over 24 weeks) was lower than winter survival (S=0.932; 95% CI = 0.884-0.961; over 28 weeks).

The two season model (model 6, Table 2-3B) was used as a base model to test for the effect of origin (captive-born versus wild-born) and site (Washington versus Nanaimo) on survival. The most parsimonious model (model 1, Table 2-3B) included additive effect of season and origin, providing substantial evidence for the effect of origin on survival; overall, captive-born marmots had a much lower survival (S=0.605; 95% CI = 0.507-0.696) rate than wild-born marmots (S=0.854; 95% CI = 0.760-0.915). Survival of captive-born marmots was lower than that of wild-born marmots during both seasons, with a more pronounced difference during the

active season (Figure 2-4). There was no evidence for the cost of release (compare models 9 and 10 in Table 2-3B).

We also used a subset of data containing only captive-born marmots to test for the effect of age-at-release on survival. There were 46 marmots released as yearlings (74 marmot-years) and 50 marmots released as two-year-olds or older (80 marmot-years). Using a 2-season model (the same seasonal model as in previous analysis), we found that the inclusion of age-at-release improved the model ($\Delta AIC_c = 1.71$). Annual survival for marmots released as yearlings was lower (0.602; 95% CI = 0.459-0.729) than for those released as two-year-olds or adults (0.774; 95% CI = 0.649-0.864).

Cause-Specific Mortality

There was a significant difference in mortality rates between captive and wild-born individuals from eagles, cougars, and over winter ($p = 0.018, 0.039, 0.010$, respectively). For each of these causes, mortality was higher for captive-born marmots than wild-born marmots (Figure 2-5). Mortality due to unknown causes was higher for captive-born marmots than wild-born marmots ($p = 0.054$). Wolf predation was the only cause for which wild-born marmots had higher mortality than captive-born; however, there was not a significant difference between these rates ($p = 0.150$).

Predation by eagles was the most important known cause of death for captive-born marmots, whereas predation by wolves was the primary known cause of death of wild-born marmots (Figure 2-5). As a percentage of known mortality (i.e. cause-specific mortality rate/total mortality rate), eagle predation accounted for 25% of captive-born deaths and 13% of wild-born deaths. Cougar predation and winter mortality also were relatively more important sources of mortality for captive-born marmots than wild-born marmots. In contrast, wolf predation accounted for 30% of known wild-born marmot mortality and only 6.4% of captive-

born marmot mortality. Mortality due to unknown causes accounted for about a third of known deaths for marmots of both origins and was mostly due to predation events where the type of predator could not be identified.

Analysis of Combined (Radio-Telemetry and CMR) Data

Using the combined dataset, we first tested for the effect of age, sex, and additive and interactive effects of the two on survival and recapture rate (Table 2-4A). There was evidence to support age-specificity; the most parsimonious model included 3 age-classes for survival (pups, yearling=adult, and two-year-olds) and 2 age-classes for resighting rate (yearlings=adults and two-year-olds). Estimated annual survival rate was lowest for pups (S=0.500; 95% CI = 0.375-0.616), but generally high for yearlings and adults (S=0.656; 95% CI = 0.604-0.705), and two-year-olds (S=0.649; 95% CI = 0.527-0.754). Recapture rate was high for yearlings and adults (ρ =0.917; 95% CI = 0.844-0.958) and lower for two-year-olds (ρ=0.677; 95% CI = 0.464-0.836), the dispersing age class (Model 1, Table 2-4A)

Apparent survival differed between sexes only in the two-year-old age-class, with females surviving better than males. Survival for two-year-old males was much lower (S=0.471; 95% CI = 0.331-0.615) than survival of two-year-old females (S=0.792; 95% CI = 0.629-0.895; Figure 2-6A). Therefore, we continued our analysis with the model including age-specific survival and recapture rates and sex-specific survival in the two-year-old age-class only (Model 1, Table 2-4A).

Next, we tested for the effects of habitat type (natural or clearcut) on survival. We found evidence for an effect of habitat type on apparent survival in the two-year-old age-class only. The most parsimonious survival model included the additive effects of both sex and habitat type on the apparent survival of two-year-old age-class (model 1, Table 2-4B). Two-year-olds in clearcut habitat had lower apparent survival (S=0.446; 95% CI = 0.263-0.646) than those in

natural habitat (S=0.719; 95% CI = 0.569-0.833). The additive effects of both sex and habitat type on the apparent survival of two-year-old age-class are presented in figure 2-6B. There was evidence for site-specific differences in apparent survival (model 1, Table 2-4B), with marmots at Washington surviving better than those at Nanaimo.

Discussion

Low numbers, restricted and sparse habitat, small geographic distribution, and anthropogenic influences on marmot habitat continue to cause concern regarding the persistence of Vancouver Island marmots. Given the extremely small population size, the marmot population is at substantial risk of extinction due to demographic stochasticity alone (Caswell 2001; Caughley and Gunn 1996; Morris et al. 2002). This risk is exacerbated by the harsh and dynamic environment *M. vancouverensis* inhabits, and with changing ecosystem and predator-prey dynamics. Thus, it is likely that conservation measures are necessary in the foreseeable future to ensure long-term persistence of marmots. Our goal was to assist Vancouver Island marmot conservation efforts by providing rigorous estimates of survival rates, evaluating factors influencing survival of marmots, and making recommendations for the reintroduction program.

Survival Rates and Sex- and Age-Specific Differences

Using radio-telemetry data (1992-2007), the overall annual survival of marmots (excluding pups) was 70.9%. There was no evidence that survival differed between sexes or among age classes. Our results regarding the effects of sex on survival of radio-tagged marmots as well as estimates of annual survival rate are similar to those reported by Bryant & Page (2005).

Analyses of combined dataset (i.e., radio telemetry and mark-resight) revealed strong evidence for age-specific differences in survival, with annual apparent survival of pups (S=51.6%) being substantially lower than that of other age-classes ($S\geq$65%). Pups typically

remained close to and hibernated at their natal burrow, and resighting rate of pups (as yearlings the next year) was generally high.

Sex effect was apparent only in apparent survival of two-year-old marmots. Survival of two-year-old males (47%) was much lower than survival of two-year-old females (79%). Vancouver Island marmots typically disperse at two years of age, and males in most species of marmots have a greater propensity to disperse than females (Armitage 1999; Arnold 1990; Barash 1989; Bryant 1998; Van Vuren and Armitage 1994). We believe that low apparent survival for two-year-old males may be a consequence of male-biased dispersal. This speculation was further supported by the observation that capture probability for two-year-olds was substantially lower than that for other age-classes.

The low apparent survival rate for the dispersing age class has been observed in other species of marmots (Farand et al. 2002; Ozgul et al. 2006). While it is often thought that dispersing marmots face a greater risk of mortality and therefore have lower survival (Ozgul et al. 2006; Van Vuren and Armitage 1994; Van Vuren 2001), this trend was not apparent in the known-fate analysis of radio-telemetry data. The lower apparent survival of two-year-old males obtained from CMR analysis than survival estimated from radio-telemetry data most likely was due to the fact that CMR-based methods cannot distinguish between death and permanent emigration (Williams et al. 2002).

Our findings (based on the analysis of combined data) that survival of pups was lower than that of other age-classes, and that apparent survival of dispersing age class was lower than that of yearling and adult marmots, are similar to those reported for other species of ground-dwelling sciurids (Armitage 2003; Bronson 1979; Bryant 1998; Farand et al. 2002; Griffin et al. 2008; Ozgul et al. 2006; Sherman and Runge 2002). However, annual apparent survival for pups

(50%) was lower than those reported for Alpine marmot pups (62%, Farand et al. 2002), yellow-bellied marmot pups (Ozgul et al. 2006), and most relevantly, Olympic marmot pups (60% from tagging, Griffin et al. 2008). Our estimates of age-specific apparent survival for older age-classes of *M. vancouverensis* were generally lower than those reported for other species of marmots (Farand et al. 2002; Ozgul et al. 2006).

Seasonal and Site-Specific Variation

Analysis of radio-telemetry data revealed substantial seasonal variation in survival (Table 2-2B, Figure 2-3), with higher survival during hibernation than during late summer/fall (also see Bryant & Page 2005). However, support for two, three, and four-season models was similar, suggesting that the primary cause of seasonal variation was the substantially higher survival during hibernation than during the active season. Marmots are not exposed to predators and other mortality factors linked with activity above ground during hibernation, and are thought to be efficient hibernators (Bryant & McAdie 2003); consequently, survival rates are higher during winter than during the active season. Comparison of our results with those of Bryant & Page (2005) suggests that seasonal variation in survival, throughout the year and particularly during active season, may have become less pronounced in recent years (i.e., mortality is more evenly spread throughout the active season, instead of higher mortality during August and fall relative to spring and early summer).

Both the known fate radio-telemetry data and combined telemetry and CMR data suggest that survival at the Mt. Washington site was higher than in the Nanaimo Lakes region. The two areas are quite different; Mt. Washington is a ski hill, where most marmots live on ski slopes. These ski slopes are technically clearcuts; however, they more closely resemble natural meadows due to stumps being removed and maintenance to prevent regeneration. Apparently, the ski

slopes are suitable habitat, although differences in vegetative composition and how this affects fitness and survival of marmots have not been formally tested.

The other major difference is the amount of human activity at each site. Whereas much of the land inhabited by marmots in the Nanaimo Lakes region is private land inaccessible to the public, Washington is a popular ski slope with lots of human traffic. Griffin et al. (2007) found that high levels of tourist traffic did not negatively affect demographic rates of Olympic marmots in Olympic National Park. Although the majority of human activities at Mt. Washington occur during winter months while marmots are hibernating, summer activities have become increasingly popular in recent years. While human presence may not have a direct effect on demographic rates of marmots, there could be indirect effects (Griffin et al. 2007).

