THE ENDANGERED VANCOUVER ISLAND MARMOT: ALLEE EFFECTS AND REINTRODUCTION SUCCESS

by

JEFFERY R. WERNER

B.Sc., University of British Columbia, 2001

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA

December 2005

© Jeffery R. Werner 2005.
Abstract

The Vancouver Island marmot (*Marmota vancouverensis*) is a large social rodent endemic to Vancouver Island, whose population has declined by 80-90% since the 1980s. It is one of the most highly endangered mammals in North America. Compared to its congeners this marmot has received little research, and many questions concerning basic ecology remain unanswered.

The first objective of this study was to compare information on contemporary animals (2002-2004) with those of an earlier time period (1973-1975). Data on time allocation, social activity and ranging behaviour of several colonies in the late stages of decline were compared with historical data collected under more stable conditions. Contemporary marmots interacted with conspecifics less, had larger home ranges, devoted more time to vigilant behaviour, and did not exhibit bi-modal activity patterns previously described for this and other marmot species. Contemporary marmots also fed less, gained daily mass at a lower rate, and may have entered hibernation later than members of historical populations. These findings suggest an Allee Effect; a positive connection between aspects of fitness and population size imply the need to identify threshold group sizes necessary for recovery.

The second objective of this study was to compare wild marmots with captive-raised marmots released into the wild (2002-2005). Time budgets, wariness to potential sources of danger, and home range activities were compared. Despite similarities in behaviour, released marmots continued to have lower survival than wild marmots. Sources of mortality included predation and unsuccessful hibernation: High mortality is likely linked to dispersal from the release site. Release methods are discussed which may foster cooperative behaviours and philopatry among reintroduced marmots intended to form new colonies. Applying our new understanding of marmot ecology to captive breeding programs may improve the success of conservation efforts for this highly endangered species.
# Table of Contents

Abstract...........................................................................................................ii

Table of Contents............................................................................................iii

List of Tables....................................................................................................iv

List of Figures...................................................................................................v

Acknowledgments.............................................................................................vi

Chapter 1 Introduction......................................................................................1  
  Background.................................................................................................1  
  Study Objectives......................................................................................4

Chapter 2 Behavioural Changes within a Declining Population.....................6  
  Introduction...............................................................................................6  
  Methods.....................................................................................................9  
  Results.....................................................................................................16  
  Ranging....................................................................................................19  
  Time Budgets..........................................................................................20  
  Sociality...................................................................................................23  
  Weight gain.............................................................................................23  
  Discussion.................................................................................................24

Chapter 3 An Assessment of Captive-rearing and Reintroduction Strategies....39  
  Introduction...............................................................................................39  
  Methods.....................................................................................................41  
  Results.....................................................................................................46  
  Survival.....................................................................................................46  
  Home ranges and movement..................................................................47  
  Sociality...................................................................................................48  
  Time allocation.......................................................................................49  
  Flight distance........................................................................................49  
  Discussion.................................................................................................50

Chapter 4 Summary and Recommendations..................................................59

References......................................................................................................63

Appendices.....................................................................................................77

iii
List of Tables

Table 2.1: Predicted trends in contemporary VIM relative to historical reference data.....9

Table 2.2: Changes in social and maintenance activities between the 1970s and 2000s...18

Table 2.3: A comparison of kernel range estimates and minimum recorded distances between successive independent locations for males and females during 2002-2004.................................................................20

Table 3.1: The composition of captive-bred release groups at each study site..........41

Table 3.2: Home range sizes for captive-bred and wild marmots at the 95% kernal density..............................................................................................................48
List of Figures

Figure 2.1: Location of Vancouver Island study sites ..................................................10

Figure 2.2: Estimates of the wild VIM population, since 1972-2004. .........................11

Figure 2.3: Demographic composition of modern and historic study sites .................19

Figure 2.4: Proportion of total observation time marmots devoted to feeding, below
ground activity, and resting (sitting and/or lying) above ground for
‘historic’ and ‘modern’ populations. Bars are SE calculated from hourly
means.............................................................................................................21

Figure 2.5: Diurnal activity during July, compared with M. Caligata and historical
VIM .....................................................................................................................22

Figure 2.6: Schematic of some positive feedback mechanism that could potentially
operate as causes and effects in a population of declining VIM .........................33

Figure 2.7: A simplified model of Allee Effects using an individual’s risk of mortality
as an example ....................................................................................................35

Figure 3.1: The major southern release sites geographically relative to one another.
These mountains are in the vicinity of the southern diamond in Fig. 2.1.
Distance between the ‘Haley Bowl’ and ‘Green Summit’ reintroduction
sites is approximately 7 km. Contours are 20m intervals ...............................42

Figure 3.2: Flight distances for released and wild marmots during 2003 and 2004 ......50
Acknowledgements

I am grateful to Justin Brashares for trusting me to conduct thesis work as a part of the project he initiated on the Vancouver Island marmot. Justin was an unofficial advisor whose leadership was essential to the success of this project.

Many field assistants have helped shape the direction of this project through their leadership and dedication to data collection. I will not attempt to describe the difficult conditions under which these people did so much work. Yannick Cobassau, Raenelle Parker, and Rob Landucci made our first difficult season possible. Hard work from Felice Griffiths, Shelley Marshall, Corinna Wainwright, and the plant expertise of Francis Iredale enabled us to expand our research priorities in the second year to include reintroductions. The addition of Michelle Connoly and Mike Champion and leadership from Scott Donker in later seasons further raised the quality of our research and the number of questions I was able to entertain.

My advisors Jamie Smith and Tony Sinclair, and my advisory committee Kathy Martin and Justin Brashares have provided support and advice throughout my tenure as a student. The time and energy that Jamie Smith invested in discussing my thesis was humbling, and the keen interest with which he approached the world around him puts me to shame.

This project was funded by generous support from The Science Advisory group of the Vancouver Island Marmot Recovery Fund, and Environment Canada. Additional monies came from Natural Sciences and Engineering Research Council of Canada and the University of British Columbia. Field work benefited from logistical support provided by the Marmot Recovery Foundation.

None of this research would have been successful without collaboration from Don Doyle and Doug Janz from the Ministry of Water, Air and Land Protection and their related field staff led by Jerry MacDermott.

Note: all data are available from the author upon request. Contact werner@zoology.ubc.ca.
Chapter 1 Introduction

Background

A primary goal of conservation research is to predict how small populations respond to changes in environmental conditions, demographic parameters, and genetic composition. Advances in conservation science have improved our understanding of how stochastic factors operate in small populations and what practical measures may reverse declines. This growing science has also expanded its directions of inquiry beyond genetics, population biology and landscape ecology to include the study of behaviour (Sutherland 1998; Caro 1998).

Despite these advances, applied conservation research runs the risk of being viewed as irrelevant because its results lack high certainty or may be too idiosyncratic to hold wider application. The political nature of endangerment often precludes certain forms of experimentation. Although the threats to small populations are generally well understood, lingering uncertainties characterize many attempts to perceive causes of decline (Caughley 1994). The window of time suitable for understanding these causes, and the challenges posed for recovery, can be narrow. As a consequence, rigorous research may be deferred in order to fulfill an immediate need to bolster survival and foster reproduction. Notwithstanding these challenges of studying small populations, and the sensitive conditions under which species at risk research is often conducted, conservation biologists are making valuable contributions to our understanding of populations in decline (Sutherland 1998). It is my hope that the research reported herein will support attempts to conserve the Vancouver Island Marmot (Marmota vancouverensis; hereafter VIM), while also providing a case study for those concerned with the broad challenge of conserving small populations.

The VIM is a highly endangered colonial ground squirrel endemic to Vancouver Island, Canada (Nagorsen 1987, 2004); it has been studied, to varying degrees, since the early 1970’s (Heard 1977). Subalpine clearings were historically important habitat; however researchers have yet to identify what constitutes critical habitat (Elner 2000). Historical colonies are thought to have been typically small (n≈8.5; Heard 1977; however
group sizes often vary in social marmot species, e.g., 2-36 in *M. caligata*; Karels et al. 2004), and to have exhibited a classic metapopulation structure whereby subpopulations experienced local extinctions and recolonizations through time (Bryant 1998). Historical populations were highly social, and exhibited complex behaviour similar to other montane marmot species (Heard 1977; Bryant 1996).

VIM is a long-lived social species with low rates of reproduction. The benefits of sociality include: increased thermoregulation (Arnold 1993; Alaine and Theuriau 2004), potential for cooperative breeding (Blumstein and Armitage 1999; Clutton-Brock 2002), delayed dispersal (Barash 1974), predator recognition and avoidance (Hauber and Sherman 1998), mate-finding (Allaine 2000), and maintenance of complex burrow systems (Barash 1989). Females typically require three years to mature, and rarely reproduce in consecutive seasons, suggesting that life-long reproductive performance is low (Bryant 1996) relative to many other Sciurids (Blumstein and Armitage 1999). Females tend to be philopatric while the males typically disperse to other colonies. Dispersal in VIM is delayed at least until after first hibernation and may be deferred well beyond reproductive maturity (3-6 years). Delayed dispersal is common to all marmots living in harsh environments (Barash 1989).

The entire VIM population declined rapidly in the 1980s from 300-500 animals (Bryant 1998) to about 25 in summer 2003, making this marmot one of the most endangered mammals in North America (IUCN Red List 2005). Current adult annual survival is approximately 72% (Bryant 2004; Janz et al. 2000). VIM conservation managers have successfully raised a modest captive population (about 120 animals), and it is generally accepted that the few, isolated remaining wild animals are unlikely to restore the species without augmentation and active management (see management rationale and protocols in Janz et al. 2000). It is believed that recovery will therefore be realized through a series of reintroductions to generate individuals that survive and reproduce in the wild. The reintroduction of artificially raised marmots began in 2003 (n=4) and continues every year (2004 n=8, 2005 n=12). With the exception of Mount Washington (n=12), all active colonies are located within several adjacent watersheds (n=10) on south-central Vancouver Island.
No single factor has been identified as the primary cause of past decline, but a number of factors have been proposed. Forestry practices above 600m are believed to have created “sink” habitats that attract marmots but cannot support viable populations (Bryant 1996; Bryant 2004). These clearings may also have reduced the likelihood of inter-colony dispersal (Janz et al. 2000). Predation is now viewed by many as the principal threat to the current persistence and recovery of VIM (Bryant 2004; Bryant and Janz 2002). A substantial portion of annual mortality is caused by predators (83% of known fate mortality events since 1992: Bryant and Page 2005). Predators include wolf (Canis lupus), cougar (Felis concolor), golden eagle (Aquila chryaetos), and bald eagle (Haliaeetus leucocephalus).

One possible explanation for the recent change in population dynamics is an Allee effect (sometimes called an ‘underpopulation effect’) which is defined by a positive relationship between aspects of fitness and population size caused by conspecific cooperation and/or facilitation (Stephens et al. 1999). The importance of Allee effects for metapopulations has recently been recognized (Amarasekare 1998), especially for populations of social species (e.g., Aviles and Tufino 1998; Creel and Creel 1995; Courchamp et al. 2000). Research on other marmots (e.g., Armitage 2003; Blumstein 1996) and other species (Burger 2003; Roberts 1996) suggests that moderate group sizes confer fitness benefits to their members. Possible mechanisms that increase individual fitness in larger groups include mate choice, a diffusion of costs associated with vigilance and predator avoidance, a lowered probability of individuals being attacked (‘dilution effect’: Hamilton 1971), or a reduction in energy expended to modify habitat (Barash 1989; Mooring et al. 2004) and survive overwinter (‘social thermoregulation’: Arnold 1988).

The likelihood that group effects will modify population growth depends upon the role sociality plays in each species (Courchamp et al. 1999a), with obligate cooperators experiencing the strongest influence (Courchamp et al. 1999b). A strong beneficial relationship between fitness and conspecific abundance may lead to demographic effects which result in reduced per capita growth (sometimes negative) in small populations (Taylor and Hastings 2005). Reduced rates of population growth can therefore be caused by lowered individual fitness that accompanies the loss of a critical density, group or
population size (Courchamp and McDonald 2001). The effect of group size on behaviour is well documented in other species (Roberts 1995; Blumstein et al. 2003; Stephens and Sutherland 1999). At low numbers social organisms must balance the risks of being eaten with the need to feed and find suitable mates (Stephens and Sutherland 1999). In marmot species, the time and energy allocated to foraging, vigilance and movement, and the realized benefits of alarm calls may vary with group size, and distance to neighbors (Armitage 2003; Barash 1989; Carey and Moore 1986). Species that exhibit strong cooperation, such as the colonial-living VIM, may therefore be especially sensitive to changes in the abundance and composition of conspecific communities. This possibility serves as one of the central foci of this study.

Study Objectives

The primary objective of my study was to investigate whether a positive relationship exists between population size and individual fitness and to explore whether such a relationship may have contributed to the decline of this endangered marmot. Chapter 2 compares research on wild VIM conducted during 1973-1975 to contemporary data that I collected during 2002-2005. The specific focus was on individual ranging behaviour, sociality and time-activity budgets. By focusing on several social mechanisms purported to affect the fitness of individuals I assess what role inverse density dependence may have played in recent VIM declines. This investigation not only contributes to our understanding of marmots, but may change the approach we take towards recovery of populations of social species.

The study’s second objective was to assess the efficacy of reintroduction methods now being used to found new populations of captive-bred individuals. Baseline data on wild animals are used to assess the performance of reintroduced individuals. When reintroductions fail such comparisons help us develop testable predictions concerning the influence of captive breeding on survival strategies, and the persistence of captivity-induced behavioural abnormalities. Specifically, I ask: How have reintroductions of VIM during 2003, 2004, and 2005 contributed to the recuperation of colonies in the wild? Are
there important differences between wild and artificially-reared marmots that drive potential differences in survival? How can conditions in captivity and the methods used to release marmots be changed to improve reintroduction success? Chapter 3 provides tentative answers to these three questions and proposes a set of hypotheses that could be used in future experimental releases to distinguish reintroduction investments of primary importance (i.e., the minimum actions necessary to achieve success) from those which might be viewed as optional; i.e., whose contribution to overall success is small relative to their cost.

Chapter 4 summarizes the main findings, their general application for conservation and suggests types of complementary research that should be conducted in the future.
Chapter 2 Behavioural Changes Within a Declining Population

Introduction

The contributions of density-dependent and independent processes to population persistence is an enduring theme in ecological research (e.g., Chitty 1960; Richter-Dyn and Goel 1972; Sinclair 1989; Berryman et al. 2002; Henle et al. 2004). Attempts to understand processes that drive population decline and recovery are evident in a broad range of applied and more theoretical work. Recent efforts have connected a classical notion, Allee effects (Allee 1931), with investigations of linearity and non-linearity in rates of population growth (Chen et al. 2002; Oborny et al. 2005). In particular, the idea of threshold relationships, wherein species exhibit abrupt shifts in the pace or direction of change at low population size, has become a fundamental topic for those concerned with the management of small populations and the evolution of animal sociality (Allee 1938; Creel and Creel 1995; Courchamp et al. 1999a; Aviles 1999; Stephens et al. 2002; Clutton-Brock 2002).

