Metapopulation ecology of Vancouver Island marmots (*Marmota vancouverensis*)

by

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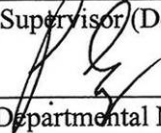Requirements for the Degree of

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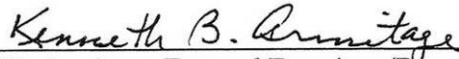
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Supervisor: Dr. D.S. Eastman

ABSTRACT

Vancouver Island marmots (*M. vancouverensis*) rank among the world's most critically endangered mammals. There were probably fewer than 100 marmots in 1998, with 90% distributed south of Alberni Inlet, and the remainder on or near Mount Washington. This represents a 60-70% decline in numbers during the past 10 years, and a considerably reduced geographic range during the past several decades.

I used data from marked animals, radio-telemetry and population counts to test whether population dynamics were consistent with predictions made under five hypotheses: habitat tracking, sink-connectivity, weather, predators and disease. Estimates of demographic rates from intensive mark-recapture work and population counts were generally consistent, although estimation of adult survival from counts was problematic because of the difficulty of distinguishing surviving marmots from immigrants. There was no apparent influence of mark-recapture on survival or reproduction, and intensively studied colonies showed similar dynamics to colonies that were visited infrequently.

There was little evidence for habitat tracking in natural habitats. Few colonies showed chronically low reproduction or survival, which would be the predicted result of a gradually deteriorating environment. Declines were more often abrupt and catastrophic. Marmots did not colonize clearcuts in proportion to their temporal or spatial availability, and ultimately colonized only a minuscule fraction of the potential habitat. However, marmots already inhabiting clearcuts represent a special case of habitat tracking; survival rates were significantly lower at clearcuts of more advanced seral age (i.e., >11 years after harvest).

Evidence for source-sink and landscape connectivity processes was relatively strong. Marmots inhabiting clearcuts had chronically lower survival rates (by 5-10%). Per female reproductive contribution in clearcuts was half that of females inhabiting natural environments. However not all clearcuts acted as sinks, or acted as sinks in all years. Colonizations of clearcuts were spatially concentrated and none occurred at distances greater that 5 km from an existing natural colony. Apparent adult survival was significantly associated with isolation but juvenile survival was not, which is consistent with the prediction that isolated colonies should receive fewer immigrants. However the spatial pattern of extinctions was unexpected. Isolated and closely-clustered colonies had similar probabilities of extinction.
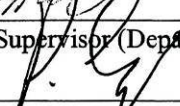
Weather significantly influenced marmot survival and reproduction but explained only small amounts of variation. Survival was significantly associated with rainfall, temperature and snowpack depth. Reproduction was negatively associated with snowpack and temperature. Slope aspect was significantly associated with survival, perhaps suggesting the importance of snowmelt patterns. Natural and clearcut colonies responded differently to weather.

Indices of wolf and cougar abundance were inconsistent and probably do not reflect true population sizes. Deer abundance was weakly associated with marmot survival in natural habitats, which could suggest switching of predator hunting effort. Marmot survival was spatially correlated, which is consistent with the idea that a few individual predators may focus hunting efforts at adjacent colonies. Field observations and radio-telemetry corroborated the importance of predators. In natural habitats, disappearances were uniformly distributed throughout summer, as predicted. In clearcuts, disappearances were more heavily skewed towards late summer, suggesting that winter mortality was more important.
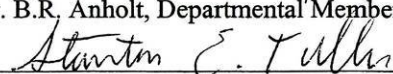
Spatial correlation of survival is also consistent with the disease hypothesis. Survival was lower in colonies with high relative density of adults, which is a predicted result given the prediction of increased risk of disease transmission. The incidence of high mortality events increased during the 1990s, and the degree of spatial correlation also increased despite a more fragmented population structure. These trends are consistent with a hypothesis of a new disease organism or increased risk of infection.

Forestry appears to be the primary cause of recent population dynamics in the Nanaimo Lakes region. Logging reduced overall marmot survival, inhibited their ability to re-colonize sites, and concentrated the population, making colonies more susceptible to predators and disease. The prognosis for continued survival remains hopeful provided that current plans for captive-breeding and reintroduction are pursued aggressively.

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FRONTISPIECE

The Marmot

On an early spring morning a marmot is born.

It eats grass but not any corn.

It lives in a burrow and not in a tree.

Its life is interesting and carefree.

Now you know a bit about the marmot.

If you read my story you'll learn a lot.

Alex Dezan (at age 7)

Stanstead Journal, Quebec, Jan. 7 1996

(reprinted by kind permission of the author's parents)

"...it might be worth while getting to know a little about geology or the movements of the moon or of a dog's tail, or of the psychology of starlings, or any of those apparently specialized or remote subjects which are always turning out to be the basis of ecological problems encountered in the field."

Charles Elton (at age 26)

Animal Ecology (1927)

"How often have I said to you that when you have eliminated the impossible, whatever remains, however improbable, must be the truth?"

Sir Arthur Conan Doyle (at age 31)

The Sign of the Four (1890)

INTRODUCTION

Marmota vancouverensis

The Vancouver Island marmot (*Marmota vancouverensis*: Swarth 1911) is endemic to Vancouver Island, British Columbia (Nagorsen 1987). Like all 14 currently recognized species in the genus, *M. vancouverensis* is fossorial, herbivorous and hibernates during winter (Barash 1989). The species was described from specimens collected in 1910 (Swarth 1912). *Marmota vancouverensis* is distinguishable from other marmots by karyotype (Rausch and Rausch 1971), skull characteristics (Hoffmann et al. 1979), pelage (Nagorsen 1987), behavior and vocalizations (Heard 1977, D. Blumstein, University of Kansas, pers. comm.). In most respects it is a typical alpine-dwelling marmot, showing slow maturation, a relatively long life span, and a complex degree of social organization (Bryant 1996). The species is notable for its highly restricted range and pronounced metapopulation structure (Bryant and Janz 1996).

Virtually nothing was known about the ecology or distribution of *M. vancouverensis* prior to the 1970s (Heard 1977). Since then it has been the subject of systematic population counts (reviewed by Bryant and Janz 1996), behavioral studies (Heard 1977), habitat and diet investigations (Milko 1984, Martell and Milko 1986), palaeontological research (Nagorsen et al. 1996), genetic work (Bryant 1990) and demographic analyses (Bryant 1996). These studies greatly improved our knowledge of the species and its precarious conservation status.

Marmota vancouverensis is listed as endangered under the B.C. Wildlife Act and regulations (Munro et al. 1985). It is similarly listed by the Committee on the Status of Endangered Wildlife in Canada (Munro 1979), the U.S. Endangered Species Act (Federal Register, Jan. 23 1984), and the International Union for the Conservation of Nature (Groombridge and Mace 1994). A Recovery Team was struck in 1988 and a recovery plan was prepared in 1990 (Bryant 1990), published in 1994 (Janz et al. 1994) and recently revised (Janz et al. in prep). *Marmota vancouverensis* has the dubious distinction of being the only endemic mammal species in Canada that is listed as endangered (Bryant 1997), and is arguably one of the rarest animals in the world.

The origin and evolutionary history of marmots on Vancouver Island is inextricably linked to climatic and glacial processes and associated changes in sea levels and habitat conditions. It remains unclear when marmots first colonized Vancouver Island. Heard (1977) speculated that marmots crossed to Vancouver Island via land connections that existed during the Illinoian glacial period, approximately 100,000 years ago, and survived subsequent glacial maxima on nunataks

and narrow coastal refugia or both. Nagorsen (1987) suggested the possibility of a more recent colonization, after the retreat of the Cordilleran Wisconsin glaciation some 10,000 to 13,000 years ago (see Pielou 1991). Existing evidence does not permit exclusion of either hypothesis. However, DNA analyses currently underway may clarify the phylogenetic relationships between *M. vancouverensis*, Olympic marmots (*M. olympus*) and hoary marmots (*M. caligata*), together with the timing of their divergence (R. Hoffmann, Smithsonian Institution, pers. comm.).

Retreat of the Cordilleran glacier during the past 10,000 years ensured that marmots became increasingly restricted as forest succession occurred (Nagorsen et al. 1996). Since then *M. vancouverensis* has apparently been confined to sites at which snow movement or fire maintained open meadows in sub-alpine habitats (Milko 1984). Habitat restriction is the fundamental reason why *M. vancouverensis* is rare and may also explain some aspects of its morphology and behavior. For example, Hoffmann et al. (1979) suggested that the rich dark fur of *M. vancouverensis* represents a melanistic phase that became genetically fixed in a small founder population. Similarly, the highly social nature of *M. vancouverensis* compared to other marmots (Heard 1977) has been interpreted as reflecting the evolutionary importance of being tolerant towards unrelated strangers (Bryant and Janz 1996). Under this interpretation, social acceptance of immigrants would encourage "rescue effects" (Brown and Kodric-Brown 1977) or colonization of unoccupied habitats.

Changes in distribution and abundance

Location records indicate that Vancouver Island marmots inhabited a considerably broader geographic range in the recent prehistoric (Nagorsen et al. 1996) and historical past (Bryant and Janz 1996). They apparently disappeared from substantial portions of Vancouver Island north of Alberni Inlet within the last several decades (Figure 1). Unfortunately, population data do not exist with which to evaluate either their recent (post-1900) abundance or the timing of declines on central Vancouver Island. Currently the species is restricted to fewer than 25 sites on 13 mountains. Apart from small colonies on Mount Washington, all active sites are located within 5 adjacent watersheds on southern Vancouver Island (Nanaimo, Cowichan, Chemainus, Nitinat and Cameron River drainages).

Population trends on southern Vancouver Island within the last 25 years are intriguing. Many colonies expanded during the early 1980s and this was accompanied by colonization of some new habitats created by clearcut logging of forests above 700 m elevation. However the expansion into clearcuts was limited in geographic and temporal terms (Bryant and Janz 1996).
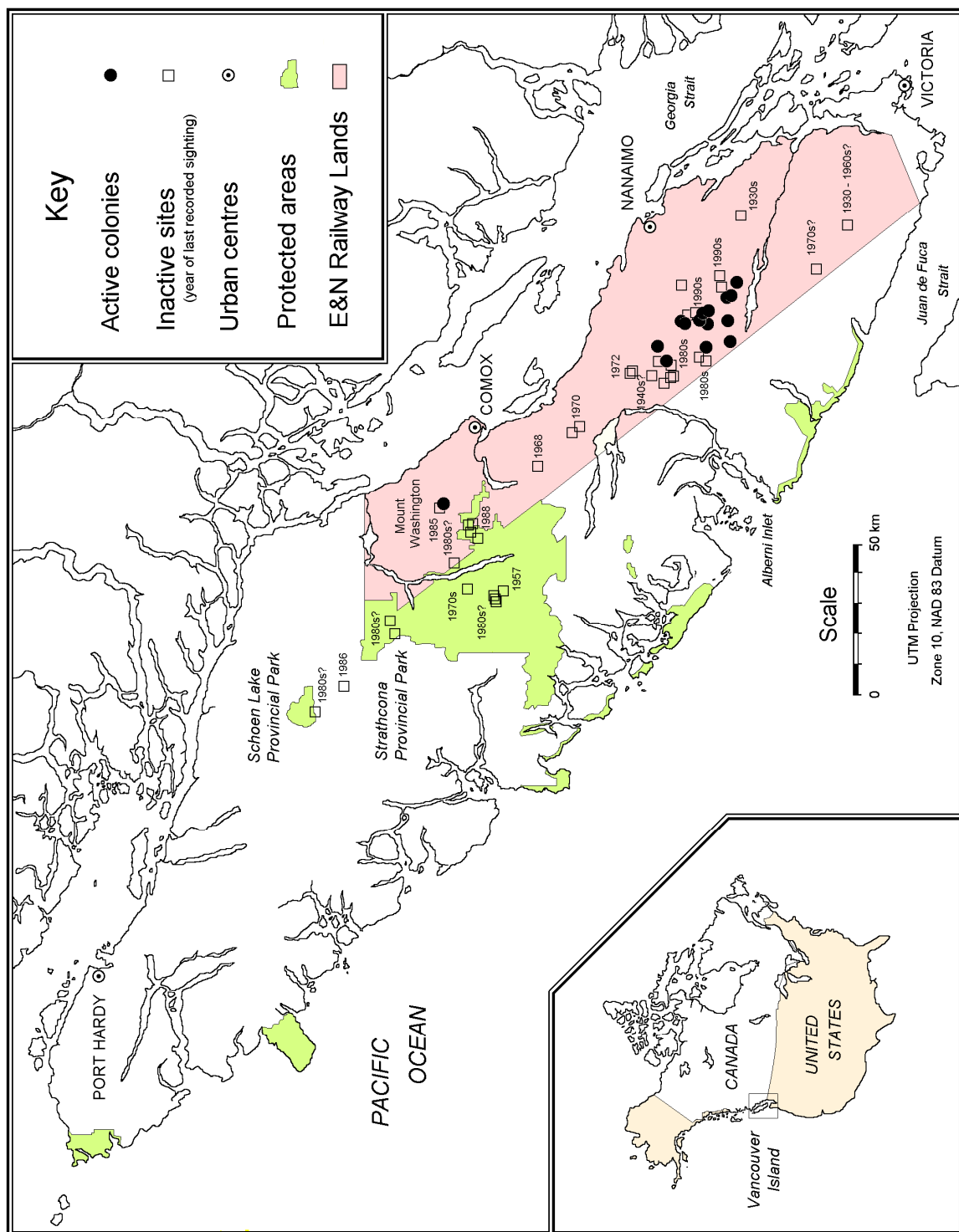
Figure 1: Historical and current distribution of Vancouver Island marmots. Extinction dates are approximate and based on sighting reports, burrow conditions and specimen data. Most of the population is found in a small area (150 km²) on private lands owned by MacMillan Bloedel Limited and TimberWest Forests. A few marmots live on lands owned by Mount Washington Ski-hill Corporation. Land tenure in this region has an interesting and convoluted history resulting from the Esquimalt and Nanaimo Railway Land Grant Act of 1883.

Despite evidence of reproduction and survival in new habitats created by forest harvesting, marmot numbers subsequently declined from a peak of over 300 animals during the mid-1980s to the present total of fewer than 100 animals. At least five hypotheses have been proposed to explain recent population dynamics in *M. vancouverensis*.

1) Habitat tracking hypothesis
2) Weather hypothesis
3) Sink-connectivity hypothesis
4) Predator hypothesis
5) Disease hypothesis

The hypotheses are not mutually exclusive and there is no *a priori* reason to imagine that a single factor is responsible for observed population trends. However, such hypotheses are useful in structuring thought and generating testable predictions. In that sense they are critical to pursuing what Caughley and Gunn (1996) described as the "diagnostic" phase of endangered species management. Without understanding there can be no hope of identifying the causes of decline or reversing them.

Habitat tracking hypothesis

Thomas (1994) suggested that many rare species "track" habitat conditions, becoming locally extinct when conditions are no longer suitable and colonizing sites when conditions improve. However, issues of temporal and spatial scale are important to understanding the processes and potential significance of habitat change. Vancouver Island marmots may be tracking habitat conditions at a variety of different scales.

Over periods spanning centuries or millennia, habitat tracking could be caused by global climate change and consequent reduction in the geographic area over which suitable conditions occur. Discovery of *M. vancouverensis* remains from sites well outside its historical range provides support for this idea (Nagorsen et al. 1996), as does similar distribution of alpine marmot (*M. marmota*) remains in parts of western Europe (Preleuthner et al. 1995). While undoubtedly correct, interpretation of habitat tracking at this temporal or spatial scale does not provide useful insight into recent *M. vancouverensis* dynamics.

However, tracking could also occur over a temporal scale measured in marmot generations and a spatial scale measured in hectares. Vegetation changes could result in altered survival or reproductive rates. In natural sub-alpine meadows, possible mechanisms of habitat change include

invasion by trees or bracken ferns (*Pteridium* spp.), fire or changing food-plant availability (Milko 1984, Martell and Milko 1986, Laroque 1998). Forestry is the principal agent of change for other habitats relevant to *M. vancouverensis*. Clearcutting and subsequent forest regeneration are exceptional because they can act over a temporal scale measured within the lifetime of individual marmots. Specifically, the extent of clearcuts and timing of their availability would be expected to influence colonization events because marmots do not inhabit mature forests (Bryant and Janz 1996). Rapid forest regeneration in clearcuts could influence demographic performance or make habitats unsuitable within a few years.

The tracking hypothesis predicts that marmots will respond to habitat change in deterministic fashion. However, the speed of the response would necessarily be related to the rate of habitat change. For colonies in natural sub-alpine meadows, gradual processes such as tree invasion lead to the expectation of slow decline in survival or birth rates as individual habitats become increasingly unsuitable. There is no reason to expect that change would occur simultaneously at all sites. Given the short duration of this study compared to rates of change in sub-alpine meadows (Kuramoto and Bliss 1970, Schreiner and Burger 1994), one would therefore expect to observe chronic low birth or survival rates at a subset of natural colonies.

For marmots inhabiting clearcuts the expectations are somewhat different because habitat change occurs more rapidly. The successional state of regenerating clearcuts could influence birth or survival in linear fashion (i.e., a gradual reduction as a function of increasing forest age). Alternatively it could be manifested by a threshold effect, in which conditions become unsuitable for birth or survival over a period of a few years. Finally, a basic premise of the tracking hypothesis is that marmots should increase in proportion to habitat availability and decrease when habitats become unsuitable. The colonization process would necessarily be limited by the number of potential colonists in the area. However, there exist numerous cases in which marmots expanded from zero to more than 20 individuals within a short period (Bryant and Janz 1996). One therefore predicts that marmot populations would increase numerically and spatially in relation to clearcut availability and population size.

Weather hypothesis

Annual weather patterns could result in altered survival or reproduction, particularly because marmots are presently restricted to such a small geographic area. One author attributed Vancouver Island marmot expansion during the early 1980s to a period of "mild winters" although he did not explain precisely what "mild" meant or how it would relate to hibernating marmots

(Smith 1982). However, snow depths, timing of snowpack melt and summer rainfall have been associated with demographic success in other marmot species (Barash 1973, Van Vuren and Armitage 1991, Armitage 1994,) and it is possible that weather could exert important and measurable effects upon *M. vancouverensis*.

The basic prediction of the weather hypothesis is that one would expect to observe high annual variance in survival or reproductive rates corresponding to years of "good" or "bad" weather. Although some effects of weather could be influenced by site-specific conditions (e.g., different snowmelt patterns at high and low elevation colonies), the expectation is that all colonies within the Nanaimo Lakes metapopulation would experience similar weather. There should therefore be no correlation of demographic trends as a function of between-colony distance (i.e., uniform spatial correlation). In addition, weather patterns would presumably vary randomly over time. The prediction is therefore that mortality or reproductive rates would show "episodes" of low performance due to unsuitable conditions, and that these would also occur randomly over time.

Sink-connectivity hypothesis

Pulliam (1988) suggested that populations could be regulated by differential habitat quality. He demonstrated mathematically that organisms can be most abundant in particular habitat "patches" but be less successful there (sink habitats) provided that continued influx of individuals occurs from nearby areas in which organisms do relatively well enough to provide a surplus (source habitats). Complementary ideas have focused on the ability of organisms to disperse successfully through a complex landscape (Dunning et al. 1992), form new subpopulations (Hanski and Gilpin 1991) or "rescue" subpopulations that have experienced poor survival or reproduction.

For Vancouver Island marmots the sink-connectivity hypothesis followed from suggestion of reduced marmot survival in clearcuts (Bryant 1990, 1996) together with spatial concentration of colonization events (Bryant and Janz 1996). The essential idea is that clearcut habitats may intercept dispersing marmots by offering nearby habitats in which to settle (Bryant 1990). If these habitats act as "sinks" the result may be to reduce long distance dispersal by intercepting dispersers and providing them with attractive but sub-optimal habitats in which to settle. If this hypothesis is correct then *M. vancouverensis* should not respond in proportion to clearcut habitat availability. Instead, the prediction is that clearcut colonies should show chronic low demographic performance. Metapopulation theory also predicts that more isolated colonies should receive fewer immigrants and show higher extinction rates. Finally, the sink-connectivity hypothesis predicts

that colonizations of clearcuts should be spatially concentrated and that colonizations would rarely occur at more isolated locations.

Predator hypothesis

Predators can play a significant role in regulating prey populations, particularly when prey populations are low (reviewed by Flowerdew 1987). For example, mustelids apparently spend much effort hunting voles even when vole density is low (Fitzgerald 1977). Such situations may result in what has come to be known as the "predator-pit" phenomenon, in which predators exert pressure on low-density prey populations sufficient to prevent their recovery (Haber 1977). Predators could act as a limiting factor for Vancouver Island marmots, particularly given the small size of colonies and their limited geographic distribution.

The predation hypothesis follows from evidence of mortality caused by predators such as cougars (*Felis concolor*), wolves (*Canis lupus*) and golden eagles (*Aquila chrysaetos*). *Marmota vancouverensis* apparently evolved in the presence of these predators, so the problem is not simply that of exposure to a "novel" predator (see Vitousek 1988 for a description of this problem for island endemics). However there are several possible mechanisms that may have increased predation pressure. These include increased predator populations, depressed alternative prey abundance and consequent "switching" of hunting effort (Bergerud 1983), increased predator mobility or increased hunting success by individual predators (Bryant 1997).

One prediction of the predation hypothesis is that marmot survival would be associated with predator abundance (or abundance of alternative prey such as deer if the "switching" idea is valid). However, spatial or temporal patterns of mortality could also be relevant. It is unlikely that mortality due to predation would show episodic pattern and be concentrated within particular years or at individual colonies. Most potential marmot predators are long-lived compared to marmots. In addition the ability to become successful at hunting marmots presumably represents learned behavior that would not be exercised sporadically. While most predators are highly mobile compared to the 150 km² area of the Nanaimo Lakes metapopulation, it also seems logical to predict that they would focus hunting efforts in areas where success is maximized. For these reasons a basic prediction of the predation hypothesis is that marmot survival should be spatially correlated as a function of decreasing between-colony distance. Finally, because predation does not occur during winter, mortality should be evenly distributed throughout the summer active season.

Disease hypothesis

Recent *M. vancouverensis* dynamics may be caused by disease or parasites. The disease hypothesis originated after four marmots died during hibernation after being transplanted (Bryant et al. in press). In this case the presumptive cause of death was a bacterial infection (*Yersinia fredericksenii*). Although *Yersinia* was detected in other marmot species (Bibikov 1992), to my knowledge this represents one of the few cases in which marmot mortality has been directly associated with disease. It remains unclear what factors precipitated the disease event, or whether the organism is native to Vancouver Island. It is possible that the bacterium was present on the release site or caused extinction of marmots at sites elsewhere in the past. It is also possible that the organism represents a new disease, that introduced species such as eastern cottontail rabbits (*Sylvilagus floridanus*) are acting as novel disease vectors, or that "normal" low-level marmot health problems are exacerbated by environmental conditions.