Habitat Changes and Vancouver Island Marmots

The landscape of Vancouver Island has undergone substantial change, especially since logging intensity increased in the 1950s. High elevation clearcut logging created patches of open meadows that resembled natural marmot habitat. These newly created habitats were colonized by marmots, and by the 1990s, nearly half of the known marmot population inhabited clearcuts (Bryant 1996; Bryant and Janz 1996). However, most marmot colonies in clearcut habitats have disappeared and very few marmots have been observed in clearcuts in recent years. Why did marmots disappear from the clearcut habitats where they thrived during 1980s?

One explanation is that clearcut habitat served as an ecological or evolutionary trap (Robertson and Hutto 2006; Sherman and Runge 2002). While marmots may have persisted in clearcuts that initially resembled natural meadows, subsequent forest regeneration rendered clearcut habitat unsuitable for marmots over a few years or decades. In addition, clearcut logging substantially changed the landscape structure and local marmot population density. These changes could have caused an increase in mortality of marmots due to predation through several

mechanisms: (1) an increased proportion of open habitat in the landscape, making the area more attractive to avian predators; (2) an increase in secondary growth and edge habitat, where predation by wolves and cougars would be higher; (3) logging roads could have acted as conduits for the movement of both predators and marmots, possibly increasing the probability of encounters; and/or 4) an increase in secondary growth altering the abundance of other prey species, and consequently the abundance of predators. We note that these mechanisms are not mutually exclusive.

Captive Breeding, Cause-Specific Mortality, Age-at-Release and Conservation of *M. vancouverensis*

Our results clearly show that captive-born marmots suffer a higher mortality than wild-born marmots, and these results are consistent with findings of Jule et al. (2008). In addition, causes of mortality also differed between the two groups; captive-born marmots were much more vulnerable to avian predators than their wild-born counterparts. These results suggest that, whereas captive-born marmots exhibit anti-predatory responses to mammalian predators (Blumstein et al. 2001; Blumstein et al. 2006), their ability to detect and/or avoid avian predators may be compromised. Pre-release anti-predator training improves survival in the wild for some species (Shier and Owings 2006; van Heezik et al. 1999). Exposing captive-born marmots to predators (particularly, golden eagles) before they are released may enhance their survival in natural habitats and contribute to the success of the release program; this however, is unproven and would be financially and logistically challenging to implement.

In some species, reintroduced individuals suffer a higher mortality during the first year after release; however, the survival may be similar to those of wild-born individuals thereafter (Bar-David et al. 2005; Le Gouar et al. 2008; Sarrazin et al. 1994). We tested for this effect, and

found no evidence that survival of captive-born marmots improved after their first active season, winter, or full year in the wild.

Age at which captive-bred individuals are released can also influence demography of reintroduced populations (Green et al. 2005; Sarrazin et al. 1994; Sarrazin and Legendre 2000). Marmots released as two-year-olds had an approximately 17% higher probability of survival than marmots released as yearlings (survival of marmots released as yearlings: 0.602 ± 0.070; survival of marmots released at age two and older: 0.774 ± 0.055). Thus, marmots released at >2 years of age are more likely to survive to reproductive age and contribute to the population growth via reproduction. The initial increase in costs associated with rearing marmots for an extra year may be well worth it if, as our results suggest, it can increase the probability of success of the release program.

Table 2-1. Summary of records included in each analysis. For known fate analyses, value represents number of marmot-years (one record per marmot per year); for the analysis of combined radio-telemetry and mark-resight data, values represent number of mark-recapture histories (roughly equal to number of marmots; however, one marmot can be included in the capture-mark-resight group in one year and the radio-telemetry group in another year depending on implantations and radio failures).

	Age Class				Sex	
Data Set	Pups	Yearlings	Two-Year-Olds	Adults	Male	Female
Radio-Telemetry (1992-2007)	0	92	89	186	206	161
Radio-Telemetry (2003-2007)*	0	66	74	115	148	107
Combination	70	98	102	316	136	137
	Habitat Type		Site		Origin	
Data Set	Clearcut	Natural	Nanaimo	Washington	Captive	Wild
Radio-Telemetry (1992-2007)	31	336	262	105	154	213
Radio-Telemetry (2003-2007)*	0	255	178	77	154	101
Combination	93	180	33	240	48	225

*Subset of radio-telemetry data were used to test for the effect of origin

Table 2-2. Analysis of the influence of (A) intrinsic (sex and age) and (B) extrinsic factors on survival (S) of the Vancouver Island marmot using radio-telemetry data (1992-2007) and known-fate models. Akaike's Information Criterion corrected for small sample size (AICc), differences in AICc values (ΔAICc), AICc weights (w_i), and the number of parameters (np) are shown for each model. The most parsimonious model in the first set of analysis testing (for intrinsic differences in survival) was used as the base model for the second set of analysis testing for effects of extrinsic factors. In both analyses, the most parsimonious models are highlighted in bold.

No.	Model	AICc	Δ AICc	w_i	np
A)*					
1	**S(.)**	**593.65**	**0.00**	**0.275**	**1**
2	S(sex)	594.21	0.56	0.208	2
3	S(2-age-class)	595.17	1.52	0.129	2
4	S(2-age-class+$sex_{\geq 2yr}$)	595.26	1.61	0.123	3
5	S(2-age-class+sex)	595.74	2.08	0.097	3
6	S(3-age-class)	597.09	3.44	0.049	3
7	S(2-age-class*sex)	597.25	3.59	0.046	4
8	S(3-age-class+sex)	597.61	3.96	0.038	4
9	S(3-age-class+sex_{2yr})	597.74	4.09	0.036	4
B)**					
1	**S(4-season+$site_{A,F}$)**	**552.75**	**0.00**	**0.645**	**5**
2	S(4-season+site)	555.59	2.84	0.156	5
3	S(4-season+$site_{S,A,F}$)	556.69	3.94	0.090	5
4	S(4-season)	557.86	5.11	0.050	4
5	S(3-season)	558.27	5.51	0.041	3
6	S(2-season)	560.10	7.34	0.016	2
7	S(time)	567.32	14.57	0.000	13
8	S(site)	590.91	38.16	0.000	2
9	S(.)	593.65	40.90	0.000	1
10	S(habitat)	595.22	42.47	0.000	2

*Age-classes are yearlings, two-year-olds, and adults for the 3-age-class models. Age classes for 2-age-class models are yearlings and adults. Subscripts indicate age-class(es) for which the model allows the age class to affect survival (≥2yr = 2 -yrs of age or older; 2yr = 2-yr olds; ad = adults).

**The 4 "seasons" were spring/early summer (*S*, emergence-July 31), August (*A*, August 1-28), fall (*F*, August 29-immergence), and winter (*W*, hibernation); the 3 season model combined August and fall; and the two season model combined the entire active season. Subscripts indicate allowing survival to differ between sites only during season(s) noted. Pluses (+) indicate additive effects and asterisks (*) indicate interactive effects. The dot (.) indicates a constant parameter value.

Table 2-3. Analysis of the influence of (A) intrinsic (sex and age) and (B) extrinsic factors on survival (*S*) of the Vancouver Island marmot using a subset of the radio-telemetry data (2003-2007) and known-fate models. Akaike's Information Criterion corrected for small sample size (AICc), differences in AICc values (ΔAICc), AICc weights (w_i), and the number of parameters (np) are shown for each model. The most parsimonious model in the first set of analysis testing (for intrinsic differences in survival) was used as the base model for the second set of analysis testing for effects of extrinsic factors. In both analyses, the most parsimonious models are highlighted in bold.

No.	Model	AICc	Δ AICc	w_i	np
A)*					
1	S(sex)	488.66	0.00	0.322	2
2	S(2-age-class+sex)	489.79	1.13	0.183	3
3	**S(.)**	**490.21**	**1.54**	**0.149**	**1**
4	S(2-age-class)	490.77	2.11	0.112	2
5	S(3-age-class+sex)	491.43	2.77	0.081	4
6	S(2-age-class+$sex_{\geq 2yr}$)	491.44	2.77	0.080	3
7	S(3-age-class)	492.56	3.89	0.046	3
8	S(3-age-class+sex_{2yr})	493.58	4.92	0.028	4
B)**					
1	**S(2-season+origin)**	**455.82**	**0.00**	**0.368**	**3**
2	S(2-season*origin)	456.19	0.37	0.305	4
3	S(2-season+origin+$first_{A,F}$)	457.25	1.43	0.180	4
4	S(2-season+origin+$first_{W}$)	457.69	1.87	0.145	4
5	S(4-season)	467.92	12.10	0.001	4
6	S(2-season)	468.29	12.46	0.001	2
7	S(3-season)	470.24	14.42	0.000	3
8	S(origin)	479.60	23.78	0.000	2
9	S(.)	490.21	34.38	0.000	1
10	S(first)	491.79	35.97	0.000	2

*Age-classes are yearlings, two-year-olds, and adults for the 3-age-class models. Age classes for 2-age-class models are yearlings and adults. Subscripts indicate age-class(es) for which the model allows the age class to affect survival (≥2yr = 2 -yrs of age or older; 2yr = 2-yr olds; ad = adults).

**The 4 "seasons" were spring/early summer (*S*, emergence-July 31), August (*A*, August 1-28), fall (*F*, August 29-immergence), and winter (*W*, hibernation); the 3 season model combined August and fall; and the two season model combined the entire active season. Subscripts indicate allowing survival to differ between sites only during season(s) noted. The "first" covariate refers to the "release cost" effect, where survival is different the first year for released marmots (or first season only as indicated by subscript) than post-first year. Pluses (+) indicate additive effects and asterisks (*) indicate interactive effects. The dot (.) indicates a constant parameter value.