More than 70 years ago, W. C. Allee (1931; 1938; Allee et al. 1949) first speculated that social changes accompanying the attrition of aggregated populations (e.g., impairment of mate-finding) might reinforce declines, or lengthen the time needed for populations to recover. Recent interest in what has become called the Allee effect has led authors to consider how forms of social mediation may influence individual fitness and potentially cause inverse density dependence at low population sizes (i.e., a positive relationship between per capita rate of population growth and population density or size). Potential mechanisms for these effects in small populations include: reduced predator detection/avoidance, reduced foraging because of increases in vigilance, changes in habitat selection or habitat modification, reduced resilience to environmental shock, and the loss of genetic variation (Stephens 1998; Stephens and Sutherland 2000). Allee effects have implications for metapopulation persistence as they will increase the likelihood of patch extinction (Amarasekare 1998; Hui and Li 2004). The connection between aspects of individual fitness and conspecific abundance is now well documented.
Theoretical predictions about the scale and impact of Allee effects under a broad range of scenarios (e.g., Boukal and Berec 2002; Dennis 2002) have now been substantiated by experimental studies of exploited, peripheral and reduced populations (e.g., Halliday 1980; Davis et al. 2004; Kuussaari et al. 1998; Morris 2002; Forsyth 2003; Cappuccino 2004; Hutchings and Reynolds 2004). In other cases, the effect of rarity on population dynamics have been identified through invasions of exotic species, reintroductions and translocations (Hopper and Roush 1993; Green 1997; Grevstad 1999; Taylor and Hastings 2005). It is now widely accepted that group size effects are not limited to certain taxonomic systems, body sizes or mating systems, and have particular relevance for management of species at risk of extinction (Gascoigne and Lipicus 2004; Stephens and Sutherland 2000; Kokko and Sutherland 2001). In spite of promising advances in our understanding of the importance of conspecifics, few empirical studies have demonstrated the mechanisms which drive inverse density-dependence in small populations (Dennis 1989; Stephens et al. 2002).

The purpose of this study was to examine the potential role of Allee effects in the decline of the endangered Vancouver Island marmot (VIM), and to identify component mechanisms that may drive such an effect. In the case of VIM, Allee effects might be driven by changes to mate searching, mating success, foraging efficiency, and predator recognition and/or avoidance rendered by changes in group or population size. My specific focus was on ranging behaviour, sociality and activity budgets. I suspected that changes in these attributes might constitute the mechanistic underpinnings of shifts in density dependence and, thereby, contribute to observed population declines. My hope was that identifying these mechanisms would have direct relevance for strategies to recover this species and, perhaps, many others.

With the exception of biological control and large scale reintroduction studies, opportunities to investigate experimentally the effect of population size on components of fitness, or on establishment and persistence, are limited. Conducting such studies may be viewed as impractical or unethical, particularly for species of conservation concern. Because experimental attempts to cause Allee effects are difficult and rare, "natural experiments" that take advantage of catastrophic events or intensive studies of endangered populations across different stages of decline represent some of the best
opportunities to study Allee effects in nature (Courchamp et al. 1999a). In both of these cases, past research conducted on ‘healthy’ populations could serve as a baseline against which more recent data on the same populations can be compared. Despite the limitations of comparing data collected at different times by different people, the careful use of reference studies can help identify possible causes of decline and fruitful directions for future research.

If a dispersal oriented colonial population was suffering from a lack of conspecifics, I would expect to find reduced sociality as numbers decline, the structure of existing colonies change, and the benefits that follow critical population size and/or compositions are lost. Specifically, I predicted 1) VIM would exhibit fewer social interactions and cooperative behaviours than in the past when the population was larger. Because the use of space is affected by social behaviour, I predicted 2) that ranging would increase to accommodate elevated mate searching, and that males would exhibit the greatest increases. Home ranges of most social marmot species are small (0.13 – 13.8 ha) and overlap greatly with other colony members (Armitage and Blumstein 2002). I therefore predicted that in colonies where social ‘break down’ occurred, VIM would range more widely, presumably in search of conspecifics. How individuals allocate limited daylight hours to different behaviours will affect their fitness and can reflect trade-offs between competing demands such as vigilance, foraging, resting, and reproduction (Stephens and Krebs 1986). Therefore my third prediction was that (3) VIM time budgets would show a shift towards increasing vigilance and reduced foraging and resting time as the benefits of sociality were lost with reductions in group size or changes to group composition as population size decreased. I also expected these shifts would have consequences for energetic requirements and exposure to predators (Sutherland 1998). Solitary VIM should allocate more time to vigilance, to the use of refuges, and to predator avoidance. These predictions are summarized in Table 2.1.
Table 2.1: Predicted trends in contemporary VIM relative to historical reference data.

If a collapse or decay of sociality drives solitary animals to forage less, then I would expect to observe a positive relationship between group size and annual rate of body growth. Furthermore, because healthy body condition is likely required before hibernation is initiated by marmots (Barash 1989), I predicted that solitary animals would require more days of foraging to gain sufficient body mass for overwinter survival and, thus, would show later hibernation dates in the fall. These additional predictions are also addressed.

Methods

Study animal

The VIM is a large (adults >6 Kg) endangered rodent (global population <150 of which over 100 live in captivity) endemic to Vancouver Island. The species is distinct from the other 13 species of marmots in skull morphology and pelage (Nagorsen 1987), behaviour (Heard 1977), and vocalizations (Blumstein 1999). Animals are diurnal, consume a wide variety of grasses and forbs (Martell and Milko 1986) and use underground burrow systems during the approximately 5 month active season (May thru September) prior to hibernation (October thru April) during the winter. VIM are relatively long-lived (at least 12 years in captivity, 8 years in the wild) and are believed to be primarily monogamous. There is a single breeding season in May shortly after
emergence from hibernation. Young males (2+ years) may disperse to new colonies (Bryant 1999).

Study population

Ten, 12 and 13 of the approximately 30 total wild VIM were studied at the northern Mt. Washington Colony (4945'N 12517'E) in 2002, 2003 and 2004 respectively. Data were also collected from three more southern colonies (Fig. 2.1) on Vancouver Island: Green Mt. (4903’N 12420’E; N=2 animals in 2002), Mt. Moriarty (4900’N 12427’E; N=2 in 2004), and Heather Mt. (4900’N 12416’E; N=3 in 2003). All of these colonies have been continuously inhabited by marmots for at least 50 years (Nagorsen 1996). VIM inhabit steep forested slopes at elevations of 700-1300 meters surrounding isolated patches of rock talus and sub-alpine meadow. Habitat at Mt. Washington includes several ski runs (Demarchi et al. 1996). See Appendix 1 for illustrations of these habitats.

Figure 2.1: Location of Vancouver Island study sites.
Detailed research on the VIM began in 1973 when Heard (1977) studied their behaviour and ecology at two colonies at the Mt. Haley site (fig. 2.1) over three consecutive years. My research is part of an ongoing program of study of the biology of wild VIM (Martell and Milko 1986; Nagorsen 1987; Bryant 1998; Blumstein et al. 2001; Janz et al. 2000; Sinclair et al. 2004; Bryant and Page 2005; Casimir 2005).

From 1980 to 2002 the total abundance of wild VI marmots declined by approximately 87%, but with some temporal heterogeneity. Historical population counts (Fig. 2.2) are not confidently known, but the species range has collapsed by hundreds of kilometers (Nagorsen et al. 1996). It is estimated that overall numbers of individuals remained fairly stable until about 1985 at which time marmots occurred in moderate sized social groups (average colony size = 8.3; Heard 1977) in natural habitat and adjacent clear-cuts. From the late 1980s, however, numbers declined steeply and marmots disappeared completely from many sites, including all re-growing clear cuts. There does not appear to be a detectable geographic pattern to this decline. Due to unequal sampling effort and changes to sampling methods across the years, population estimates are not accurate enough to draw quantitative conclusions about rates of change throughout the decline. A recovery program was instituted in 1988, employing captive propagation with plans for future reintroductions which began officially in 2003.

Figure 2.2: Estimates of the total number of wild Vancouver Island marmots, 1980-2005. [Updated from Bryant (1998). The estimates are not accurate to infer density-specific rates of decline.]
Field methods

Data on ranging, sociality and activity budgets were first collected by Heard (1977) in 1973, 1974 and 1975 when VIM populations appeared to be stable (N=350 animals). To test for changes in the ecology of VIM that might indicate an Allee effect I used methods comparable to Heard’s to gather similar data on time budgets, social interactions and ranging activity during 2002, 2003 and 2004, a period late in this decline (N=23-31). Limited intermediate data from reports and communications (e.g., A. Bryant pers. comm.) are used to fill in some of data gaps within this 29 year interval between the two intensive studies.

My study was limited to wild marmots that were individually ear marked and implanted with radio transmitters for telemetric tracking. Bryant (1998) describes the transmitters, and capture and implant techniques. All marmots studied were of known sex and age. During 2002 to 2004, 21 individual marmots were followed in detail from emergence (May 1) to the onset of hibernation (mid-October). Because some individuals were studied in multiple years, I obtained a total of 38 animal-years across the three seasons. This sample included roughly 70% of the surviving wild population.

Home ranges

Home ranges were mapped using locations collected daily across the five-month active season. When a marmot was first located, the observer recorded its exact position using a hand-held Global Positioning System receiver (GPS). Data points were plotted using Home Range, Movement and X-tools extensions in ArcView 3.2 Geographical Information Systems Software (ESRI 1996; Hooge 1999) and the Home Ranger program (Hovey 1998).

During 2002 to 2004 I used a minimum of 35 distinct locations distributed evenly from May to October (mean=88, range 35-129) to estimate annual VIM ranges over the season (Seaman et al. 1999). A maximum of one location was gathered per day. In 2004, collection was intensified in order to estimate range size by month. When estimating home ranges for each month in 2004, I took a maximum of two measurements per animal per day > five hours apart (typically in the morning and afternoon), totaling >
34 measurements per animal per month. Measurements of location and altitude were considered accurate to within ± 6 m.

My sampling was designed to minimize the potential for temporal or other biases. The use of locations from an individual over a short time period can result in spatial autocorrelation, and thus misleading estimates of range size (Swihart and Slade 1995; McNay et al. 1994). Nevertheless, accuracy and precision of kernel home range estimates can improve as the time interval between locations is shortened, despite increasing autocorrelation among sightings (de Solla et al. 1999; Harris et al. 1990). The sampling approach chosen for this study attempted to balance these concerns.

**Sociality and time budgets**

To ensure equal coverage of animals and sample times, and to minimize observer and sampling biases related to the duration, onset and termination times of a sampling event, a randomized protocol was used. Individual marmots were located and observed according to schedules constructed 14 days in advance. Behavioural data were gathered using a “focal sampling” approach (Altman 1974), similar to Heard (1977), thus allowing direct comparison of data between 1973–1975 and 2002–2004. To ensure proper comparison with Heard (1977) I adopted his entire ethogram and definitions (See Appendix 2 for the list of behaviours). In focal sampling, instantaneous activity was scored for each animal at one minute intervals for 60 consecutive minutes. Recorded were the body position (sitting, lying, standing, moving, alert posture), head position (up or down), orientation (up, down, or across-slope), social interactions (e.g., nose touching, fighting, chasing, grooming, sniffing another), feeding, movement, and the use and maintenance of burrows (Heard 1977; Barash 1989). All behaviours were observed from a distance of 40-300 m from the animals with 10x binoculars and 60x spotting scopes. All animals were habituated to human presence, and were identified from their radio telemetry frequencies, ear tags and molt patterns.

Every month, each marmot was observed for >3 hours when the animal’s transmitter was active (typically 6 am – 6 pm; transmitters function on a 12-hour on-off cycle to prolong battery life). Small amounts of additional behaviour data were collected before and after transmitters were activated each day. The 38 focal individuals were
studied for a combined total of more than 1800 observation hours across the three year study. Each year one or two individuals were added to the population (i.e., were discovered and implanted), died or were removed to augment the captive stocks. As a result, some marmot individuals were not sampled across the entire study period or across all of the 5 ½ month active season.

Analysis

The Kolmogorov-Smirnov test was used to compare distributions and the Mann-Whitney U test to compare medians when data were not distributed normally. Data were pooled only if within-individual variance was larger than those between individuals and sample sizes were similar (Leger and Didrichsons 1994). Following previous studies of marmot/ground squirrel behaviour and ecology (Blumstein and Arnold 1998; Hoogland 1995; Salsbury and Armitage 1994; Barash 1989), observations of individuals from different years were treated as independent. Results are presented as x ± SE. Where historical data on VIM were not available, I refer to other studies of congeners for comparison (Blumstein et al. (2001) discuss the merits of this approach for VIM). There were no significant inter-annual differences between activity budgets and rates of behaviour for 2002, 2003 and 2004; therefore, data were pooled across years unless otherwise noted. Appendix 3 contrasts data collected in different years and for different sex and age classes.

Home ranges

Home ranges were plotted using the fixed non-parametric kernel (density probability) method with a grid resolution = 255. Fixed kernels reflect the intensity of use, do not assume a single center of activity or a particular shape (Worton 1995; Seaman and Powell 1996), and exhibit less error in surface fit than adaptive kernels (Seaman et al. 1999). The h values (smoothing factor) were calculated as outlined by Worton (1989) and account for the high number of multiple observations in identical locations within the data set (Silverman 1986; Tufto et al. 1996; Seaman, Griffith and Powell 1998). As a check, and to avoid overestimation, each kernel estimate was compared to a home range
estimate obtained using the minimum convex polygon technique (MCP; Burt 1943; Kenward 1987). The MCP method has been used extensively in past studies. It tends, however, to over-emphasize peripheral data, while including areas which are not actually visited by the animal (Worton 1987). In almost all cases, kernel estimates were smaller than MCPs.

The minimum linear distance between successive independent locations was used rather than range size to assess travel costs and to determine if patterns in movement differed between males and females. This was measured using the following formula:

\[ d = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2} \]

where, \( d \) is the shortest distance between two successive locations and \( x_1, x_2 \) and \( y_1, y_2 \) are the Northing and Easting bearings for each point in Universal Transverse Mercator (UTM). Changes in elevation during travel were not accounted for. Consequently, both home range size and travel distance reported here may be underestimated compared to reports of other marmot species (e.g., Salsbury and Armitage 1994) where the effects of topography have been taken into account.

**Sociality and time budgets**

To quantify activity budgets for feeding, resting (lying or sitting) and time spent in-burrow, I followed the methods of Martin and Bateson (1993). Other less frequent behaviours, such as social interactions, were expressed as occurrences per animal per observation hour. Individual marmots were treated as statistically independent. When necessary, I excluded data from over-represented hourly periods to ensure that each hour of the work day had equal weight in calculations of means for each individual. When reporting time budgets the contribution of each month to an individual mean value was similarly equalized to ensure results were not biased by unequal sampling across the active season. Because the degree of sociality in a marmot colony likely depends on the number of its members, and to ensure that interaction rates from the past and present came from similar group sizes, interaction rates from Heard’s (1977) two main southern study sites (mean colony size=8.3; monthly range 4-17, Mt. Haley, Green Mt.) were compared with my largest northern study colony (mean local population size=12.0; range 5-15, Mt. Washington; Fig. 2.1). Any colony size bias here should favour higher rates of
social behaviour at the more recently studied Mt. Washington site. Data that I collected from smaller southern colonies (Green, Moriarty, Heather; fig. 2.1) showed rates of social interaction similar to those recorded at Mt. Washington. Bias related to slight latitudinal differences between sites are not expected to effect my results.

Weight gain
During the study, observations of changes in ranging, behaviour, sociality and time budgets raised a question about whether these changes affected growth rates of afflicted individuals across the active season. Therefore, to examine the potential for energetic repercussions of Allee effects in VIM, I analyzed body mass data collected for VI marmots from 1975-2004. These data were collected by Heard (1977) in 1975, and by the VI marmot recovery team (e.g., Bryant 2004) between 1987 and 2004. Individual weights were plotted against time to explore how seasonal variation in marmot body mass varied between a stable period (reported in Heard 1977) and the more recent decline phase of 1987-2004. To estimate summer growth rates I fit a linear regression of body mass against the number of days since emergence from hibernation (Armitage et al. 1976).

Results
Historical (Heard 1977) and contemporary VIM data were compared for ranging, sociality, time budgets, and growth rates. Marked and statistically significant differences were observed between historical and contemporary populations. Home range sizes of 'modern' VIM were consistently larger than those recorded for the same species in the 1970’s. Similarly, 'modern' marmots show a loss in colony structure, sociality and the amount of time individuals allocate to foraging. Contemporary VIM devoted more of their day to being vigilant and appeared to acquire mass during the summer at a lower rate than did animals in larger, more stable VIM populations during the 1970s. Table 2.2 summarizes many of these differences in ecology, behaviour and physiology between
current and past VI marmots. Figure 2.3 shows the age structure of the modern and historical VIM study populations.
Table 2.2: Changes in social and other activities in VIM between the 1970s and 2000s. [Data are conveyed as mean ± SE; [Range]; (n)].