Disease-induced mortality could show episodic pattern if the organism is particularly virulent. In this case mortality would be expected to be concentrated at particular colonies or years. Alternatively, mortality due to disease could show chronic pattern if the effect of the organism is to slightly depress survival rates. This leads to the contrary prediction that mortality would be temporally correlated within colonies and among years. However, epidemiological theory (e.g., May and Anderson 1972) suggests that in either case one would expect mortality to be spatially correlated. Disease events would be more likely to occur in areas of high marmot density and, depending on the mode of transmission, would be expected to occur more frequently at nearby colonies.

Finally, much of the potential impact of disease depends on the nature of the organism and its history of interaction with *M. vancouverensis*. For example, pathogens that are native to the environment would be expected to cause abrupt pulses of mortality followed by a return to normal conditions after virulence decreases (either because surviving marmots are more resistant or because other conditions change; e.g., Blake et al. 1991). Alternatively, a non-native organism (or a non-native means of exposure) might be expected to produce a growing incidence of high mortality events with no subsequent recovery.

Non-exclusive hypotheses, testable predictions and practical significance

The question of why *M. vancouverensis* is declining is inherently complex. The five general hypotheses are not mutually exclusive and result in many testable predictions. Some predictions are related to only one of the hypotheses, but others relate to two or more. For this reason my

approach was to construct sets of predictions that were both amenable to analysis and would allow inference to be made based on the cumulative "weight of evidence" (Platt 1964).

The predictions and expected nature of the relationships are as follows:

	Tracking	Weather	Sink	Predator	Disease
1. Reproduction and survival will be chronically low at some natural colonies.	yes	no	-	-	-
2. Reproduction and survival will be associated with habitat type or site characteristics such as elevation or aspect.	no	-	yes	-	-
3. Colonization of clearcuts will occur in proportion to their availability.	yes	-	no	-	-
4. Reproduction and survival will be associated with age of regenerating clearcuts.	yes	-	-	-	-
5. Reproduction and survival will be associated with weather measurements.	-	yes	-	-	-
6. Reproduction and survival will be chronically low in clearcuts.		-	yes	-	-
7. Isolated colonies will show higher extinction rates.	-	-	yes	-	-
8. Isolated colonies will show lower apparent survival due to reduced immigration.	-	-	yes	-	-
9. Colonizations of clearcuts will be spatially concentrated.	no	-	yes	-	-
10. Survival will be spatially correlated.	no	no	no	yes	yes
11. Survival will be density-dependent.	no	no	no	-	yes
12. Survival will be associated with abundance of predators or alternative prey such as deer.	-	-	-	yes	-
13. Episodes of high mortality will occur randomly over time.	-	yes	-	no	maybe

	Tracking	Weather	Sink	Predator	Disease
14. Incidence of high mortality episodes will increase over time.	-	no	-	maybe	maybe
15. Most mortality will occur during summer.	-	-	-	yes	-

The practical significance of the hypotheses is that they suggest different interpretations about the feasibility of recovering *M. vancouverensis* populations and about the direction of management activities.

Specifically, if marmot declines are primarily caused by long-term changes in climate (habitat tracking) then efforts to re-establish colonies on central Vancouver Island will likely fail and there may be little that can be done to recover marmot populations. On the other hand, if habitat tracking is manifested by marmot response to tree invasion, then removal of trees could be a simple and inexpensive habitat enhancement technique. Retention of the weather hypothesis would yield few management possibilities but might offer hope that recent dynamics represent a temporary aberration and that conditions will improve on their own. If forestry has created "sink" habitats and influenced dispersal (sink-connectivity hypothesis), then marmots on southern Vancouver Island are in serious jeopardy and the only possible strategy is the one currently proposed: captive-breeding combined with reintroductions. Retention of the predator or disease hypotheses would reinforce this interpretation and raise additional management issues such as predator control and removal or quarantine of animals from the wild.

STUDY AREAS

The Nanaimo Lakes marmot metapopulation is located within the Coastal Western Hemlock and Mountain Hemlock biogeoclimatic zones of the Georgia Depression Ecoprovince (Demarchi 1988). This region is characterized by an effective rain shadow in the lee of the Vancouver Island Mountains, and consequently is much dryer than sites on the west coast of Vancouver Island (Campbell et al. 1990*a*). Mountains are typically lower in elevation and somewhat less rugged than are the mountains of central and northern Vancouver Island.

Population data were obtained from the entire Nanaimo Lakes metapopulation (Figure 2). Data from Mount Washington colonies on central Vancouver Island were excluded because of small sample sizes, because colonies were infrequently sampled, and because it is unlikely that dispersal occurs between that mountain and the southern metapopulation (Bryant and Janz 1996). Five intensively studied colonies illustrate the variety of habitats occupied by Vancouver Island marmots.

The Haley Lake and Green Mountain sites are steeply sloped (30° to 45°) south or southwest-facing meadows kept free of trees by snow-creep and avalanches. Elevations are 1040 and 1420 m respectively. Common plant species included *Phlox diffusa*, *Castilleja* spp., *Erythronium grandiflorum*, *Saxifraga ferruginea*, *S. occidentalis*, *Anaphalis margaritacea*, *Aster foliaceus* and *Lupinus latifolius* (Milko 1984, Milko and Bell 1985). Both sites had numerous boulders and rock outcrops that marmots use as "loafing spots". The mountain summits above the marmot meadows are parklands of mountain hemlock with small ponds and a heavy shrub layer of *Vaccinium* spp*., Phyllodoce empetriformis,* and *Rhododendron albiflorum*. Soils on the meadows themselves consist of colluvial veneers (<1m) overlying bedrock. Bedrock outcrops occur on the upper slopes, with deeper colluvium on the lower slopes. The Haley Lake and Green Mountain colonies were 8 km apart, but connected by a ridge system that runs north-south. Both sites have a long history of marmot occupancy, with records dating from 1915 (Haley Lake) and 1954 (Green Mountain).

The Vaughan Road clearcut colony is located 1 km west of the Haley Lake natural colony, in an area that was logged between 1974 and 1978 (elevation is 940 m). Marmots were first observed there in 1983. Aspect is west-southwest and the site is surrounded by steep hills to the east and west. The Pat Lake site is a steep north-facing bowl surrounding a shallow lake 16 km southeast of Haley Lake and 2 km east of Mount Whymper, where marmots also occur.
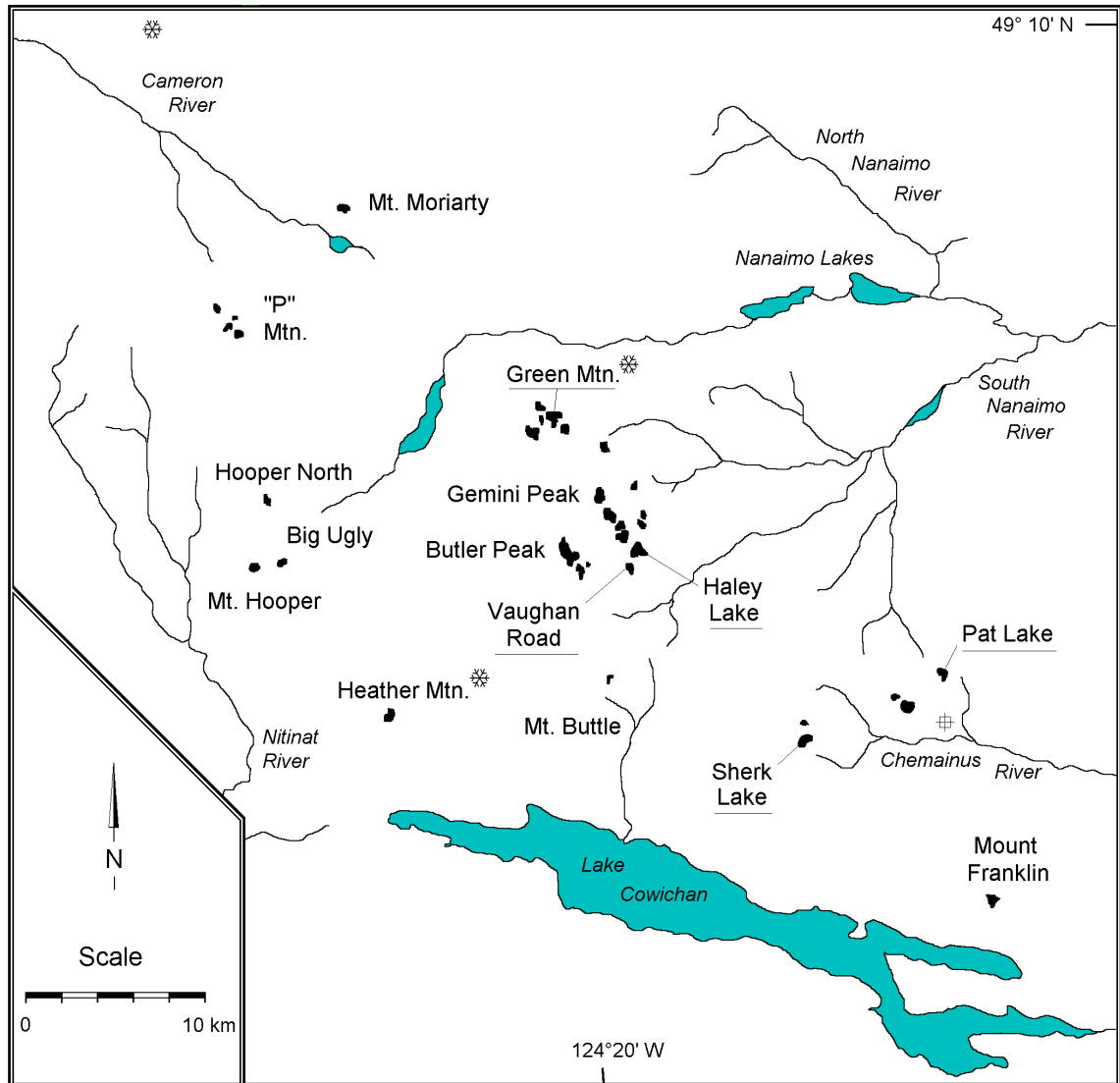
Figure 2: The Nanaimo Lakes metapopulation. This map illustrates cumulative conditions. Not all colonies were occupied simultaneously. Locations of intensively studied colonies are underlined. Snowpack sampling stations (✻) and the Copper Canyon weather station (⊕) are also indicated.

Elevation at Pat Lake was 900 meters. The site was logged between 1978 and 1979, and marmots were first discovered there in 1985. The Sherk Lake site was a south-facing slope at 980 m elevation on the southern flank of Mount Landalt. The area was logged in 1977, and marmots were first reported there in 1992. The Sherk Lake colony was within 2 km of another Mount Landalt location where marmots were reported in natural meadows during the 1980s and not subsequently. Vegetation at clearcut colonies differs from that at natural sub-alpine meadows, although systematic vegetation work has not been performed on them. Trees were generally dominated by alder (*Alnus sitchensis*) and regenerating conifers. Many wildflower species found at natural meadows were not present in the clearcut sites, although *L. latifolius*, *A. margaritacea* and *Epilobium angustifolium* were common.

M. vancouverensis inhabits other vegetation types as well. For example, the habitat on Mount Buttle is dominated by scattered alpine fir *(Abies lasiocarpa)* and mountain hemlock *(Tsuga mertensiana)* interspersed with dwarf juniper *(Juniperus communis)* and blueberries *(Vaccinium* spp.). Marmots on the northwest ridge of "P" Mountain live on steep cliffs and talus slides, while those on Mount Heather and Westerholm Basin live amidst willow *(Salix)* thickets interspersed with rock slides.

METHODS

Population counts

Marmot counts were made by many persons (see Acknowledgments). Methods were basic: scanning meadows and cliffs with binoculars or spotting scopes, listening for marmot whistles and searching for burrows, scat and mud-stains on rocks, stumps or logs. Marmots were classified as adults, yearlings or pups (young-of-the-year) based on size and pelage. The latter are readily identifiable by their small size and dark, almost black, pelage (Nagorsen 1987). Yearlings can be distinguished by their uniform pelage color and small relative size, although it becomes more difficult in late summer. Most counts were conducted before 1100 hours to coincide with known marmot activity rhythms (Heard 1977). Counts of pups were made after early July, when they first emerge from their natal burrows (Bryant 1996).

Count data provided minimum numbers of adults, yearlings and pups present for each site-year combination. Daily count tallies were considered as repeated measures (Krebs 1989), and I took the highest annual count for each age-class to represent minimum population sizes for each colony (hereafter the "observed" number). For each site I also defined the long-term average number of adults, yearlings and juveniles across years as the "expected" number. The extent of annual count coverage was estimated by summing the expected numbers from the colonies that were actually counted, and expressing this as a proportion of the expected total had every colony been counted. Count intensity was expressed as the total number of counts made per site-year combination.

Population estimation

To estimate population size I first calculated sums of observed and expected numbers using those sites that received at least one count. The $\Sigma_{observed}/\Sigma_{expected}$ ratio is therefore an index of the extent to which observed numbers differ from long-term average. I also summed the expected numbers from all colonies presumed to be occupied ($\Sigma_{occupied}$). To do this I assumed that all natural colonies were occupied even if they did not receive counts (i.e., I included their contribution). However for clearcuts I assumed that they were not occupied prior to the year of discovery, and that they would become unsuitable 20 years after logging. If one assumes that trends in the overall population are reflected by colonies that received counts, then a crude estimate of population size can be obtained by multiplying $\Sigma_{observed}/\Sigma_{expected}$ by $\Sigma_{occupied}$.

The assumption that trends at colonies receiving counts are representative of trends elsewhere is probably reasonable for years in which count effort was extensive (1980-1986 and 1992-1997).

It is more tenuous for years in which few colonies were counted (1972-1979 and 1987-1991). To minimize error I did not calculate $\Sigma_{observed}/\Sigma_{expected} * \Sigma_{occupied}$ for years in which fewer than five reproductive colonies in natural habitats (25% of the total colonies and 35% of $\Sigma_{occupied}$) were counted.

Finally I applied correction factors to account for probable count underestimation. The correction factor for adult marmots was based on the average number of counts made per site-year at non-intensively studied colonies, using a regression formula obtained from the probability of resighting tagged marmots at intensively studied colonies (Bryant and Janz 1996). In practice, the correction factor varied from 1.19 to 1.66 (average = 1.40, a value similar to that obtained for alpine marmots: 1.25: Cortot et al. 1996). Because juvenile marmots typically emerge in July there is little time in which to conduct repeated counts and the same statistical approach could not be used to correct the results. Instead a constant multiplier (1.2) was used. This multiplier was obtained from average litter size at intensively studied colonies divided by average litter size at other colonies (Bryant and Janz 1996). Correction factors were applied to the total observed numbers of adults and juveniles within natural and clearcut habitat classes and not to individual colonies. Correction of individual site-year estimates was unjustifiable because some colonies were probably counted accurately despite receiving few repeated visits.

Capture, handling and age-assignment

Marmots were ear-tagged and monitored at five colonies from 1987 through 1998 (Green Mountain, Haley Lake, Pat Lake, Sherk Lake and Vaughan Road). At these sites most animals were ear-tagged and some animals were radio-telemetered. Numerous repeated visits provided accurate population estimates for most years (Bryant 1990, 1996). Capture rates were high and reproductive performance, persistence, and immigration rates could therefore be estimated with precision.

Marmots were captured using raccoon-sized single-door Havahart traps (model 1079, Woodstream Corporation, Littitz, PA) baited with peanut butter. Once trapped, marmots were transferred to a cone-shaped canvas handling bag. The large opening was placed around the Havahart trap and the door was opened, whereupon the marmot would run into the bag and be physically restrained as the bag narrowed.

A mixture of Ketamine hydrochloride (Rogarsetic®, Rogets Pharmaceuticals, Vancouver, BC) and Midazolam (Versed®, Hoffman-La Roche Ltd., Missisauga, ON) was used to facilitate animal

handling. Dosage was normally 40 mg/kg of Ketamine and 5 mg/kg of Midazolam, following guidelines established through experience and veterinary collaboration (Woodbury 1997). Injections were made intramuscularly, in the lumbar muscles, through the handling bag. Note that with this dosage and protocol, animals were sedated but not completely immobilized. The drug normally took effect within five minutes of injection and the animal could then be removed from the handling sock. A Bacitracin-Neomycin-Polymyxin ophthalmic ointment was used to protect the animal's eyes during handling (Vatropelycin[®]; Altana Inc., New York, NY).

Morphological data were recorded at time of capture: sex, weight, total length including tail, body length excluding tail, tail length, neck circumference, chest circumference, length of hindfoot from toe to edge of pad, and length of foreleg from toe to elbow. Weights were measured to the nearest 100 grams using a spring scale; all external measurements were made with a flexible plastic metric tape to the nearest mm. Sex determination was made by everting the genitalia, palpating for testes and/or by measuring the distance from anus to genital opening (Heard 1977). Pelage characteristics, abundance of parasites, fat condition and any external characteristics, such as scars, which could aid in re-identification were noted. Marmots were placed in one of four age-classes at time of capture using the following criteria:

Juveniles (young-of-the-year): small body size (body length = 30-47 cm, forearm length = 10.1-13.0 cm, weight = 1-3.75 kg), uniformly dark pelage (Nagorsen 1987) with no faded fur, first observation in late June or early July (Bryant and Janz 1996, Heard 1977), and observed emergence from natal burrows.

Yearlings (1 year-olds): Any small, dark marmot captured prior to mid-June was unquestionably a yearling (Bryant and Janz 1996, Heard 1977). In practice, juveniles and yearlings were distinguishable well past this date, as yearlings were larger (body length =35-54 cm, forearm = 12.0-15.5 cm, weight = 2.0-4.75 kg). By late August, most yearlings are either in faded overall pelage, or are in partial molt (unpublished photographs of known-age yearlings).

Sub-adults (2 year-olds): Most "first-time" captures were assigned to this category by default. Marmots in this age-class were full-sized (body length = 44.2-55.5 cm, forearm = 12.7-17.1 cm, weight = 3.5-5.5 kg) but were non-reproductive. In May and June, 2 year-olds have usually completed their first molt and exhibit a uniformly dark pelage, but often show a patch of faded (rufous) fur on the dorsal surface at the base of the tail (unpublished photographs of known-age animals, this study).

Adults (3 years and older): Large-bodied males (>60 cm, forearm >16 cm, weight >5.5 kg) and all reproductive females were initially classified as 3 year-olds. Molt patterns are unpredictable beyond age 2 (unpublished photographs of known-age animals, this study) but typically show a mottled appearance of old (faded) and new fur.

Data from animals originally captured as juveniles or yearlings were coded as "known-age" data, and data from other animals were coded as "presumed-age" data. My aging protocol was intentionally conservative, and undoubtedly underestimated the true age of older animals. The reverse is not true. It is unlikely that I overestimated marmot ages using the above criteria. Marmots were equipped with ear-tags in both ears (monel self-piercing tags, style #1005-3, National Band and Tag Company, Newport, KY).

Surgical implantation and radio-telemetry

Radio transmitters were surgically implanted in order to determine causes of mortality and movement patterns. I used two types of radio transmitters (from Custom Telemetry, Watkinsville, GA, and Telonics, Mesa, AZ). The former were identical to those used by Van Vuren (1989), but performance was characterized by weak signal strength and relatively short battery life (overall dimensions = 110 x 20 mm, weight = 35 grams). In 1994 I switched to Telonics units (model IMP 300), which contained a larger battery (overall dimensions = 89 x 23 mm, weight = 40 grams). Both transmitters featured temperature-dependent pulse rates (50-60 beats per minute at 35 C°). Transmitters were encased in beeswax and sterilized by soaking in povidone-iodine solution for 24 hours prior to implantation.

Surgical implants were performed in the field by veterinarians (see Acknowledgments). After preliminary sedation with injectable agents to facilitate handling, marmots were anaesthetized using 2.0-3.0% isofluorine gas (Aerrane®, Anaquest, Missisauga, ON) administered with bottled oxygen and an Isotec® vaporizer (Ohmeda, Madison WI) mated to a small animal mask. Oxygen flow rates were 2 to 3 liters per minute. After induction, anesthesia was maintained at reduced isofluorine concentration (1.5-2.0%). This practice shortened recovery time to 15-30 minutes and allowed precise control of the depth of anesthesia. Transmitters were implanted in the intraperitoneal cavity while animals were restrained on a portable steel operating table. Other deviations from Van Vuren's procedure included incision through the linea alba to minimize muscle trauma and blood loss, and the use of methyl-methacrylate glue (Vetbond®, 3M, St. Paul, MN) to reinforce stitches. Antibiotics were not dispensed routinely, although enrofloxacin (Baytril®) was used on several occasions after animals received superficial abrasions from traps.

Sterile saline solution was used in place of a povidone-iodine wash to irrigate incisions and clean transmitters prior to implantation.

Instruments, masks, capes and drapes were autoclaved prior to use, and sterile conditions were maintained as far as was possible. The surgical "drug kit" and "surgery kit" were carried in backpacks and a waterproof plastic case, weighed <80 kg in total, and could be quickly positioned by 3-4 persons even in steep terrain. Surgeries in low elevation habitats with good road access were often performed by two persons. All animals were released within 1.5 hours of initial capture.

Transmitters were monitored using a Telonics receiver (model TR-2) and either a two-element "H" (model RA-2A) or folding three-element "yagi" antenna (model RA-3). The former gave superior directionality. Signal-bounce from steep terrain often made radio-telemetry difficult. Unless the animal was plainly visible, the normal procedure was to "walk down" the signal rather than attempt to triangulate from compass bearings (e.g., White and Garrott 1990). Searches for missing animals were conducted on foot, by road and occasionally by helicopter. Close proximity to marmots was evaluated by removing the antenna to determine whether the signal was still audible; in practice this typically occurred when transmitters were within 3-5 meters of the receiver.

Colony-specific demographic rates

The finite rate of population increase (λ) is the essential measure of colony success. By definition, a population will increase if $\lambda > 1.0$, be stable if $\lambda = 1.0$ and decline if $\lambda < 1.0$. There are several methods to calculate λ but I used Pulliam's (1988) basic formula because it corresponds well to the types of data that can be obtained from marmot counts. The formula is:

$$\lambda = P_A + (P_J * \beta)$$

in which P_A is the annual probability of adult survival, P_J is the annual probability of juvenile survival, and β is the annual per capita birth rate. Colony-specific annual rates were compiled from intensively studied colonies and non-intensive marmot counts as follows:

Adult survival: At intensively studied colonies, adult survival rates were estimated from resightings of previously-tagged adults and yearlings. Given ear-tag loss, dispersal and individuals that could have been missed due to low sampling effort, resightings yield a minimum adult survival rate. At other colonies, "apparent" adult survival rates were based on consecutive annual counts of yearlings plus adults and apparent survivors (i.e., minimum numbers of adults excluding yearlings

in the following year). Presence of immigrants ensures that this will yield an inflated survival rate (using Pulliam's terminology, this actually represents "*i-d-e*" or net immigration-death-emigration). For cases in which numbers of adults increased in the consecutive year, apparent survival was assumed to be 1.0, with the remainder assumed to represent immigrants.