Table 2-4. Analysis of the influence of (A) intrinsic (sex and age) and (B) extrinsic factors on survival (*S*) and recapture rate (ρ) of the Vancouver Island marmot using a combination of radio-telemetry and capture-recapture data and multi-state models. Akaike's Information Criterion corrected for small sample size (AICc), differences in AICc values (ΔAICc), AICc weights (w_i), and the number of parameters (np) are shown for each model. The most parsimonious model in the first set of analysis (testing for intrinsic differences in survival) was used as the base model for the second set of analysis testing for effects of extrinsic factors. In both analyses, the most parsimonious models are highlighted in bold.

No.	Model	AICc	Δ AICc	w_i	np
A)*					
1	**S(3-age-class+sex$_{2yr}$)ρ(2-age)**	**765.81**	**0.00**	**0.644**	**6**
2	S(3-age-class+sex$_{2yr}$)ρ(2-age+sex$_{2yr}$)	767.59	1.77	0.265	7
3	S(2-age)ρ(2-age)	771.44	5.62	0.039	4
4	S(4-age+sex$_{\geq 2yr}$)ρ(2-age)	773.02	7.21	0.018	7
5	S(3-age)ρ(2-age)	773.15	7.33	0.016	5
6	S(.)ρ(2-age)	774.73	8.92	0.007	3
7	S(4-age)ρ(2-age)	775.18	9.37	0.006	6
8	S(.)ρ(3-age)	776.95	11.14	0.002	4
9	S(sex)ρ(.)	778.97	13.16	0.001	3
10	S(.)ρ(.)	779.54	13.73	0.001	2
11	S(sex)ρ(sex)	780.56	14.75	0.000	4
12	S(.)ρ(sex)	780.81	15.00	0.000	3
B)					
1	**S(3-age+sex$_{2yr}$+site+habitat$_{2yr}$)ρ(2-age)**	**755.28**	**0.00**	**0.753**	**8**
2	S(3-age+sex$_{2yr}$+site)ρ(2-age)	758.04	2.76	0.189	7
3	S(3-age+sex$_{2yr}$+habitat$_{2yr}$)ρ(2-age)	761.49	6.21	0.034	7
4	S(3-age+sex$_{2yr}$+site$_{\geq 2yr}$)ρ(2-age)	763.72	8.45	0.011	7
5	S(3-age+sex$_{2yr}$+habitat$_{\geq 2yr}$)ρ(2-age)	765.12	9.85	0.005	7
6	S(3-age+sex$_{2yr}$)ρ(2-age)	765.81	10.54	0.004	6
7	S(3-age+sex$_{2yr}$+habitat)ρ(2-age)	766.02	10.75	0.003	7

*Age-classes are pups, yearlings, two-year-olds, and adults. For recapture rate, 3 age-class models consider yearling, two-year-old, and adult differently; and, 2 age-class models consider yearling and adult recapture rate to be equal but different from two-year-old recapture rate. For apparent survival, 2 age-class models are pups and older marmots (>1 yr); 3 age-class models are where pup and two-year-old apparent survival differ, and yearling and adult survival are set equal. All subscripts refer to the age-class(es) for which the individual covariate was considered (≥2yr = 2-yrs of age or older; 2yr = 2-yr olds; ad = adults). Pluses (+) indicate additive effects and asterisks (*) indicate interactive effects. The dot (.) indicates a constant parameter value.

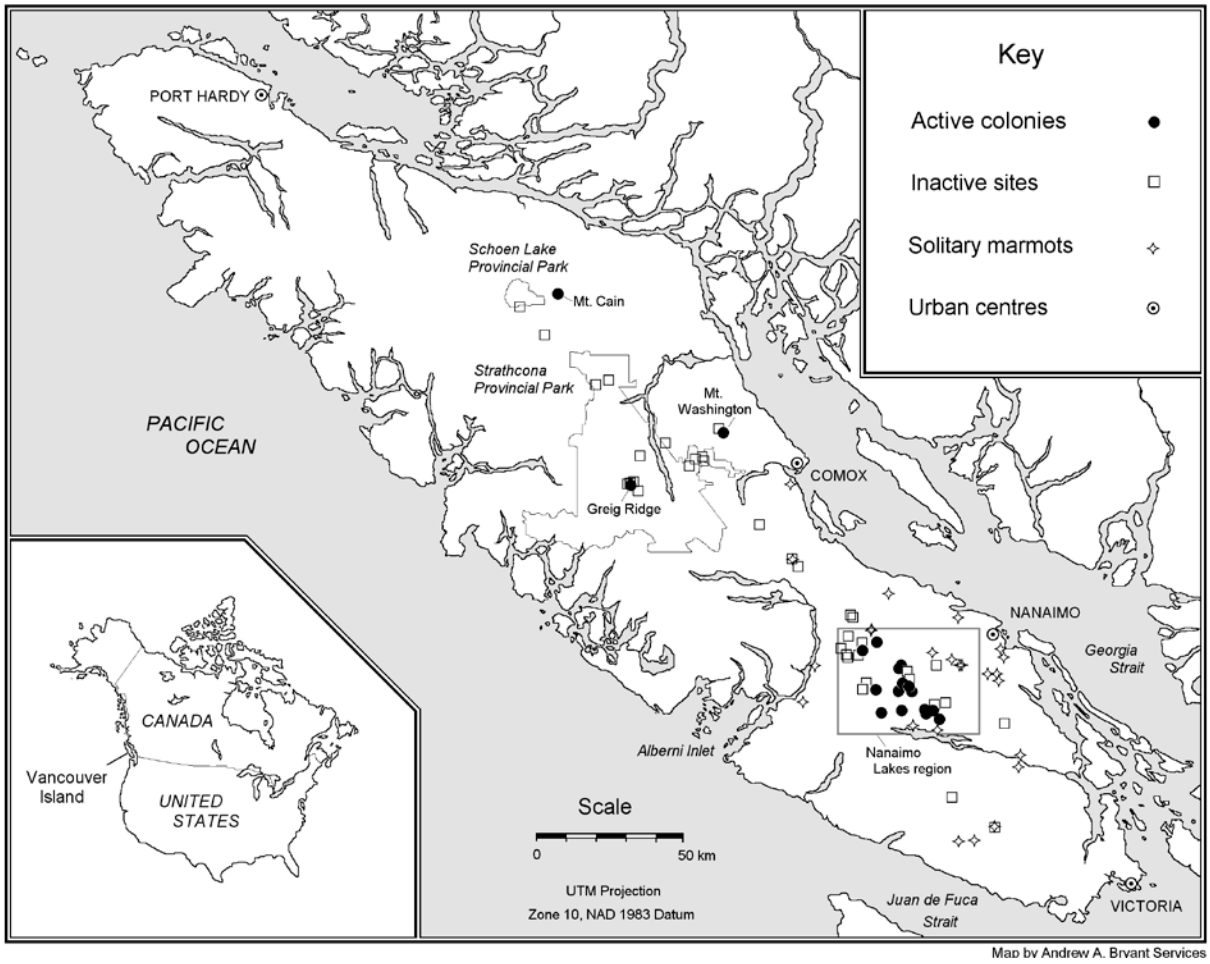

Figure 2-1. Historically occupied (squares) and recently occupied (circles) sites for *M. vancouverensis*. The rectangle encompasses recently-active colonies within the Nanaimo Lakes region, from which the majority of survival data were obtained. Locations of the isolated Mt. Washington sub-population, and recent reintroductions at Mt. Cain and Greig Ridge are also shown.

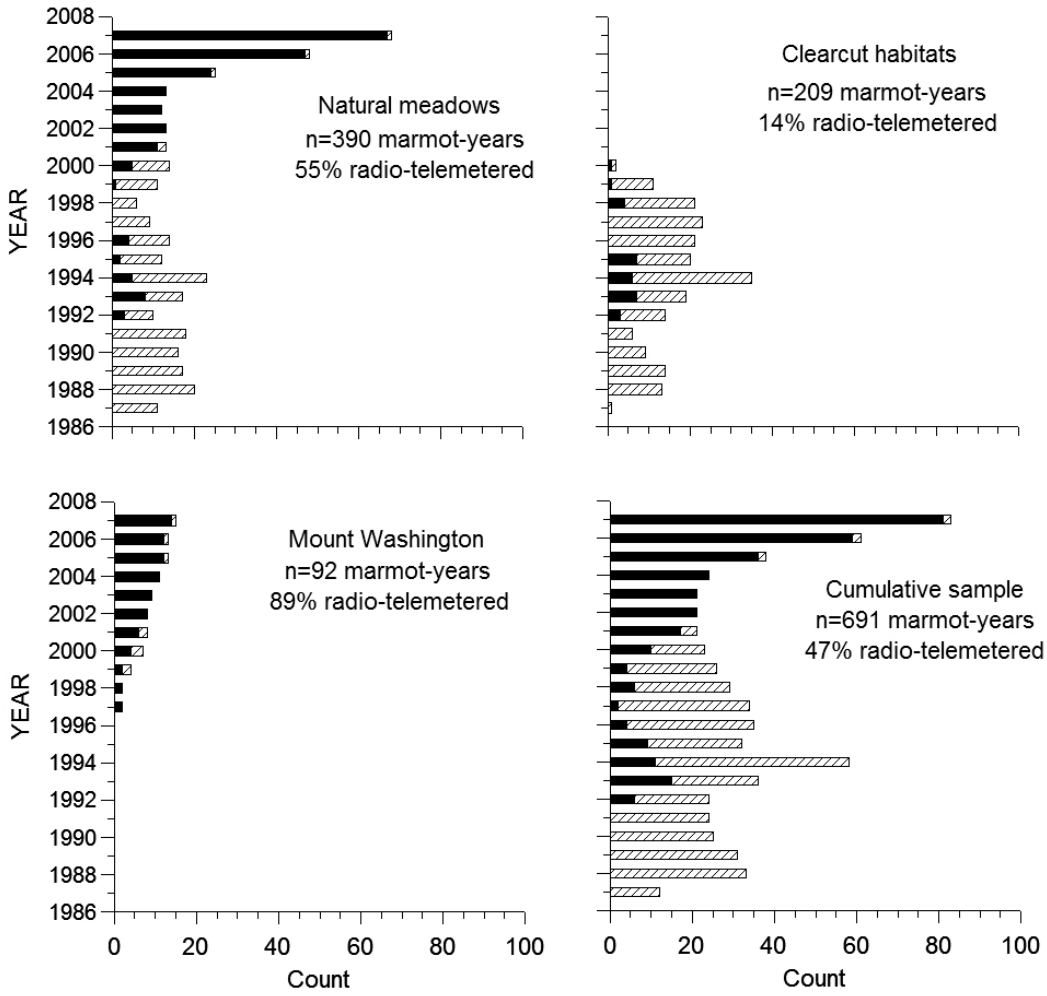

Figure 2-2. Changes in numbers of ear-tagged (hatched bars) and radio-telemetered (solid bars) marmots for which annual survival data were available. Almost half of the sampled marmots were telemetered, with the Mt. Washington sub-population being particularly well-represented. The overall trend illustrates greatly increased reliance upon radio-telemetry in recent years, largely driven by growing numbers of reintroduced captive-born marmots.