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ranging</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Home Range (ha)</td>
<td>2.0* [0.5-4.0] (8)</td>
<td>81.6 ± 8.8** [25-201]</td>
<td>(19♂, 10 ♀)</td>
</tr>
<tr>
<td><strong>Time Budgets</strong>*</td>
<td>Fig. 2.4</td>
<td>Fig. 2.4</td>
<td>NA</td>
</tr>
<tr>
<td>Monthly activity</td>
<td>Fig. 2.4</td>
<td>Bimodal</td>
<td>Unimodal</td>
</tr>
<tr>
<td>Daily activity²</td>
<td>Bimodal</td>
<td>Unimodal</td>
<td>NA</td>
</tr>
<tr>
<td>Total time allocated to feeding</td>
<td>25.0% ± 4.5</td>
<td>3.5% ± 0.4</td>
<td>U=25, n₁=5, n₂=5, p&lt;0.001</td>
</tr>
<tr>
<td>Total time allocated to resting</td>
<td>34.3% ± 4.4</td>
<td>23.4% ± 1.6</td>
<td>U=23, n₁=5, n₂=5, p=0.03</td>
</tr>
<tr>
<td>Total time allocated to burrow use</td>
<td>35.0% ± 7.6</td>
<td>64.0% ± 4.6</td>
<td>U=23, n₁=5, n₂=5, p=0.03</td>
</tr>
<tr>
<td><strong>Sociality</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Greeting rate³</td>
<td>0.55 ± 0.06</td>
<td>0.052 ± 0.02</td>
<td>U=25, n₁=5, n₂=5, p&lt;0.001</td>
</tr>
<tr>
<td>Interaction rate⁴</td>
<td>1.12 ± 0.27 (28)</td>
<td>0.182 ± 0.04 (29)</td>
<td>U=25, n₁=5, n₂=5, p&lt;0.001</td>
</tr>
<tr>
<td>Affiliative : Agonistic interactions</td>
<td>1.68</td>
<td>0.54</td>
<td>U=18, n₁=5, n₂=4, p&lt;0.05</td>
</tr>
<tr>
<td>Alarm call rate</td>
<td>0.34/hr</td>
<td>0.07/hr</td>
<td>x²=157, df=1, p&lt;0.01</td>
</tr>
<tr>
<td><strong>Other</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult weight gain</td>
<td>24.5 ±2.15 g/day (r²=0.91, N=31, F=135.0, p&lt;0.001)</td>
<td>9.5 ±2.5 g/day (r²=0.19, N=63, F=14.33, p&lt;0.001)</td>
<td>Unpaired t-test df=92, p&lt;0.001</td>
</tr>
<tr>
<td>Hibernation date¹</td>
<td>Sep. 18 [Sep. 16-21] (28)</td>
<td>Oct. 7 [Oct. 3-19] (26)</td>
<td>U=710, n₁=28, n₂=26, p&lt;0.001</td>
</tr>
</tbody>
</table>

*Colority range size, n=8 colonies. Heard also reports the home range of four individuals at one colony site to be about 3 ha. In another colony the territory sizes of two males were 4.5 and 2.2 ha.

**Adjusted by gender.

***Tests and standard errors calculated using a single mean for each month which combines all individuals across all years. Heard (1977) did not report standard errors or mean activity budgets for individuals. These three tests must therefore be interpreted with caution. Figure 2.4 show these monthly data. Where slight discrepancies exist between means for 'modern' marmots described in table 2.2 and reported elsewhere in this document, data reported in the text should be treated as most reliable and may be assumed to be based on means of individual marmots rather than means from all marmots combined by month.

¹Calculated from Heard (1977: 35-36). n=animals.

²See Figure 2.5.

³Calculated from monthly means. Rates are incidence per animal per hour of observation.

⁴All marmots, all social acts combined. Rates are incidence per animal per hour of observation.

⁵1994-2004.
Ranging

I expected ranges of females, which are typically philopatric, not to change as the density of local populations diminished and as colonies became more isolated, but for males to have larger ranges and move more in search of unrelated mates. As anticipated, home ranges of males from 2002-2004 were 30-45 times larger than values for VIM home ranges recorded in 1973-1975 (Table 2.2). Current home ranges of male VIM were more than ten times larger than that observed in any previous study of a social marmot. However, female territories in 2002-2004 (including three females that weaned young) were 30 times larger on average than those recorded for this species in 1973-1975.

Despite dramatic differences in historic and current home ranges of both male and female marmots, the 90% kernel range size for ‘modern’ females (66 ha; Table 2.3) was about one third smaller than that of ‘modern’ males (98 ha). Nevertheless, current home ranges of females are an order of magnitude higher than those observed for males in 1973-75 and higher than those observed for males of any other species of social marmot. Minimum distances moved between independent locations also differed by sex, with
males moving almost twice as far (Table 2.3). Except for two adult females whose home ranges were distinct, all 99% annual kernel estimates for Mt. Washington overlapped, as did home ranges from the three other colonies (Green Mt., Heather Mt., Mt. Moriarty). Appendix 4 summarizes the 99%, 90%, 75% and 50% kernal density estimates for each age and sex class.

Table 2.3: A comparison of non-parametric kernel range estimates and minimum recorded distances between successive independent locations for males and females during 2002-2004 (range shown in square brackets).

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Male (n=19)</th>
<th>Female (n=10)</th>
<th>Statistical Significance*</th>
</tr>
</thead>
<tbody>
<tr>
<td>90% Estimate (ha)¹</td>
<td>97.7 ± 11.7 [27-201]</td>
<td>65.6 ± 11.1 [25-110]</td>
<td>U=135, n₁=10, n₂=19, p=0.03</td>
</tr>
<tr>
<td>Movements (m)²</td>
<td>264.0 ± 23.2</td>
<td>145.0 ± 19.5</td>
<td>U= 171, n₁=19, n₂=10, p&lt;0.001</td>
</tr>
</tbody>
</table>

¹ Mean value for Swihart and Slade’s autocorrelation index is low (0.6). Only one male marmot showed significant levels of serial autocorrelation (index >1.5).
² Minimum distances between successive independent locations.

* Mann-Whitney U test.

Time budgets

VIM now enter hibernation in the first week of October, approximately three weeks later than they did 30 years ago (p>0.001; Table 2.2). Immergence dates from the 1980s (September 26 - October 3, n>70) (Bryant and Page 2005; Bryant and McAdie 2003) are intermediate, and consistent with this trend.

VIM fed less in 2002-2004 than they did in 1973-1975 (Table 2.2, Fig. 2.4). The contemporary population allocates less time to above-ground activity during the beginning (May—June) and end (September—October) of each active season (Fig. 2.4 middle). The proportion of total time each month that VIM spend resting above ground has also decreased (Fig. 2.4 bottom). Peak values for all three activities in 2002-2004 generally correspond to periods of low activity during 1973-1975.
Figure 2.4: The percentages of total observation time (1724 hours) that 'modern' VIM devoted to feeding, below ground activity, and resting (sitting and/or lying) above ground during May through September with historical comparison (626 hours). Bars are SE calculated from hourly means for all marmots in a given month.
In addition to monthly shifts in time allocation, contemporary VIM also differed from historical colonies in their daily time budget. In general, contemporary marmots were less active in the morning and evening periods, and were more active at midday than in the 1970s. Figure 2.5 also illustrates how VIM deviated from the pattern of bimodal activity reported for Hoary marmots (*M. caligata*) from the Washington Cascades (Barash 1974b; 1989). Bimodal activity patterns are reported for virtually all montane marmot species (Barash 1989).

![Figure 2.5: Diurnal in burrow activity of VIM during July. (*M. caligata* data adapted from Barash (1989). Early VIM data adapted from Heard (1977).)](image)

Time spent in the burrow accounted for 63% ± 2.5 of all observations, and remained relatively constant until late evening. Only 6.3% ± 0.3 of above ground activity during focal observations was spent moving. Far more time above ground was devoted to vigilance ("head-up"=66% ± 2.2) than non-vigilance ("head-down"=34% ± 1.8). Time allocated to feeding as a fraction of all activity equaled 3.5% ± 0.4, and as a fraction of above ground activity was 7.5% ± 0.7; the percentage of time spent vigilant during foraging bouts was 60.1 ± 2.14. In general, marmots now devote less than one seventh of the time to acquiring food than did populations during the 1970s (Table 2.2).
Sociality

Mean greeting rates were one tenth and social interaction rates one twentieth as frequent as during 1973-1975 (Table 2.2; p<0.001). There was also a shift in the ratio of greetings to agonistic behaviours over the 30 years. Animals made fewer greetings and were involved in relatively more fighting and chasing in my data than in Heard’s data (Table 2.2; mean ratio of greetings/(fights + chases) = 1.68 in 1973-75 vs. 0.54 in 2002-04; p<0.05). Timing of maximum social activity shifted from a single peak in June (2.2 interactions per animal hour; Heard 1977) to both May (0.33/hr) and August/September (0.39/hr). Social marmot species generally spend ≈ 90% of their time close to other colony members (K. B. Armitage, 2005 personal communication). In contrast, contemporary VIM lead relatively solitary lives. The fraction of above ground time spent near (<100m; a distance within which marmots are likely to detect alarm calls and maintain visual contact) any conspecific during 2002-2004 was 38.5%. When data from nearest neighbours that are below ground were excluded, this value falls to 14.5% (mean distance between conspecifics=25.5m, SD=31.3m, n=7665 measurements). Wild marmots within 10m of a paired conspecific engage in social interactions at levels similar to animals currently in captivity (Casimir 2005), suggesting that inter-specific distance may partly account for low sociality.

Ten alarm calls were recorded in more than 1200 hours of focal sampling in 2002-2004 (an additional 68 calls were recorded outside focal samples; call rate=0.07/hr) whereas Heard recorded 212 alarm calls in 626 hours of focal observation (call rate=0.34/hr) (Table 2.2). Alarm calling (“whistle behaviour”) is also now comparatively rare at other colonies.

Mean inter-hibernacula distances (Green Mt., Mt. Washington, Mt. Moriarty combined) were 1016.5m (n=20, range=390-1440), almost ten times larger than they were historically at Mt. Haley (≈ 100m; locations of hibernacula at Haley provided by A. Bryant).

Weight gain

Adult marmots gained mass each summer after emerging from hibernation. However, the rates of growth between historical and modern VIM were significantly
different. Marmots are currently growing more slowly throughout the season than in the past (Table 2.2). Historic (1974) mass accumulation for adult females was 26.3 ± 3.07 g/day ($r^2=0.92$, $N=14$, $F=62.0$, $p<0.001$), for adult males was 21.0 ± 3.50 g/day ($r^2=0.88$, $N=15$, $F=40.1$, $p<0.001$), and for adults combined was 24.5 ± 2.15 g/day ($r^2=0.91$, $N=31$, $F=135.0$, $p<0.001$). Modern growth rate for adults (1994-2004, sexes combined) was 9.5 ± 2.5 g/day ($r^2=0.19$, $N=63$, $F=14.33$, $p<0.001$).

Discussion

Data comparability of recent and reference studies

There are unavoidable difficulties with comparing data collected by different people at different times and places. For example, while Heard’s study relied mainly on marking methods to identify and locate focal animals, my study benefited from radio transmitters. Also, the location and composition of historical colonies were slightly different; Heard mainly depended upon two study sites, whereas I used data from four sites. Historical VIM research also had a lower sampling effort.

Without the use of radio telemetry, historical movements were likely underestimated. However, Heard’s reported home ranges are not for individuals but for entire colonies and his measurements are consistent with reports from other marmot species (Blumstein et al. 2001 and references therein). To address potential bias the ranges that I reported are purposely conservative and cross checked with home ranges generated using the historical MCP method. That the present home range sizes are larger than reports from historical VIM and other marmot species, some of which used radio telemetry (e.g., Salsbury and Armitage 1994; Karels and Hik 2005 progress report), suggest that observed differences in space use are genuine.

Because historical VIM may have been more difficult to locate without telemetry, individuals that left Heard’s study sites may sometimes have been misidentified as being underground. If so, Heard’s activity budgets would have over emphasized time in-burrow, and under estimated the time spent above ground feeding, resting or engaging in social activity. This potential bias does not detract from the results reported in my study.
because I observed a reduction in social, resting and feeding activities. If Heard’s marking techniques biased his results then the behavioural differences I observed between historical and contemporary populations may even be stronger than they appear.

Although Heard found no differences in the activity budgets between males and females, or old and young, it is possible that changes in colony composition between past and present are partly responsible for reported differences in behaviour. Figure 2.3 depicts the age and sex composition of the past and present study populations. The age structure is approximately the same (inset graph Figure 2.3). However due to the large number of unidentified adults in Heard’s population, it remains unclear whether my study sites were comparatively male biased. Assuming that Heard’s ratio of male to female adults is representative, and that the proportion of unidentified adult males and females follows this pattern, the composition of historical and contemporary study populations would be similar. However, the data do not allow for conclusions about demographic dynamics over the past decades. The proportion of males to females in my study population was male biased and it is possible that historical colonies had more equal sex ratios (but see Blumstein and Arnold 1998 for examples of naturally occurring male biases in other social marmots).

I now examine the evidence in support of Allee-type density dependence and identify how population decline might bring about these unstable dynamics by emphasizing behavioural mechanisms that may drive small populations even smaller.

**Ranging**

The home range estimates from 2002-2004 are approximately 20 times larger than for populations of social marmots reported in the literature (Blumstein et al. 2001 and references therein), and over 40 times the average two ha size of entire colonies described by Heard (range 0.5-4.0 ha, n=8 colonies). Both range size and movement patterns remained large throughout the active season. Individual marmots made exploratory travels in excess of two km, and these 85 ha range sizes expose animals to a greater variety of risks. Large home ranges occur in part because some individuals make large movements. For example, a 3-year old male moved 2.4 km during the last three days of May 2004 and a further three km a week later. On eleven occasions in 2002-2004,
project field staff inadvertently intercepted individuals in the process of moving large distances (~1 km). Marmots making these long moves were at higher risk because they were in unfamiliar terrain. In the absence of burrows these animals hid under logs, in snow depressions around tree bases, within thin cover (40 cm high Vaccinium spp.), climbed trees, or took flight, sometimes moving greater than 600m without pause. Large movements may be particularly risky in the spring when the ground is covered in snow (Barash 1989). At current range sizes one adult VIM will use an area equivalent to sixteen entire Olympic marmot colonies (Barash 1973; Edelman 2003), and 25 Golden marmot colonies (Blumstein and Arnold 1998) during the course of one summer. In contrast to VIM, individual ranges of yellow-bellied marmots do not increase with reduced population density (K. Armitage personal communication, 2005); however, this may be because fluctuations in populations of yellow-bellied marmots which determine the number, size, and distance between colonies rarely reach levels comparable to current VIM. Reduction in the size and number of colonies, changes to colony composition, and an increase in the distance between subpopulations may have resulted in larger territories, raising an individual’s risk of predation and it’s energetic needs. Large increases in home range size at low density may therefore serve as one indicator of a component Allee effect.

**Sociality and time allocation**

Distortions of sex ratio and age composition in a population at low numbers reduce mate availability and the effective population size. Also, as the number of possible pairs is reduced, mating with close relatives may increase (Caughley 1994) despite changes in behaviour designed to avoid inbreeding. Time and energy may therefore be diverted from social or maintenance activities to either defending or searching for a mate while actively avoiding inbreeding. Additionally, increased mortality rates may have destroyed the family units that form the cooperative structure of this social species. During the course of this study I observed very few stable cooperative social groups (where individuals spent time in the proximity of one or more conspecifics), even though some reproduction was observed. Although most individuals over-wintered with another of the opposite sex, I found almost no cooperative relationships (defined as individuals
with similar overlapping home ranges that spent a significant proportion of their time in the presence of the other) during the active season. Almost every animal remained ‘single’ despite opportunities to join another. When this data was constrained to periods when paired marmots were within 10m of the other, interaction rates were higher and were similar to marmots housed as pairs in captivity (Casimir 2005). During hibernation, the distance between modern overwintering groups located on the same mountain may be larger than for historic populations. Mean inter-hibernacula distances (Green Mt., Mt. Washington, Mt. Moriarty combined) are now 1016m (n=20, range=390-1440), almost ten times larger than were historically at Mt. Haley (~100m; Bryant personal communication 2004) and similarly larger than reported for other social marmots (e.g., Golden marmot: interhibernacula distance=146m, n=18 social groups, Blumstein and Arnold 1998; Hoary marmot interhibernacula distance=259m, Holmes 1984). Whether these distances are determined by the availability of high quality hibernacula, the distribution of resident females (Holmes 1984), or the current social structure of modern colonies is not known.