Juvenile survival: Survival of pups (young-of-the-year) was estimated by comparing counts of pups with counts of yearlings in the following year. Pups and yearlings apparently do not disperse (Bryant 1996) so survival estimates should be robust if sufficient sampling effort was made. Resightings of tagged pups at intensively studied colonies provided an independent estimate of survival.

Per capita births: For all colonies I defined per capita birth rate as the total number of pups divided by the total number of non-pups. I also calculated the probability of breeding (number of litters divided by the number of non-pups) and average litter sizes (pups per litter) to test whether per capita births accurately reflected these variables.

Relative density: Observed/expected ratios provided a measure of "saturation" or relative density. This was calculated as the observed number of animals divided by the long-term expected number for that colony. Relative density was estimated separately for adults and pups.

Immigration-emigration: Data were insufficient to estimate dispersal (emigration) rates. However, some inference could be obtained from four independent sources of data. First, resightings of tagged marmots at new colonies provided empirical information about the magnitude and direction of dispersal movements, and sometimes allowed inference about the timing of dispersal. Second, measurement of untagged immigrants at intensively studied colonies permitted inference about the age-sex composition of immigrants. Third, location records for solitary marmots in low elevation, non-typical habitats were compared with the location of the nearest colony known to be active in that year. Resulting between-location distances permitted estimates of minimum dispersal distances (these will be underestimates unless animals originated in the nearest colony, which is unlikely). Fourth, those cases for which apparent adult survival >1.0 (see above) permitted assessment of when and where large influxes of immigrants may have occurred.

Mortality: Mortality patterns were impossible to describe with precision. Radio-telemetry provided useful data about causes of death but sample sizes were small. Disappearances of tagged marmots yield a maximum mortality rate (because some tagged marmots probably dispersed and survived but were not seen again). To gain additional insight about possible factors I evaluated the

timing of last observation for each marmot that disappeared. My reasoning was that disappearances that were concentrated at particular times could suggest dispersal (spring disappearances) or mortality during hibernation (late-season disappearances). Conversely, disappearances that were distributed throughout the active season could represent the effect of constant mortality factors such as predation.

Lifetime reproductive performance: Tagged females that disappeared for at least one active season (and were presumed to have died) were used to calculate lifetime reproductive performance (i.e., the total number of juveniles produced by that female). Females confirmed to be alive in 1997 were excluded as they could reproduce again.

Colonizations and extinctions: Count records were used to compile discovery dates (earliest record of occupancy), colonization date (for clearcuts only; many natural colonies probably existed long before they were first visited by observers and extinction date (previously occupied sites that had been vacant for at least 2 years prior to the 1997 season). Records of non-reproductive "potential" colonies (Bryant and Janz 1996) were excluded. It is possible that these records represented marmots "in transit" that did not remain at the location. For clearcuts, I calculated longevity (extinction date minus colonization date). This calculation could not be made for natural colonies because of the uncertainty over dates of colonization. To test whether clearcut location was important to colonizing marmots, I randomly sampled 30 clearcuts of appropriate age and elevation, within the apparent dispersal capability of marmots, in order to compare the spatial location of these sites with those clearcuts that were actually colonized.

Landscape conditions

To measure conditions at marmot colonies, landscape change and potential clearcut marmot habitats over time, I used a Geographic Information System (ARC/INFO; Environmental Systems Research Institute, 1994) to create digital landscape maps. These maps contained topographic features, forest cover data, roads and marmot locations. Software developed by the same manufacturer (ARCVIEW 3.0) was used to query the resulting maps and measure landscape conditions.

Colony-specific habitat conditions: Habitat variables included type (natural versus clearcut), elevation (m above sea level), aspect (degrees of compass bearing) and patch size (in hectares; clearcut habitats were excluded as it was normally impossible to accurately define the spatial extent of marmot use). For clearcut colonies, the age of the regenerating forest was measured

(current year minus date of logging). Spatial locations were tabulated in UTM units (Universal Transverse Mercator projection using the 1983 North American Datum). Two measures of isolation were calculated: isolation (median distance of that colony to all other active colonies, expressed in km), and nearest neighbor proximity (distance to the nearest active colony, also expressed in km). To facilitate exploratory analyses, resulting data were then dichotomously coded based on the median value obtained (i.e., high versus low elevation, exposed versus sheltered aspect, large versus small habitats, young versus old clearcuts, and isolated versus clustered colonies).

Landscape conditions: The size of the GIS study coverage was 1006 km² and included all extant marmot colonies south of Alberni Inlet. Landscape measurements included the annual area of forests classified by forest companies as mature (old-growth) and the annual area logged above or below 700 m elevation. This demarcation was selected based on the apparent inability of marmots to colonize low elevation habitats (Bryant and Janz 1996). Potential clearcut marmot habitat was defined as the area of logged clearcuts above 700 meters in elevation and between the ages of 0 and 15 years after logging. This definition probably overestimates the area of habitat that could actually be used by marmots because it included sites of all slopes and aspect. Most marmot clearcut colonization events occurred on north-west to south-east-facing slopes and on relatively steep slopes.

Dates of logging road construction were unavailable from the raw digital data, although the cumulative (1996) extent of the road network was available. I therefore assumed that roads were constructed in relative proportion to the extent of logging activities, and queried the digital map for roads that intersected current and previous clearcuts. This calculation yielded a minimum estimate of road density. Logging roads deteriorate rapidly in the Vancouver Island climate and typically become unusable after a few years if not maintained. However, because my purpose was to explore the possibility of enhanced marmot or predator mobility, I reasoned that animals would continue to use them long after they became impassable to vehicles, and therefore made no allowance for forest regeneration along roads. Road densities were expressed as linear km of roads/km².

Weather

Summer precipitation and temperature data and winter snowpack data were available from several sources. Summer data included daily midday temperatures and total daily rainfall from an automated weather station located in a clearcut at 840 m elevation in Copper Canyon (unpublished

data, B.C. Ministry of Forests). Average daily temperature and precipitation data were also available from Nanaimo Airport (unpublished data, Environment Canada). Snowpack data were available from Green Mountain (1400 m), Heather Mountain (1170 m) and Mount Cokely (1190 m: unpublished data, B.C. Ministry of Environment, Lands and Parks). From these raw data I calculated several variables of possible relevance to marmots. These data cannot be assumed to represent conditions at specific colonies but should reflect annual weather trends for the study area as a whole.

Summer rainfall and temperature: I constructed variables that may influence adults (spring conditions) or adults and juveniles (late summer conditions). Variables included average midday temperature during May and June (in °C), average midday temperature during July and August, total precipitation during May and June (in mm) and total precipitation in July and August. Drought and nutritional effects upon vegetation could be also caused by differences in the timing of rainfall. For this reason I also calculated the number of days with significant (>5 mm) rainfall events in May and June, and number of days with significant rainfall events in July and August. Finally, because early-spring snowmelt patterns could be driven by both rainfall and temperature, I constructed additional variables that were "offset" by one year (to evaluate the possibility that next year's spring weather might influence survival of this year's marmot cohort).

Winter snowpack: Monthly snowpack measurements were averaged among sites and expressed in cm. Two variables were constructed to represent "early" snow conditions that may influence hibernation physiology (average January-February conditions) and "late" conditions that could influence hibernation duration or food availability (June). The latter was also offset by one year to reflect the possibility that next year's snowmelt affects survival of this year's marmot cohort. As with the case of the summer weather station, snowpack sampling locations did not correspond precisely with marmot colonies and cannot therefore be interpreted to reflect local conditions at specific marmot colonies.

Predator-prey trends

Predators: Currently the only long-term measure of terrestrial predator abundance on Vancouver Island comes from sightings made by deer hunters (unpublished data, Ministry of Environment, Lands and Parks). Numbers of cougars (*Felis concolor*) and wolves (*Canis lupus*) seen by deer hunters were expressed per 100 hunter-days. These "hunter-sighting indices" have not been tested for reliability against a known population, and data were obtained from an area considerably larger than the area occupied by marmots (>1500 km²). Additional data were

available concerning numbers of animals "removed" due to trapping, hunting, animal control programs and road-kills. It remains unknown how well these estimators reflect actual abundance. I used both estimators for both species and constructed two additional variables by pooling relevant data to estimate "terrestrial predator abundance" and "terrestrial predator removal". No data were available with which to assess abundance of hawks or eagles.

Prey: Predator impacts upon marmots could also be influenced by "switching" of hunting effort. For this reason I included an abundance measure for black-tailed deer (*Odocoileus hemionus*), an important prey species for wolves and cougars. I reasoned that deer abundance may be inversely related to marmot survival. Abundance was estimated from systematic night counts (Harestad and Jones 1981) and expressed as annual numbers of deer seen per km. The area of deer counts (~150 km²) was centered on the Nanaimo Lakes metapopulation (unpublished data, Ministry of Environment, Lands and Parks).

Statistical analyses

Preliminary analyses were conducted to assess the repeatability and coherence of the data. How consistent were population counts and resulting population estimates? How well did estimates of demographic rates from counts conform with those obtained from marked animals? Were there obvious mechanisms (e.g., ear-tag loss, differential capture or dispersal rates) that rendered the data unusable? Was it possible that mark-recapture efforts themselves caused population declines? Exploratory analyses were pursued to uncover fundamental patterns in the data. Were there temporal, spatial or habitat-specific trends in marmot survival or reproductive rates? Did such trends facilitate testing of more detailed hypotheses? Results from exploratory analyses permitted finalization of the data sets, removal of outliers and development of detailed predictions. Final analyses were designed to test these predictions.

I used mean successive difference tests to evaluate consistency of population counts among successive survey years (Zar 1974). Adult counts, juvenile counts and per capita birth rates were tested separately. I also used intraclass correlation coefficients to assess the repeatability of adult counts. Repeatability (*R*) varies from 0 to 1.0 depending upon the similarity of repeated measurements (Krebs 1989). For this analysis I used raw count data in which the repeated measures were multiple counts made for a given site-year. To determine whether count performance differed with season, I also plotted the "success" of counts against number of days after 30 April and fitted a locally weighted regression curve (LOWESS; Cleveland 1979). Success was defined as the ratio of a given count to the highest count obtained for that site-year.

I also used LOWESS to plot population trajectories for individual clearcut and natural colonies. For this I used the maximum adult count. Pup data were excluded because small numbers of reproductive-age females at most colonies combined with the two-year breeding cycle of most females (Bryant 1996) would induce high variance and would not assist in evaluation of trend. Adult counts were square-root transformed prior to plotting to make the data more easily interpreted. Pearson correlations were used to test for association with year.

To test whether marmots colonized clearcuts in proportion to their availability, I used Spearman rank correlation of the number of colonizations with availability of clearcut habitat above 700 meters elevation in any given year. I used Student *t* tests to determine whether the nearest-colony-neighbor distance of actual colonizations was different from that of randomly selected clearcuts within the study area.

Chi-square tests were used to evaluate independence of demographic rates calculated from intensively studied colonies and non-intensive counts. The same method was used to test for independence among subsets of colonies (high versus low elevation, exposed versus sheltered, natural meadows versus clearcuts, and isolated versus clustered). Mean litter sizes, birth rates, female lifetime reproductive success, and mean age at first reproduction were compared across habitats using Mann-Whitney *U* tests or Student *t* tests for discrete and continuous variables, respectively. Sex ratios of animals first captured as juveniles were tested against an expected 1:1 ratio using χ^2 goodness-of-fit methods (Zar 1974).

Demographic trends were evaluated using life-table analysis and mark-recapture models. Life-tables were constructed using resightings of tagged marmots and raw frequencies of sex and age-specific disappearances (Caughley 1977, Method 2). All rates were calculated from frequencies of sex and age-specific disappearances (d_x). To verify that the tagged marmot cohort reasonably reflected actual trends, I re-calculated life-tables using a) tagged pup data alone, b) all pup data including observations of surviving but untagged yearlings, c) fecundity estimated using the observed ratio of male:female pups, and d) fecundity estimated assuming a 1:1 sex ratio at birth. Fecundity was calculated using observed ratios of male:female pups. Because age-specific samples were so small I did not smooth the L_x values (Krebs 1989) or test for differences in survivorship curve shape (Pyke and Thompson 1986).

I used Cormack-Jolly-Seber models (Pollock et al. 1990) to estimate parametric survival rates and 95% confidence limits. This analysis was performed using SURGE (Cooch et al. 1996) and

followed the Lebreton et al. (1992) approach in seeking the most parsimonious model that explained the data. I also performed a basic elasticity analysis (Caswell 1989) to evaluate which life-history characteristics were most important driving population growth. The analysis involved modifying each of adult survival, pup survival and fecundity estimates in turn by proportional amounts and by calculating the relative effect of each variable upon λ (finite growth rate in years). I used RAMAS/age to calculate λ (Akcakaya and Ferson 1990).

I used stepwise logistic regression (Cox 1975) to test whether environmental conditions were associated with survival or probability of reproduction. Logistic regression is similar to normal multiple regression techniques except that it is designed to explain variation in a binary response variable (i.e., a variable with a value of 0 or 1). Independent variables may be either continuous and categorical. For this analysis I used coded marmot survival data (alive = 1) and reproductive data (produced a litter = 1) together with sets of continuous or categorical environmental variables associated with the predictions. Logistic regression uses McFadden's *Rho²* statistic to evaluate the amount of variation explained by independent variables. Like the analogous *r²* used in linear regression, larger *Rho²* values indicate stronger relationships. However, *Rho²* is generally much smaller, with values of 0.2 to 0.4 considered to indicate extremely powerful relationship (Hensher and Johnson 1981). Logistic regression also yields an "odds ratio" that represents the "odds of making a correct prediction." Negative influences upon a binary response variable produce odds ratios <1.0 while positive influences produce odds ratios >1.0. Overall regression significance was evaluated by likelihood-ratio χ^2 tests (Hosmer and Lemeshow 1989). Tests were performed using Systat 7.0 (SPSS Inc. 1997).

I used Moran's *I* coefficient (Sokal and Oden 1978, Sawada 1998) to evaluate spatial autocorrelation of survival rates. This statistic is analogous to Pearson's *R* except that it is designed to evaluate whether events are similar or dissimilar in a spatial context. Coefficients close to 1.0 indicate that similar values tend to cluster together, and values approaching -1.0 indicate that dissimilar values tend to cluster together. The formula is:

$$I = \sum_i \sum_j W_{ij} \Delta_{ij}$$

in which Δ_{ij} is a measure of the proximity of the variate (in this case apparent survival) between the $_i$th and $_j$th spatial positions and W_{ij} is a spatial weighting function that is a measure of connectivity or "contiguity" of the locations. On a regular grid (quadrat data), contiguity (W_{ij}) is typically set to equal 1 for nearest neighbors and 0 if otherwise (Haining 1990). For spatially complex data (such

as locations of marmot colonies), contiguity can be assigned by applying an "effects radius" relevant to the research question (Smith and Gilpin 1997). In this case only those neighbors within a pre-defined radius are considered to be contiguous ($W_{ij} = 1$).

I reasoned that mortality due to weather would occur over the entirety of the study area but that mortality from predators or disease would occur over progressively smaller areas. I therefore tested for spatial autocorrelation using cumulative effects radius established at 1 km intervals up to a maximum of 15 km (at which the entire metapopulation was included in the effects radius). Reasons of sampling effort (not all colonies were counted in any year), measurement error (annual variation in survival was high) and predicted effects (predators are long-lived) suggested that I evaluate change in spatial autocorrelation over two time periods: "early" (1979-1988) and "late" (1989-1998). Annual survival estimates were treated as repeated measures within the two groups, with care being taken to ensure that nearest-neighbor distances were measured only within years. Significance of Moran's I was evaluated using Z test scores (Sokal and Oden 1978). The null hypothesis is that the observed distribution of events is no different from a distribution in which values are randomly assigned to the same set of spatial locations.

Some analyses resulted in tests with low statistical power (Zar 1974) despite being based on a large fraction of the extant marmot population. I caution that results may resemble parameters more than they resemble sample statistics. I employed a conventional ($\alpha=0.05$) decision rule to accept or reject null hypotheses, but leave it to readers to judge whether observed differences might be biologically significant despite lack of statistical significance (Krebs 1989).

RESULTS

Part 1: The environment

Weather

Summer weather patterns on Vancouver Island varied considerably (Figure 3). Late summer (July-August) measures of cumulative precipitation obtained from Nanaimo airport and Copper Canyon stations were highly correlated (Pearson $r = 0.89$, $n = 22$ years, $P < 0.01$) but early summer (May-June) measures were not ($r = 0.31$, $n = 22$ years, $P > 0.05$). Similarly, average daily temperatures at Nanaimo airport in late summer (July-August) were correlated with average midday temperatures from Copper Canyon ($r = 0.53$, $n = 22$ years, $P < 0.05$) but early spring (May-June) temperatures were not ($r = 0.37$, $n = 21$ years, $P < 0.05$). Both temperature and rainfall data varied more at Copper Canyon. This result is expected. Nanaimo airport is located in a low elevation (100 m) coastal environment on the leeward side of the Vancouver Island mountains. The weather station at Copper Canyon is located at higher elevation (840 m) and is therefore more prone to "mountain weather". Given the probability of site-specific effects of weather upon marmots, there was no *a priori* reason not to use data from Copper Canyon, which is closer to the mountains inhabited by marmots (Appendix 1).

Overall, some years were extremely hot and dry (1979, 1982, 1985 and 1994) and some years were relatively cold and wet (1975, 1976, 1991 and 1993). Annual variation was high. In some years there was snowfall in June (1988 and 1991) and in some years there was virtually no rainfall during summer (1994 and 1996).

Winter conditions are less easily evaluated. Annual and monthly snowpack conditions from Mount Cokely, Green Mountain and Heather Mountain were strongly correlated (r values from 0.68 to 0.83, $n = 18$ years, $P < 0.05$) but data were available from only a single location (Green Mountain) after 1995. The general pattern is that snow begins to accumulate in December and increases through April (Figure 4). There were substantial differences in snowpack accumulation and melt patterns among study sites and among years (my unpublished photographs). Snowpack data must therefore be interpreted as reflecting "average" annual conditions and not site-specific snow depths (Appendix 2).

A) Average midday temperature

B) Average daily rainfall
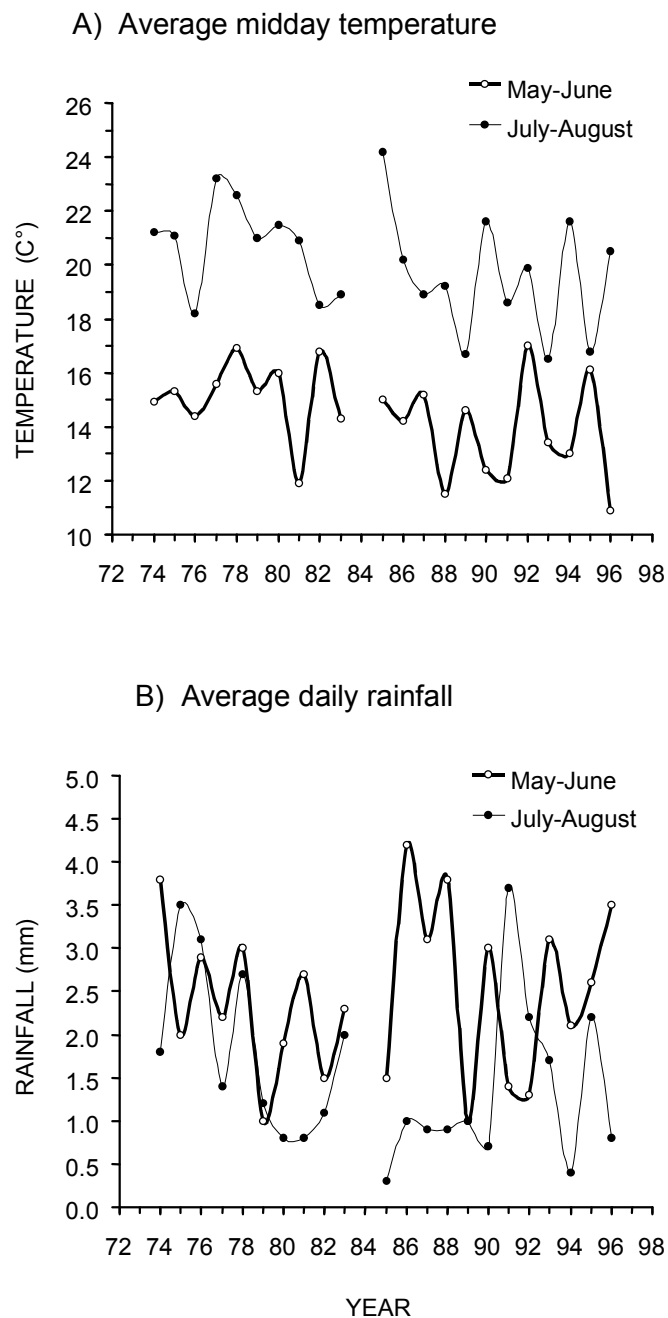
Figure 3: Four measures of summer weather conditions. Data are (A) daily noon temperatures averaged across May-June, and July-September, and (B) average daily rainfall averaged across the same periods at Copper Canyon.

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A) Snowpack accumulation

B) Annual snowpack trends
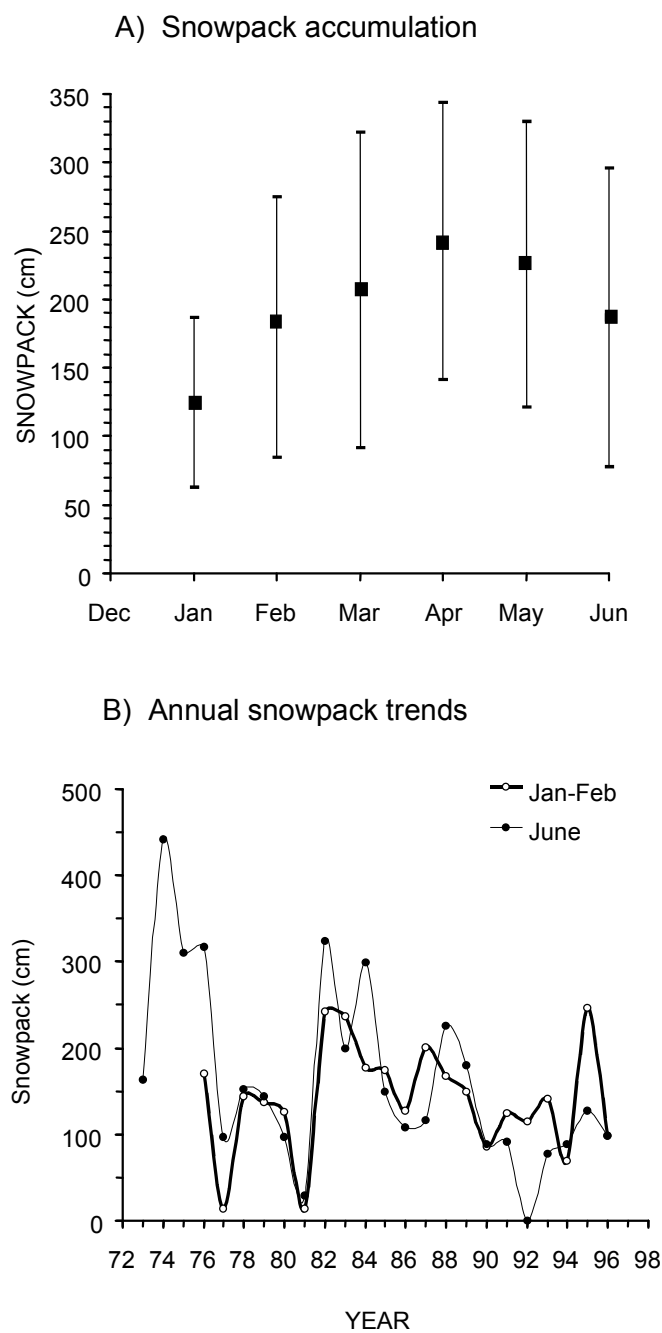
Figure 4: Two measures of snowpack conditions. Data are (A) average and SD
monthly snowpack depths, and (B) early and late winter snowpack depths
across years.