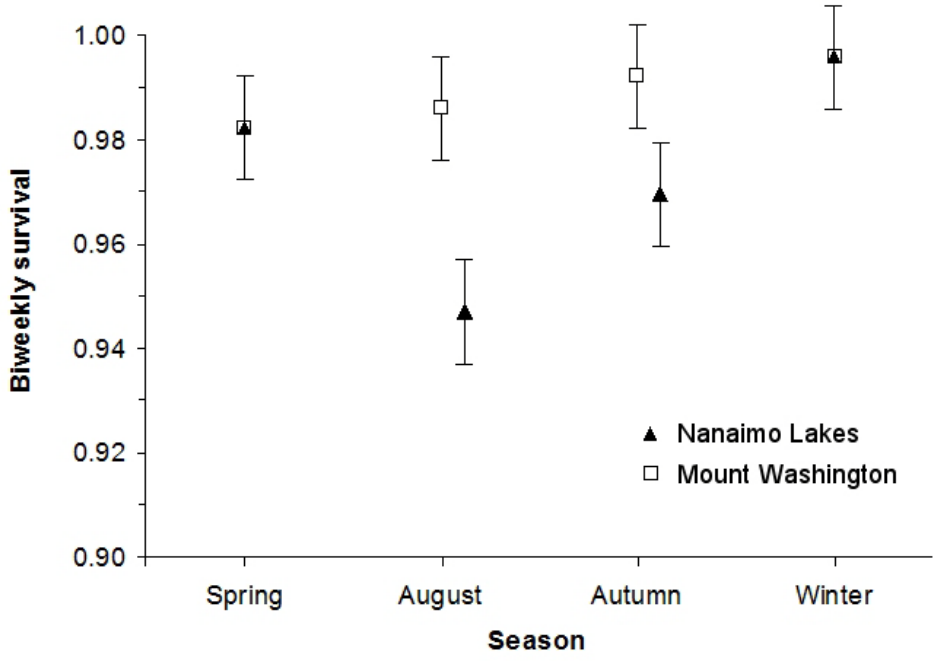

Figure 2-3. Estimates of biweekly survival rates (± 1SE) estimated using the most parsimonious model of the known-fate analysis (Table 1-2b, model no. 1). Survival differed between sites during August and fall, but not during spring/early summer or winter. For the winter interval, survival was estimated over a two-week interval as a derived parameter; therefore, winter survival is directly comparable to biweekly survival rates during other seasons.

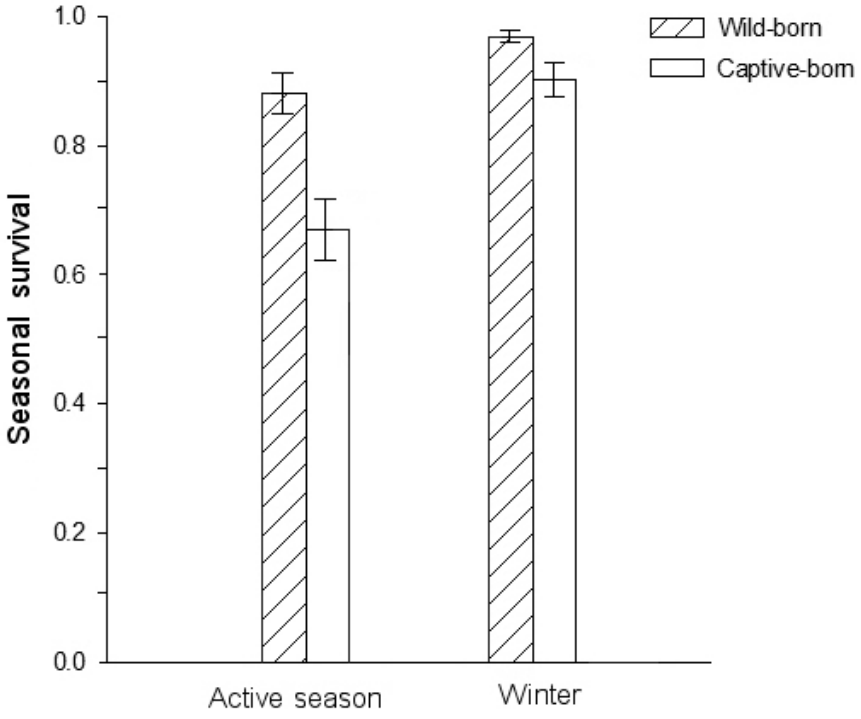

Figure 2-4. Estimates of seasonal survival rates (± 1SE) for captive-born and wild-born marmots estimated using the most parsimonious model from the subset analysis (Table 1-3b, model no. 1). Active season survival spans 24 weeks, and the winter season spans 28 weeks.

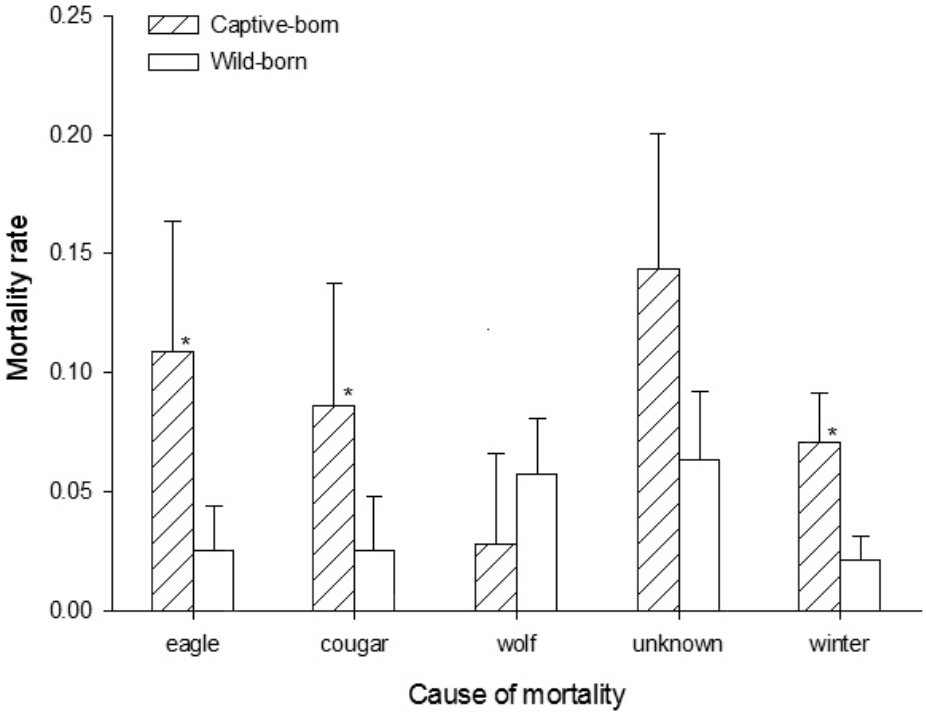

Figure 2-5. Estimates of cause-specific mortality rates (mean ± 1SE) for captive-born and wild-born marmots estimated using the nonparametric cumulative incidence function estimator. Significant differences are indicated by an asterisk (*). Most of the "unknown" cases of mortality represented cases in which predation was known to have been the cause of death, but for which forensic clues precluded identification of the predator species involved