Predators are considered to be one cause of the decline in current VIM numbers (Bryant and Page 2005). Predation rates may become elevated when, as colony sizes decrease, marmots call less and the effectiveness of their social warning system diminishes. Calling rates have fallen since the 1970s, and agonistic behaviours have become more common relative to greeting. Reduced levels of cooperative behaviour, elevated aggression and shifts towards larger space use may be a consequence of low population size and/or consequent changes to demographic composition and genetic relatedness.

In general, VIM fed less in 2002-2004 (3.5% of all activity) than they did in 1973-1975 (25% of all activity), and also less than other marmot species. Armitage et al. (1996), for example, reported foraging as a major activity for Marmota flaviventris, which occupied between 12 and 23% of each day. Marmota caudata spends upwards of 30% of their time feeding (Blumstein 1998); and foraging constituted 35% of all above ground activity in Marmota caligata (Karels et al. 2004). In addition to this reduced foraging, VIM spend more foraging time scanning for predators (60%) than many other species: Marmota flaviventris (10.2%; Carey and Moore 1986), Marmota monax (20.2%;

Lone marmots typically devote more time to vigilant behaviour than more social individuals (Svendsen 1974; Armitage 1962). Being vigilant reduces time available for foraging and/or reduces foraging efficiency (Carey and Moore 1986; Blumstein et al. 2004) and might be expected to reduce mass gain during the active season. Low mass gain, in turn, can delay hibernation (Shubin et al. 1978) and lead to over-winter mortality (Formozov 1966; Barash 1989). Barash (1973) found similar costs of solitary life in *Marmota olympus*; lone marmots doubled the time they devoted to vigilance and scanning compared to colonial individuals. Schwartz and Armitage (1997) found that group-living raised lifetime reproductive fitness in yellow-bellied marmots. Less social marmots may spend more time being alert, indicating that predator avoidance is more costly in solitary animals. Compared to my value (60% foraging in the looking up position), Blumstein et al. (2001) reported lower, but still high levels of vigilance for VIM (40%) in 1998 when there were about 100 wild marmots, which are intermediate between this study and those from other stable populations of marmots listed above (10-32%).

My data suggest that VIM avoid predation by spending more time below ground and by being more vigilant when above-ground (Kotler et al. 2004). However, the loss of bimodal activity (elevated activity in the early morning and a lull at midday; Fig. 2.5) is puzzling. It may reflect avoidance of mammalian predators which tend to hunt in the morning or evening (Beier et al. 1995). Neuhaus et al. (1992) describe how alpine marmots alter the timing of their daily above ground activities to avoid exposure to perceived threats posed by human activity.

**Growth rate**

VIM are now gaining mass 40% as fast as they did in 1974-1975. This disparity however must be treated with caution due to Heard’s limited sampling, although his reported growth rates are consistent with accounts of other marmots (Armitage et al. 1976). Some, but non-significant, reduction in weight gain were found between data
pooled into two categories: 1987-1993 and 1994-2004. Marmots that live in harsh environments appear incapable of increasing growth rate, and likely maximize weight gain throughout the season (Armitage et al. 1976). Reproductive females, for example, cannot accelerate their weight gain to compensate for giving birth, and therefore accumulate less fat than barren females during the same year (Armitage and Blumstein 2001; Salsbury and Armitage 2003; Karels 2005, personal communication).

Poor weight gain can cause females to forgo reproduction, and cause both males and females to delay hibernation (Armitage et al. 1976). Slow growth also prolongs vulnerability to predators in late summer when marmots are metabolically less active (Salsbury and Armitage 2003; Kilgore and Armitage 1978; Edwards 1997). The possibility that marmots now hibernate later might exacerbate late season predation, which is a major known mortality source in VIM (Bryant and Janz 2002; Bryant 2004). Marmots appear to enter hibernation about three weeks later than they did in 1973-1975. There is some uncertainty as to the magnitude of this effect because, although dates of entry into hibernation were measured accurately (± 1 day), it is less clear how accurately Heard estimated immergence dates and this result should be treated with caution.

Summer temperature (mean temperature in degrees Celsius July through September: 1973=13.0, 1974=15.5 (Heard 1977), 2002=15.8, 2003=13.1, 2004=14.7) did not differ between the two study periods, and do not appear to explain observed changes in the ecology of VIM.

Between-litter intervals are significantly shorter for females in captivity (1.36 years) than for females in the wild (1.88 years) and captive litters are skewed towards males where wild litters are not (Bryant 2005). These differences may suggest that female wild VIM are in comparatively poorer body condition (Trivers and Willard 1973), or simply that captive females are ‘over-fed’. Mean survival of wild pups also dropped between the intervals 1987-1993 (survival=0.65) and 1994-2001 (survival=0.25) (p<0.001, Karels and Bryant 2004, unpublished data). A positive relationship between population size and juvenile survival suggest that young of the year are more reliant on the benefits of group life, because they are naïve to predators and have less time to accumulate the fat reserves necessary to survive hibernation (Karels et al. 2004b).
Overwinter survival

Bryant and Page (2005) attribute 10% of all known wild VIM deaths to overwinter mortality, and report the probability of these events to be low ($P_{\text{death}} = 0.016$). VIM are efficient hibernators (Daily Mass Loss=0.95g/day in captivity) (Bryant and McAdie 2003) and wild solitary marmots have hibernated successfully. However, during the winter of 2004/2005, which had low snow accumulation (~10%), many marmot colonies experienced high mortality; Mt. Washington, which has high recent annual survival (84% from spring 2002 thru spring 2004), lost an estimated 40% of the colony (n=10) during the 2004/2005 winter/early spring.

Previous studies (e.g., Bryant 1998; Blumstein et al. 2001) claimed that VIM are highly social, live in family groups and thermoregulate socially, all of which is consistent with observations of closely related species (Barash 1973, 1974a, 1989). In hoary marmots, for example, the number of subadults (male and female) in a social group affects pup survival; the odds of survival increased 1.4-fold for every sub-adult retained in the group (Karels and Hik 2005). Recent translocation experiments have resulted in high overwinter mortality (67%; Bryant et al. 2002) and during years of low snow hibernation success has dropped. Solitary VIM will sometime join others by digging into hibernacula whose entrances have already been plugged by over-wintering marmots, presumably to avoid solitary hibernation. The 38% decrease in juvenile survival between the periods 1987-1993 and 1994-2001 could be explained by a shortage of suitable conspecifics with which to hibernate (Allaine et al. 2000; Arnold 1993).

Causes of VIM decline

Although Allee dynamics represent a significant challenge for short term recovery, they are not among the putative agents of initial decline. Other factors must have contributed to VIM declines, and may pose future challenges for recovery. Climate change may account for historical range contraction through its effects on habitat availability (Nagorsen 1987; Hebda 1996; Hebda et al. 2004) and fire (Gavin et al. 2003). However, habitat change alone probably does not adequately explain the recent precipitous decline. Space and food are currently not limiting, as most suitable meadows are now vacant. Changes in mass patterns, territory sizes, and time allocations are
unlikely due to limitations in quantity or quality of available food. Vegetation surveys in historically occupied habitats indicate that these meadows are still rich in species and have many abundant food plants for VIM. Though some sites have experienced moderate tree encroachment (Laroque 2001), descriptions and photographs of plant communities at both Mt. Washington and Haley Mt. have changed little from the early 1970’s (Heard 1977), through the 1980’s (Milko 1984; Martell and Milko 1986), 1990’s (Demarchi 1996), and early 2000’s (Werner, personal observations and unpublished data). Moreover, I could discern no difference in the quality of habitat, as estimated by quantity of preferred foods, between extinct and extant colony sites (Werner and Brashares 2005, unpublished data).

Although predation is an important mortality source (Bryant and Janz 2002), this may change in the future. An index of predator density and of total population on Vancouver Island has dropped substantially (Don Doyle 2005, data from BC MWLAP Region 1). Also, over four years of field study (cumulative 20 months of observation) I observed far fewer combined eagle attacks/over-flights (<0.05 flights/hr, no recorded attacks) than Milko (1984) reported for the month of May (0.42/hr). Therefore, predation may not be exerting as much pressure on the population as in the past.

Evidence from the past 20 years suggests that VIM may have made maladaptive habitat choices—another phenomenon potentially driven by numerical rarity (Kokko and Sutherland 2001). Artificial clearings generated by logging can serve as ecological traps for dispersing marmots. In the 1980s much of the existing wild population settled in clear cuts, where survival was poor (Janz et al. 2000) and the steep decline in numbers began. Since then efforts have been made to relocate marmots which settle in clear cuts.

Methods for gauging habitat choice using density isodars (Morris 2002) have opened up new opportunities for identifying potential Allee effects by observing where population density does not match habitat quality. Unusual habitat choice has recently been noted in VIM. Many animals on Green Mt., Mt. Moriarty and Mt. Washington now spend large portions of the active season in forested habitats (~50% observation time). There are no previous reports of substantial forest habitat use by VIM, and this suggests that habitat selection may become more variable at low density. This is in contrast to Borgo (2003) who found that less dense populations of alpine marmots (Marmota
*marmota* showed more restrictive habitat choice consistent with Ideal Free Distribution Theory (Fretwell and Lucas 1970). In some cases, such as with the Bearded vulture (*Gypaetus baratus*) individuals living in unsaturated environments exhibit strong selection for high quality habitat, and colonization patterns of reintroduced stock are used as a deliberate tool for identifying the most important habitat (Hirzel et al. 2004). Future research could focus on why habitat use in VIM becomes more variable at low population size.

**Possibility of Allee effects**

Knowing what factors affect the fitness of individuals in diminished populations is of critical importance to conservation. Theoretical models of Allee effects hypothesize such potential adverse impacts (Dennis 1989; Schreiber 2003; Henle et al. 2004). Despite this expectation, few empirical studies actually support Allee effects and fewer still have demonstrated the mechanisms that were involved. Figure 2.6 illustrates a subset of the potential positive feedback mechanisms that may be caused by and further contribute to population decline in the VIM.
Figure 2.5: A limited hypothetical example of positive feedback in a declining population of VIM.
Patterns of non-linear accelerating decline due to increasing proportional mortality, coupled with what appears to be slow recovery, are anecdotal signs of an Allee dynamic. However, crucial parameters for testing an Allee hypothesis should extend beyond population growth. Inverse density dependence can be driven by other, unrelated processes such as predation (Sinclair et al. 1998) and components of individual fitness may change without causing critical extinction thresholds. I suggest that reduced body mass growth rates concomitant with reduced population size are consistent with an Allee effect. Changes in sociality, movement, and time allocation suggest mechanisms which contribute to energetic expenditures, predation risks and population trajectories. Unlike Gascoigne and Lipcius (2004), however, I do not attribute negative density dependence via predation to an Allee effect without supplemental evidence that such declines are related in some way to changes in the behaviour or vulnerability of the prey species. Accelerated declines in prey species can and do occur in small populations without recourse to an Allee explanation. I also do not advocate that the large body of theory on positive density dependence and stability in ecological interactions be incorporated wholesale into discussions of Allee-type dynamics. Rather, Allee effects serve as a framework for exploring the antecedent conditions for, benefits of, and evolution in sociality. Allee-type dynamics may help us predict threshold low-densities which mark significant losses to group living, and reductions in measures of individual fitness, per capita growth and population persistence that may accompany social breakdown.

To illustrate the point that Allee effects are not themselves driven by predation, I propose a simplified conceptual model for considering how low density or population size can affect components of individual fitness. I use predation as an example (Fig. 2.7). This model is a useful reference for disentangling mechanisms that drive Allee effects from other exogenous factors that may also suppress population growth. For any individual, the probability of dying \( m \) due to some agent of mortality (e.g. a predator or a bad winter) can be expressed as the probability of that dangerous event occurring (e.g., an encounter with a predator) \( e \) multiplied by an individual's vulnerability to that event \( V \); such that \( m = e \times V \). This description is similar to how one might express risk (Slovic 1987). A measurable Allee effect (which might be viewed as the cumulative
expression of all possible $m$, but scaled to a population) is brought about by a negative relationship between $V$ and population density. In healthy social populations, $V$ is buffered because most individuals profit from group life. For example, as the population of wild VIM declined and the benefits from social facilitation decreased, individual marmots developed higher vulnerabilities to predator encounters, poor winters and the like.

Figure 2.7: A simplified conceptual model of an Allee effect using an individual’s risk of mortality as an example. [Allee effects are driven by increases in $V$ that happen when members of a small population no longer receive the same benefits from conspecifics, are forced to incur costs as solitary individuals, or take on greater risks while searching for and associating with appropriate social partners. This relationship can be modified to describe reduction in other components of fitness, such as fecundity. In this case probability of reproductive failure for a given time period ($m$) is the theoretical
probability of mating with a conspecific \((e)\), multiplied by \(V\) (where \(V\) represents the vulnerability to failure related to whether it can find that hypothetical mate, and whether that mate is genetically compatible. At low density, \(V\) may increase when reproduction is socially facilitated). According to this model, the mechanisms that cause Allee effects must contribute to an individual’s vulnerability. Cases where the relationship between components of fitness and number of conspecifics is strongly positive should cause positive feedback between per capita rate of growth and population size over some, or several, ranges of \(N\) (growth may remain positive at low \(N\) or, in extreme cases become negative).

We observe from this relationship that changes in the function or numerical response of predators can increase \(e\) and, in and of itself, cause local extinctions without reference to changes in \(V\). A mechanism that contributes to an Allee effect is therefore something that increases values of \(V\). \(M = e^*V\) is a simple description of a complicated phenomenon and it could be further modified to account for a greater proportion of the complexity observed in population declines. For example, in some cases lone individuals may themselves contribute to elevated \(e\) by exposing themselves more often to potential sources of danger at low density. Modeling Allee dynamics in this way would be difficult, and require a series of nested \(V\) for each age and sex class, with multiple vulnerability—density relationships to describe the various component mechanisms that can affect an individual, each at potentially different population levels. These drawbacks, to my knowledge, do not change our observation that the causes of Allee effects are more internal and less the consequence of external biotic or environmental forces. Under some circumstances members of a small population may have high \(V\) values and yet continue to persist because the agents of mortality \((e)\) have been removed. Higher survival rates at Mt. Washington may be an example of this case, wherein a high level of human activity throughout each summer shelter marmots from predators.

This illustrates the fact that changes in components of individual fitness do not inevitably lead to impacts on net population growth such as inverse density dependence. The net effect of a particular population size on an individual’s total fitness must depend upon the competing benefits and drawbacks of conspecifics. This has led some authors (Stephens et al. 1999) to distinguish between ‘component’ vs. ‘demographic’ Allee
effects. A component Allee effect is manifest by a component of fitness, while it’s demographic analogue is manifest at the level of total fitness. Whether a component effect will translate to an observable change in a population’s proportional rate of growth will therefore depend upon the strength of density dependent processes (e.g., competition for resources). The terms ‘strong’ and ‘weak’ Allee effects have therefore been used to distinguish cases where per capita growth is positively related to population size (the former) from those where it is not, and the terms “critical” and ‘non-critical’ Allee effects to further distinguish cases where per capita growth becomes negative (the former; indicating critical extinction thresholds) from situations where it does not (Taylor and Hastings 2005). In the case of VIM, determining the strength of Allee effects and their specific implications for future recovery will only be possible through thoughtful experimental reintroductions in conjunction with the use of population models.