Landscape change

GIS measurements illustrate the extent of commercial forestry operations on privately-owned lands in the Nanaimo Lakes region. There was little forest harvesting prior to 1956 and much of what occurred was concentrated along valley bottoms. This pattern continued through the 1960s. Harvest rates increased during the 1970s, particularly at higher elevations. By 1976 over 75% of the annual harvest occurred above 700 meters in elevation. At least 60% of all forests classified as mature by forest companies within the Nanaimo Lakes region were harvested in a 25 year period (Figure 5). Road development took place at a similar pace and increased fivefold in density during the same period (Figure 6). Potential clearcut marmot habitat was first created during the late 1960s and large amounts (>10,000 hectares) became available during the 1970s (Appendix 3).

Predator-prey abundance

Black-tailed deer abundance declined dramatically from the mid-1970s through the mid-1990s. Current populations are about 40% of the long-term average (Figure 7). Deer abundance estimates were not highly correlated among the 4 sampled areas in the Nanaimo Lakes region, but all showed substantial declines (Appendix 4). Within each sub-region estimates were serially correlated among years (mean square successive difference tests, range of C values = 0.49 - 0.87, $P < 0.05$). This is an expected result given deer longevity, and suggests that systematic roadside night counts provided realistic estimates of deer abundance.

Wolf and cougar abundance indices varied greatly among years (Figure 7). Indices were not correlated among years (mean square successive difference tests, $C = 0.34$ for wolves and 0.14 for cougars, for both species $n =15$ years, $P > 0.05$). These results are unexpected given probable predator longevity and territoriality. Localized predator control activities and incidental kills occurred in the Nanaimo Lakes region throughout the study but were higher in some years. In some years substantial numbers of predators were removed from the area (e.g., 24 wolves and 11 cougars in 1985; Appendix 5). However, there was no congruence between "removal" data and hunter-sighting index in the following year (for wolves, Pearson $r = 0.06$, and for cougars, $r = 0.04$, $n = 15$ years, $P > 0.05$). For both species the hunter sighting index was just as likely to increase as it was to decrease following years of high numbers of removals. I conclude that hunter-sighting indices and removals probably do not reflect actual abundance of cougars and wolves.
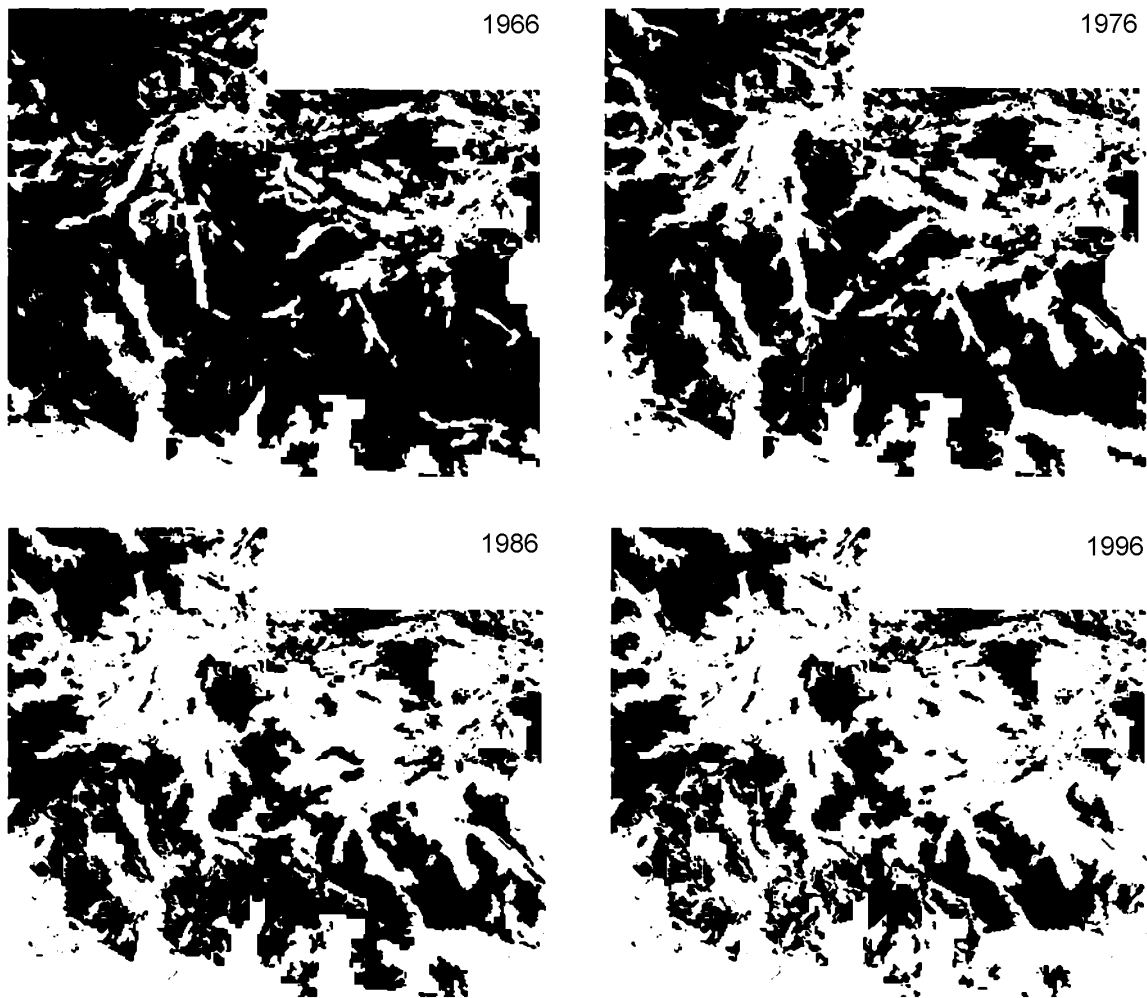
Figure 5:   Extent of forest harvesting over time. Data are unharvested habitats including non-forested habitats (black areas) and harvested forests (white areas) sampled at 10 year intervals from 1966 through 1996. Size of the GIS study coverage was 1006 km², which corresponds almost exactly with the extent of the Nanaimo Lakes metapopulation shown in Figure 2.

A) Forest conditions
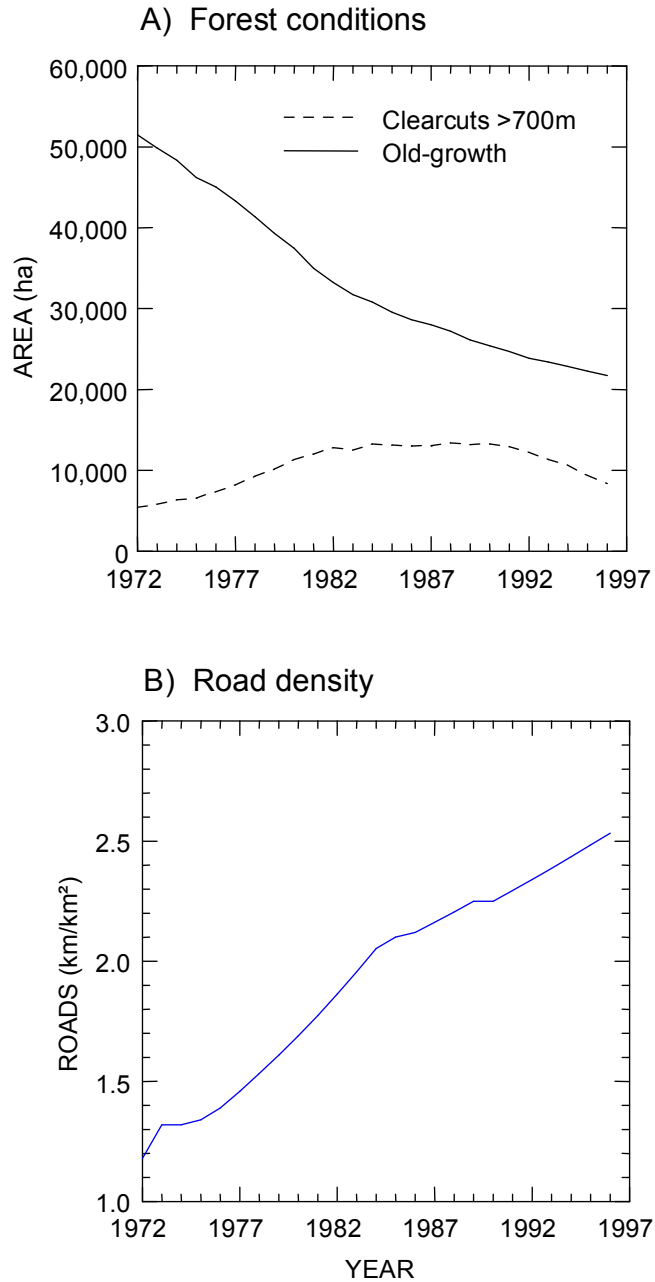
B) Road density

Figure 6: Two measures of landscape change. Data are A) hectares of old-growth forest and potential clearcut marmot habitats (clearcuts above 700 m in elevation and 0-15 years old), and B) road densities (expressed as linear km of road per km²).

A) Deer abundance

B) Predator abundance
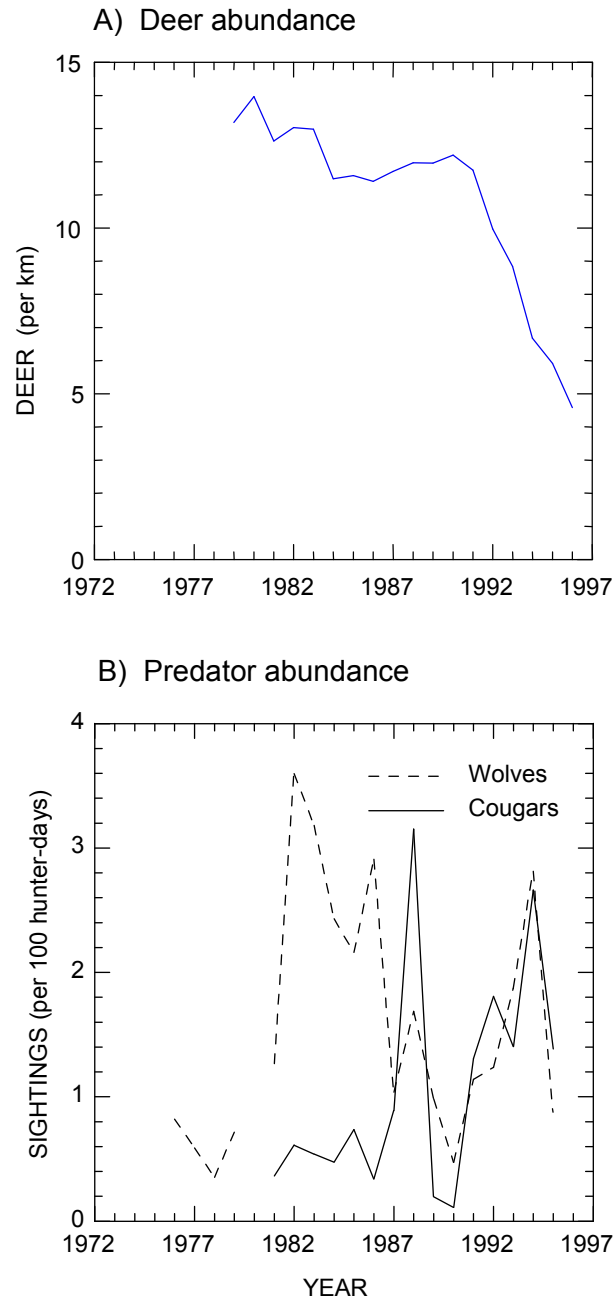
Figure 7: Predator-prey trends. Deer abundance (A) was estimated from nocturnal counts and expressed as numbers seen per kilometer. Wolf and cougar abundance (B) was a "hunter sighting index" and expressed as numbers seen per 100 hunter-days.

Part 2: Sampling effort

Population count efforts

Observers counted marmots on 1711 occasions at colonies or potential colonies within the Nanaimo Lakes metapopulation between 21 April and 7 October during the years 1972-1997. Count coverage was relatively low prior to the 1980s and during the late 1980s. Not every site was visited in each year. Coverage was particularly low in years in which I worked alone or with a single technician (1987-1991). Coverage was higher in years for which dedicated crews were available to count marmots at known colonies (1979-1986 and 1992-1997). In years of low count coverage, efforts were focused on the relatively large and well-known colonies within the Gemini-Green-Haley-Butler core area of distribution. For this reason single-count coverage was obtained for 30-90% of the expected number of marmots in the Nanaimo Lakes metapopulation in every year after 1980 (Figure 8).

Count intensity also varied with time. The five intensively studied mark-recapture colonies typically received more than 10 counts annually with greatly increased effort after 1992. Other colonies were counted 2-4 times per year, with higher frequencies during the peak of count efforts in the early 1980s and after 1992. Coverage for pups (counts after 1 July) was generally consistent with adult coverage (all counts) except for 1985 and 1987, when few late summer counts were made.

Repeatability of marmot counts

Of the 1711 marmot counts, 206 (12%) constituted the only count for a particular site-year. An additional 173 counts (10%) resulted in no marmots or fresh burrows observed, and 227 counts (17%) recorded fresh burrows but no marmots. The remaining 1332 counts constitute repeated measures of colonies known to be active (grand mean = 3.8 counts per site-year combination). Of these, 352 counts (26%) produced maximum counts of adults and 799 (60%) recorded fewer than maximum numbers.

Results from resampled counts of tagged animals suggest that ~ 9 repeated visits are necessary to obtain accurate population sizes but that 2 to 3 counts provide a reasonable index of abundance. On average, single counts resulted in detection of 44% of tagged adults known to be present (Figure 9). Accumulated success for counts repeated 2, 3, and 4 times was 63%, 73% and 78%, respectively. The success of counts is greatly improved if they are made before August (Figure 10).

A) Count coverage
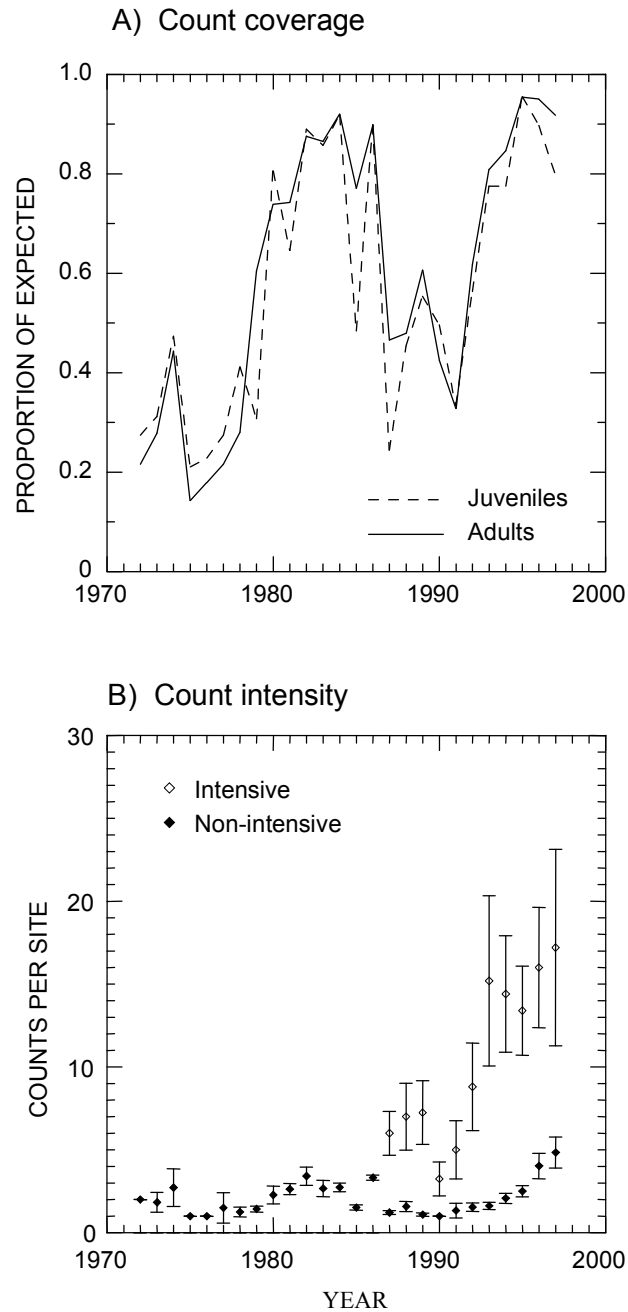
B) Count intensity

Figure 8: Population count extent and intensity. Count extent (A) was estimated as the annual proportion of expected number of marmots contained in habitats that received at least one visit. Count intensity (B) was expressed as $\overline{x}$ (SE) number of counts per site-year at intensively studied and other colonies (see Appendix 6).
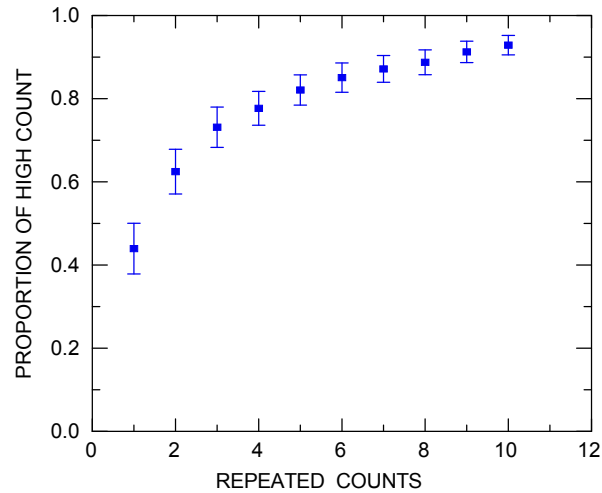
Figure 9: Probable accuracy of marmot counts. Counts at colonies with known numbers of adults ($n = 437$) were resampled in random order to create 100 trials of 10 counts each. Data are mean accumulated success and 95% confidence limits.
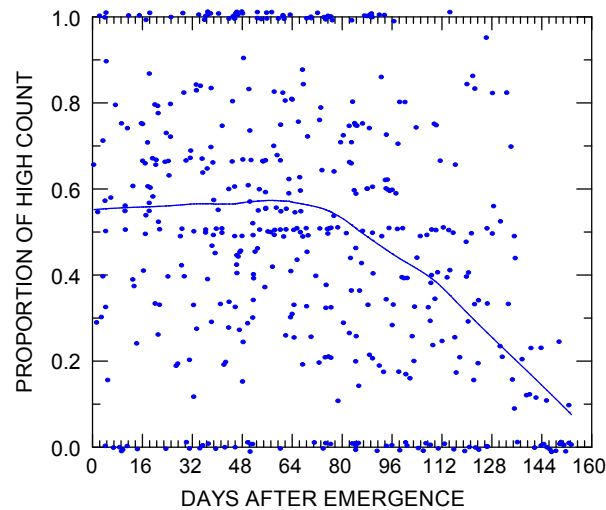
Figure 10: Seasonal effects upon marmot count success. A locally weighted regression (LOWESS) line is shown, and slight "jitter" has been introduced to make the data points more legible. May 1 was defined as the date of emergence.

Count repeatability was moderate (66%). Data from intensively studied colonies showed lower repeatability despite increased numbers of measurements (Table 1). This result appears counterintuitive but in fact is explainable. The intensively studied colonies in which animals were marked commonly experienced some turnover of individuals within a given season (due to mortality,

dispersal and immigration). This had the effect of inflating the annual maximum count because all marked individuals were considered in the total, despite the fact that not all individuals were present at any time. For other colonies it was not possible to distinguish such turnover. The annual maximum count more closely approximated the number present at any given time, with the result of establishing an artificially low target for repeated measures.

Table 1: Repeatability of count data for adults. Cumulatively the data showed moderate (66%) repeatability. Single counts are not likely to produce reasonable estimates of marmot abundance.

	SOURCE OF DATA		
	Cumulative	Intensively studied	Non-intensive counts
N of counts	1332	450	882
N of site-years	254	30	224
Effective n of counts (n_0) *	5.23	14.87	3.93
Num./denom. df	253/1078	29/420	223/658
Repeatability (R)	**0.656**	**0.465**	**0.700**
upper 95% confidence limit	0.695	0.509	0.737
lower 95% confidence limit	0.622	0.430	0.669

* Nomenclature follows Krebs (1989), in which n_0 signifies the average effective number of repeated counts for each site-year combination.

Mark-recapture effort

A total of 144 individual marmots were tagged and monitored at five intensively studied colonies from 1987 through 1998 (Appendix 7). This involved 635 visits, 817 person-days, 1204 trap-days and 306 marmot captures, with approximately equal effort spent at the 2 natural and 3 clearcut colonies. Most (62%) animals were eventually tagged at these colonies. Ear-tag loss rate was low (5%) and loss of both tags was very rare (Appendix 8). Given probable abundance it is likely that ear-tagged individuals represented approximately 10-15% of the entire *M. vancouverensis* population over the 11 year mark-recapture period.

Part 3: Population trends

Probable marmot abundance

Marmot abundance within the Nanaimo Lakes metapopulation changed dramatically during the past two decades. Comparison of observed and expected numbers from 1972 through 1998 showed systematic trends (Figure 11). For adults, observed numbers were consistently above average (134-159%) from 1981 to 1984, and near or below average (53-99%) from 1990 to 1998. The magnitude of annual change was generally small ($\overline{x}$ absolute change = 19.7%, SD = 15.9). Application of a correction factor based on count intensity suggests that adult numbers decreased from a peak of 200-250 during the mid-1980s to fewer than 100 in 1998 (Appendix 9). Probable adult numbers were highly correlated with values in the preceding year (mean square successive difference test, $C = 0.63$, $n = 22$ years, $P < 0.01$), which is a predicted result given known marmot longevity and suspicion that marmots do not disperse after becoming sexually mature and establishing themselves within a colony. I conclude that population counts provide relatively consistent estimates of adult abundance.