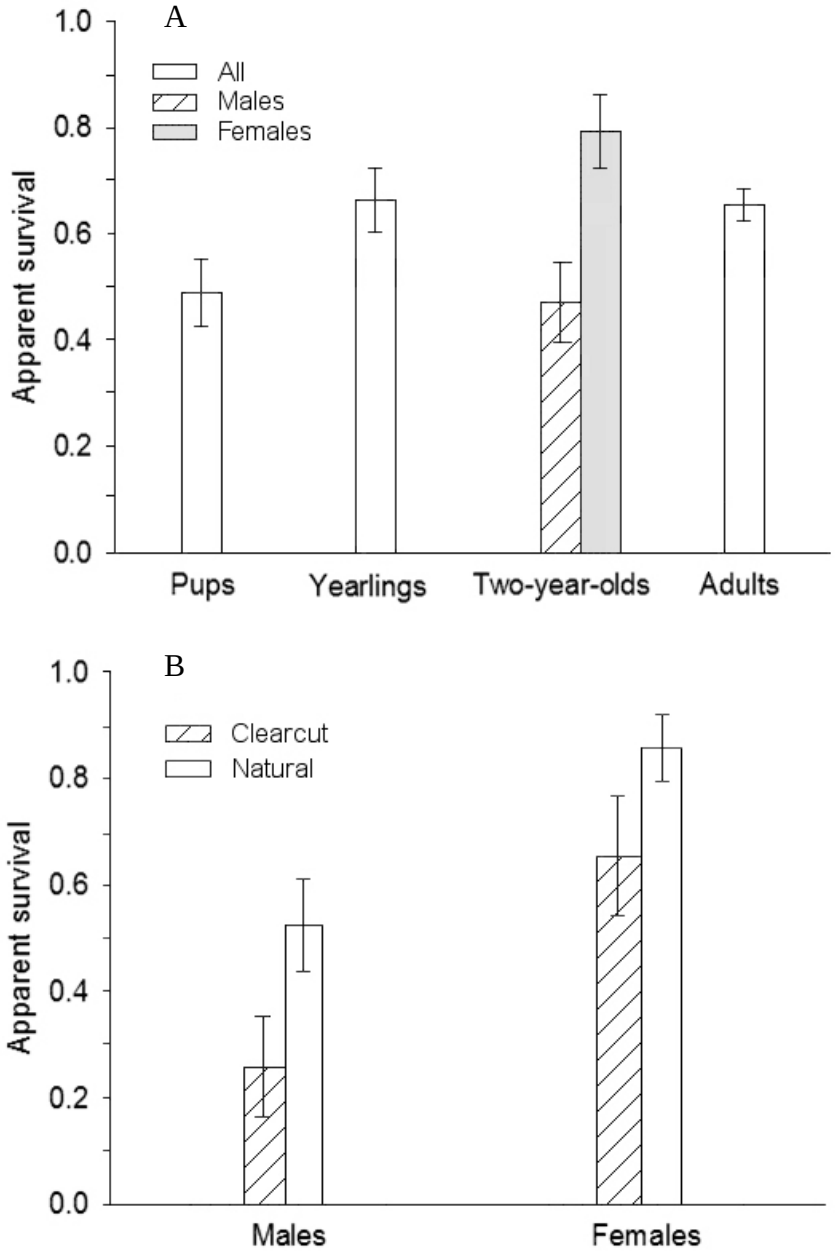

Figure 2-6. Apparent survival rates from combined data analysis. A) Age-specific annual apparent survival rates (means ± 1SE)) estimated using model no. 1, Table 1-4a. Apparent survival rates differed between males and feamales only for two-year-olds. B) Sex-specific annual apparent survival rates for two-year-old marmots by habitat type at Nanaimo Lakes based on model no. 1 in Table 1-4b.

CHAPTER 3
POPULATION ECOLOGY OF THE ENDANGERED VANCOUVER ISLAND MARMOT

Introduction

Captive-breeding and reintroduction are frequently used for the conservation of rare or endangered species (Caughley & Gunn 1996; Sarrazin & Legendre 2000). However, few reintroduction programs have achieved success, due in part to poor understanding of the population-level effects of alternative release strategies (Armstrong & Seddon 2008; Grenier et al. 2007; Sarrazin & Legendre 2000; Seddon et al. 2007). Furthermore, the reintroduction literature largely consists of descriptive accounts of success or failure of reintroduction programs; progress in this branch of conservation biology has been slow due to the lack of quantitatively rigorous analysis of data generated from well-designed comparative or experimental studies (Armstrong & Seddon 2008). Demographic models can provide valuable insights into likely results of conservation efforts, and allow for evaluation of the population-level impacts of release strategies; however, few reintroduction programs have benefitted from such models (Caswell 2001; Meretsky et al. 2000; Sarrazin & Legendre 2000).

The Vancouver Island marmot (*Marmota vancouverensis*) is an endangered mammal inhabiting subalpine meadows on Vancouver Island, British Columbia (Janz et al. 2000; Nagorsen 1987). The *M. vancouverensis* population went through several range restrictions leaving the population in only two locations on the island by the 1970s (Figure 3-1). The marmot population increased to 300-350 individuals during the mid-1980s as marmots colonized the openings created by high-altitude logging that resembled marmot habitat (natural meadows, Bryant & Janz 1996). This increase in population size was short-lived, as most marmot colonies in clearcut habitats disappeared by 2000 and the population declined to an estimated 35 individuals by 2003 (Bryant 2005). The disappearance of marmots from clearcut habitat is likely

due to forest regeneration reducing the suitability of clearcuts as marmot habitat (Bryant 1998). Changes in landscape structure following logging probably had direct and indirect impacts on the entire marmot population through predator-prey interactions (Aaltonen et al. in review; Bryant & Page 2005). With the marmot population on the brink of extinction, a captive-breeding program was initiated in 1997 with facilities established both on and off Vancouver Island (Bryant 2005). During 2003-2008, 155 captive-born marmots were released into various sites at both Mt. Washington and Nanaimo Lakes (Kruckenhauser et al. 2009; unpublished minutes, Vancouver Island Marmot Recovery Team, Dec. 2008).

The reintroduction program has contributed to an increase in population size in the wild (COSEWIC 2008). However, recent work has shown that captive-born marmots suffer substantially higher mortality compared to their wild-born counterparts, and that causes of mortality differed substantially between captive-born and wild-born marmots (Aaltonen et al. in review). Moreover, survival of released marmots in the wild was found to be influenced by the age at which they were released. Marmots released as two-year-olds or older survived better than those released as yearlings. These findings may have important consequences for the reestablishment of a viable population and for the consideration of alternative management scenarios.

Although some estimates of demographic rates exist (Aaltonen et al. in review; Bryant 2005; Bryant & Page 2005; COSEWIC 2008), only limited information on the population ecology of Vancouver Island marmots is currently available. Our intent was to narrow this gap in knowledge by providing better information on population ecology of Vancouver Island marmots and evaluating potential population-level impacts of alternative release strategies.

In this paper we (1) use estimates of demographic variables to parameterize age-structured matrix population models, (2) analyze the matrices to calculate population growth rates, and (3) calculate the elasticity of the population growth rate to vital demographic parameters. We also estimate target demographic rates for recovery of the species and investigate population-level effects of releasing marmots either as yearlings or as two-year-olds, and the effects of a reduction in mortality of captive-born marmots after they have been released into their natural habitats. Our findings are expected to guide future release strategy and other management efforts aimed at the conservation of this critically endangered species.

Methods

Study Species

Vancouver Island marmots live in small, subalpine meadows characterized by colluvial soils, diverse vegetation, and rocky outcrops (Heard 1977; Milko & Bell 1986). They are generalist herbivores (Martell & Milko 1986) and are active during the spring and summer (approximately, early May through early October). They hibernate in underground burrows during the winter for an average of 210 days (SE ± 7.6 days, Bryant & McAdie 2003). They exhibit slow maturation, delayed dispersal, and large body size relative to most marmots, but similar to other members of the *M. caligata* group (Armitage 1999; Barash 1989; Griffin et al. 2008).

Study Area

This study was conducted on Vancouver Island, British Columbia, Canada. The present distribution of marmots consists of two main populations: Nanaimo Lakes and Mt. Washington (COSEWIC 2008). The Mt. Washington population is relatively small, and data were insufficient for estimating age-structured demographic parameters. Thus, we focused on the data collected from the larger population, Nanaimo Lakes. The Nanaimo Lakes population is located

on the southern part of the island, and is characterized by mountains of lower elevation and less rugged terrain than the central and northern regions. All colonies within the Nanaimo Lakes population are concentrated in an area encompassing 840 km^2 within 5 adjacent watersheds (Bryant 1998). Marmot habitat in the Nanaimo Lakes region is described in detail elsewhere (Bryant & Janz 1996)

Field Methods

From 1987-2008, marmots were captured using single door Havahart traps baited with peanut butter, transferred to a tapered handling bag to restrict marmot movement, and sedated using procedures described in Bryant (1996). Each marmot received a pair of numbered metal ear tags. Individuals were classified into one of four age-classes: pup (0-1 years), yearling (1-2 years), two-year-old (2-3 years old), or adult (≥3 years old). Age was accurately known for marmots captured for the first time as pups or yearlings; it was estimated for marmots captured for the first time as two-year-olds or adults (Bryant 1998). The majority of trapping occurred during the months of July and August. Marmot resightings were made throughout the active season using 60x spotting scopes, usually before 1100 hours when marmots were most active.

Radio-telemetry of marmots began in 1992, with an increasing proportion of the marmot population radio-tagged since 2000. Types of transmitters and methods used for surgical implant of transmitters are described in detail by Bryant and Page (2005). Radio-tagged marmots were tracked from the ground or from a helicopter. Non-dispersing marmots typically remained close (≤ 100 m) to home burrows, and thus could be tracked from the ground. However, helicopter flights were necessary to reach remote colonies and to track dispersing marmots. The frequency of tracking varied depending on funding, weather, road access problems and research priorities in various years of the study (Bryant & Page 2005).

Marmota vancouverensis pups are born in early June, emerge from their natal burrows in early July, and typically stay near natal burrows for the first few weeks post-emergence (Bryant 1996). The number of weaned pups per female was counted when pups first emerged from their natal burrows during the first weeks of July. Pups were not trapped immediately post-emergence due to small size (Bryant 1998), therefore, there is a possibility of pup mortality both prior to emerging from the natal burrow and post-emergence but prior to tagging. Two-year-old females breed infrequently; most female marmots breed for the first time as 3 or 4-year-olds (Bryant 2005).

Estimates of Survival and Fecundity Rates

From 1987-1992, the *M. vancouverensis* population was monitored by capture-mark-resight (CMR) method only. Resightings were considered visual recaptures, and were included in CMR analysis. From 1992-1999, ≤10% of the known population was radio-tagged; from 2000-2006, > 60% of the known population was radio-tagged, with an estimated maximum of 95% radio-tagged in 2006. Analysis of radio-telemetry data is the method of choice for the estimation and modeling of survival because it provides estimates of true survival rates and also allows determination of cause of death (Williams et al. 2002). However, radio-telemetry data were sparse or non-existent until about a decade ago. Also, only a few pups were radio-tagged, so pup survival could not be estimated using radio-telemetry. Thus, we estimated age-specific survival rates using both capture-resight and radio-telemetry data (Aaltonen et al. in review).