Testing the key predictions that are needed to authenticate and tease apart Allee effects is difficult because of the nature of positive feedback. Just as these effects are both a consequence and a potential cause of low density, so the various components may act both as mechanism and byproducts of one another. Mate limitation, for example, can reduce population growth, while triggering search behaviours that further contribute to low survival or reproduction. The mechanisms that cause negative density dependence may be cryptic and hard to identify, and can relate to increased vulnerabilities. Situations where changes to $V$ are not balanced among age and sex classes, may cause demographic skew and reduce the effective population size, despite these processes commonly being attributed to stochasticity.

**Conclusion**

When compared to historical baseline data collected when the VIM population was relatively large, I predicted that marmots at currently low densities would exhibit:

1) fewer social interactions and fewer incidences of cooperative behaviours;

2) larger home range sizes consistent with elevated mate searching;
3) less foraging activity, more time devoted to the use of below ground cover, and more time in scanning/vigilant postures when above ground.

The results from my study confirm these predictions, thereby strengthening the possibility that individuals now suffer from a loss of suitable conspecifics, and that individuals may experience lower total fitness as a consequence. The observation that marmots may now gain weight more slowly and delay the timing of hibernation further strengthens an Allee hypothesis.

To further test this hypothesis, future research should examine the expectation that per capita growth will increase as the VIM population recovers, and that current trends in the behaviour and movement of marmots will revert towards similar conditions described by Heard (1977). Just as I used historical data to test for predicted mechanisms that reduce the fitness of individuals (and may cause inverse density dependence), so too may future research use this study as a reference point to assess the survival benefits of group life and the critical population sizes that might have to be achieved before these benefits are realized.

This study points to the malady of presuming that a species basic ecology will remain static at low abundance and highlights fruitful methods for enriching our limited understanding of population decline. Previous field studies have diagnosed Allee effects largely by qualitative patterns of population growth and have not identified the mechanisms that are required to distinguish Allee dynamics from other causes population decline. Changes to home range, social behaviour, and time budgets may provide a more convincing demonstration of component Allee effects. Several social factors, other than mate encounters, may contribute to population decline and impede subsequent rates of recovery. Social cohesion, time allocation and space use can be tractable and measurable indicators of potential Allee dynamics. They may eventually prove useful when estimating target population sizes for species at risk. Further, these effects should be considered when structuring successful release groups for future reintroductions (Grevstad 1999) of captive-reared marmots (Chapter 3).
Chapter 3 An assessment of Captive-rearing and Reintroduction Strategies

Introduction

Reintroduction techniques are sometimes necessary for mammalian conservation. Some approaches, however, tend to produce better results than others. For example, reintroductions of captive-bred animals are generally less successful than translocating wild-born individuals (Ginsberg 1994; Fischer and Lindenmayer 2000). Soft releases often work better than hard releases (Bright and Morris 1994), and pre-release training usually raises initial survival (Biggins et al. 1999). Releasing a minimum number frequently improves the status of reintroductions from outright failure to conditional success (Wolf et al. 1996, 1998; Veltman et al. 1996; Green 1997). The use of intact historical habitat can improve site fidelity for released animals (Griffith et al. 1989). When attempted reintroductions do not succeed, failure is often attributed to insufficient time necessary for individuals to adapt to novel environments and acquire social, hunting, foraging and/or anti-predator skills (Price 1989; Gipps 1991). A perennial question, therefore, is what minimal pre-release and post-release measures are necessary to achieve persistence and reproduction in a reintroduced population (Mathews et al. 2005).

The critically endangered Vancouver Island Marmot illustrates several tradeoffs that recovery teams face when they endeavor to resuscitate a species from near extinction. There are about 30 VIM living in the wild; a forecasted supply of approximately 12 captive-bred marmots will be available for release every year. During the initial years (2003-2006) most candidates for release are males (2:1 sex ratio in captive-born pups) and between one and two years of age.

Preliminary reintroductions were made in 2003-2005. The major objective of this study was to assess whether captive conditions exert an influence on the ecology of released marmots and to develop best practices for discharging animals into natural meadows. These experiments are expected to clarify whether further remedial measures are needed to maximize survival during the first year after release. Detailed contemporaneous studies of wild VIM provide a baseline against which the behaviour
and ecology of captive-bred individuals are interpreted. Though we have seen (Chapter 2) that wild VIM have changed their social activity, movement, time budgets and vigilant behaviours from when historical populations were larger, released stocks must survive as well as their wild counterparts. In the short term, therefore, an important measure of success for reintroduced animals may be that they behave and perform, under similar conditions, in similar fashion to wild born marmots. If the survival of artificially-reared VIM be lower than expected, comparison with wild VIM would provide the first testable hypotheses concerning why this may be so and what procedures might improve the success of future attempts to release captive VIM.

The objective of this study was to determine if captive-rearing and release methods influence the survival, movement and behaviour of VIM liberated into suitable vacant habitat. Studying both wild and reintroduced captive groups in similar natural habitat circumvents the difficulties of comparing data drawn from marmots in wild and artificial conditions. I was particularly interested to know whether captive-bred marmots would lack effective survival skills (Price 1989) or exhibit abnormal behaviours (Gipps 1991).

Based on the results from Chapter 2, my hypothesis is that several characteristics which could contribute to survival—such as home ranges and movement, sociality, time allocation and flight distances—would be different in captive-reared compared with wild marmots. Specifically, because current release groups were small (1-7 marmots), male biased (approximately 2:1), and composed of primarily young unrelated animals of the same cohort (typically two years of age) I expected to observe low social cohesion among reintroduced animals and a tendency toward large exploratory movements consistent with the need to relocate to a suitable colony. Many of the survival skills employed by wild VIM potentially have a learned or socially transmitted component. Because current captive-rearing practices provide little opportunity to identify natural forage and sources of risk, or to acquire the skills necessary to balance tradeoffs, I expected to observe reduced vigilance, a lowered sensitivity to potential sources of danger, and a different allocation of time from wild VIM under similar ecological conditions.
Methods

Study population

Twelve captive raised marmots were released on sites with either an active colony (Mt. Washington 2004) or vacant sites that recently supported wild VIM (Green Mt. and Mt. Haley in 2003 and 2004) and monitored during the summers of 2003 and 2004. Of these released animals, four two-year olds (2 female, 2 male) were introduced in July 2003 to Green Mt. (4903’N 12420’E). The following year, six two-year olds were released at Mt. Haley (2 female, 4 male; 4860’N 12417’E) and two were placed on Mt. Washington (2 females, aged two and four; 4945’N 12517’E) (Table 3.1). With the exception of Mt. Washington, which has an active colony of wild marmots (n≈10), all released animals were situated in vacant, but recently occupied habitat. An additional 14 marmots (7 yearlings at Haley, 5 marmots aged 2 on Green and one marmot aged 4 on Mt. Washington) were released in 2005 (total n=25). Because these reintroductions were still in progress, data from these 13 individuals were limited to an analysis of patterns of movement from July to emergence. Figure 3.1 illustrates the major southern release sites geographically relative to one another.

<table>
<thead>
<tr>
<th>Year</th>
<th>Green Mt.</th>
<th>Mt. Haley</th>
<th>Mt. Washington</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>2♀ + 2♂</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>2004</td>
<td>--</td>
<td>2♀ + 4♂</td>
<td>2♀</td>
</tr>
<tr>
<td>2005</td>
<td>2♀ + 3♂</td>
<td>2♀ + 5♂</td>
<td>2♂</td>
</tr>
</tbody>
</table>

Table 3.1: The composition of captive-bred release groups at each study site. [Data from 2005 are included only in the analysis of long distance movement.]

For comparison, data on 21 wild VIM (36 animal years) were collected from three colonies during May to October 2002, 2003, 2004, and spring of 2005. Mt. Washington was studied most intensively, with additional data collected from Green Mt. (2002 only); Mt. Morarity (4900’N 12427’E) and Heather Mt. (4900’N 12416’E). Details of the study sites, study animals, and historical research are described in Chapter 2.
Figure 3.1: Location of primary release efforts. These mountains are in the vicinity of the southern diamond in Fig. 2.1. Distance between the ‘Haley Bowl’ and ‘Green Summit’ reintroduction sites is approximately 7 km. Contours are 20m intervals.

Field methods

Released and wild marmots were monitored daily to record behaviour, movement, habitat use, and survival from emergence from hibernation (May) or time of release (July) to the onset of hibernation (October); a census the following May (2003, 2004, and 2005) determined whether they survived the winter. A soft release (temporary cover,
electric fencing, fladry, and food supplementation) approach was used, where marmots were generally placed as pairs in wooden nest boxes open to a burrow system. After 24 hours the boxes were opened; this holding period was intended to acclimatize individuals to burrow systems and natural surroundings. Boxes were left for about 30 days to provide initial shelter, protection from predators and a reference point for marmots to return to during exploratory episodes (specific release techniques are described in Bryant et al. 2002).

Home ranges and movement

Home ranges were mapped using locations collected once per day across the 5½ month active season (2½ months for released marmots). Each day when a marmot was first located, the observer recorded its exact position.

A minimum of 35 locations recorded at regular intervals over the season were used to estimate annual home ranges (mean=88 for wild marmots, 61 for released marmots). Locations gathered the same day were recorded in the morning and afternoon, and a minimum of four hours apart. A marmot’s precise location and altitude were measured using a hand-held Global Positioning System (GPS) receiver accurate to ± 6m. Methods for constructing individual home ranges are described in Chapter 2. Dispersal-like movements were excluded from home range analyses and evaluated separately. Large movements away from the reintroduction meadows were measured by the linear distance between the release site and the furthest recorded location that an animal was known to have visited. Some of the very distant locations were supplemented by helicopter searches conducted by BC government officials (locations were provided by Don Doyle, MWALP). Because marmots tend to use ridges when moving between mountains, an additional “least resistance” estimate of travel distance was calculated by measuring the distance between the release site and each individual’s peripheral location by following the most direct ridge systems.
Sociality and time allocation

Individual marmots were located and observed each day according to schedules constructed 14 days in advance to ensure field observers did not bias results by choosing when to initiate or terminate a focal observation. Behavioural data were gathered using a focal sampling approach (Altman 1974). Specifically, a single marmot’s activity was scored at one-minute intervals for 60 consecutive minutes. Recorded were the animal’s body position (sitting, lying, standing, moving, alert posture), head position (up or down), orientation (up, down, or across-slope), social interactions (Heard 1977), feeding, movement, and use of burrows. Also recorded were other less frequent activities used in analyses of marmot behaviour (Barash 1989). Approximately 300 hours of behavioural observations were collected for the 12 marmots released in 2003 and 2004, and over 1500 hours were collected for 21 wild marmots (36 animal-years). Most focal observations were conducted between 6 am and 6 pm when transmitters were active. Behavioural sampling methods and the construction of activity budgets are described in Chapter 2. Individuals were identified from their radio telemetry frequencies, ear tags and molt patterns. Behaviours were observed from 40-300 meters with 10x binoculars and 60x spotting scopes and all animals were habituated to human presence.

Flight distances

The remains of most VIM killed by predators are found within several meters of a burrow. For this reason, each flight distance is an estimate of how close individuals will allow a potential threat to advance before finally retreating to the safety of a burrow. Initial flight distances were therefore not measured, as these typically occurred in excess of 40m. Individual marmots were approached from proximities of over 100m within five minutes of being located. When the marmot entered a burrow, the distance between the observer and the animal’s chosen refuge was recorded. Single animals were approached steadily at a walking pace of 0.5m/second from a position across slope until a marmot entered a burrow or refuge (talus, cliff face). A 60m tape measure was used to determine the linear distance between the marmot’s point of entry and the observer’s last position. An equal number of measurements in the morning and afternoon were undertaken. No more than one flight measure was taken per marmot per day between July 15 and mid
October. Three released and nine wild individuals were removed from this analysis due to insufficient observations or poor coverage across the entire active season.

Analysis

The Kolmogorov-Smirnov test was used to inspect distributions and the Mann-Whitney U test to compare medians of data that were not distributed normally. Results were considered significant when $p<0.05$, and are presented in text as $x \pm SE$. Data reported for wild marmots were limited to the seasonal duration of the experimental releases (marmots were released in July) if the constrained data produced significantly different results from those when the entire data on wild marmots were considered.

Home ranges and movement

Home ranges were plotted using the fixed non-parametric kernel (density probability; Worton 1987) method (grid resolution = 255). Data points were plotted using Home Range, Movement and X-tools extensions in ArcView 3.2, Geographical Information Systems Software (ESRI 1996; Hooge 1999) and the HomeRanger program (Hovey 1998). Kernels reflect the intensity of use, and do not assume a single center of activity or a particular shape (Worton 1995; Seaman and Powell 1996). The adaptive kernel method was not employed because it is more subject to bias and exhibits greater error in surface fit (Seaman et al. 1999). The $h$ values (smoothing factor) were calculated as outlined by Worton (1989) rather than the least squares cross validation method, because of the number of multiple observations in identical locations within the data set (Silverman 1986; Tufto et al. 1996; Seaman, Griffith and Powell 1998). The minimum distance between successive independent locations was used to assess travel costs and to determine if patterns in movement differed between males and females.

Sociality and time allocation

Methods for quantifying activity budgets for feeding, resting (lying or sitting) and in-burrow follow those of Martin and Bateson (1993). Infrequent behaviours, such as social interactions, were expressed as occurrences per animal per hour of observation.
Data of activity budgets and rates of behaviour for wild marmots during 2002, 2003 and 2004 were pooled after I found no significant inter-annual differences (Appendix 3).

Results

Upon release, most VIM used the temporary nest boxes and fed on supplemental food pellets and water for several days, before adapting to local forage, appearing to selecting forbs over grasses and flower heads over leaves/stems. Non-dispersing marmots soon relocated to other nearby burrow complexes which contained talus and large boulders. Some dispersed long distances during the first several weeks of release. Twenty-one of the twenty-six animals from 2003-2005 made exploratory or dispersal movements away from their release burrow, ranging from 350m to well over ten km. During 2003-2004 seven of the dispersers selected appropriate habitat on relatively open south facing meadows or boulder slopes. One two-year-old male settled in a clear cut and was subsequently translocated to join a dispersing female on Green Mt. Another male spent the bulk of the active season in steep, heavily forested habitat which held few natural burrows and little forage.

Survival

Survival for ex-captives during the first summer (2003 and 2004 combined; July to immersgence) was 58% (7/12). In 2003, none of the reintroduced marmots survived long enough to hibernate in the wild; three were preyed upon (by cougar or eagle), and the fourth was recaptured and returned to captivity because managers believed its predation was imminent (I scored this animal as having not survived). In 2004 seven of the eight released individuals survived to hibernation; the overwinter/early spring survival of these animals was 43% (3/7). Overall, for the two seasons, survival from release (July) through to July of the following season was 25%. During this study survival for wild marmots at Mt. Washington and Green Mt. was 84% (27/32). The long term annual survival estimate (1984 - present) for wild marmots at all sites was $74\% \pm 4$ (Bryant and Page 2005).
Of those six marmots that survived to hibernation, two (1 female, 1 male; Mt. Haley) remained at the release site, used the traditional hibernaculum, and survived the winter. Two animals (1 female, 1 male) relocated to another mountain (>7km away; Green Mt.) and jointly hibernated in an unknown burrow that had no previous history as a hibernaculum. Both these animals died overwinter. A further two marmots (1 female at Mt. Washington, 1 male at Mt. Haley) remained above ground late into the fall as solitary individuals. Then, in October, they removed the plug and dug into a hibernaculum that already contained two hibernating marmots. One of these late hibernators (Mt. Washington) died during the winter/early spring before emergence. The other was preayed upon early the following season. Average body mass of three released adult marmots (2 females, 1 male) that died during winter of 2004/2005 and were later excavated in May was 1.9 kg and all were severely emaciated (range 1.8-2.2 kg) (McAdie 2005, personal communication).