For pups the ratio of observed to expected numbers fluctuated more dramatically during the same period (range of annual proportion of expected numbers = 26% to 210%). Magnitude of annual change was greater ($\overline{x}$ absolute change = 79.9%, SD = 50.3%). Probable abundance of pups was not correlated with values observed in the preceding year ($C = 0.01$, $n = 18$ years, $P > 0.05$) but this is not surprising. There is no reason to expect consistent annual reproduction. In fact the reverse is true. Small colony sizes combined with infrequent breeding in adult females ensure that most colonies would not be expected to reproduce in consecutive years. Limited population count effort in some years and consequent extrapolation of trends from a small number of colonies would be expected to exaggerate the variance of observed/expected ratios. I consequently remain less confident of pup abundance estimates.

Colonizations and extinctions

Recent population dynamics were accompanied by a profound change in the spatial structure and habitat associations of the metapopulation. Prior to 1981, marmots were confined to steep natural sub-alpine meadows at elevations above 900 m. Beginning in the early 1980s increased proportions of the Nanaimo Lakes metapopulation inhabited recently harvested (0-15 year old) clearcuts. In the last five years 58% of the probable marmot population inhabited clearcuts (Figure 12).

A) Observed/expected marmots
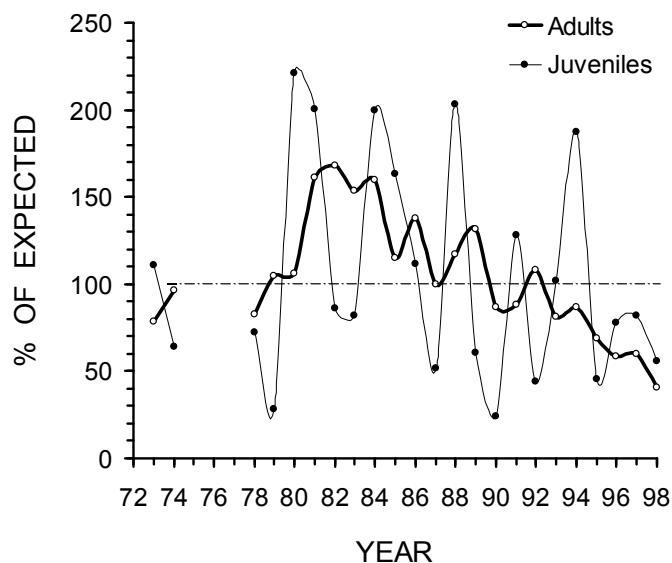
B) Probable marmot abundance
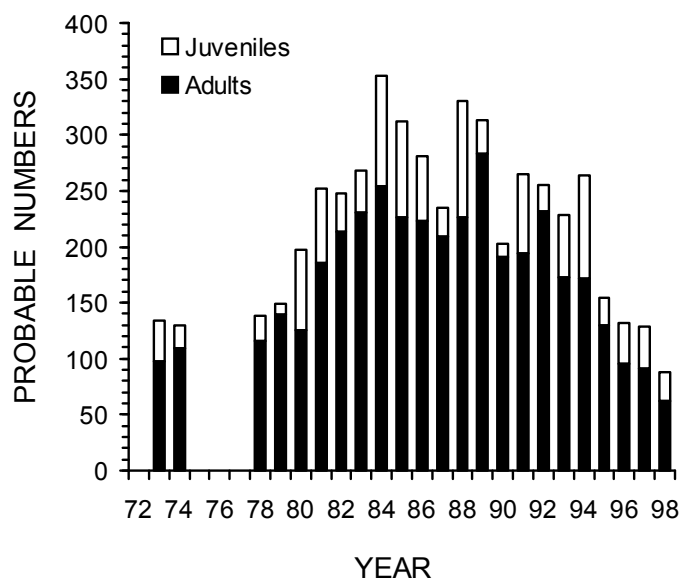
Figure 11: Marmot population trends over time. Percent of expected values (A) were calculated using only those sites counted in any year. Probable marmot numbers (B) were estimated by applying a correction factor based on count effort, by excluding clearcut habitats for years prior to colonization, and by excluding years in which fewer than four sites were counted.
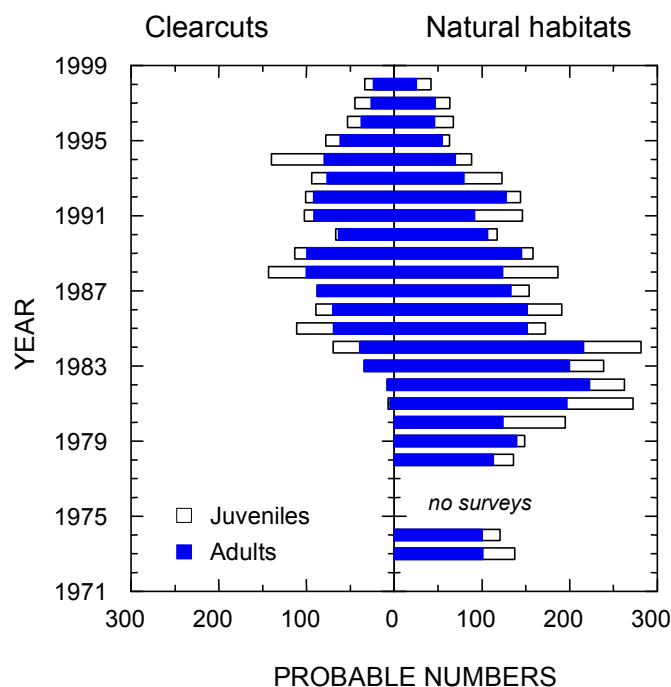
Figure 12: Probable marmot numbers in natural and clearcut habitats. Neither juvenile nor adult abundance was correlated among habitat types (Pearson r = -0.19 for adults and -0.02 for juveniles). The current population probably contains fewer than 100 animals, of which ~50% are found in clearcut habitats.

Marmots apparently first colonized a clearcut in 1981 (Appendix 10). At least seven additional sites were colonized between 1982 and 1985 and in several cases population increases were dramatic. Marmots also apparently colonized some natural meadows during the early 1980s, although it is impossible to confirm which of these represented true colonization events and not belated discovery dates.

Only two new colonies were discovered during the 1990s despite greatly increased search effort and public awareness. Both (Mount Franklin and Sherk Lake) were in clearcut habitats and certainly represent actual colonization events because the habitat was unsuitable for marmots before forest harvesting occurred. In addition, several new habitat patches were discovered on several mountains (e.g. Mount Moriarty and Big Ugly). However, in these cases reproduction has not been confirmed and they may represent sites used only occasionally by marmots. In addition, for reasons identified above it is impossible to distinguish colonization events from pre-existing colonies that were only recently discovered.

Population trends among colonies

Sequential population estimates could not be made for many colonies because of gaps in sampling coverage, but LOWESS regressions were useful in exploring trends over time. Apparently no colony remained stable over the study period (Figure 13). Marmots numbers in natural habitats declined systematically with year. The data suggest a definite upward bulge that occurred in 1983, which probably reflects high reproduction in 1982 or earlier. Numbers of marmots in clearcuts increased greatly during the late 1980s (the Butler "west roads" colony was the largest) but since about 1992 most colonies declined rapidly.

Part 4: Population ecology

Survival

Population dynamics are the inevitable result of differences in birth and death rates. Robust estimates of both processes are essential if causal factors are to be understood.

Juvenile survival: At least 25 of 56 (45%) tagged pups at the intensively studied colonies were confirmed as surviving their first winter. Survival of untagged pups at the same colonies was slightly higher (88 pups and 46 yearlings; persistence = 52%) but not significantly so ($\chi^2 = 0.80$ with 1 df, P=0.37). From these data there seems little reason to suspect that capture influenced pup survival. I therefore used pooled data from tagged and untagged pups to estimate annual survival rates all subsequent analyses. The single exception was that of possible sex bias in survival, which could only be evaluated from tagged pups. Survival was independent of sex. At least 12 of 25 (48%) tagged males survived their first winter, as did 13 of 31 (42%) tagged females ($\chi^2 = 0.21$ with 1 df, P=0.65).

Survival varied dramatically across years and colonies (Appendix 11). Relatively low survival occurred over the winter of 1989-90 (13 survivors of 31 juveniles; 42%), 1990-91, (0 of 8; 0%) and 1994-95 (8 of 27; 30%). Relatively high juvenile survival was observed in 1991-92 (10 of 16; 63%) and 1993-94 (17 of 23; 74%).

The short late summer trapping window precluded any meaningful analysis of dates of last observation to assess the timing of mortality. However, sampling effort was sufficient to confirm that loss of complete litters occurred on at least 12 occasions. This resulted in loss of 43 of the 73 juveniles (59%) that disappeared. Partial mortality of nine litters was also confirmed. This resulted in loss of another 13 of the 73 disappearing juveniles (18%). For the remainder of

A) Natural habitats

r = - 0.385, n=233, P<0.001

ADULTS (square-root)

1978 1983 1988 1993 1998

B) Clearcuts

r = - 0.103, n=87, NS

ADULTS (square-root)

1978 1983 1988 1993 1998

YEAR
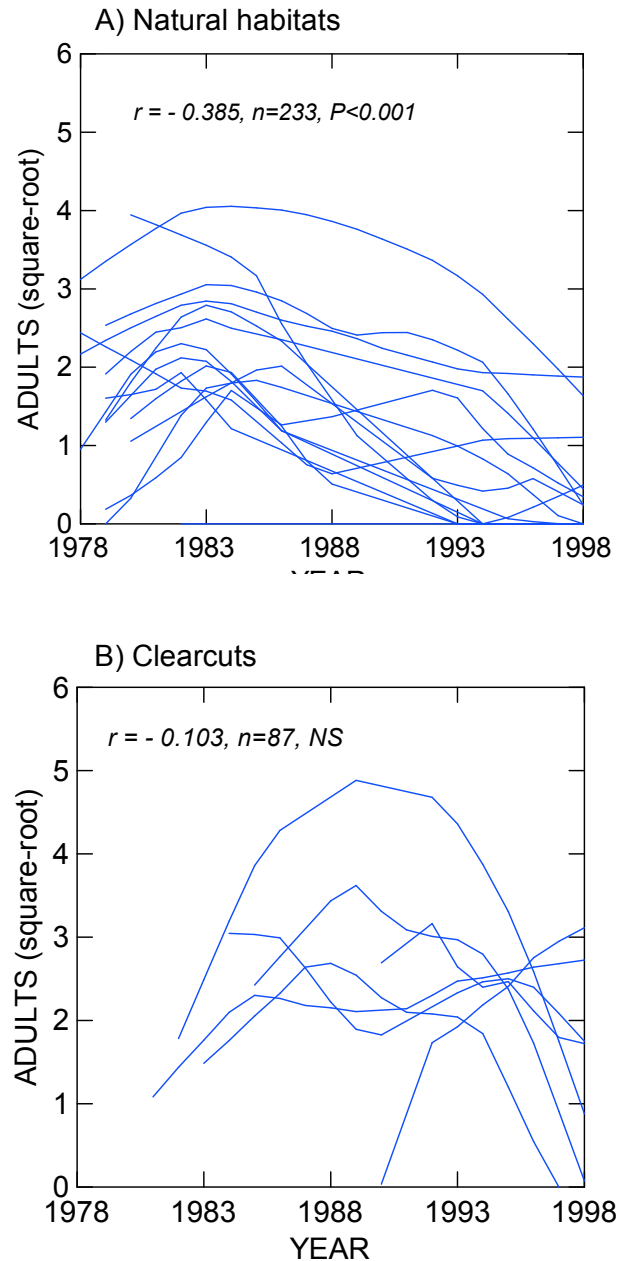
Figure 13: Marmot population trends within and among colonies. The data are LOWESS regressions of annual adult numbers at natural meadows (A) and clearcuts (B). Numbers of adults were square-root transformed to facilitate comparison of trends among colonies. Marmots in natural colonies declined significantly over time (Pearson correlations) but increased during the early 1980s. Marmots in clearcuts increased later but most colonies subsequently declined.

disappearing juveniles (23%), incomplete trapping or the presence of multiple litters prevented me from distinguishing complete losses of litters from partial losses. The high mortality involving loss of complete litters is intriguing because it suggests that the entire group was exposed to a single mortality factor, as would be the case if animals died during communal winter hibernation. On four occasions monitoring was sufficient to verify that this was the case (i.e., all animals were seen in mid September but not in April-May). In all 12 cases involving the loss of complete litters, disappearance of associated adult female parents increased my suspicion that entire family groups succumbed during winter hibernation.

Adult survival: In theory, survival estimated from consecutive annual counts (N_{t+1}/N_t) of marmots will provide accurate estimates of survival only if emigration equals immigration. If successful emigration occurs more frequently than animals immigrate, consecutive counts will underestimate survival. The reverse is also true. If emigration is lower than immigration, survival estimates based on N_{t+1}/N_t will overestimate true survival.

Following this reasoning, calculating survival from marked animals should underestimate survival because some individuals emigrate successfully but will never be recorded again. But the reverse is not true. For a marked population there is no question of confusing immigrants from surviving animals because immigrants will be untagged (or they will be known immigrants from other study areas). However, even for a marked population of marmots there remains the problem of re-observability (i.e., some animals remain undetected in a given sampling period). Low re-observability would result in underestimates of survival.

Initial results suggested that annual adult survival was independent of whether animals were tagged (persistence:disappearance ratio = 159:96; persistence rate = 62%) or untagged (persistence:disappearance = 45:26; persistence rate = 63%; $\chi^2 = 0.03$ with 1 df, $P=0.874$). Similarly, the question of observability of tagged marmots appeared to be essentially irrelevant provided that sufficient monitoring efforts were made. Only in a few cases ($n=7$ in a sample of 255 adult-years) did marmots older than juveniles apparently disappear (for at least one year) and then reappear at the same colony. In no case did a non-juvenile disappear for more than one active season and then reappear at the same site. Formal testing of recapture (resighting) probability using Cormack-Jolly-Seber mark-recapture models indicated that the most parsimonious model was that of assigning a value of 1.0 (Table 2), and I did this for all subsequent analyses.

Table 2: Cormack-Jolly-Seber estimates of adult survival and recapture probability. This analysis was based on a model of constant survival and recapture rates (i.e., no time or age-dependence). The model including a fixed recapture probability produced a lower Akaike Information Criterion (AIC) and is therefore more parsimonious. Nomenclature and methods follow Lebreton et al. (1992).

Parameter	Estimate	lower 95% limit	upper 95% limit	AIC
Sex-biased survival and recapture (ϕ,p)				433.3
Male survival probability	0.545	0.451	0. 476	
Female survival probability	0.684	0.610	0.750	
Male recapture (resighting) probability	0.935	0.776	0.983	
Female recapture (resighting) probability	0.940	0.834	0.964	
Sex-biased, fixed recapture (ϕ,p=1.0)				428.6
Male survival probability	0.545	0.451	0. 656	
Female survival probability	0.684	0.609	0.751	
Pooled sex survival and recapture (ϕ,p)				429.7
Survival probability	0.629	0.570	0.683	
Recapture (resighting) probability	0.933	0.867	0.968	
Pooled sex, fixed recapture (ϕ,p=1.0)				398.7
Survival probability	0.623	0.565	0.678	

The sex-biased model was less parsimonious (higher AIC) although survival estimates were substantially lower for males than for females. Life table analysis also suggests that adult survival was sex-biased, implying differential mortality or dispersal or both (Table 3). Relatively few males survived beyond the age of four years compared to females. For females the general pattern is that of a Type III survivorship curve (e.g., Begon and Mortimer 1986), in which mortality is concentrated in the younger age classes. For males, lower adult survival suggests a pattern that more closely resembles a Type II curve, with relatively constant survival among age-classes. As was the case for juveniles, there was high variation across years and study colonies (Appendix 12). Sensitivity analysis suggested that the population is more sensitive to changes in adult survival than to changes in pup survival, probability of breeding or litter size (Figure 14).

Table 3: Cumulative life-table for Vancouver Island marmots. Net reproductive rate (R_O) is congruent with other estimates of a severely declining population. Nomenclature and methods follow Caughley (1977; Method II)*.

	MALES					FEMALES						
	f_x	d_x	q_x	p_x	L_x	f_x	d_x	q_x	p_x	L_x	$b_x^{\ddagger}$	l_x*b_x
Juveniles [†]	-	-	0.51	1.00	1000	144	73	0.51	1.00	1000	0.00	0.00
Yearlings	26	9	0.35	0.49	493	31	10	0.32	0.49	493	0.00	0.00
2 year-olds	30	14	0.47	0.65	322	34	13	0.38	0.68	334	0.07	0.02
3 year-olds	25	12	0.48	0.53	172	35	8	0.23	0.62	206	0.85	0.18
4 year-olds	13	7	0.54	0.52	89	26	7	0.27	0.77	159	0.66	0.11
5 year-olds	6	3	0.50	0.46	41	16	5	0.31	0.73	116	0.57	0.07
6 year-olds	3	2	0.67	0.50	21	10	4	0.40	0.69	80	0.75	0.06
7 year-olds	1	0	0.00	0.33	7	7	2	0.29	0.60	48	0.41	0.02
8 year-olds	1	0	0.00	1.00	7	3	1	0.33	0.71	34	0.96	0.03
9 year-olds	1	1	1.00	1.00	7	3	1	0.33	0.67	23	0.77	0.02
10 year-olds	0	0	0.00	0.00	0	1	1	1.00	1.00	15	0.00	0.00
											$R_O =$	**0.50**
											$\lambda =$	**0.88**

Notes:

* Data are f_x (frequency of marked animals per age-class), d_x (frequency of disappearances), q_x (disappearance rate), p_x (probability of persistence), L_x (standardized survivorship), b_x (per female fecundity), l_x*b_x (reproductive value), and R_o (net reproductive rate).

The data reflect 255 tagged adult- years (n =96 individuals), 56 tagged juvenile-years and 88 untagged-juvenile years at the five intensively studied colonies. An additional 17 adult- years were included from 6 tagged individuals at non-intensively studied colonies.

† Juvenile survival based on counts of juveniles and yearlings in the following year. I assumed no sex bias in juvenile survival and used the same rate for males and females.

‡ Fecundity was calculated using the observed juvenile sex ratio (40:28 in favor of females). Assumption of a 1:1 sex ratio at birth reduced R_o to 0.44.
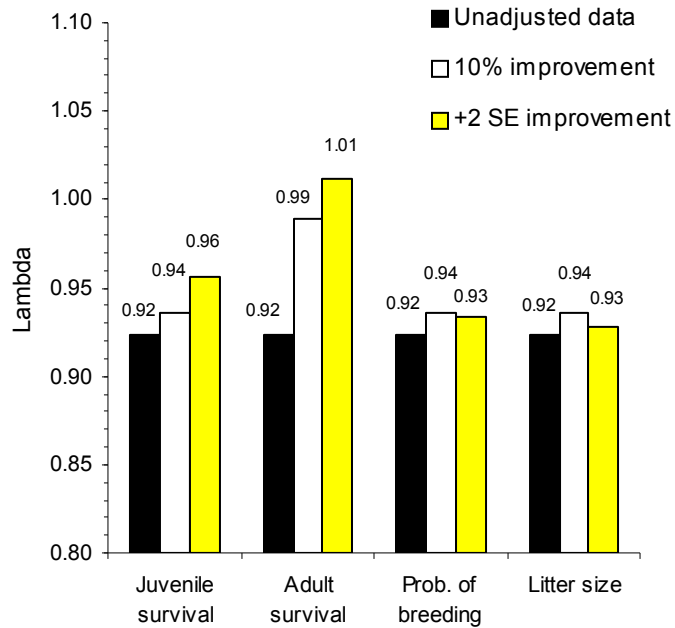
Figure 14: Sensitivity of finite population growth rate (λ) to changes in demographic
rates. Each of the four variables was adjusted by adding either a 10%
proportional increase, or by using the upper 95% confidence limit as the
estimate (the "best-case" interpretation of observed data). Adult survival
exerted a disproportionate effect. This analysis assumed constant survival and
fecundity among adults older than 2 years and therefore exhibits higher λ
values than observed.

Reproduction

Per capita birth rates (β) reflect the probability of breeding (P_b) multiplied by the magnitude of
reproductive events (litter size). The probability of breeding at a given colony is influenced by
intrinsic life-history traits (the period over which a marmot can breed and frequency with which it
can breed) and by the age-sex structure and reproductive history of the animals within a colony. It
is therefore not surprising that reproductive rates varied greatly among colonies and years
(Appendix 13).

Most females that eventually reproduced first did so at age three or four ($\bar{x}$ age of first
reproduction = 3.87, SD = 0.92, range = 2 to 5 years). A single female apparently reproduced at
age two. Females were capable of breeding in the oldest age classes (maximum age = nine years)
and age-specific fecundity was relatively stable after the age of two (range of values from 0.41 to
0.98 females per adult female year). The probability of producing a litter was 0.29 (SD = 0.45,

n=137 animal years) for tagged females older than 1 year and 0.37 (SD = 0.46, n=103 animal years) for females older than two years. There was usually a non-reproductive interval of at least one year between litters ($\overline{x}$ interval = 2.0 years, SD = 0.67, n=10). Litter production in consecutive years was confirmed twice. Litters normally contained three or four pups, with litters of two or five observed infrequently ($\overline{x}$ litter size = 3.28, SD = 0.85, n=43). Variation in lifetime reproductive performance of individuals was high. A few females accounted for the majority of reproductive events. This was particularly evident at the Haley Lake colony, where three of 12 reproductive-age females (i.e., >2 years old) produced 30 of the 58 pups (52%) born from 1987 through 1997 at that site (Appendix 14).

Emergence of pups was generally synchronous among colonies and years. The earliest date that pups were seen was 22 June, but most (29 of 34 litters for which emergence data exist) were first observed aboveground between 28 June and 7 July. Sex ratio of 68 animals initially captured as pups was skewed towards females (40:28) but this ratio did not significantly differ from 1:1 (χ^2 = 2.12 with 1 df, P=0.14). Addition of 21 animals initially captured as yearlings produced a similar result (cumulative sex ratio =52:37 in favor of females, χ^2 = 2.53 with 1 df, P=0.11). Sex determination is more difficult for pups. On two occasions recapture revealed that I had initially mis-identified the sex. Despite this problem, results make it difficult to exclude the possibility of a skewed sex ratio in favor of females.

Immigration-emigration

Dispersal is the "glue" that allows metapopulations to survive (Gilpin 1987). In the case of *M. vancouverensis*, the importance of dispersal may be exaggerated because small colony sizes presumably lead to increased vulnerability from stochastic processes (Hanski and Gilpin 1997). Timely appearance of immigrants (rescue effects) could therefore be very important. On two occasions I observed reproduction that became possible only after untagged animals immigrated into a colony (Haley Lake in 1988 and Sherk Lake in 1993). Conversely, on several occasions I observed reproductive-age animals that could not reproduce because of the absence of a possible mate (Green Mountain in 1990 and 1995, Bell Creek in 1996, Pat Lake in 1997).