We merged radio-telemetry and CMR data because the combined dataset (a) spanned a longer period of time (1987-2007), (b) allowed estimation and modeling of survival of pup survival, and (c) had larger sample sizes which would increase the precision of estimates of survival. We used multi-state Cormack-Jolly-Seber models implemented in Program MARK (White & Burnham 1999; Williams et al. 2002) to estimate stage-specific survival from the

combined dataset. The states used were four age classes chosen based on the biology of the species: pup (0-1 years), yearling (1-2 years), two-year-old (2-3 years), and adult (≥3 years). We estimated survival over the entire study period (1987-2007) and also over the population decline before reintroduction began (1987-2002).

We used known fate models implemented in Program MARK (White & Burnham 1999; Williams et al. 2002) to estimate and model survival of marmots using radio-telemetry data. The subset of radio-telemetry data collected from 2003-2008 contained both wild-born and captive-born individuals that were released into natural marmot habitat. This subset was used to estimate age-specific survival rates for the entire population, and the wild-born and released individuals separately over the past five years. We used pup survival estimates from CMR methods for this time period as pups were not tracked by radio-telemetry.

Using data from females in the wild, we estimated age-specific litter size as the number of weaned pups per litter produced by a female of age *x*, and fecundity rate as one-half times the average number of pups produced by females (including females that did not reproduce that year) of each age-class. There was no evidence of temporal variation in litter size; the primary sex ratio in the wild did not vary significantly from 1:1 (Bryant 2005).

Construction and Analysis of Population Model

The parameter estimates described above were used to construct several age-structured matrix population models (Table 3-1). We used four age-based stages: 1) pup, age 0-1; 2) yearling, age 1-2; 3) two-year-old, age 2-3; and adult, ages 3 and older. Age-specific fertility rate was estimated using the post-breeding census formulation (Caswell 2001):

$$F_i = P_i m_i$$

where m_i is age-specific fecundity and P_i is age-specific survival rate.

Using these estimates of survival and fertility rates, we constructed a population projection matrix A (Figure 3-2), where subscripts refer to age-class (p=pups, y=yearlings, t=two-year-olds, a=adults).

Deterministic population growth rate, λ (lambda), was calculated as the dominant eigenvalue of the population projection matrix. We calculated sensitivity of λ to vital demographic rates as partial derivative of λ with respect to vital rates, and elasticity of λ to vital demographic variables as (Caswell 2001):

$$e_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \frac{a_{ij}}{\lambda}$$

where e_{ij} is the elasticity of λ to ijth entry of the population projection matrix, and $\partial\lambda/\partial a_{ij}$ is the sensitivity of λ to ijth entry of the matrix.

Results

Estimates of Survival and Fecundity Rates

Survival rates varied depending on time period and origin of the population (wild-born or captive-born marmots released into the wild). Pup survival ranged from 0.460 (0.339-0.585; 1987-2007; model 1) to 0.492 (0.372-0.613; 1987-2002; model 4), depending on the time period over which survival was estimated (Table 3-1). Yearling survival ranged from 0.618 (0.559-0.674; 1987-2007; model 1) to 0.893 (0.756-0.958; 2003-2008; model 6). Two-year-old survival ranged from 0.736 (0.425-0.913) to 0.923 (0.756-0.979). Adult survival ranged from 0.456 (0.307-0.613) to 0.812 (0.688-0.894). For yearlings, two-year-olds, and adults, the highest estimate of survival rate was based on the model that used just the post-release subset of radio-telemetry data for wild-born individuals only (model 6, Table 3-1). For two-year-olds and adults, the lowest survival rate was estimated from the same data and survival model, but for captive-born marmots only (model 7, Table 3-1).

Fecundity did not vary over time or with origin (wild or captive-born), but did vary with age. Reproductive output increased with age, two-year-old fecundity being much lower than that of older females (m_x = 0.129, 0.420, and 0.616, for 2-year-olds, 3-year-olds, and$\geq$ 4 -year-olds respectively). A much smaller proportion of two-year-old females breed and they had a smaller average litter size compared to older females (Figure 3-3A). Overall, average litter size was 3.39 (±0.13; *N*=66 litters; Figure 3-3A) and average age of first reproduction was 3.33 (±0.22; *N*=24; Figure 3-3B).

Population Growth Rate and Elasticities

Asymptotic population growth rate, λ, ranged from 0.721 (model 7, Table 3-1) to 1.038 (model 6, Table 3-1), depending primarily on the subset of the data used to estimate survival rates. Both of these growth rates represent hypothetical populations in which populations consist of entirely captive-born, released individuals (λ=0.721) or entirely of wild-born marmots in recent years (2003-2008; λ=1.038). The population growth rate estimated for the entire population (both wild and captive-born) since releases began in 2003 was 0.876 (model 5, Table 3-1). Population growth estimated using parameters estimated from combined (i.e. radio-telemetry and CMR) data over the entire study period (model 1, Table 3-1) was 0.821. All estimates of population growth rate for the entire population over any duration, using parameters from either combined or radio-telemetry data and from any model, were in the range of 0.821 to 0.878. This indicates population decline of at least 12% and up to 18%, encompassing various time periods and methods of parameter estimation.

In general, population growth rate was more sensitive to proportional changes in survival rates than fertility rates. Specifically, the population growth rate was proportionally most sensitive to changes in survival of adults, followed by pups, yearlings, and two-year-olds. These trends of relative importance of various demographic rates to population growth rate was

consistent for all the models we tested ($e(P_a) > e(P_p) > e(P_y) > e(P_t) > e(F_a) > e(F_t) > e(F_y)$; Table 3-2). The population growth rate was proportionally much more sensitive to changes in survival of adults than to changes in any other parameter for all models, with $e(P_a)$ twice as large as any other elasticity (Table 3-2, Figure 3-4), except for the model representing captive-born individuals only (Table 3-2, model 7). For released marmots, survival of younger age-classes was similar in importance to adult survival (Figure 3-4).

Discussion

Population modeling is a necessary, but often missed, step in recovery planning for endangered species (Meretsky et al. 2000; Sarrazin & Legendre 2000). We must have an understanding of what the population dynamics were like during the decline of a species, including which demographic rates drove the population decline (Caswell 2001). If population dynamics in recent years are similar to dynamics during population decline, then the goal of ensuring population persistence in the wild may not be met unless conditions change. Through population modeling, we can determine goals for demographic rates in the wild and evaluate alternative reintroduction scenarios (Bar-David et al. 2005; Caswell 2001; Sarrazin & Legendre 2000); this information is needed but was not available for the Vancouver Island marmot population until this study.

Population Decline

The Vancouver Island marmot population crashed from an estimated 300-350 marmots in the mid-1980s to less than 50 marmots by 2002, representing a drastic decline in just 15 years. We estimated population growth rate over the entire study period (1987-2007) to be between 0.82 and 0.85. Our estimates may slightly underestimate the population growth rate due to the limitations of CMR-based survival parameters; however, a 15% decline annually appears reasonable when compared to the observed trend.

Several populations of other marmot species are not in decline. Yellow-bellied marmots (*M. flaviventris*) in western North America and various alpine marmot (*M. marmota*) populations throughout Europe appear stable or even slightly growing (Farand et al. 2002; Ozgul et al. 2006; Ozgul et al. 2009; Stephens et al. 2002). Our estimates of age-specific survival were generally lower than those estimated for these populations (Oli & Armitage 2004; Ozgul et al. 2006). Reproductive parameters were also slightly lower; however, both the yellow-bellied and alpine marmot exhibit a faster life history so this is to be expected (Armitage 2003). Reproductive rates of yellow-bellied and alpine marmots are comparable to those estimated for the Vancouver Island marmot only in situations of high population density. Reproductive suppression has been a commonly cited explanation for low proportions of females breeding in colonies of high population density (Griffin et al. 2008; Ozgul et al. 2006). Low densities of Vancouver Island marmots make reproductive suppression an unlikely mechanism for any decrease in reproductive output.

On the other hand, the population growth rate recently estimated for the Olympic marmot (*M. olympus*) suggests a decreasing population at a rate of 7% annually from 2002-2006 (Griffin et al. 2008). The Olympic marmot, like the Vancouver Island marmot, is a species with limited geographic range and slow life-history compared to other species of marmot. Survival of Vancouver Island marmot pups was slightly lower than survival of Olympic marmot pups; however, survival rates for all other age-classes were similar (Griffin et al. 2008; Griffin et al. 2007b).

Reproductive rates of Vancouver Island marmots were also similar to those reported for Olympic marmots in recent years and slightly lower than historic estimates, from a time of presumed stability for the Olympic marmot population (Barash, 1973; Griffin et al. 2008; Griffin

et al. 2007a). Griffin (2008) considers the slight decline in reproductive output a secondary effect of increased mortality of adult females. This was also the case in the collapse (>95% decrease from 1987-1999) of a Northern Idaho ground squirrel population where decreased reproductive rates was a result of a low proportion of adult females in the population (Sherman & Runge 2002).

It is apparent that low survival due to predation is the proximate cause of the Vancouver Island marmot population crash. As primary evidence, population growth rate was much more sensitive to proportional changes in survival than to proportional changes in reproduction. Furthermore, any decrease in reproductive output of the population is most likely a result of high adult mortality through two mechanisms. First, high adult mortality leads to lower adult population density, which may lead to mate-finding Allee effects. Second, fewer adult females in the population causes a shift in age structure towards younger individuals of lower fecundity. These demographic causes of proximate population decline are similar to those cited for both the crash of a Northern Idaho ground squirrel population (Sherman & Runge 2002) and the recent decline of the Olympic marmot population (Griffin et al. 2008).

Potential for Recovery

In recent years (2003-2008), population growth rate has improved slightly to 0.876. While there has been an increase in population size due to release of captive-born marmots, models still predict a 12% decline per year. If population size has increased in the wild solely due to addition of released marmots, this effect will persist only for the duration of releases, unless the population growth rate improves.