*Home ranges and movement*

All released and wild marmots had large ranges (Table 3.2), but the daily movements of captive marmots were about half as long as those of wild marmots. For example, the minimum distance between successive independent locations (excluding dispersal movements) for released animals in 2004 was 129.9 ± 28.9m versus 226.3 ± 22.4m for wild marmots during the same year (U=53, n₁=10, n₂=6, p<0.01). There was no significant divergence between combined male and female wild (84.6; range 25-201 ha) and released (79.8; range=8-250 ha) 90% kernel home ranges. The mean 90% kernel home range for released marmots (52.5 ± 14.0 ha) was not significantly different from wild animals. However, home ranges of released females (33.2 ha) were roughly half the size of wild females (65.5 ha) (U=57, n₁=7, n₂=10, p=0.03). The range size of released males (123.9; range=33-250 ha), though not smaller than wild males (97.6; range=27-201), exhibited greater variation (sample variance= 6078 vs. 2585). Several captive-reared marmots that did not disperse or undertake large exploratory movements (~300m) had relatively small ranges (~30 ha).
Table 3.2: Home range sizes for captive-bred and wild marmots at the 90% kernal density. Mean ± SE.

<table>
<thead>
<tr>
<th></th>
<th>90% kernal (ha)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Released ♀ + ♂</strong></td>
<td>79.8 ± 20.9</td>
<td>12</td>
</tr>
<tr>
<td><strong>Wild ♀ - ♂</strong></td>
<td>84.6 ± 8.8</td>
<td>30</td>
</tr>
<tr>
<td><strong>Released ♀</strong></td>
<td>33.2 ± 10.0</td>
<td>7</td>
</tr>
<tr>
<td><strong>Wild ♀</strong></td>
<td>65.5 ± 11.1</td>
<td>11</td>
</tr>
<tr>
<td><strong>Released ♂</strong></td>
<td>123.9 ± 31.8</td>
<td>6</td>
</tr>
<tr>
<td><strong>Wild ♂</strong></td>
<td>97.6 ± 11.7</td>
<td>19</td>
</tr>
</tbody>
</table>

*Includes one additional home range from a female that dispersed to a new mountain.

The mean linear dispersal distance for marmots that permanently left the release site and maximum linear “exploratory” movement for animals that did not disperse during 2003, 2004 and 2005 was 3.14 km ± 0.57 (n=26, range=0.3-10.8 km; raw movement estimates provided in Appendix 5). Movements recalculated based on the assumption that reintroduced marmots followed ridges between mountains increased this estimate to 4.25 km ± 0.81 (range=0.3-16.0 km).

**Sociality**

Numbers of social interactions per animal per hour (all combined) for 2003 through 2004 for released marmots averaged 0.23 ± 0.04, and were significantly greater than for wild marmots during 2002 through 2004 (0.18 ± 0.04; Mann-Whitney U test: U=246 n₁=28 n₂=12 p<0.05). Both wild and released populations exhibited a bimodal pattern of social activity. Peak activity occurred during the months of emergence (May; 0.33 ± 0.05) and immersence (September/October; 0.38 ± 0.07) for wild marmots, and the months of release (July; 0.244 ± 0.05/hr) and immersence (September/October; 0.233 ± 0.04/hr) for released marmots. The number of unsolicited whistles recorded for captive-bred individuals during the first ten days post-release (65; ≈0.54/animal/day) exceeded the number recorded for wild marmots during any single year of study (highest count in 2003 was 31; ≈0.03/animal/day).
Time allocation

Reintroduced VIM spent 67.7% ± 3.5 of their time in burrow, compared to 60.0% ± 2.5 for wild animals. Percentage of time spent vigilant (head-up) during bouts of foraging did not differ between released (55.0 ± 2.3) and wild marmots (60.1 ± 2.1); but released animals spent more time in the bipedal alert posture (6.5% ± 1.08) than wild individuals (1.2% ± 0.31) (U=314.5; n₁=30, n₂=12; p<0.001) during periods of feeding. Overall, the fraction of above ground time spent being vigilant (head up) vs. non-vigilant (head down) was almost identical between wild (hu=66% ± 2.2, hd=34% ± 1.8) and released (hu=67% ± 3.2, hd=33% ± 2.8). Time allocated to feeding as a fraction of all activity was 4.0% ± 0.8 for released and 3.5% ± 0.4 for wild individuals. In short, these two groups allocated their time similarly above vs. below ground, in scanning vs. feeding, and in the proportion of time spent being wary vs. other activity. The only distinction was that released individuals conducted more of their scanning in an alert posture.

Flight distances

After removing individuals with insufficient data, 122 observations were used from nine released individuals (5 females, 4 males) and 67 observations from 11 wild marmots (6 males, 5 females). Flight distances were twice as large for released (25.3 ± 2.8 m) vs. wild (13.0 ± 2.0 m) marmots for all months combined (Fig. 3.2; U=89.0, n₁=9, n₂=11, p<0.01). Released marmots exhibited a pattern of increased wariness during the first few weeks in their new environment, and flight distances steadily decreased as the summer progressed (Figure 3.2). To determine whether differences between wild and captive-raised marmots were an artifact of elevated wariness in released animals during the initial stages post reintroduction, the data were further partitioned into July 12—August 15 and August 15—immergence (mid October). Early season discrepancies between aboriginal and captive raised animals were highly significant (U=93.5, n₁=9, n₂=11, p<0.01), but were indistinguishable during the later period (U=34, n₁=9, n₂=11, p>0.1). Flight measurements are summarized by individual in Appendix 6.
Discussion

Conditions in captivity may alter how infants develop into adults in at least three broad ways. First, captive animals are insulated from some of the environmental stimuli normally experienced by wild individuals. On release, these animals must learn to recognize sources of risk, compulsory habitat, and suitable forage. Most captive VIM are raised in small artificial cages that do not provide individuals opportunities to dig, forage, or move moderate distances. Second, most rearing facilities do not allow animals to associate freely, thereby hampering the development of social skills. Although VIM are typically housed in high density environments where individuals may see and hear others in enclosures nearest them, they have no control over who they have contact with. Cages that separate individual marmots also limit the degree to which they can interact socially. This is important because in mammals, skills used for recognizing and avoiding predators
are often socially transmitted (Curio 1993; Zohar and Terkel 1995). Thirdly, captive-rearing may encourage novel behaviours that are conducive to captive life, but which may be non-functional—even maladaptive—in the wild. For example, over several generations VIM who are bold may suffer less stress and reproduce more successfully than marmots who are fearful of their handlers; however, behaviours such as boldness may be deleterious in the wild. Captive animals may also live in conditions that do not promote the acquisition of defensive behaviours or competition for burrows and food resources.

In this chapter I explore whether marmots raised in artificial settings behaved similarly to wild marmots when released in natural marmot habitat. I address the implications of this behaviour on population establishment and recovery. Some aspects of wild and released animal behaviour were similar (e.g., home ranges and time budgets); however, others differed. Most newly released animals dispersed from the release site, some soon after being liberated. Although some wild animals also dispersed the frequency and extent of long range movements made by reintroduced marmots greatly exceeded those in the wild population. In the following discussion I account for some of the similarities and differences between captive and wild VIM behaviour, and raise some implications for the success of the captive breeding program.

**Survival**

Survival of ex-captives was poor, with major sources of mortality being predation and unsuccessful hibernation. Whether released animals in the future will continue to survive poorly, or whether future attempts will be successful, will not be known until different reintroduction methods can be compared. Low initial survival rates have characterized some other reintroduction efforts (e.g., Scheeper and Venzke 1995; Black et al. 1997; Bryant et al. 2002; Green et al. 2005).

Animals which have never before seen predators, eaten native forage, or navigated through natural habitat, often have low survival once released (e.g., Priddel and Wheeler 1994; Stoinski et al. 2003; Mathews et al. 2005). Abnormal manners developed in captivity or absent wild-type activity caused by limited experience may explain reduced survivorship (Price 1989; Snyder et al. 1996). Reintroduced marmots face the
additional challenge of having to prepare for hibernation and choose an appropriate hibernaculum during the first three months post-release. The low body mass (1.8 kg when recovered) of several artificially-raised animals that died overwinter in 2004-2005 (a year of low snow deposits) indicates that they either did not accumulate sufficient fat reserves, or did not chose appropriate habitat to survive the winter. It is also possible that solitary marmots that later joined existing hibernating pairs (who had already plugged the burrow entrance) were forced to use separate chambers and did not receive the benefits of social thermoregulation or were not deep enough underground to avoid cold temperatures (Arnold et al. 1991). Future monitoring will enable researchers to verify whether lone animals have poor survival and whether overwinter losses will continue to be a significant source of mortality during years of average snowfall. A more rigorous test of the social thermoregulatory hypothesis can be carried out in captivity by comparing rates of mass loss during hibernation among solitary and group hibernators. Isolating individuals by age and sex would also clarify whether some demographic groups benefit more from the presence of conspecifics during hibernation.

The similarities in general behaviour, time budgets, and hibernation dates between wild and released VIM are encouraging. They suggest that many important survival strategies are innate. Also, the first efforts to found a new colony by reintroducing VIM into vacant habitat have been partially successful. One male and one female now live on Mt. Haley and it is hoped that this pair will reproduce soon. However, because the current captive breeding program can produce only 10-20 yearly candidates for release, these observed successes may be insufficient to recover the wild population.

Home ranges and movement

The fact that captive-reared VIM make shorter daily movements than their wild counterparts may be a sampling artifact, as marmots that traveled to other mountains during the course of the study were located less often than those that remained at the release site and because dispersal movements were excluded from the analysis. Large movements (3-4 km) from the release site were common (range 0.3-16 km) and represent a major challenge for monitoring the success or failure of future reintroductions. The length of dispersal and exploratory movements reported here were underestimates.
because individuals were assumed to travel directly from the release site to a peripheral location. For example, one two-year old male released at Mt. Haley moved an accumulated distance of over 30 km among several mountains during 2004 before being eaten. In contrast to the length of 'routine' movements made by VIM, the largest recorded movement during 6 years of study for the Golden marmot (Marmota caudata aurea) was a 950m dispersal event (Blumstein and Arnold 1998). Long movements influence survival by exposing marmots to hostile habitat and by reducing the probability that animals will settle near conspecifics. Prolonged movements in search of mates or other social companions take prospective time and energy away from activities necessary for successful hibernation (burrow excavation, fat accumulation). The only marmots which, interestingly, survived their first year did not disperse, and rarely strayed from the release site. Bremner-Harrison et al. (2004) also found that larger movements were related to lower survival for reintroduced Swift Foxes (Vulpes velox). Although philopatry is often associated with habitat quality (Haughland and Larson 2004), in the case of VIM release sites were carefully chosen based upon criterions of previous use, considerations of historical population dynamics at those sites, and estimates of food availability. It is therefore unlikely that poor habitat quality drove most of the reintroduced marmots to leave these mountains. However, a comparison of burrow densities, food plant abundance and community composition between release and settlement sites might reveal whether dispersing marmots choose habitats that provide better opportunities for finding cover or acquiring food.

The composition of released groups (sex and age), pairing into nest boxes (each nest box held at least two marmots during each release), and the distance between boxes (<200m) within meadows may have been important factors that contributed to the results of these initial reintroductions. Release groups near to one another exhibited higher levels of aggression within and among nest pairs. Antagonistic encounters between released marmots may explain why some VIM left the site within one week. In 2004 all three dispersing individuals, including a female, were not seen to visit and use natural burrow systems prior to their departure. Movements away from the release site may therefore have been related, early on, to competition for limited numbers of females and the small space around each artificial shelter wherein marmots were familiar and capable.
of finding cover. The use of male biased sex ratios likely increased inter-individual aggression during 2004. Heard (1977) reported that males rarely interact with one another, and my observation was that when they did it was often to fight. Later in the summer, exploratory movements were made most often by solitary males with no mates.

Reintroduced marmots chose a variety of habitats. Some of these areas had been historically occupied by wild marmots, and were consistent with popular conceptions of what constituted “suitable habitat.” Other marmots, however, did not settle in meadows but instead used forest or clearcuts. The use of dense forest is curious, given the availability of vacant meadows, the theoretical expectation (Fretwell and Lucas 1970) that low density should result in animals using a narrow range of optimal habitats, and the confirmation that other marmot species exhibit this pattern of habitat selection (Borgo 2003). Perhaps solitary animals manage predator risk by making use of forest cover (Chapter 2). Yet another possibility is that marmots draw information from each other when assessing how suitable a local environment is for settlement (Kiester 1979); identifying optimal habitat where marmot density is low might then be less effective as individuals rely less upon conspecific cues. Both of these explanations predict that habitat use should become more predictable as density increases and marmots no longer live in isolation. Estimating predation rates in each habitat type could help distinguish cases where the use of forest habitat has survival benefit from cases where it does not. Mapping marmot locations and kill sites onto air photographs would also help determine whether predators select prey in proportion to each area’s probability of containing a marmot.

Big home ranges pose an added challenge. Large movements increase the amount of time spent being solitary and away from refuge. For a social species living at low densities, the release of larger group sizes or the addition of animals to existing colonies could mitigate extravagant ranging. Limited experience with supplementing the Mt. Washington population in 2004-2005 suggests that when naïve marmots join their wild counterparts, their daily movements are reduced and their home ranges are smaller than with insular reintroductions at Mt. Haley and Green Mt.
Sociality

The density of marmots housed in captivity is high (McAdie 2004, personal communication). Although normal social activity is not possible among all members of a captive population, the presence of conspecifics may benefit released individuals by fostering social predispositions—especially alarm calling. Marmots that stayed at the release site and survived to the following summer exhibited more cooperative behaviours than observed in the wild population. For example, individuals alternated vigilance during bouts of feeding, and readily communicated sources of danger to conspecifics. Pre-release exclosures could be developed in breeding facilities to provide a more “normal” social setting and to identify suitable social companions amongst genetically compatible candidates. A small portion of the captive population housed at Mountain Wood Farms, for example, is currently provisioned with some of these options (G. Blankstein 2005, personal communication) but captive managers have yet to foster these ideas at other institutions which currently hold VIM. By recording the quality and quantity of social interactions among a number of release candidates housed together, managers could select those which appear to be compatible. These predictions could then be tested by simultaneously releasing groups whose composition was chosen at random with groups whose members were selected based on behavioural criteria. Releases could then be monitored to verify whether post-release pairs bond and survive to reproduce the following spring.

Time allocation

Reintroduced marmots partitioned time in similar fashion to their wild counterparts. Time budgets for wild VIM, however, differed from those seen in historical studies conducted when the population was larger and thought to be stable (Heard 1977) and from other similar marmot species (Chapter 2). The fact that marmots raised in contrasting environments allocated time similarly suggests that the manner in which competing costs are balanced amongst foraging, resting and apprehension has a genetic component. Also, a large proportion of time was allocated to vigilance (head up ~60%) for both wild and captive-reared VIM, when compared with congeners (e.g. Barash 1973, 1989; Carey and Moore 1986; Blumstein et al. 2001). This change may reflect the high
costs of solitary life that most individuals now lead. Because the marmots that I studied spent most of their time alone, levels of vigilance between solitary and socially integrated animals could not be compared. Future attempts to found new colonies and/or bolster existing populations would provide opportunities to test whether vigilant behaviour is linked to conspecific presence. As reintroduction methods designed to keep individuals near the release site become more refined, observations from a range of group sizes would enable researchers to identify the number of conspecifics necessary to raise foraging efficiency and limit the need for such high levels of wariness.

Flight distances

Measures of responses to potentially dangerous stimuli can be used as a predictor of poor success in reintroductions. For example, boldness (low fear) often predicted poor survival in release candidates of swift foxes (e.g., Bremner-Harrison et al. 2004). Elevated wariness in VIM may have contributed to high survival (100%) during the first month post-release. That naive marmots were generally more apprehensive during this critical first month may lessen the need for extensive soft-release methods. Nevertheless, predation of VIM was concentrated in late summer (Bryant and Page 2005), a time when marmots are metabolically less active (Barash 1989) and their sensitivity to perturbations are lessened. The use of aversive mid-season training could instill an enduring wariness toward potential predators and a more cautious response to approaching danger. Over time, flight measurements of wild and released VIM may help gauge the degree to which captive rearing influences sensitivity to sources of danger.