Five tagged animals dispersed from intensively studied colonies and were observed alive at new locations. A two-year-old male and a female, probably age two, moved 7.4 km from the Pat Lake clearcut colony to the Mount Franklin clearcut colony in 1992 or earlier. The female produced a litter in 1993 and was observed in 1998. The male was still resident on Mount Franklin in 1997 and remains the oldest male recorded during the study (age 10). Another two-year-old male moved

5.9 km from the Vaughan Road clearcut colony to the Green Mountain colony in 1994. This animal was photographed at a hibernaculum entrance on 4 May 1995 but disappeared shortly thereafter. Two additional tagged animals were seen outside their original colony briefly (at Bell Creek and Mount Holmes), but tag numbers could not be recorded. It appears that none of the latter animals became resident at the new location. Their eventual fate remains unknown. Heard (1977) reported another dispersal movement in which an adult male moved 0.9 km from Haley Lake to Bell Creek in 1974.

All 39 immigrants observed at intensively studied colonies were judged to be young adults, and 19 captured immigrants were definitely so (8 females, 11 males). These animals were invariably larger than pups or yearlings but typically smaller than known-age adults of reproductive age. Most immigrants had relatively uniform pelage color, which is typical of two-year-olds in late summer or three-year-olds in early spring. No immigrant had the "mottled" molt pattern that is typical of older adults, and no female had the prominent nipple development that is characteristic of animals that reproduced in the current or previous year. My data do not preclude the possibility that some yearlings dispersed, but it appears unlikely. Radio-telemetry provided little additional information about dispersal. Transmitter limitations, battery failure and small sample sizes combined to ensure that few dispersal-aged animals were successfully monitored. However, two radio-equipped marmots at Pat Lake made extensive movements and disappeared for over a month in 1994, when the brother and sister were two years old. The brother disappeared; the sister survived and is now in captivity at Toronto Zoo.

Pups and adults that have reproduced apparently do not disperse. Sub-adult (two or three-year old) marmots made sizable dispersal movements (~10 km) through the landscape. Records of solitary marmots in low elevation habitats provide another means of estimating the length of dispersal movements. For example, at least two animals were observed near Nanaimo, including one animal that hibernated successfully near the Cassidy airport in 1991 (assuming that this animal originated at the nearest known active colony, it dispersed at least 20 km). The seasonal timing of dispersal is more difficult to evaluate although records of solitary marmots suggest that dispersal could occur as early as mid-May (Appendix 15).

Dispersal is an infrequent event and the majority of marmots present at intensively studied colonies were apparently born there. Of 105 animals in the two-year-old age-class, at least 78 (74%) were born at that site. Using pooled data from two and three-year-old age classes, at least 130 of 166 animals (78%) were not immigrants.

Mortality factors

It was rarely possible to determine causes of mortality. Golden eagles, cougars and wolves take an undeniable toll on marmots. Disease and unsuccessful hibernation are probably equally or more important.

Avian predators: Observers recorded three cases of predation by golden eagles (*Aquila chrysaetos*), all apparently involving pups or yearlings. Many unsuccessful attacks were also seen and most colonies were frequently hunted by that species. Bald eagles (*Haliaeetus leucocephalus*) were rarely seen at high elevations, but a few unsuccessful attacks were observed. Sharp-shinned hawks (*Accipiter striatus*) and Cooper's hawks (*Accipiter cooperii*) were commonly observed "dive-bombing" marmots but in these cases the relative sizes of the animals suggested "play" or "training" behavior on the part of the hawks rather than a serious predation attempt. Other raptors were occasionally seen throughout summer (especially northern goshawks *Accipiter gentilis*). Raptors such as red-tailed hawks (*Buteo jamaicensis*) and northern harriers (*Circus cyaneus*) were sometimes seen, particularly during fall migration. There are no recorded attacks on marmots by the latter three species.

There is essentially no overlap in diurnal activity patterns of owls and marmots. Pygmy owls (*Glaucidium gnoma*) were common in the study area but do not represent a threat to marmots because of their small size. Great horned owls (*Bubo virginianus*) were recorded twice and one barred owl (*Strix varia*) was seen in a low elevation clearcut colony.

Terrestrial predators: Cougars were observed "stalking" marmots twice, at the Haley Lake and Bell Creek colonies. Heard (1977) also reported a probable case of cougar predation at the former site. It is possible that terrestrial predators benefit from easier movement along logging roads and from learned behavior. On four occasions I observed cougar tracks in the snow surrounding hibernacula exits in late April or early May, and on two occasions I followed cougar tracks along roads as they led from the Vaughan Road clearcut colony into the nearby Haley bowl natural colony. Wolves are another known predator. Wolf scat collected from Gemini Peak in 1984 contained marmot hair (D. Nagorsen, Royal B.C. Provincial Museum, pers. comm.). On two occasions wolf packs produced pups in areas within 1 km of marmot colonies in clearcut colonies (at Sherk Lake in 1995 and Green Mountain in 1998).

Radio-telemetry provided useful information about mortality (Appendix 16). Of seven animals equipped with radio transmitters in 1994, three were confirmed to have been killed by terrestrial

predators. Similarly, of six animals equipped with transmitters in 1998, three were killed. In no case was it possible to definitively identify the predator species. Tooth marks and mangled transmitters were found on two occasions, perhaps suggesting wolf predation. Similarly, on four occasions transmitters were found in relatively pristine condition, which may reflect the more "surgical" nature of cougar feeding habits (D. Doyle, B.C. Wildlife Branch, pers. comm.). The relative importance of cougar and wolf predation remains unknown. Given the wariness of Vancouver Island marmots and the fact that they rarely stray far from the safety of a burrow, I suspect that a "lurk and pounce" technique would be the most effective hunting strategy, and this might suggest cougars more than wolves. Cougars stalk and pounce on their prey much as domestic cats do (Banfield 1977), whereas wolves typically run down their prey (Carbyn 1987).

The possibility of predation by mustelids cannot be discounted. Pine marten (*Martes americana*) are reasonably common in the study region, although they were rarely reported in high elevation habitats. In 1990 I photographed an ermine (*Mustela erminea*) at the Green Mountain summit colony but that constituted my single observation of this species in a habitat occupied my marmots. Predation by black bears (*Ursus americanus*) is probably rare if it occurs at all. Observers often recorded black bears grazing in close proximity to marmots, particularly in the early spring at natural subalpine colonies. Marmots were invariably wary but normally did not respond by whistling or retreating into burrows. In this respect marmots behaved much as they do while in the presence of humans, which is quite different from their response to predators such as cougars or golden eagles. Throughout the project there was no evidence of attempts by any predator to excavate marmots from their burrows.

Some terrestrial predators that are important for other marmot species are irrelevant for   *M. vancouverensis*. There are no coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*), fishers (*Martes pennanti*) or long-tailed weasels (*Mustela frenata*) on Vancouver Island. Predation by wolverines (*Gulo gulo*) is unlikely because of the extreme rarity of that species on Vancouver Island (there are fewer than 20 confirmed sightings in the past fifty years; D. Janz, B.C. Wildlife Branch, pers. comm.). From the accumulated evidence I conclude that cougars, wolves and golden eagles are the principal predators upon Vancouver Island marmots, probably in that order of importance.

Unsuccessful hibernation: Unsuccessful hibernation is a commonly cited mortality factor in marmot ecology (e.g. Armitage 1994) but is extremely difficult to confirm from field observations. Incontrovertible evidence of overwinter mortality was obtained only once. Four animals that were

transplanted to Mount McQuillan in June of 1996 as part of an experimental reintroduction died during hibernation (Bryant et al. in press). Three of the four animals were recovered in the following June. The adult female could not be retrieved but radio-telemetry confirmed her presence in the same burrow system. Relatively large body mass of recovered corpses suggested that death did not occur because of depletion of fat reserves. Initial necropsy results suggested that mortality was due to a bacterial infection (*Yersinia frederiksenii*) but more recent cultures also identified *Y. enterocolitica* and *Carnobacterium divergens* from the same tissue samples. At present it is impossible to identify any particular pathogen as the presumptive cause of death, or to exclude the possibility that bacterial infection occurred post-mortem.

No other animals were confirmed as dying during winter although radio-telemetry provided some suggestive results. Excluding transplanted animals, the sample of animals that entered hibernation with functioning transmitters was small ($n = 27$). In 19 cases both the marmot and the transmitter survived. In five cases the transmitter failed during winter but the marmot was confirmed to be alive in the subsequent spring by recapture or resighting. In three cases (11%) the transmitter failed and the animal was not seen in the following spring. One disappearance of a telemetered animal involved a yearling that hibernated with a sibling at the Pat Lake clearcut colony; neither animal was seen again. On another occasion a telemetered pup vanished along with two siblings and the mother at the Sherk Lake clearcut colony. Another adult male disappeared at the Sherk Lake colony in the following year, but unfortunately in that instance the hibernaculum and hibernation group remained unidentified.

On 12 occasions I observed the disappearance of entire family groups that included juveniles. In all cases animals were observed using particular burrows in late August or early September. In the following spring these burrows showed no evidence of use by marmots or were occupied by new marmots. For example, my last day at Haley Lake in 1996 was on 17 September, when four of the seven juveniles born at that site were confirmed alive. No yearlings were observed in the following spring despite visits beginning on 22 April and three additional visits made prior to 15 May. Similarly, two of three juveniles born at Vaughan road clearcut colony were recorded as late as 22 September. Neither the adult female nor surviving yearlings were observed despite observations that began on 21 April in the following spring. I conclude that evidence for unsuccessful hibernation is circumstantial but compelling.

Effect of research on mortality: There was little evidence to suggest that research efforts caused significant mortality. A single fatality occurred in 1992, when an adult male overheated

while being moved prior to implantation of a radio transmitter. In addition a yearling male was killed in 1994 after a trap was set and left open by unknown visitors to the site. For 16 of the 144 tagged animals (11%), dates of first capture and last observation were identical. In these cases the date of initial capture tended to be late in the season (mean capture date = 13 August, SD = 29.2 days) and few later visits were made to the site before onset of hibernation (mean number of later visits = 1.6, SD = 0.5). However the possibility cannot be discounted that capture stress contributed to mortality at a later date. To address this possibility I compared demographic rates from the intensively studied mark-recapture colonies with those that received only limited visitation by count crews.

Congruence among estimates from intensively studied colonies and counts

Overall demographic rates obtained from intensively studied colonies and other sites were quite similar with one exception (Table 4). Average litter size estimated from non-intensive population counts was significantly lower. This trend probably reflects the relatively late date of litter counts at many of the non-intensively studied colonies (mean date of count = 29 July, SD = 19.9 days) compared to the intensively studied sites (mean = 14 July, SD = 16.2 days). When counts made after 30 July were removed from the data the difference disappeared (Pooled mean litter size = 3.01 juveniles, SD = 1.12, Mann-Whitney U = 1142, P = 0.127).

For the above reason I used the probability of producing a litter rather than per capita births or litter sizes for subsequent analyses. The latter measure is less likely to be biased by later dates of observation than is litter size (seasonal bias would be expected if some summer mortality of juveniles occurs, or if vegetation growth makes it harder to obtain accurate counts, or if expanding foraging movements make it more difficult to assign litter membership). Probability of reproducing would be less sensitive to such bias, because a count of two juveniles and one litter would produce the same probability of reproduction as would a count of five juveniles and one litter.

Adult survival and pup survival were independent of whether colonies were intensively or non-intensively studied. Pup survival rates were virtually identical, suggesting that capture and marking at intensively studied colonies did not increase mortality. Annual demographic rates among intensively and non-intensively studied colonies were uncorrelated. This probably represents real variation in birth and survival rates. The exception to this trend was adult relative density (observed/expected), which was strongly correlated between the two data types and which

had the largest sample size (11 years of relevant data). This pattern is consistent with overall population decline.

Table 4: Marmot demographic rates from intensively studied colonies and non-intensive counts. Tests were χ^2 tests of independence or comparisons of means using two-tailed t tests or Mann-Whitney U tests as appropriate. Pearson correlations were used to compare annual rates. Note that adult survival from intensively studied colonies reflects "apparent" survival based on counts (net survival after immigration-emigration) and that not all animals were necessarily ear-tagged.

Variable and type of data						
Breeders: nonbreeders	breeder	nonbreeder	gross rate	χ^2	P	Correlation (annual rates)
Intensively studied	39	296	**0.11**	0.10	0.749	0.16, *n*=9 years, *NS*
Other colonies	142	1146				
Juvenile survival	persist	disappear				
Intensively studied	71	69	**0.49**	0.24	0.63	-0.19, *n*=4 years, *NS*
Other colonies	98	106				
Adult survival (n+i-d-e)	persist	disappear				
Intensively studied	194	118	**0.65**	1.21	0.27	0.65, *n*=5 years, *NS*
Other colonies	562	294				
Mean litter size	N	mean	SD	U	P	
Intensively studied	39	**3.39**	0.82	3814	0.007	-0.48, *n*=5years, *NS*
Other colonies	155	**2.90**	1.08			
Per capita births	N	mean	SD	U	P	
Intensively studied	335	**0.39**	1.12	217368	0.978	0.16, *n*=9 years, *NS*
Other colonies	1297	**0.35**	1.01			
Adult relative density	N	mean	SD	t	P	
Intensively studied	44	**1.02**	0.51	-0.854	0.394	0.72, *n*=11 years, *P<0.01*
Other colonies	158	**1.11**	0.68			

Part 5: Tests of predictions

Effect of habitat on demographic rates

Demographic rates were influenced by some habitat variables and not others (Table 5). Survival of pups was lower in clearcut versus natural and high versus low elevation habitats (note that these habitat classes often represented the same colonies, as there are few natural habitats below 1200 m and no clearcuts above that elevation). Breeder:nonbreeder ratios were independent of habitat class, although there were more breeders in the early (1983s) period when most colonies had high relative densities. Adult survival was also higher during the same period, although it is impossible to evaluate the relative importance of immigrants and surviving residents. There were no apparent differences in demographic rates among exposed (southeast to southwest-facing) and sheltered (west-southwest to east-southeast facing colonies) colonies. Peripheral colonies had relatively low apparent adult survival but birth rates and pup survival were independent of isolation class.

Life-table analysis from resighting data suggested a reduction of 5-10% in survival of pups and reproductive-age females (age three and older) living in clearcuts. There was no apparent difference in survival of yearlings or two-year-olds among the two habitat types (Figure 15). Age-specific reproductive contribution in clearcuts (R_o =0.35) was slightly more than half that observed at natural sites (R_o =0.65; Appendix 17). Cormack-Jolly-Seber estimates of adult survival also suggested site or habitat specific differences in survival (Figure 16). However, sample sizes were insufficient to resolve these differences at the 95% confidence level. The most parsimonious model was a hypothesis of no site or habitat specific differences, and therefore a single pooled estimate of annual survival (survival probability = 0.623, with lower and upper 95% boundaries of 0.565 and 0.678 respectively).

For reasons of low statistical power I caution against rejecting a hypothesis of habitat or colony-specific effects. The Sherk Lake clearcut colony had high adult survival compared to other sites, although this estimate was based on the smallest number of years with relevant data. Similarly, although age-structured data suggest a distinct sex bias in adult survival, mark-recapture modeling was unable to reject the hypothesis of no difference. Small changes in survival rates could produce biologically significant results but current data are inadequate to resolve such small differences. This is problematic because sample sizes are not likely to be materially improved in many cases. For example, the Vaughan and Pat Lake clearcut colonies are extinct and the Haley Lake natural colony currently contains only two adults.

Table 5: Effect of habitat, time period and relative density on marmot demographics. Data are pooled from intensively studied and other colonies. Tests are χ^2 tests of independence. Adult survival is apparent survival based on counts (net survival after immigration/emigration).

Habitat class	Adult survival				Juvenile survival				Breeder: non-breeder ratio			
	survive	disap.	χ^2	P	survive	disap.	χ^2	P	breeder	non.	χ^2	P
Natural meadows	484	254	0.57	*0.45*	103	84	5.81	***0.02***	70	497	1.11	*0.29*
Clearcuts	270	156			66	91			111	935		
High (>1200 m)	346	193	0.15	*0.70*	61	46	3.86	***0.05***	77	665	1.59	*0.21*
Low (<1200 m)	217	408			108	129			102	720		
Sheltered (245-150°)	164	106	2.51	*0.11*	42	49	0.44	*0.51*	134	1044	0.02	*0.88*
Exposed (151-244°)	590	304			127	126			45	341		
Core area	598	305	3.70	*0.06*	133	133	0.36	*0.55*	141	1063	0.37	0.55
Peripheral	156	105			36	42			38	322		
High density (>1.0)	426	261	3.83	***0.05***	144	151	0.08	*0.78*	147	960	17.6	***0.00***
Low density (≤1.0)	269	127			25	24			31	470		
Early (1980s)	377	188	5.43	***0.02***	59	63	0.00	0.99	87	814	5.28	***0.02***
Late (≥1990)	261	177			83	89			69	437		

There was a discrepancy in the proportions of immigrants to surviving tagged animals at the two natural colonies (13 immigrants versus 116 surviving residents) and three clearcut colonies (26 immigrants versus 140 surviving residents; $\chi^2 = 9.36$, $P = 0.002$). It appears that turnover of individuals was higher at clearcut colonies. In addition, loss of complete family groups including juveniles occurred more frequently in clearcuts (8 cases of complete loss and 11 cases of partial or complete survival; loss rate = 43%) compared to natural habitats (4 cases of loss and 20 cases of partial or complete survival; loss rate = 17%) and this difference may be significant ($\chi^2 = 3.41$ with 1 df, $P = 0.07$).

The seasonal timing of disappearances differed among habitat types and could provide insight about causes of mortality (Figure 16). Dates of last observation of tagged adults were not independent of month (single-sample goodness-of-fit $\chi^2 = 17.1$ with 4 df, $P=0.002$). Most tagged adults were last recorded alive in August or early September. Dates of last observation do not necessarily equate with dates of mortality. The September data are probably biased

A) Female survivorship

B) Age-specific contribution
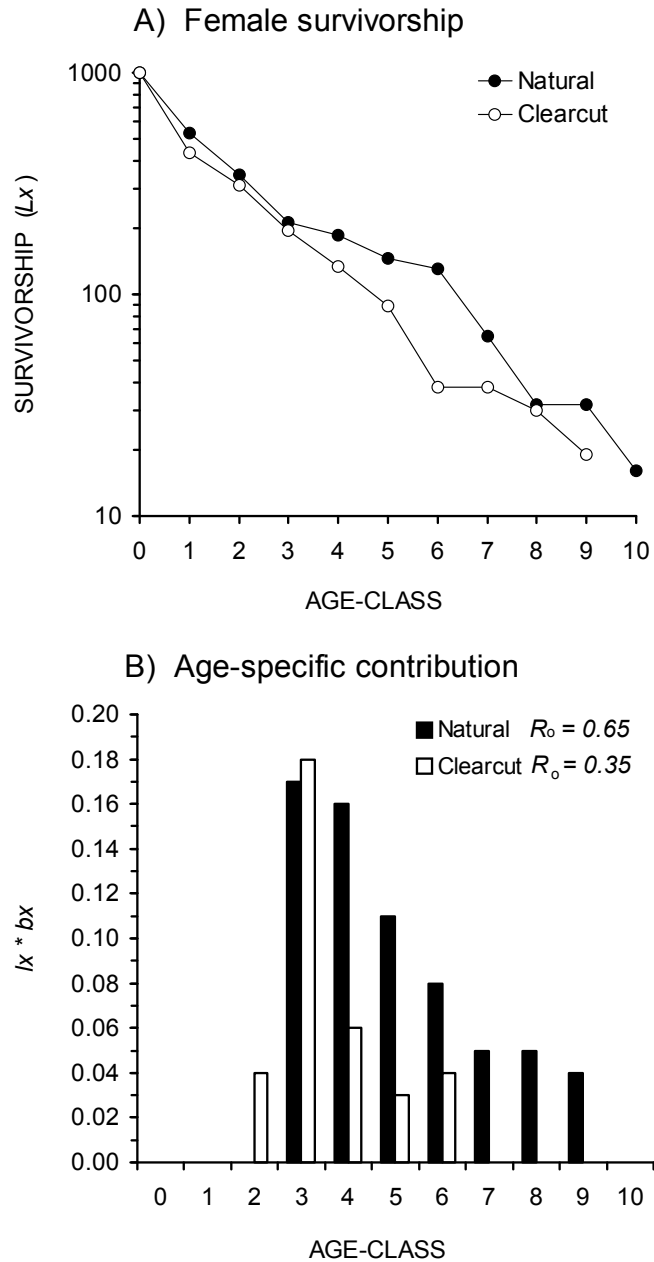
Figure 15: Effect of habitat type on age-specific reproductive performance. Life-table analysis suggests that female survival rates (A) were 5-10% lower in clearcut habitats. The consequence was reduced lifetime reproductive performance (B). Data are from tagged adult females monitored from 1987 through 1998 (*n*=34 in natural habitats and *n*=51 in clearcuts).

A) Habitat class

B) Colony
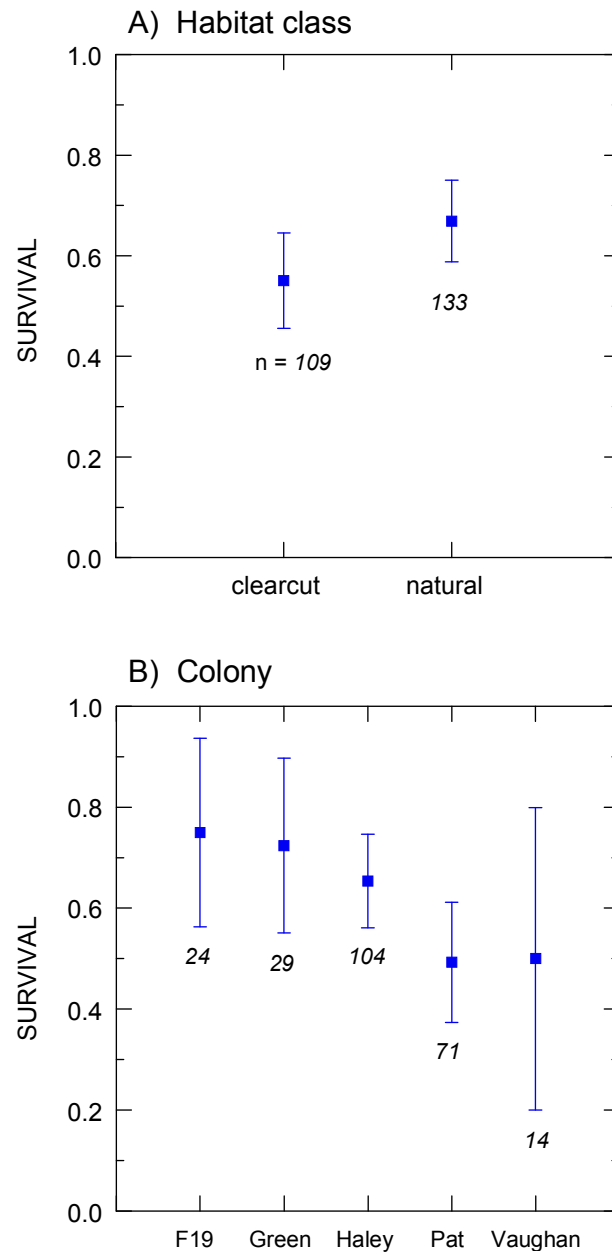
Figure 16: Cormack-Jolly-Seber estimates of adult survival. Data are mean annual survival rates and 95% confidence limits based on 88 tagged adults and 242 marmot-years of observation. Confidence limits overlap and the most parsimonious model is that of no habitat or colony-specific differences in adult survival.
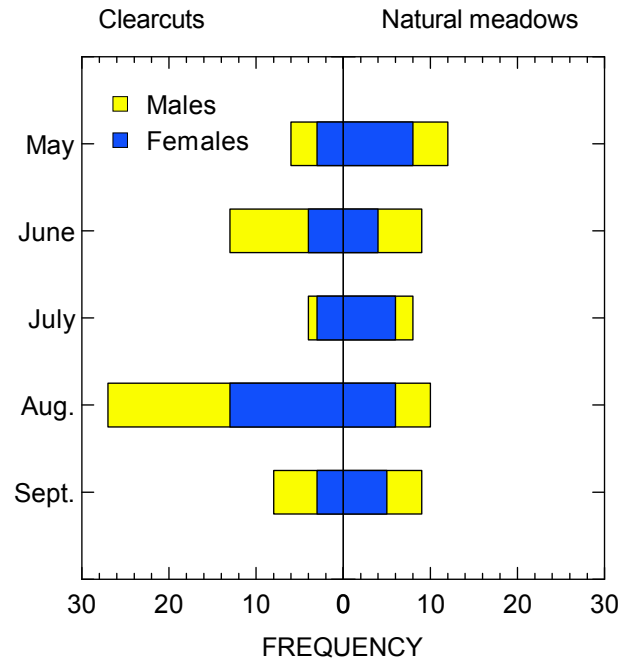
Figure 17: Timing of last observation of tagged adults in natural and clearcut habitats. Data are based on 48 adults that disappeared from natural habitats and 58 adults that disappeared from clearcuts. Dates of last observation of animals in clearcuts are skewed towards late summer. Most animals enter hibernation by mid-September.

downward because of relatively low monitoring effort in that month and because many individuals enter hibernation in mid-September. August data are probably skewed upwards because of these trends. Timing of last observation was independent of sex ($\chi^2 = 5.45$ with 4 df, $P=0.25$). I conclude that males and females have similar seasonal patterns of mortality and that pooling of the data was justified for subsequent analyses.