To investigate what level of demographic success is necessary to create a persistent population in the wild, we estimated two hypothetical population growth rates representing best-case and worst-case scenarios. The first, a population of captive-born, released individuals only;

and the second, using demographic rates of only wild-born marmots in recent years. Estimated growth rate for a population of entirely captive-born individuals was 0.721. With a decline of nearly 30% a year, the current demographic rates of released individuals will not lead to a persistent reintroduced population.

However, some hope lies with the marmots born in the wild in recent years. The population growth rate we estimated for a population of these wild-born marmots was 1.03; the only model we examined which predicted a growing population. If enough marmots are released into the wild, and if enough of these marmots survive to reproductive age, than their offspring might contribute to a viable population. This strategy may require the release of a large number of individuals over a number of years, if we must wait for the next generation of marmots to survive sufficiently in the wild to produce a persistent population. It also requires that marmots are released and remain in a spatial distribution at high enough densities to minimize mate-finding Allee effects.

Over the past 3 years, some released female marmots which do survive to reproductive age and are in the presence of a male have reproduced in the wild. As additional evidence, although sample sizes are small, we were unable to detect an effect of origin (captive or wild-born) on reproductive rates. It also seems as though a second generation effect of captivity on survival is unlikely because the high survival rate estimated for wild-born marmots in recent years is comprised of both offspring of wild-born individuals and of offspring of released marmots,.

Survival of captive-born marmots released into the wild must be improved to produce a persistent population in the wild. If marmots continue to be released as yearlings, with an extremely low survival rate (lower than those released at age two or older, Aaltonen et al. in review), the probability that they contribute to population growth through reproduction is low.

Releasing marmots at an older age (i.e. shorter time required to survive until age with maximum reproductive value) would likely increase the success of the reintroduction program.

We do not have sufficient data on predator populations nor sufficient understanding of the interaction between the altered landscape and predator-prey dynamics on the island to know if the cause of low overall marmot survival (and hence the proximate cause of population decline) has been removed. It is possible that the difference in survival rates between captive-born and wild-born marmots is due to selective predation on captive-born marmots because of some decreased ability of released marmots to avoid or escape predators, particularly avian predators. If released individuals can survive long enough to produce an increasingly wild-born population, there are multiple possible outcomes. As captive-born individuals become less abundant, wild-born individuals could become increasingly depredated and survival of wild-born individuals could decrease. Alternatively, wild-born offspring could be more capable of avoiding predation and survival of wild-born individuals could remain high.

Currently, reproductive rates of the Vancouver Island marmot seem adequate, although the only true evidence is by comparison with historic reproductive rates of the Olympic marmot and comparison with other members of the *M. caligata* group (Bryant 2005; Griffin et al. 2008). If reproduction is insufficient at all, it is most likely due to fewer older-aged females (with higher reproductive value) being alive to breed.

Matrix population models project a continuing decline of greater than 10% annually unless vital rates improve. We have found that low survival is an extremely important driver of population decline, and this is likely to be the case if survival of captive-born marmots in the wild is not increased. These findings suggest that management strategies aimed at increasing survival rates would be required to ensure the long-term persistence of the Vancouver Island

marmot. Further population modeling and use of alternative reintroduction strategies within an experimental design are necessary to improve knowledge about survival in the wild, the overall recovery strategy, and the probability of achieving a persistent wild population of Vancouver Island marmots.

Table 3-1. Description of data used, time period, and estimates of age-specific survival rates used in each matrix population model

				Parameter			
Model	Dataset*	Time Period	Population§	P_p	P_y	P_t	P_a
1	Combined	1987-2007	entire	0.460 (0.339 - 0.585)	0.618 (0.559 - 0.674)	0.807 (0.638 - 0.908)	0.618 (0.559 - 0.674)
2	Combined	1987-2007	wild-born	0.490 (0.370 - 0.611)	0.646 (0.588 - 0.700)	0.825 (0.662 - 0.919)	0.646 (0.588 - 0.700)
3	Combined	1987-2007	entire	0.490 (0.370 - 0.611)	0.63 (0.573 - 0.684)	0.799 (0.631 - 0.902)	0.63 (0.573 - 0.684)
4	Combined	1987-2002	wild-born	0.492 (0.372 - 0.613)	0.638 (0.572 - 0.699)	0.825 (0.613 - 0.933)	0.638 (0.572 - 0.699)
5	Radio-telemetry	2003-2008	entire	0.490 (0.370 - 0.611)	0.777 (0.604 - 0.888)	0.835 (0.588 - 0.947)	0.628 (0.510 - 0.733)
6	Radio-telemetry	2003-2008	wild-born	0.490 (0.370 - 0.611)	0.893 (0.756 - 0.958)	0.923 (0.756 - 0.979)	0.812 (0.688 - 0.894)
7	Radio-telemetry	2003-2008	captive-born	0.490 (0.370 - 0.611)	0.651 (0.441 - 0.815)	0.736 (0.425 - 0.913)	0.456 (0.307 - 0.613)
8	Radio-telemetry	1992-2007	entire	0.490 (0.370 - 0.611)	0.712 (0.540 - 0.838)	0.802 (0.534 - 0.935)	0.659 (0.566 - 0.742)

*Data set used to estimate survival rates (either radio-telemetry data only or a combined data set including radio-telemetry and capture-mark-resight data)

§Population or subset of population for which survival rates were estimated (Model 4 is automatically wild-born only, because no captive-born marmots had been released yet)

Age-specific survival rates: Pp is pup survival from first tagging through July/August the following year; Py is survival of yearlings; Pt, survival of two-year-olds; Pa, survival of adults, age 3 and older

Table 3-2. Estimates population growth rate (λ) and elasticities from each matrix population model

				Elasticity							
Model	Dataset	Time period	Population	P_p	P_y	P_t	P_a	F_y	F_t	F_a	λ
1	Combined	1987-2007	entire	0.165	0.156	0.127	0.388	0.009	0.029	0.127	0.821
2	Combined	1987-2007	wild-born	0.165	0.156	0.127	0.388	0.009	0.029	0.127	0.858
3	Combined	1987-2007	entire	0.166	0.157	0.127	0.384	0.009	0.029	0.127	0.839
4	Combined	1987-2002	wild-born	0.166	0.157	0.128	0.383	0.009	0.029	0.128	0.851
5	Radio-telemetry	2003-2008	entire	0.180	0.169	0.133	0.337	0.012	0.036	0.133	0.876
6	Radio-telemetry	2003-2008	wild-born	0.152	0.144	0.121	0.433	0.008	0.023	0.121	1.038
7	Radio-telemetry	2003-2008	captive-born	0.212	0.196	0.140	0.240	0.017	0.056	0.140	0.721
8	Radio-telemetry	1992-2007	entire	0.166	0.156	0.127	0.385	0.010	0.029	0.127	0.878

*Data set used to estimate survival rates (either radio-telemetry data only or a combined data set including radio-telemetry and capture-mark-resight data)

§Population or subset of population for which survival rates were estimated

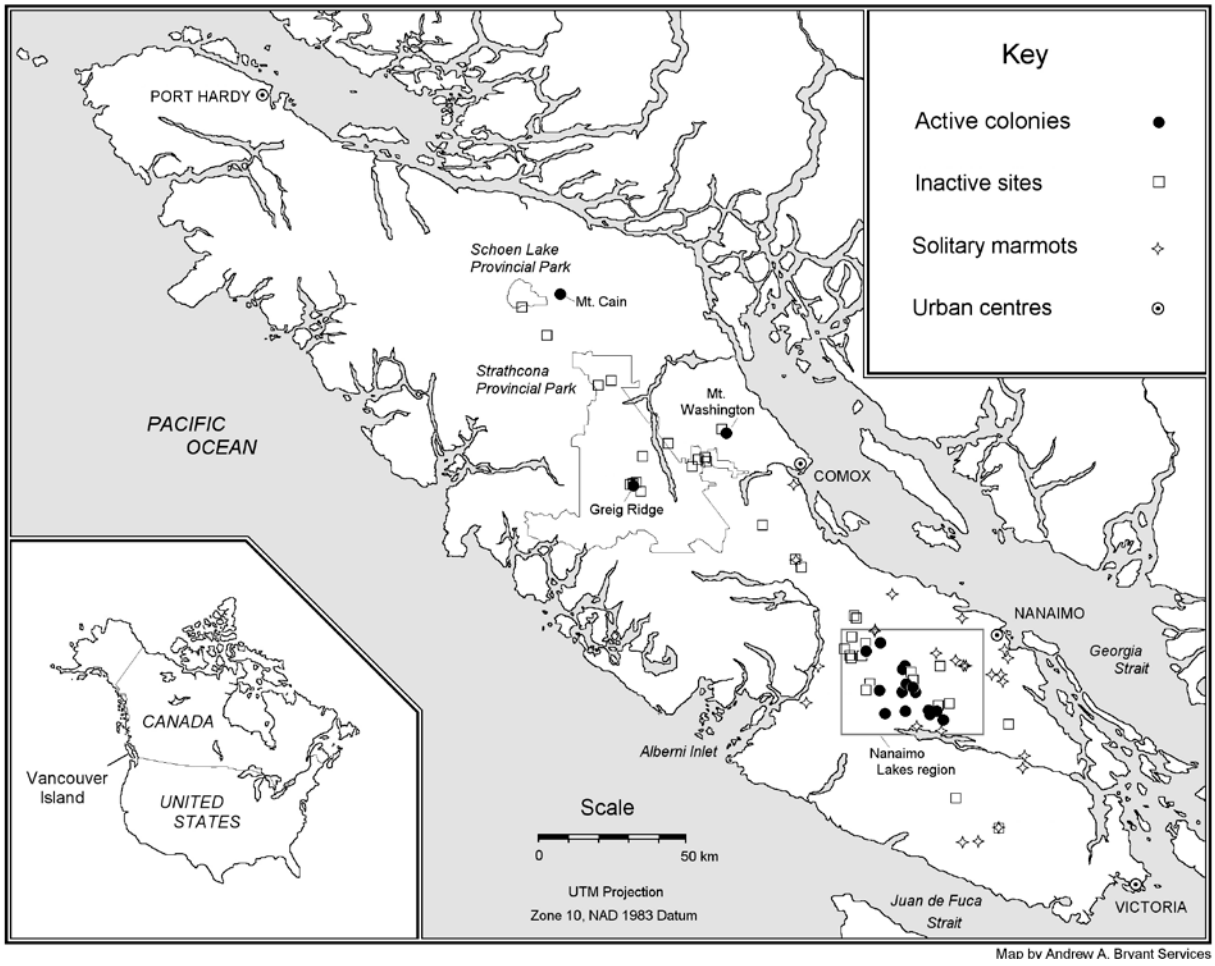

Figure 3-1. Historically occupied (squares) and recently occupied (circles) sites for *M. vancouverensis*. The rectangle encompasses recently-active colonies within the Nanaimo Lakes region, from which the majority of survival data were obtained. Locations of the isolated Mt. Washington population and recent reintroductions at Mt. Cain and Greig Ridge are also shown, but were not included in analyses.