Conclusion

I predicted that captive raised animals would have poor survival compared to wild marmots because artificially reared animals would range widely in search of colonies, exhibit less sensitivity to potential danger due to lack of experience, and be less social because the composition of release groups did not mimic natural colonies. Specifically, when compared to aboriginal VIM, I expected to observe a) changes in time allocated to
feeding, and to above vs. below ground activity; b) a reduction in social activity; c) an increase in the size of home ranges and the distance of exploratory movements; and d) a reduction in vigilance, alarm calling and flight distances.

The results from my study are mixed. Survival of artificially reared individuals released into natural meadows was low. Yet, activity budgets and social activity remained similar between captive bred and wild VIM. When captive raised VIM remained near to their release site, their home ranges and daily movements were comparable to wild animals. Most reintroduced marmots, however, either dispersed or exhibited large exploratory movements exceeding observations for wild animals both in frequency and extent. Contrary to my expectation, released VIM were wary to sources of danger. They had larger initial flight distances, spent more time in alert posture, and whistled more often than their wild counterparts.

Solitary behaviour, large dispersal-like movements and big home ranges (compared to other social marmots) may place released and wild VIM at greater risk of being depredated, and also raise their energetic expenditures. The conditions of captivity and the composition of groups released into the wild appear to a) promote dispersal behaviour, b) make individuals susceptible to predation, and c) weaken their capacity to prepare for and endure hibernation. Aversive training to predators and opportunities for digging burrows and hibernating underground may be useful elements in future captive programs. Intensive monitoring during the next several years, coupled with a commitment to experimentation, should help practitioners identify where mitigation is necessary and where it is optional.

A first step in better preparation for releases may be the establishment of “captive colonies.” Individuals receive benefit from the presence of conspecifics. Solitary marmots and/or very small groups are likely to fare less well than those which are socially integrated and remain at the release site. Any process which confers advantage to individuals in a group can lead to inverse density dependence and, hence, maximal population growth at more intermediate densities. Large ranges, social dysfunction and poor survival suggest that, like wild VIM, newly-released marmots may be vulnerable to Allee effects (see Chapter 2). Allee effects may imply a threshold abundance below which a population will tend toward extirpation, even in the absence of other sources of
decline. Whether this marmot has already crossed an extinction threshold (or whether possible Allee effects simply pose an additional challenge to recovery) is not known. If the wild population continues to diminish, future efforts to improve the status of this species will likely depend chiefly on reintroductions to reclaim threshold colony sizes and overall numbers.

Experimental releases ought therefore to focus on a range of group sizes and group compositions as a means of avoiding dispersal and promoting social behaviour. Future selection of release candidates may have to be based on more than the fulfillment of age, sex and health criteria (Bremner-Harrison et al. 2004). One avenue to pursue here is experimental work where groups of varying size and sex composition are released in separate, nearby meadows. As reintroduction programs become more sophisticated, selection of candidates may be able to use multiple criteria. The need to release a minimum number of animals of both sexes for populations to persist and grow is a common phenomenon in the reintroduction literature (e.g., Robinette et al. 1995) and assessing potential threshold release sizes should be a priority when recovering a social species.

In an ideal world, alternative approaches are first tested and their results compared in order to choose the best method for succeeding. However, because reintroduction initiatives typically have constrained budgets, managers must make difficult choices as to which methods to employ or abandon. Under just such conditions of uncertainty and financial constraint, the experimental study of reintroductions may be of most value. Adaptable releases offer a hopeful alternative to methodological prejudice informed by primarily by “experience.” For when an initial choice fails (which it sometimes does), those managing endangered species may find themselves tempted to continue trying what does not work well in the hope that it eventually will. Experimental reintroductions may, therefore, shed light on what pre-release investments and post-release measures might be necessary to achieve positive growth in a released population.
Chapter 4 Summary and Recommendations

The primary objectives of this study were:

1) To examine the evidence in support of Allee-type inverse density dependence in the VIM and to identify how population declines might bring about these unstable dynamics.

2) To assess the strengths and weaknesses in initial attempts to reintroduce captive-raised VIM, and to suggest which methods may improve the success of future releases.

The major findings were:

1. Allee effects may be a factor that contributed to recent declines of Vancouver Island marmots, and may present an imposing challenge for population recovery. My data is consistent with an Allee hypothesis and the social nature of this species makes it susceptible to group size effects. There appears to be a reduction in social behaviour between the 1970s and 2000s predicted by the Allee hypothesis, as well as a reduction in the amount of time individuals allocate to acquiring food, an increase in time allocated to being vigilant, an increase in ranging, and a reduced rate of mass accumulation in contemporary animals. These patterns likely increase the vulnerability of a marmot to predation, over-winter mortality and to low reproductive success.

2. Initial attempts to increase the numbers of this species using reintroductions have had mixed results, with most released individuals not surviving their first year. Post-release losses in reintroduced VIM are mainly due to predation and over-winter mortality. Similarities in sociality and activity budgets and several differences in measures of wariness and vigilance appear favorable for released marmots. However, animals released at low densities also appear to be under the potential influence of inverse density dependence.
Recommendations for the conduct of future releases should consider the following:

1. Potential mechanisms which drive Allee effects could serve as measurable indicators of population instability and as potential predictors of population decline. These measures could also be used as foci for assessing the progress of remediation. These mechanisms, many of which entail visible changes in the ecology of small populations, increase an individual’s vulnerability to sources of danger or reproductive failure, regardless of how frequent these events are. Furthermore, high mortality or low reproduction not caused by an increase in vulnerability should not be characterized as Allee effects—despite their importance for small populations.

2. Before a significant upturn in population growth in the wild is achieved it will be necessary for managers to intercede in order to regain intermediate population sizes, through reintroductions of captive-reared marmots and through sheltering wild animals from predation. Further attempts to found colonies of captive-raised marmots should consider releasing groups composed of various age, sex, and levels of relatedness. Conditions in captivity might be modified to enhance social relations and to promote learning among juveniles. The use of large outdoor exclosures is one possible method by which individuals would be allowed to interact with each other in a more “natural” environment.

3. If reintroductions are to achieve success, every release should be approached with the intention of encouraging captive-reared marmots to stay at the release site. Dispersal presents a significant challenge for monitoring the success of releases and for the survival of individuals that elect to move.

4. Poor survival of released compared to wild VIM may be due, in part, to chance events. Conversely, survival may be influenced by the methods used to liberate animals and the manner and conditions under which they were reared. Managers and researchers will need to structure each reintroduction as a part of a larger
experimental program if they are to distinguish which factors limit reproduction and survival.

Findings from this study suggest that the following research would be timely:

1. An analysis of habitat use and selection could identify whether and when habitat selection becomes hazardous (e.g., Morris 2002), and evaluate where future reintroductions should occur based on the distribution of secure and protected habitat patches; it could also clarify what constitutes critical habitat under Canada’s Species At Risk Act.

2. A re-analysis of time allocation in wild VIM would also be timely. Observed time budgets may be understood without recourse to an Allee effect. Specific research might evaluate whether current time allocation is driven by a need to thermally regulate by using burrows to conserve or dispense body heat.

3. Precipitating Allee effects experimentally could be attempted with non-endangered colonies of Hoary marmots (*Marmota caligata*). Our understanding of the mechanisms purported to cause Allee effects would benefit from a controlled experiment where several closely linked colonies are monitored before, during and after an induced population crash. Because the suite of possible mechanisms that cause Allee effects in social mammals have not been experimentally defined, this approach could help establish a set of principles to direct future research and conservation policy.

4. A study of the specific factors which cause dispersal in reintroduced marmots. Experimental releases could invest five years, each year testing whether the following release scenarios reduce the likelihood of large movements away from the intended reintroduction site: 1) A repetition of the past three release attempts, except that marmots are released in individual nest boxes separated in space to reduce stress. Each individual would therefore have access to his/her own refuge,
and each nest box would be separated by sufficient distance (>100m) to allow subordinate marmots to remain at the release site and avoid confrontation with aggressive animals. 2) The reintroduction of extended families. Because family groups typically form the basis of cooperative social groups in most marmot species, we could expect to observe a greater degree of tolerance and fewer aggressive acts amongst family members. 3) The use of pre-release screening (e.g., mirror image stimulation) to identify behaviour traits that are correlated with dispersal. 4) Equalize the sex ratios of founder populations or make them female biased. Females are, in general, philopatric among species of social marmots (Barash 1989). 5) Structure reintroductions as if dispersal events are to be expected. By reintroducing a large number of intermediate sized groups, core habitat could be founded with groups skewed towards males, while peripheral releases situated along natural dispersal routes could contain more females. In the event of dispersion, males moving away from a release site may be likely to encounter and settle with a peripheral female rather than wander indefinitely.
Literature Cited


Armitage, K. B., and Rumiantsev, V. Y., editors. Holarctic Marmots as a Factor of
Biodiversity- Proceedings of the 3d International Conference on Marmots,
B. A., and Horwitz, B., editors. Life in the cold: Ecological, physiological, and
Ambient temperatures in hibernacula and their energetic consequences for alpine
Arnold, W. 1988. Social thermoregulation during hibernation in Alpine marmots
Marmota marmota. Journal of Comparative Physiology - B, Biochemical,
Systemic, & Environmental Physiology. 158: 151-156.
Aviles, L., and Tufino, P. 1998. Colony size and individual fitness in the social spider
Aviles, L. 1999. Cooperation and non-linear dynamics: An ecological perspective on
Monographs. 6: 171–249.
Barash, D. P. 1974a. The social behaviour of the hoary marmot, Marmota caligata.
Barash, D. P. 1974b. The evolution of marmot societies: A general theory. Science. 185:
415-420.
Stanford, CA.
properties, and a requiem for density dependence. Oikos. 99: 600-606.


ESRI. 1996. Introduction to ArcView GIS. Environmental Systems Research Institute
Publications. Redlands, California.
Formozov, A. N. 1966. Adaptive modifications of behavior in mammals of the Eurasian
spatial and temporal distribution of fire from the west coast of Vancouver Island,
Olney, P. J. S., Mace, G. M., and Festne, A. T. C. Editors. Creative conservation:
Interactive management of wild and captive animals. Chapman and Hall, London.
365–383.
Green, R. E. 1997. The influence of numbers released on the outcome of attempts to
35.
Marbled Teal (Marmaronetta angustirostris) released back into the wild.
Biological Conservation. 121: 595-601.
Grevstad, F. S. 1999. Factors influencing the chance of population establishment:
Implications for release strategies in biocontrol. Ecological Applications. 9: 1439-
1447.


Appendix 1: Vancouver Island marmot habitat.

Typical marmot habitat can include (A; Mt. Washington) talus, (B; Green Mt.—C; Haley Mt.), sub alpine meadow (D; Moriarty Mt. and Mt. Washington) Forest and ski runs. These and other habitat photographs may be obtained from the author.
Appendix 2: Ethogram of *M. vancouverensis* behaviours

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Code</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>In burrow</td>
<td>ib</td>
<td>Underground or within a cliff refuge, either in a burrow, rock crevice, under a rock, or in talus.</td>
</tr>
<tr>
<td>Sitting**</td>
<td>s</td>
<td>Back end touching ground, usually all four legs touching ground. Ventral surface not touching ground.</td>
</tr>
<tr>
<td>Standing 4 legs s4</td>
<td></td>
<td>No portion of body touching ground except four legs.</td>
</tr>
<tr>
<td>Standing 2 legs s2</td>
<td></td>
<td>Bi-pedal standing posture.</td>
</tr>
<tr>
<td>Lying**</td>
<td>l</td>
<td>Ventral surface touching ground, animals weight not supported by legs.</td>
</tr>
<tr>
<td>Head up hu</td>
<td></td>
<td>Head positioned higher relative to rest of body.</td>
</tr>
<tr>
<td>Head down hd</td>
<td></td>
<td>Head positioned equal or lower relative to rest of body.</td>
</tr>
<tr>
<td>Tail raised tr</td>
<td></td>
<td>Tail no longer at rest, but noticeably arched and usually raised above the height of the back, hairs on tail usually erect.</td>
</tr>
<tr>
<td>Eyes closed cc</td>
<td></td>
<td>Cheek placed in long sweeping motions against a hard surface.</td>
</tr>
<tr>
<td>Scent mark sm</td>
<td></td>
<td>The contact of an individual's facial region with any region of another marmot. Used to describe both initiated and received versions of said contact.</td>
</tr>
<tr>
<td>Nose touch nt</td>
<td></td>
<td>Grooming one's fur, or that of another using either paws or mouth. Solitary vs. social preenings are noted.</td>
</tr>
<tr>
<td>Preening pr</td>
<td></td>
<td>Front or back paws employed to displace soil, or rocks. Usually associated with burrow maintenance.</td>
</tr>
<tr>
<td>Digging d</td>
<td></td>
<td>Usually by way of back legs. Grass, twigs, and small branches are picked up and transported while being held within the mouth.</td>
</tr>
<tr>
<td>Sniffing sn</td>
<td></td>
<td>One marmot rapidly following another.</td>
</tr>
<tr>
<td>Scratching sc</td>
<td></td>
<td>Typically associated with yawn; front or back legs are extended and held away from body.</td>
</tr>
<tr>
<td>Grass collecting gc</td>
<td></td>
<td>Similar to that observed in a cat; associated with stretch behaviour.</td>
</tr>
<tr>
<td>Chasing ch</td>
<td></td>
<td>One marmot straddling another with forelegs, while placing its ventral surface in Contact with the dorsal surface of the other.</td>
</tr>
<tr>
<td>Stretching st</td>
<td></td>
<td>Two marmots biting, pushing, or boxing each other. Typically both interactants are on their hind legs (s2) and push their forelimbs against the others chest or shoulders. We cannot reliably distinguish whether this activity is aggressive or not. Not taken whether vocalizations such as snarling is involved.</td>
</tr>
<tr>
<td>Yawn y</td>
<td></td>
<td>Vegetation is ingested.</td>
</tr>
<tr>
<td>Moving m</td>
<td></td>
<td>Vegetation is ingested.</td>
</tr>
<tr>
<td>Mounting mo</td>
<td></td>
<td>Not always visible, and therefore not a reliable measure. Closely associated and usually synonymous with feeding.</td>
</tr>
<tr>
<td>Play fighting Pf</td>
<td></td>
<td>Used for infrequent behaviours described by Heard (1977). These include “invitations” to playfight, anal sniff, avoidance, novel vocalizations and other rare social interactions that occur too infrequently to warrant code.</td>
</tr>
<tr>
<td>Facing North fn</td>
<td></td>
<td>Refers to body orientation rather than head orientation, which may differ. Rounding to nearest 1/8th quadrant, allowing for conjunction of two codes.</td>
</tr>
<tr>
<td>Facing South fs</td>
<td></td>
<td>See above.</td>
</tr>
<tr>
<td>Facing West fw</td>
<td></td>
<td>See above.</td>
</tr>
<tr>
<td>Facing East fe</td>
<td></td>
<td>See above.</td>
</tr>
<tr>
<td>Facing me fm</td>
<td></td>
<td>See above.</td>
</tr>
<tr>
<td>Facing upslope fu</td>
<td></td>
<td>Discrete. Similar to compass direction, but rounded to nearest slope orientation.</td>
</tr>
</tbody>
</table>

78
Appendix 1 continued

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Code</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Facing down</td>
<td></td>
<td></td>
</tr>
<tr>
<td>slope</td>
<td>fd</td>
<td>See above</td>
</tr>
<tr>
<td>Facing across</td>
<td></td>
<td></td>
</tr>
<tr>
<td>slope</td>
<td>fa</td>
<td>See above</td>
</tr>
<tr>
<td>Whistle</td>
<td>wh</td>
<td>Loud piercing alarm call. Most common vocalization.</td>
</tr>
<tr>
<td>Keaw</td>
<td>ke</td>
<td>A rare trailing alarm call unique to <em>M. vancouverensis</em>.</td>
</tr>
</tbody>
</table>

* These are combined to give an overall measure of “feeding” for comparison with other published reports.