Timing of last observation differed among natural and clearcut habitats ($\chi^2 = 11.1$ with 4 df, $P = 0.03$). Last observations in natural habitats were evenly distributed among months ($\chi^2 = 0.96$ with 4 df, $P = 0.20$). This result could suggest constant mortality pressure throughout the active season, as might occur from predation. In contrast, most dates of last observation in clearcuts were concentrated in August and September ($\chi^2 = 29.4$ with 4 df, $P < 0.001$), which may suggest a higher incidence of mortality due to unsuccessful hibernation.

Temporal effects on survival and reproduction

Adult survival estimated from mark-resighting data varied considerably among years. Low survival years included 1991 and high survival years included 1992. However 95% confidence levels overlapped and the time-independent model was more parsimonious (Figure 18). Probability of producing a litter also varied substantially across years, including some years with low or no reproduction (1989, 1990 and 1995). However, logistic regression showed no significant effect of year on the probability of producing a litter. Survival data from tagged juveniles at intensively studied colonies were too sparse to test.

Effect of clearcut age on birth and survival rates

Seral stage of regenerating clearcuts may represent a special case of environmental tracking. Logistic regression indicated that apparent adult survival was negatively associated with increased clearcut age but juvenile survival was not (Table 6). However, clearcuts coded as "old" (older than 11 years) were negatively associated with survival of all animals ($n = 583$, coefficient = -0.343, $P = 0.041$).

Pup survival results may suggest a nonlinear relationship with seral age (Figure 19). Such a situation might occur if it took initial immigrants a few years to construct successful hibernacula, or if predators benefit from forest regeneration, resulting cover and improved experience. Probability of reproduction was not significantly associated with age of clearcuts (Table 7).

Table 6: Logistic regression of clearcut age against marmot survival.

Type of data	N	odds ratio	coefficient	Rho^2	P value[*]
All juveniles (tagged and untagged)	157	0.978	-0.022	0.002	0.532
Non-intensive adult survival (counts)	284	0.910	-0.094	0.035	<0.001
Tagged adults (intensively studied)	121	0.911	-0.093	0.025	0.002

Table 7: Logistic regression of clearcut age against probability of reproducing.

Type of data	N	odds ratio	coefficient	Rho^2	P value
Adults (non-intensive counts)	412	1.045	0.044	0.007	0.124
Tagged adults (intensively studied)	121	0.984	-0.018	0.001	0.836

A) Adult survival (both sexes)

B) Reproduction
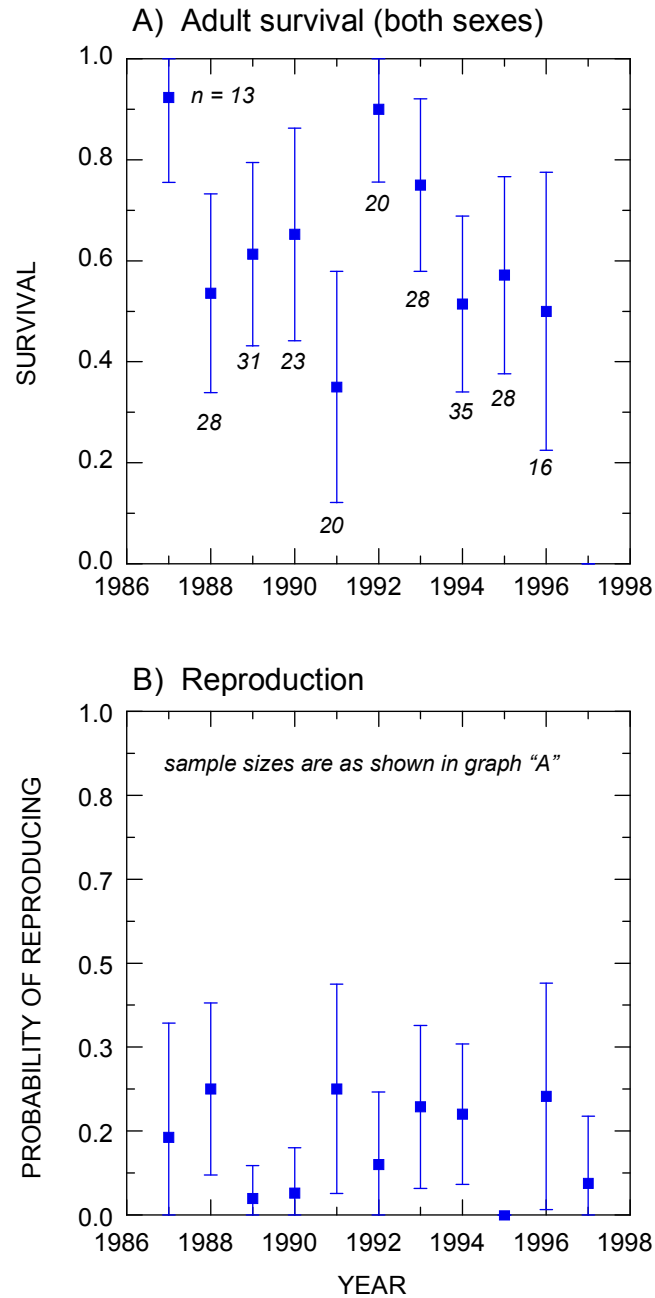
Figure 18: Temporal changes in adult survival and probability of breeding. Data are mean annual rates and 95% confidence limits based on 88 tagged adults and 242 marmot-years of observation. Sample sizes are shown. For survival, confidence levels overlap and the most parsimonious model was that of no time-dependence. For probability of reproduction, logistic regression showed no relationship between year and the probability of producing a litter.
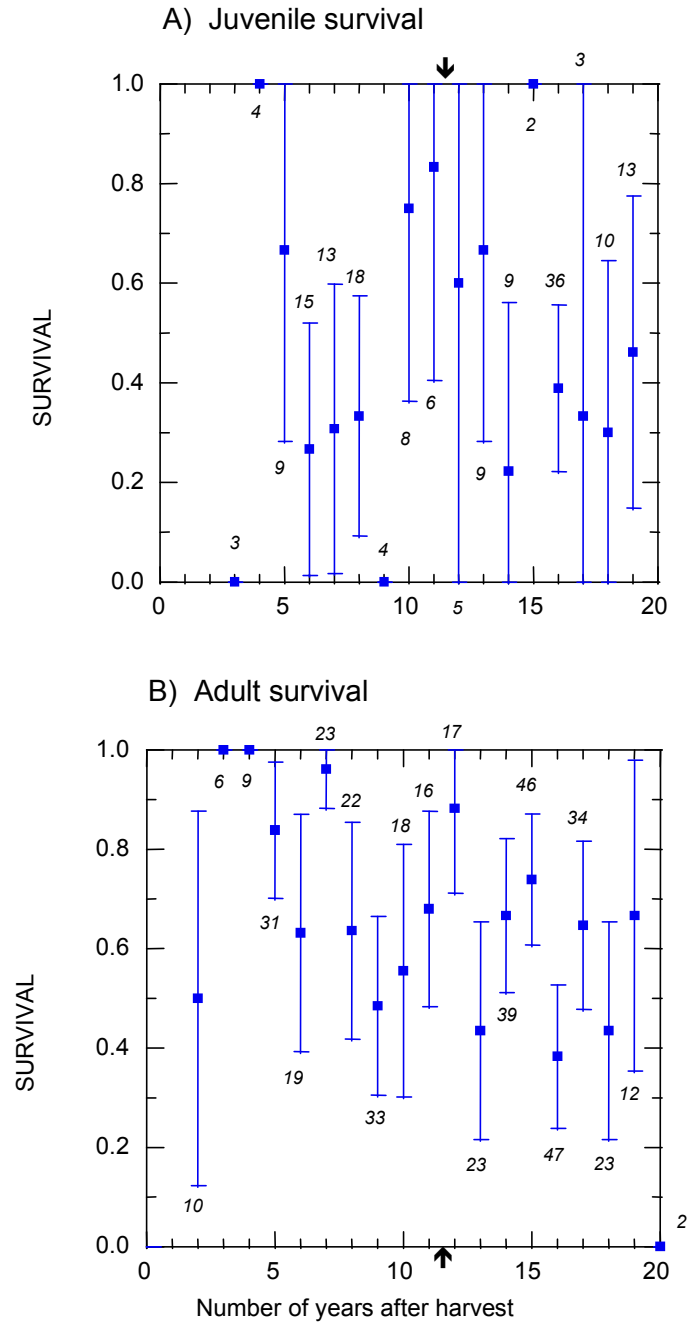
Figure 19: Effect of increasing clearcut age on marmot survival. Data are mean survival estimates with 95% confidence levels for juveniles (A) and adults (B). Sample sizes are shown. Logistic regression determined that survival of all animals was reduced in clearcuts coded as "old" (>11 years, see arrows). Clearcuts older than 15-20 years old generally become unsuitable for marmots.

Density dependence

Demographic variables were associated with changes in relative density (Figure 20). Adult survival was negatively associated with relative density (observed/expected number of adults) for both tagged and untagged samples, although density explained only a small amount of the variation in survival (Table 8). Lower survival in high density conditions could reflect increased emigration of two-year-old marmots or increased mortality from disease or predators.

Pup survival was not associated with adult relative density in linear fashion. Survival peaked during periods of moderate abundance (75 - 150% of expected) and declined when marmots were more or less abundant. The result raises questions about hibernacula availability or disease transmission under high density conditions, and about the role of communal hibernation under low density conditions.

The probability of producing a litter was positively associated with relative density of adults, although regression *Rho²* values were very small. Litter production was lower during periods of below-average adult density (i.e., <1.0) but quite stable at higher densities. This relationship was unexpected. I expected that most animals in a high density colony to represent non-reproductive yearlings and 2 year-olds, which would result in an inverse relationship between probability of reproducing and relative density.

Table 8: Logistic regression of relative adult density against survival and probability of reproducing. Samples were marmot-years (an individual alive in one year).

Variable	*N*	odds ratio	coefficient	*Rho²*	*P* value
Juvenile survival (all animals)	344	0.814	-0.306	0.002	0.254
Tagged adult survival	254	0.556	-0.547	0.011	0.059
Non-intensive adult survival (counts)	1083	0.684	-0.379	0.013	<0.001
Probability of producing a litter	1608	1.393	0.330	0.017	<0.001

Colonization events in relation to habitat availability

Since 1981 marmots colonized a small fraction (<100 ha of ~10,000 ha) of clearcuts above 700 m that were available to them assuming dispersal capability of 5-10 km. Frequency of colonization was not correlated with habitat availability (Spearman $r = 0.16$, n=11, P>0.05). This result is not surprising giving the small number of colonizations (n=10) and the compressed temporal period over which they occurred (8 colonizations between 1981 and 1986).
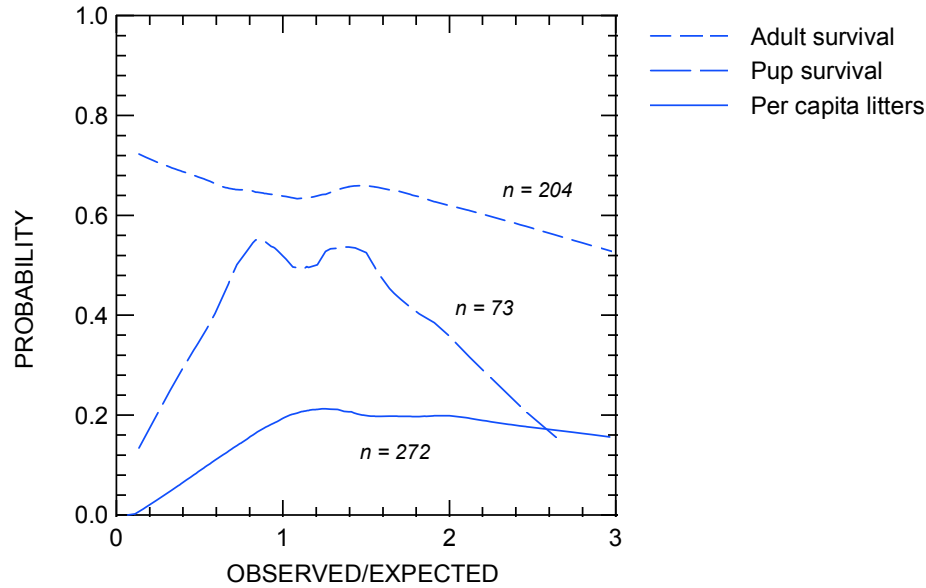
Figure 20: Effect of relative density on marmot demographics. Data are LOWESS regressions of relative density of adults against annual adult survival, pup survival and probability of reproducing. Numbers of site-years are shown.

The spatial pattern of colonization events was not random (Figure 21). All recorded colonizations occurred within 5 km of existing natural colonies and 8 of 10 events occurred within 2 km. Colonizations were significantly closer to existing natural colonies than were 30 randomly selected sites (Table 9). The data do not suggest a "stepping-stone" pattern of colonization. Instead, results suggest a "wave" of colonizations that began during the early 1980s and stopped abruptly, perhaps because of a shortage of colonists. Only two colonizations occurred after 1985.

Table 9: Nearest colony-neighbor distances for marmot colonizations and random sites. Clearcuts of appropriate age (0-15 years) and elevation (>700 m) and timing (1985) were randomly selected to represent colonization events if all locations were equally accessible by marmots. Student t test is one-tailed.

Variable	N	$\overline{\text{X}}$	SD	t	df	P value
Nearest colony-distance						
Actual colonizations	10	**1.47**	1.07	-3.61	38	<0.001
Random sample	30	**5.47**	3.37			
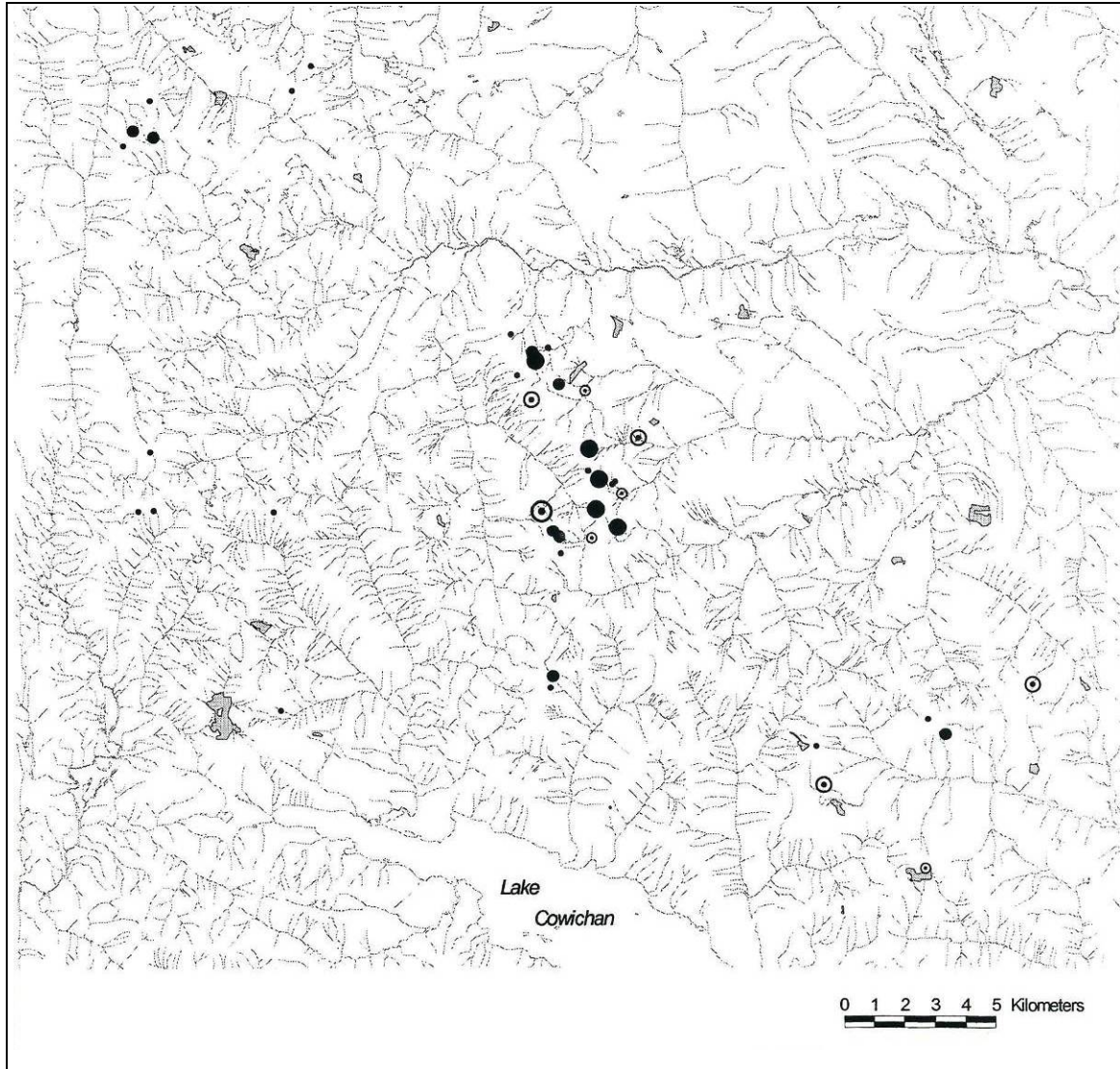
Figure 21: Colonizations and potential colonizations of clearcuts. Data are colonizations (⊙) that occurred from 1981 to 1992 and natural colonies (●) that existed during that period. The map also shows 30 randomly selected clearcuts above 700 m and between the ages of 0 and 15 years (shaded polygons) to represent "potential" colonizations given marmot dispersal capability of at least 5-10 km. These 30 sites represent only 160 hectares of the more than 10,000 hectares of potential habitat that were available to marmots in 1986. Most colonizations occurred in the central portion of the range. Sizes of dots are proportional to average numbers of adults during the 1980s.

Extinction and demographic performance in relation to isolation

Marmots apparently disappeared from 10 historically reproductive natural colonies and 8 potential colonies during the late 1980s and early 1990s (Figure 22). Timing of extinction was impossible to accurately confirm in the field. Vancouver Island marmots are apparently adapted to a lifestyle involving extremely small colony sizes and showed extreme tenacity in their persistence at some sites (e.g., Mount Washington). However it seems unlikely that inventory crews often missed reproductive colonies for periods of consecutive years. Uncertainty about extinction date precluded direct testing of extinction probabilities in relation to distance to extant colonies. An indirect test of isolation effects using apparent survival data as a measure of immigration supported the idea that isolated colonies receive fewer immigrants (Table 10), although the degree of variation explained was low ($Rho^2 = 0.070$).

Table 10: Effect of increasing isolation on apparent marmot survival. Logistic regression indicated that "apparent" adult survival was negatively associated with increased isolation, but juvenile survival was not.

Variable	N	odds ratio	coefficient	Rho^2	P value
Adult survival + net immigration	1164	0.960	-0.041	0.070	0.002
Juvenile survival	334	1.015	0.015	0.001	0.563

Sources and sinks

Although population trajectories were similar among colonies, some were apparently more successful than others. Comparison of average annual births and disappearances (net immigration-death-emigration) suggests that most colonies lost more marmots than they produced between 1979 and 1997. This discrepancy between births and losses is the fundamental cause of observed population declines, and for this reason most colonies therefore fell below a theoretical "source-sink" line above which reproduction more than balances survival (Figure 23).