$$\mathbf{A} = \begin{bmatrix} 0 & P_y m_y & P_t m_t & P_a m_a \\ P_p & 0 & 0 & 0 \\ 0 & P_y & 0 & 0 \\ 0 & 0 & P_t & P_a \end{bmatrix}$$

Figure 3-2. Population projection matrix used for all models. P_i is the age-specific survival rate and m_i is age-specific fecundity. Matrix constructed using post-breeding census technique (Caswell 2001).

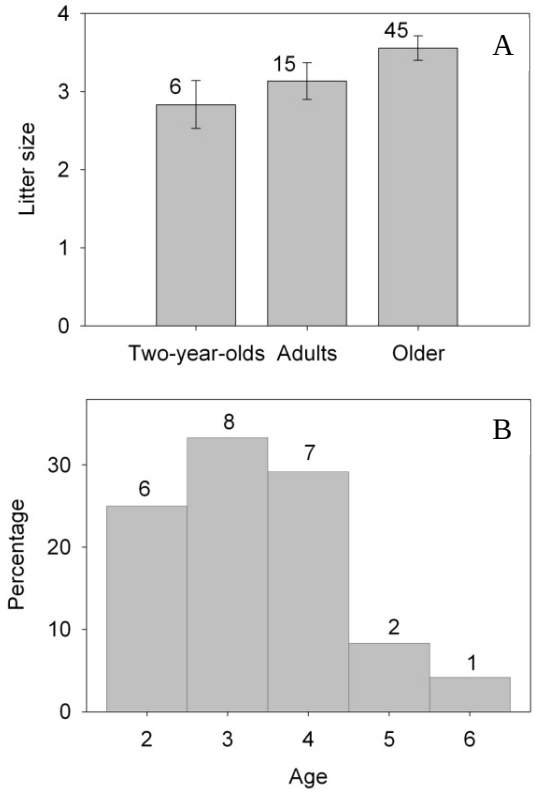

Figure 3-3. Average age-specific litter size and age of first reproduction. A) Average (±SE) litter size for two-year-olds, adults (three-year-olds), and older (four years and older) Number of litters displayed. B) Distribution of age at first reproduction (N=24)

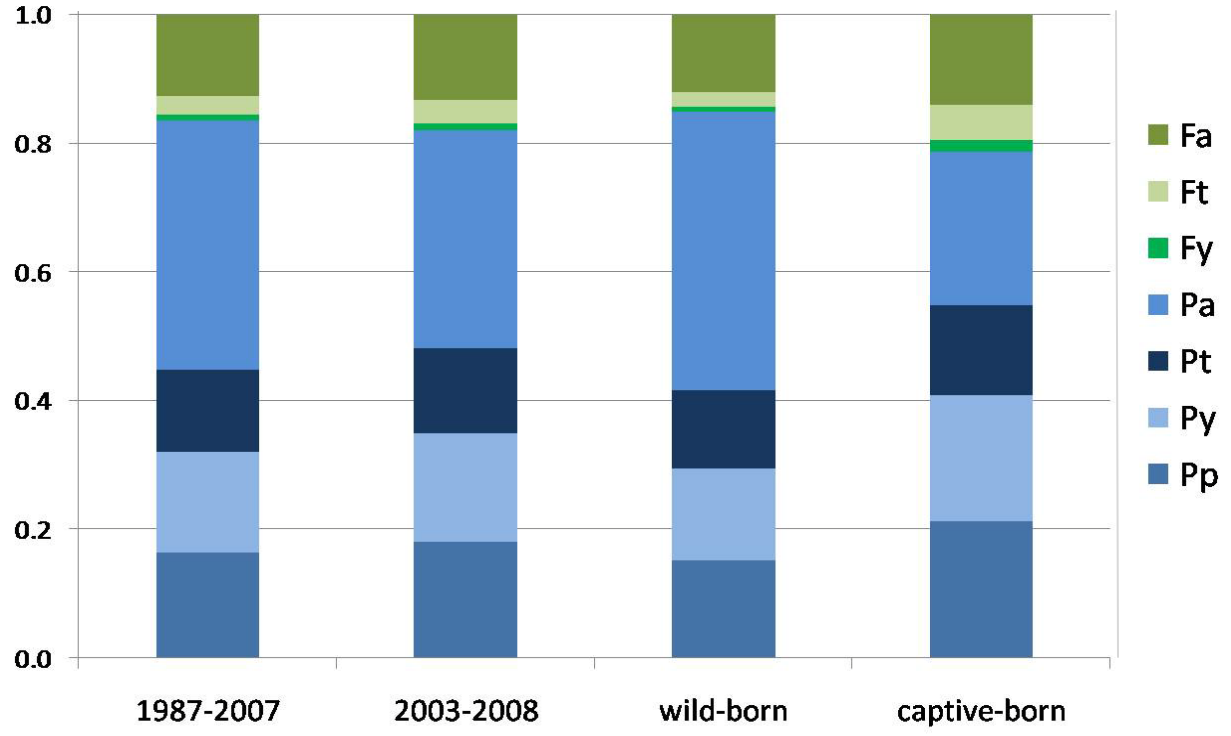

Figure 3-4. Elasticities from four models. Columns from left to right represent models 1, 5, 6, and 7 (Table 3-2). Model 5 represents the entire population from 2003-2008; models 6 and 7 represent noted hypothetical sub-population over the same time period (2003-2008).

CHAPTER 4
POPULATION ECOLOGY OF THE VANCOUVER ISLAND MARMOT: CONCLUSIONS

Survival of captive-born marmots released into the wild must be improved to produce a persistent population in the wild. If marmots continue to be released as yearlings, with an extremely low survival rate (lower than those released at age two or older, Aaltonen et al. in review), the probability that they will contribute to population growth through reproduction is low. Releasing marmots at an older age (i.e. shorter time required to survive until age with maximum reproductive contribution) would likely increase the success of the reintroduction program.

Currently, reproductive rates of the Vancouver Island marmot seem adequate, although the only true evidence is by comparison with historic reproductive rates of the Olympic marmot and comparison with other members of the M. caligata group (Bryant 2005; Griffin et al. 2008). If reproduction is insufficient at all, it is most likely due to fewer older-aged females (with higher reproductive value) being alive to breed, as suggested to be the case for Olympic marmots and a population of Idaho ground squirrels (Griffin et al. 2008; Sherman & Runge 2002).

Matrix population models project a continuing decline of greater than 10% annually unless vital rates improve. We have found that low survival is an extremely important driver of population decline, and this is likely to be the case if survival of captive-born marmots in the wild is not increased. These finding suggest that management strategies aimed at increasing survival rates would be required to ensure the long-term persistence of the Vancouver Island marmot. Further population modeling and experimental design of reintroductions are necessary to improve knowledge about survival in the wild, to improve the overall recovery strategy, and to increase the probability of achieving a persistent wild population of Vancouver Island marmots.

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BIOGRAPHICAL SKETCH

Kristen was born in West Lafayette, Indiana and grew up a Purdue fan there in the academic shadow of her older brother. High school tardies, frequent tears in the hallways, sleeping in class, and running with the infamous KLAS crew didn't keep her out of college. Much to her mother's chagrin, she left home to attend a small private university in Indianapolis for her undergraduate education. She earned a bachelor's in science from Butler University, majoring in biology with minors in mathematics and Spanish. She also walked on to the Butler Bulldogs soccer team (sans white cleats) and loved playing on the team for all four years. It was rumored that she had the best foot skills in the nation and while she made life-long friends from the team, there is speculation that they still ridicule her on occasion out of jealousy of her athleticism.

After Kristen graduated from Butler, much to her Finnish father's chagrin, she went to Uppsala, Sweden to do forest genetics research on the lignin biosynthetic pathway. She soon decided that white biology was not for her, and she needed to do something greener in nature. She had a wonderful time in Sweden, in fact the only failure of her stay in Sweden was not hooking a Swedish husband to dilute her Finnish blood.

Kristen started graduate school at the University of Florida in 2006 and quickly grew to love both ecology and conservation. Gainesville has provided her with both a beloved lifestyle of simplicity and an exceptionally diverse group of friends which she has learned much from. While she has yet to decide her future path, she is certain it will include conservation of our natural resources and sustainability. She hopes to spread awareness of the consequences our decisions have beyond our immediate perspectives and a respect for all living creatures, for all things in this world are connected. In the spirit of interconnectedness, she is very grateful for all

the much needed emotional support from friends and family over the years, she surely would have missed an insurmountable proportion of deadlines without their love and encouragement.