** These are combined to provide an overall estimate or “rest” for comparison with Heard (1977).

<table>
<thead>
<tr>
<th>Weather Codes</th>
<th></th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clear</td>
<td>cl</td>
<td>Most likely full sun, &lt; 10% cloud cover</td>
</tr>
<tr>
<td>Partly cloudy</td>
<td>pcl</td>
<td>&gt; 10% cloud cover</td>
</tr>
<tr>
<td>Overcast</td>
<td>ov</td>
<td>&gt; 90% cloud cover</td>
</tr>
<tr>
<td>Rain</td>
<td>ra</td>
<td></td>
</tr>
<tr>
<td>Wind</td>
<td>wi</td>
<td>Subjective</td>
</tr>
<tr>
<td>Breeze</td>
<td>br</td>
<td>Subjective</td>
</tr>
<tr>
<td>Snow</td>
<td>sn</td>
<td></td>
</tr>
<tr>
<td>Cold</td>
<td>co</td>
<td>Subjective (usually &lt; 10 °C)</td>
</tr>
<tr>
<td>Hot</td>
<td>ho</td>
<td>Subjective (usually &gt; 20 °C)</td>
</tr>
<tr>
<td>Warm</td>
<td>wa</td>
<td>Subjective (usually 10-20 °C)</td>
</tr>
<tr>
<td>No sun</td>
<td>nos</td>
<td>no direct sun on focal animal, as a consequence of cloud cover or angle of incidence</td>
</tr>
<tr>
<td>Poor visibility</td>
<td>pv</td>
<td>&lt; 30m visible distance</td>
</tr>
<tr>
<td>Fog</td>
<td>fo</td>
<td></td>
</tr>
<tr>
<td>Hail</td>
<td>ha</td>
<td></td>
</tr>
<tr>
<td>Thunder</td>
<td>th</td>
<td></td>
</tr>
</tbody>
</table>
Appendix 3: Time activity budgets

<table>
<thead>
<tr>
<th>Activity</th>
<th>2002 n=9</th>
<th>2003 n=12</th>
<th>2004 n=11</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>In burrow</td>
<td>Median</td>
<td>64.1</td>
<td>68.0</td>
<td>66.0</td>
</tr>
<tr>
<td></td>
<td>Average</td>
<td>13.1</td>
<td>17.2</td>
<td>18.4</td>
</tr>
<tr>
<td>Feeding</td>
<td>Median</td>
<td>2.9</td>
<td>1.5</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td>Average</td>
<td>18.8</td>
<td>12.8</td>
<td>18.6</td>
</tr>
<tr>
<td>Resting</td>
<td>Median</td>
<td>24.1</td>
<td>25.4</td>
<td>20.4</td>
</tr>
<tr>
<td></td>
<td>Average</td>
<td>17.8</td>
<td>18.3</td>
<td>13.5</td>
</tr>
</tbody>
</table>

$x^2$=1.73, df=2, p=0.42
$x^2$=3.00, df=2, p=0.22
$x^2$=1.78, df=2, p=0.41

Kruskall Wallis Test. Differences between years are not significant.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Males n=22</th>
<th>Females n=10</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>In burrow</td>
<td>64.4</td>
<td>65.6</td>
<td>U=128, p=0.48</td>
</tr>
<tr>
<td>Feeding</td>
<td>1.7</td>
<td>2.0</td>
<td>U=142, p=0.21</td>
</tr>
<tr>
<td>Resting</td>
<td>23.1</td>
<td>20.3</td>
<td>U=142, p=0.20</td>
</tr>
</tbody>
</table>

Mann-Whitney U Test, medians reported. Differences between males and females are not significant.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Age 0-2 n=11</th>
<th>Age 3+ n=21</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>In burrow</td>
<td>65.6</td>
<td>66.2</td>
<td>U=126, p=0.7</td>
</tr>
<tr>
<td>Feeding</td>
<td>4.2</td>
<td>1.8</td>
<td>U=138, p=0.39</td>
</tr>
<tr>
<td>Resting</td>
<td>18.7</td>
<td>23.8</td>
<td>U=156, p=0.11</td>
</tr>
</tbody>
</table>

Mann-Whitney U Test, medians reported. Differences between juvenile and adults are not significant.
Appendix 3 continued

Proportion of total observations spent in burrow, resting (sitting and/or lying) and feeding for 32 wild VI marmots from time of spring emergence to the onset of hibernation.

Note: all data are available from the author upon request. Contact werner@zoology.ubc.ca.
Appendix 4: Home range summaries

<table>
<thead>
<tr>
<th>Sex</th>
<th>Age</th>
<th>count</th>
<th>99%</th>
<th>90%</th>
<th>75%</th>
<th>50%</th>
</tr>
</thead>
<tbody>
<tr>
<td>female</td>
<td>0</td>
<td>1</td>
<td>110.2</td>
<td>30.3</td>
<td>21.1</td>
<td>11.4</td>
</tr>
<tr>
<td>female</td>
<td>1</td>
<td>1</td>
<td>245.8</td>
<td>109.3</td>
<td>75.7</td>
<td>25.8</td>
</tr>
<tr>
<td>female</td>
<td>2</td>
<td>3</td>
<td>268.0</td>
<td>53.7</td>
<td>21.5</td>
<td>7.6</td>
</tr>
<tr>
<td>female</td>
<td>3</td>
<td>2</td>
<td>134.7</td>
<td>40.2</td>
<td>25.8</td>
<td>12.6</td>
</tr>
<tr>
<td>female</td>
<td>4</td>
<td>2</td>
<td>256.4</td>
<td>84.1</td>
<td>60.6</td>
<td>32.0</td>
</tr>
<tr>
<td>female</td>
<td>5</td>
<td>1</td>
<td>228.6</td>
<td>81.1</td>
<td>50.8</td>
<td>23.6</td>
</tr>
<tr>
<td>female</td>
<td>7</td>
<td>1</td>
<td>163.9</td>
<td>68.9</td>
<td>51.7</td>
<td>28.6</td>
</tr>
<tr>
<td>male</td>
<td>0</td>
<td>1</td>
<td>119.9</td>
<td>34.6</td>
<td>22.2</td>
<td>12.5</td>
</tr>
<tr>
<td>male</td>
<td>1</td>
<td>1</td>
<td>124.9</td>
<td>53.1</td>
<td>38.1</td>
<td>18.5</td>
</tr>
<tr>
<td>male</td>
<td>2</td>
<td>3</td>
<td>238.2</td>
<td>90.8</td>
<td>62.3</td>
<td>26.5</td>
</tr>
<tr>
<td>male</td>
<td>3</td>
<td>3</td>
<td>310.4</td>
<td>125.7</td>
<td>88.1</td>
<td>43.5</td>
</tr>
<tr>
<td>male</td>
<td>4</td>
<td>3</td>
<td>246.1</td>
<td>107.2</td>
<td>76.8</td>
<td>36.2</td>
</tr>
<tr>
<td>male</td>
<td>5</td>
<td>4</td>
<td>379.3</td>
<td>108.5</td>
<td>67.0</td>
<td>31.0</td>
</tr>
<tr>
<td>male</td>
<td>6</td>
<td>3</td>
<td>129.7</td>
<td>43.9</td>
<td>30.1</td>
<td>12.1</td>
</tr>
<tr>
<td>male</td>
<td>7</td>
<td>2</td>
<td>194.2</td>
<td>46.3</td>
<td>26.3</td>
<td>12.4</td>
</tr>
<tr>
<td>male</td>
<td>8</td>
<td>1</td>
<td>690.3</td>
<td>192.4</td>
<td>103.5</td>
<td>41.7</td>
</tr>
</tbody>
</table>

Fixed kernal home range sizes for 32 wild animals (2002-2004) summarized by age and sex. Kernels reflect space use for the entire active season. Size measured in hectares. The 90% density estimates (in bold) were used for comparison with Heard (1977) and are reported in text.
Appendix 5: Movements of released VIM from reintroduction site.

<table>
<thead>
<tr>
<th>Animal ID</th>
<th>Age</th>
<th>Sex</th>
<th>Year</th>
<th>Release Site</th>
<th>Linear</th>
<th>Contour</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rose</td>
<td>1</td>
<td>F</td>
<td>2005</td>
<td>Haley</td>
<td>11.0</td>
<td>16.0</td>
</tr>
<tr>
<td>Lily</td>
<td>1</td>
<td>F</td>
<td>2005</td>
<td>Haley</td>
<td>1.1</td>
<td>1.5</td>
</tr>
<tr>
<td>Thelma</td>
<td>2</td>
<td>F</td>
<td>2003</td>
<td>Green</td>
<td>0.4</td>
<td>0.45</td>
</tr>
<tr>
<td>Gemeni</td>
<td>2</td>
<td>F</td>
<td>2003</td>
<td>Green</td>
<td>0.35</td>
<td>0.39</td>
</tr>
<tr>
<td>Denai</td>
<td>2</td>
<td>F</td>
<td>2004</td>
<td>Haley</td>
<td>6.5</td>
<td>8.7</td>
</tr>
<tr>
<td>Haida</td>
<td>2</td>
<td>F</td>
<td>2004</td>
<td>Haley</td>
<td>0.2</td>
<td>0.25</td>
</tr>
<tr>
<td>Virginia</td>
<td>2</td>
<td>F</td>
<td>2004</td>
<td>Wash</td>
<td>0.9</td>
<td>1.45</td>
</tr>
<tr>
<td>Dasie</td>
<td>2</td>
<td>F</td>
<td>2005</td>
<td>Green</td>
<td>1.8</td>
<td>2.6</td>
</tr>
<tr>
<td>Lucy</td>
<td>2</td>
<td>F</td>
<td>2005</td>
<td>Green</td>
<td>0.2</td>
<td>0.28</td>
</tr>
<tr>
<td>Haley</td>
<td>4</td>
<td>F</td>
<td>2004</td>
<td>Wash</td>
<td>0.7</td>
<td>0.9</td>
</tr>
<tr>
<td>Digger</td>
<td>1</td>
<td>M</td>
<td>2005</td>
<td>Haley</td>
<td>6.75</td>
<td>9.9</td>
</tr>
<tr>
<td>Ziggy</td>
<td>1</td>
<td>M</td>
<td>2005</td>
<td>Haley</td>
<td>5.25</td>
<td>6.9</td>
</tr>
<tr>
<td>Ruben</td>
<td>1</td>
<td>M</td>
<td>2005</td>
<td>Haley</td>
<td>5.25</td>
<td>6.9</td>
</tr>
<tr>
<td>Pogo</td>
<td>1</td>
<td>M</td>
<td>2005</td>
<td>Haley</td>
<td>1.5</td>
<td>2.1</td>
</tr>
<tr>
<td>Cujo</td>
<td>1</td>
<td>M</td>
<td>2005</td>
<td>Haley</td>
<td>3.2</td>
<td>3.75</td>
</tr>
<tr>
<td>Hooper</td>
<td>2</td>
<td>M</td>
<td>2003</td>
<td>Green</td>
<td>3.4</td>
<td>4.1</td>
</tr>
<tr>
<td>Onslo</td>
<td>2</td>
<td>M</td>
<td>2004</td>
<td>Haley</td>
<td>0.35</td>
<td>0.38</td>
</tr>
<tr>
<td>Macumba</td>
<td>2</td>
<td>M</td>
<td>2004</td>
<td>Haley</td>
<td>5.25</td>
<td>6.25</td>
</tr>
<tr>
<td>Dylan</td>
<td>2</td>
<td>M</td>
<td>2004</td>
<td>Haley</td>
<td>2.3</td>
<td>2.8</td>
</tr>
<tr>
<td>Newman</td>
<td>2</td>
<td>M</td>
<td>2004</td>
<td>Haley</td>
<td>7.2</td>
<td>10.9</td>
</tr>
<tr>
<td>Logan</td>
<td>2</td>
<td>M</td>
<td>2005</td>
<td>Green</td>
<td>4.0</td>
<td>4.5</td>
</tr>
<tr>
<td>Elvis</td>
<td>2</td>
<td>M</td>
<td>2005</td>
<td>Green</td>
<td>0.25</td>
<td>0.35</td>
</tr>
<tr>
<td>Clifford</td>
<td>2</td>
<td>M</td>
<td>2005</td>
<td>Green</td>
<td>11.0</td>
<td>14.1</td>
</tr>
<tr>
<td>Jack</td>
<td>3</td>
<td>M</td>
<td>2003</td>
<td>Green</td>
<td>1.3</td>
<td>2.1</td>
</tr>
<tr>
<td>Butler</td>
<td>5</td>
<td>M</td>
<td>2005</td>
<td>Wash</td>
<td>0.6</td>
<td>0.68</td>
</tr>
<tr>
<td>Mark</td>
<td>5</td>
<td>M</td>
<td>2005</td>
<td>Wash</td>
<td>1.4</td>
<td>1.68</td>
</tr>
</tbody>
</table>

Estimated minimum and cumulative distance (in km) between release site and furthest known location for 26 reintroduced marmots during 2003, 2004 and 2005.
Appendix 6: Flight distances.

<table>
<thead>
<tr>
<th>Animal ID</th>
<th>Sex</th>
<th>Age</th>
<th>Distance</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>WILD MARMOTS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PUP 2</td>
<td>F</td>
<td>0</td>
<td>10</td>
<td>5</td>
</tr>
<tr>
<td>APRIL</td>
<td>F</td>
<td>2</td>
<td>10.6</td>
<td>7</td>
</tr>
<tr>
<td>COLLETTE</td>
<td>F</td>
<td>3</td>
<td>11</td>
<td>5</td>
</tr>
<tr>
<td>SHELBY</td>
<td>F</td>
<td>4</td>
<td>10.1</td>
<td>8</td>
</tr>
<tr>
<td>LIV</td>
<td>F</td>
<td>5</td>
<td>7.6</td>
<td>5</td>
</tr>
<tr>
<td>PUP 1</td>
<td>M</td>
<td>0</td>
<td>30</td>
<td>6</td>
</tr>
<tr>
<td>CHANCE</td>
<td>M</td>
<td>3</td>
<td>11</td>
<td>7</td>
</tr>
<tr>
<td>CLINT</td>
<td>M</td>
<td>4</td>
<td>16.2</td>
<td>6</td>
</tr>
<tr>
<td>COOTER</td>
<td>M</td>
<td>5</td>
<td>9.6</td>
<td>5</td>
</tr>
<tr>
<td>WILL</td>
<td>M</td>
<td>7</td>
<td>20</td>
<td>8</td>
</tr>
<tr>
<td>SHAM</td>
<td>M</td>
<td>8</td>
<td>8.1</td>
<td>5</td>
</tr>
<tr>
<td><strong>REINTRODUCED MARMOTS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DYLAN</td>
<td>D</td>
<td>2</td>
<td>15.7</td>
<td>15</td>
</tr>
<tr>
<td>DENAI</td>
<td>F</td>
<td>2</td>
<td>32.8</td>
<td>12</td>
</tr>
<tr>
<td>HAIDA</td>
<td>F</td>
<td>2</td>
<td>19.2</td>
<td>18</td>
</tr>
<tr>
<td>VIRGINIA</td>
<td>F</td>
<td>2</td>
<td>29.5</td>
<td>12</td>
</tr>
<tr>
<td>HALEY</td>
<td>F</td>
<td>4</td>
<td>32</td>
<td>15</td>
</tr>
<tr>
<td>MACUMBA</td>
<td>M</td>
<td>2</td>
<td>38.1</td>
<td>12</td>
</tr>
<tr>
<td>NEWMAN</td>
<td>M</td>
<td>2</td>
<td>20.3</td>
<td>11</td>
</tr>
<tr>
<td>ONSLO</td>
<td>M</td>
<td>2</td>
<td>16.5</td>
<td>17</td>
</tr>
<tr>
<td>HOOPER</td>
<td>M</td>
<td>4</td>
<td>29.3</td>
<td>10</td>
</tr>
</tbody>
</table>