Extinction at three natural colonies (Gemini Peak, Westerholm basin and Mount Whymper) showed that performance is not guaranteed in natural habitats by virtue of colonies being either large or isolated. Data from clearcut colonies are also noteworthy. Clearcut colonies tended to be much larger in size but in only 2 of 10 cases did analysis suggest that these sites were net producers of marmots. These few positive data are probably also biased. Results from ear-tagged animals at 3 clearcut colonies (Pat Lake, Vaughan Road and Sherk Lake) suggest that
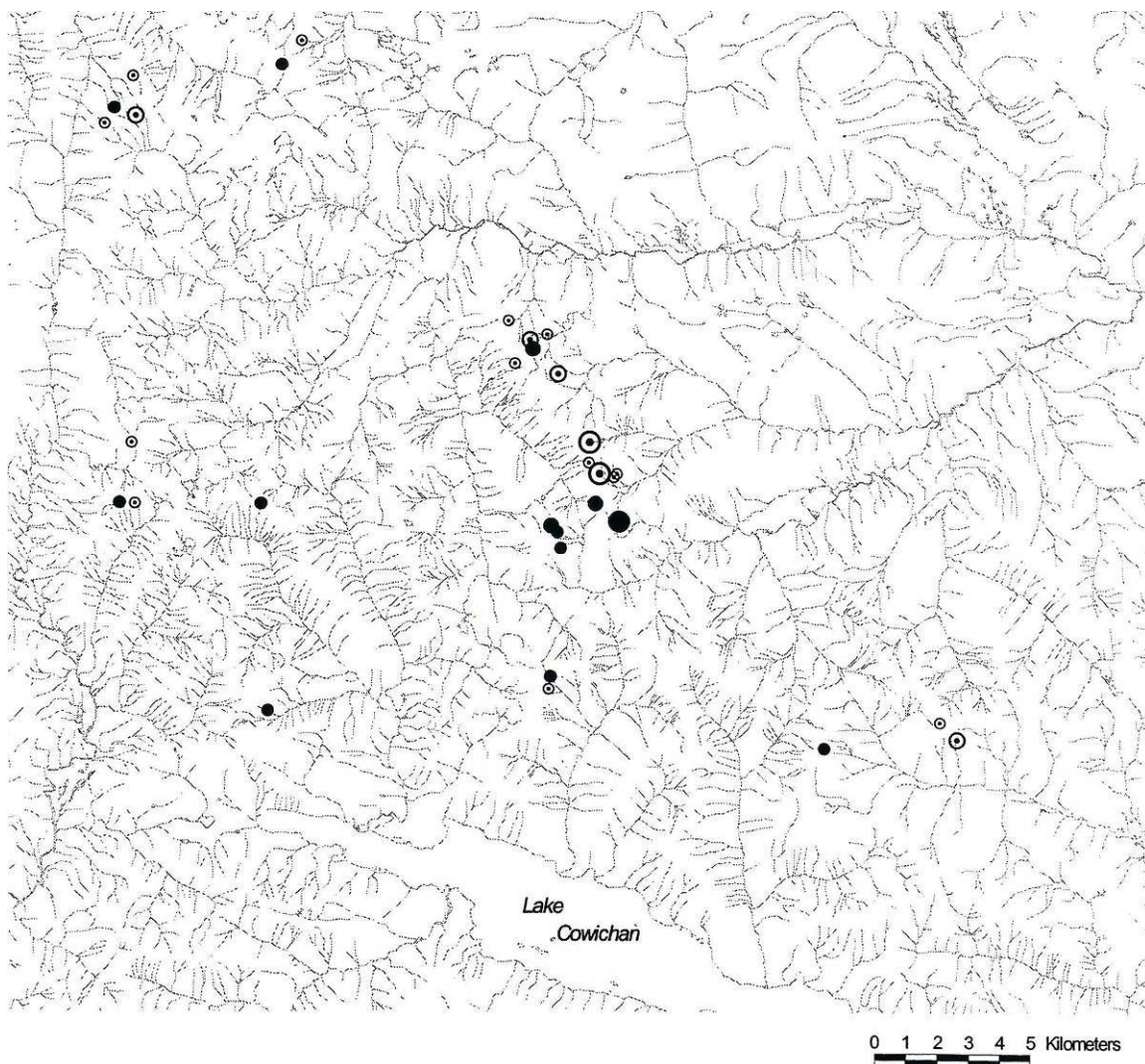
Figure 22: Extinction events at natural colonies from 1985 to 1997. The data reflect sites
with no reproduction or marmots observed despite three consecutive annual counts
(⊙). Persisting colonies are represented by (●). Data show no apparent spatial
pattern or relationship between colony size and probability of extinction. Some
large colonies in the center of the current range (e.g., Gemini Peak) suffered
extinction as did some small colonies on the periphery (e.g., "P" Mountain NW
ridge). Dot sizes are proportional to numbers of adults during the mid 1980s.
This map does not show clearcut colonies, of which 5 of 10 suffered extinction
during the same period.
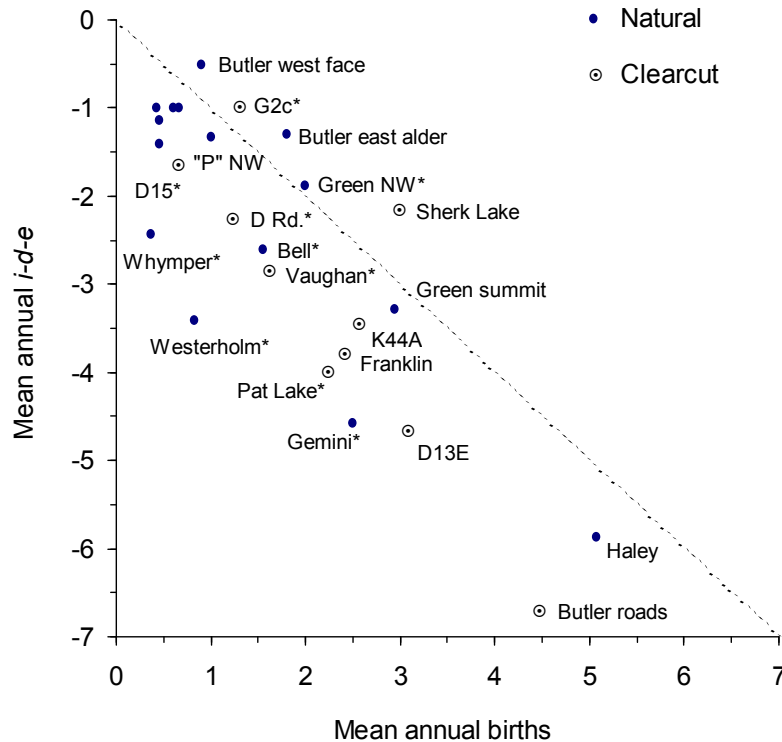
Figure 23: Colony-specific source-sink analysis. Data are mean annual births per colony (*b*) and mean annual net immigration-death-emigration (*i-d-e*) rates based on counts. Labels denote the most numerically important colonies. Sites with fewer than 5 years of observation were excluded. The dashed line indicates a predicted *b* = *i-d-e* relationship if colonies were stable and there were no source-sink dynamics. Departure from this line illustrates the degree to which various colonies acted as "sources" or "sinks" during the 1972-1997 period. For colonies that are extinct (*) this is a measure of cumulative "lifetime" colony performance.

apparently high *i-d-e* rates were disproportionately due to adult immigration compared to that experienced by natural colonies.

The above method of source-sink analysis based on cumulative data could mask important temporal or spatial patterns. For example, it is unclear whether the observed patterns reflect chronic low survival (for example, as would be the case in which habitats are slowly becoming increasingly unsuitable for marmots) or episodic low survival (as might be the case if a disease outbreak occurred or if there were "bad weather" years).

Effects of weather on survival

Weather significantly influenced marmots but generally explained only small amounts of the variation in survival (Table 11). Adults and pups responded differently, as did marmots living in natural and clearcut habitats.

In natural habitats, survival of pups and adults were positively associated with high spring temperatures, number of days with significant (>5 mm) precipitation in spring, and average June snowpack depth. The effect of these relationships may be to influence vegetation conditions more than the marmots themselves, since onset of hibernation does not occur until September, and juveniles are not born until June. Alternatively, for adults, spring weather conditions could reduce foraging opportunities or increase metabolic demands beyond levels that their remaining fat reserves can accommodate. Late-summer temperatures were unimportant but summer days with significant rainfall were positively associated with pup survival. These results suggest that pups may be particularly vulnerable to drought conditions.

Snow conditions in the following winter were significantly associated with survival of pups and adults in natural habitats. Snowpack depth in early winter (December-February following the active season) was negatively associated with survival. Late-winter (May-June following the active season) snowpack depth was negatively associated with pup survival but weakly positively associated with adult survival. Exposed aspect (southeast to southwest) was weakly associated with adult survival, suggesting that local snow melt patterns could be important. Elevation was unimportant.

For clearcut habitats, weather again explained only small amounts of the variation in survival. As was true for natural meadows, adult survival was positively associated with spring temperatures and days with significant rainfall, but negatively associated with total spring precipitation. This result is intriguing and could suggest the importance of severe weather events that deposit a large amount of precipitation over a few days (e.g., the June 1 snowstorm in 1988). Late summer days with rainfall and late-summer precipitation produced contrary relationships with survival of adults and pups. Adult survival was positively associated with days with rainfall but negatively associated with precipitation. For pups the relationships were exactly opposite (i.e., negative for days with rainfall and positive for precipitation). These results were unexpected but could suggest that pups and adults have different physiological vulnerabilities to soil moisture conditions or by having to curtail foraging during periods of inclement weather.

Table 11: Effect of weather on marmot survival in natural and clearcut habitats. Only significant factors are shown. All logistic regressions were highly significant but explained only small amounts of the overall variation in survival (McFadden's *Rho²* statistic <0.2). *

Variable	Key to variables	Odds ratio	Coefficient	*P* value	*Rho²*	overall *P* value
Natural colonies						
Juveniles (n = 162 records)					0.118	*<0.001*
MAYTEMP	May-June average temperature	2.280	0.824	0.037		
MAYDAYS	May-June days with > 5 mm rainfall	1.443	0.367	0.000		
SUMDAYS	July-August days with rainfall	1.683	0.521	0.021		
SNOEARLY	December-February snowpack	0.956	-0.045	0.003		
SNOWJUN1	June snowpack (next spring)	0.992	-0.008	0.011		
SNOWJUN	June snowpack (current year)	1.026	0.026	0.057		
Adults (n = 638 records)					0.038	*<0.001*
ASPECT	Aspect (exposed)	1.666	0.510	0.075		
MAYTEMP	May-June average temperature	1.374	0.318	0.000		
MAYRAIN	May-June cumulative rainfall	0.462	-0.772	0.002		
MAYDAYS	May-June days with >5 mm rainfall	1.337	0.290	0.000		
SNOEARLY	December-February snowpack	0.993	-0.007	0.003		
SNOWJUN1	May-June snowpack (next spring)	1.002	0.002	0.069		
SNOWJUN	May-June average snowpack	1.006	0.006	0.004		
Clearcut colonies						
Juveniles (n = 142 records)					0.056	*0.029*
MAYDAYS	May-June days with >5 mm of rainfall	1.301	0.263	0.037		
SUMRAIN	July-August rainfall	9.268	2.227	0.032		
SUMDAYS	July-August days with >5 mm of rainfall	0.516	-0.662	0.059		
SNOEARLY	December-February snowpack	0.987	-0.013	0.080		
Adults (n = 388 records)					0.055	*<0.001*
MAYTEMP	May-June average temperature	1.211	0.191	0.034		
MAYRAIN	May-June cumulative rainfall	0.260	-1.020	0.002		
MAYDAYS	May-June days with rainfall	1.232	0.209	0.006		
SUMRAIN	July-August cumulative rainfall	0.325	-1.123	0.001		
SUMDAYS	July-August days with >5 mm of rainfall	1.422	0.352	0.005		
SNOEARLY	December-February snowpack	1.004	0.004	0.086		

* The regression model statement was Survival = Elevation + Aspect + Mayrain + Maydays + Maytemp + Sumrain + Sumtemp + Sumdays + Snowjun + Snowjun1 + Snoearly

In contrast to natural habitats, survival was not associated with late-winter snowpack or aspect for either adults or pups. I suspect that timing of snow melt may be irrelevant for the relatively low-elevation clearcut colonies. Snowpack depths in early winter provided contrary results for adult and pup survival (positive association for adults and negative for pups). These results were unexpected and are difficult to reconcile; presumably the communally-hibernating marmots experience very similar microclimate conditions.

Overall, I conclude that weather significantly influences survival but is unlikely to be the principal cause of recent population trends.

Effects of weather on reproduction

Weather variables were not useful predictors of the probability of reproducing for marmots living in natural habitats (Table 12). Reproduction was positively associated with low spring temperatures but the amount of variation explained was small ($Rho^2 = 0.015$).

Weather exhibited stronger effects on reproduction in clearcuts ($Rho^2 = 0.111$). As with animals in natural habitats, probability of reproducing was positively associated with low spring temperatures. I can offer no reasonable explanation for this result except to speculate that estrous cycles or hormonal processes are somehow influenced by temperature. Adults inhabiting clearcuts were also significantly influenced by rainfall in spring of that year. Probability of reproducing was positively associated with cumulative spring precipitation and negatively associated with days having significant rainfall. Possibly spring rainfall patterns influence snowmelt patterns, a hypothesis that is supported by the negative influence of late winter (May-June) snowpack.

The probability of breeding was also associated with late-summer rainfall in the previous active season, a trend that could reflect nutritional composition of food resources. It is likely that the physiological condition of marmots entering hibernation would influence the likelihood of producing a litter in the following spring.

Despite some significant relationships, I conclude that weather patterns do not explain recent reproductive trends.

Predator-prey effects

Indices of cougar and wolf abundance were poor predictors of survival in both habitat types and for adults and pups (Rho^2 values < 0.03; Table 13). The hunter-sighting index for wolves was not associated with survival, whereas for cougars it was weakly and negatively associated with adult survival in clearcuts. These results are not surprising given the high annual variation

Table 12: Effect of weather on probability of reproducing.

Variable	Key to variables	Odds ratio	Coeff.	P value	Rho² statistic	overall P value
Probability of producing a litter (adults only, both sexes)						
Natural colonies (n = 799 records)					0.015	*0.004*
MAYTEMP	May-June average temperature	0.865	-0.179	0.050		
Clearcut colonies (n = 470 records)					0.111	*<0.001*
MAYTEMP	May-June average temperature	0.613	-0.489	0.002		
MAYRAIN	May-June days cumulative rainfall	6.155	1.187	0.091		
MAYDAYS	May-June days with rainfall	0.634	-0.456	0.005		
SUMRAIN-1	July-August rainfall (previous summer)	0.292	-1.230	<0.001		
SUMDAY-1	July-August rainfall days (previous summer)	1.697	0.529	0.003		
SNOWJUN	May-June average snowpack	0.985	-0.015	0.001		
SNOEARLY	December-February average snowpack	1.014	0.014	0.076		

* Model statement was Birthcode = Elevation + Aspect + Mayrain + Maydays + Maytemp + Sumrain (previous year) + Sumtemp (previous)+ Sumdays (previous) + Snowjun + Snoearly (previous).

Table 13: Effect of predator-prey indices on marmot survival.

Variable	Key to variables	Odds ratio	Coefficient	P value	Rho² statistic	overall P value
Natural meadows						
Juvenile survival (n = 124 records)					0.024	*0.045*
DEER	Deer/km	*6.537*	2.524	0.048		
Adult survival (all adults, n = 554 records)					0.020	*0.001*
COUGREM	Cougars removed	*0.929*	-0.074	0.003		
WOLFREM	Wolves removed	*1.044*	0.043	0.005		
Clearcuts						
Juvenile survival (n=142 records)						*>0.10*
no significant terms						
Adult survival (all adults, n = 396 records)					0.026	*<0.001*
COUGAR	Cougars/100 deerhunter-days	*0.649*	-0.432	0.000		

* Model statement was Survival = Cougar + Wolf + Cougrem + Wolfrem + Deer.

in hunter-sighting indices; I reiterate my suspicion that such indices may not accurately reflect wolf or cougar abundance.

Similarly, numbers of cougars and wolves removed from the population produced inconsistent effects despite their numbers being substantial in some years (e.g., 20 cougars and 9 wolves removed in 1989, at approximately the time that marmot colonies began to decline). In natural habitats, adult survival was positively related to numbers of wolves removed and, curiously, negatively associated with numbers of cougars removed. A suggestion that marmot survival is improved by increased numbers of cougars would be counter-intuitive to say the least.

Deer abundance was a significant predictor of juvenile survival in natural habitats only. The amount of variation explained by regressions was very small in all cases, but these results may be partially due to inconsistencies in the predator abundance data. I cannot reject the hypothesis that terrestrial predators have exerted important effects upon marmots.

Spatial correlation of survival

Apparent marmot survival (N_{t+1}/N_t) was spatially autocorrelated during both periods that received relatively thorough sampling effort (1981-1987 and 1991-1997). Moran's I coefficient varied from 0.09 to 0.52, indicating weak to moderate positive correlation at all effects radii (lag distances). However the strength of correlation varied with distance (Figure 24).

Survival was more strongly correlated at shorter distances. Significant positive correlation was obtained at the largest radii that encompassed the entire study area (15 km), but strength of the associations were low ($I = 0.09$ and 0.25). At shorter distances (< 5 km) stronger correlations were obtained ($I = 0.15$ to 0.36). Spatial autocorrelation differed between the early and late periods although the shape of the curves was similar. Survival rates were more highly correlated during the late sampling period. This is an interesting result because recent extinctions mean ensure that the metapopulation was more dispersed in the late period than in the early period.

Results supported the prediction that adjacent colonies would show similar survival rates within years. Significant positive correlation at the largest effects radii lends support for the "bad weather" hypothesis although the relationship is not strong. Stronger correlations at shorter distances are consistent with a hypothesis of localized predator effort or disease events. Most importantly, change in the magnitude of autocorrelation among sampling periods could suggest a new mortality factor (e.g., disease outbreak or changing predation patterns).
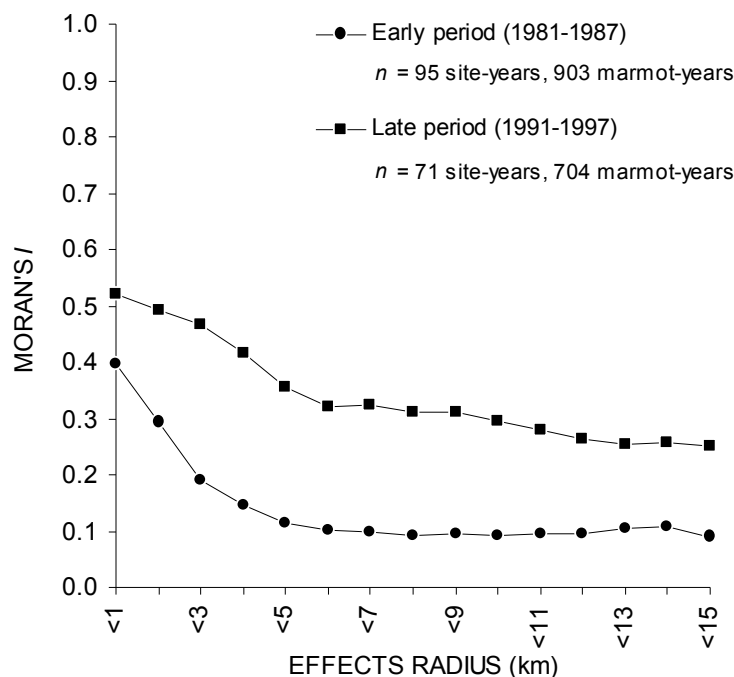
Figure 24: Spatial autocorrelation of marmot survival rates. Data are Moran's *I* coefficient calculated over increasing lag distances (effects radii) and using annual survival rates weighted by the numbers of adults and pups present. All correlations were significant and positive ($Z > 1.65$, $P < 0.05$).

Incidence of high mortality events

For some colonies survival did not vary greatly across years and there was little evidence for episodes of high mortality (Figure 25). Data from the Pat Lake and Mount Franklin clearcut colonies suggest relatively constant survival (i.e., low coefficients of variation), although neither colony showed particularly high survival for years in which they contained more than three individuals (median survival = 67% and 61%, respectively). At the other extreme, some colonies with relatively high survival also showed low coefficients of variation (e.g., Sherk Lake, with median survival of 86%). These results are consistent with a hypothesis of chronic low or high survival corresponding to "sink" and "source" habitats (Appendix 18-20).

Many other colonies suffered distinct episodes of high mortality. For example, the Gemini Peak natural colony showed relatively high survival (median = 0.82%) and low annual variability (CV = 45%) but apparently lost most of its marmots in a single year (1986-1987). Similarly, the Bell Creek natural colony exhibited high survival and low annual variation (median survival = 0.69%, CV = 36%) but suffered two high mortality events (1979 and 1995).
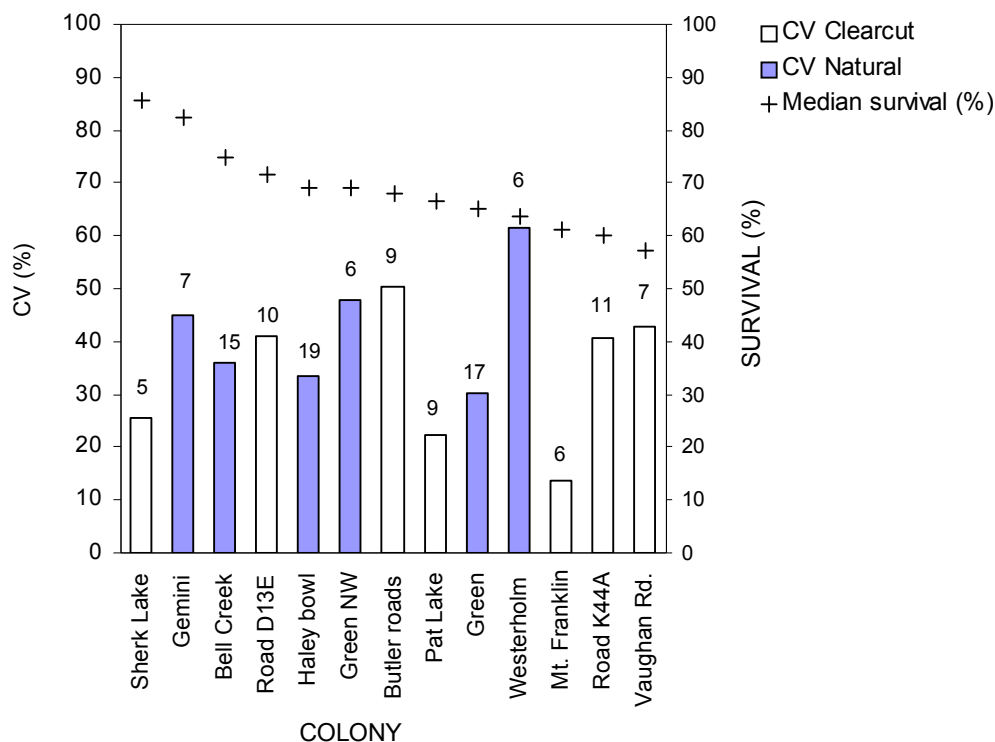
Figure 25: Colony-specific variation in apparent survival. Bars are coefficients of variation (CV) based on apparent survival of adults and pups at colonies with a relatively complete sampling history since 1979. Median annual survival rate (+) is also shown. Sites with fewer than five years of data were excluded. Numbers of years in the sample are shown.

Episodes of high mortality are a predictable fact of life for marmots because colonies are small and because marmots hibernate communally. The well-known Haley bowl and Green summit colonies have long monitoring histories and are therefore illustrative in this regard. Haley Lake had typical survival rates (median = 0.69, n = 26 years) but on six occasions lost more than half of its marmots. The Green summit colony showed similar survival trends (median = 0.65, n = 20 years), but on three occasions lost most of its marmots. Occasionally, high mortality episodes have been catastrophic: for example the apparently well-established Hooper north natural colony (4 adults, 3 juveniles and 5 active burrows) that was first discovered in 1982 has apparently not contained marmots since, despite repeated surveys in subsequent years.

High mortality events were apparently not uniformly distributed across time (Figure 26). Annual survival data coded as high mortality "events" or low mortality "non-events" using a variety of criteria suggest that the frequency of events increased over time. Using the median
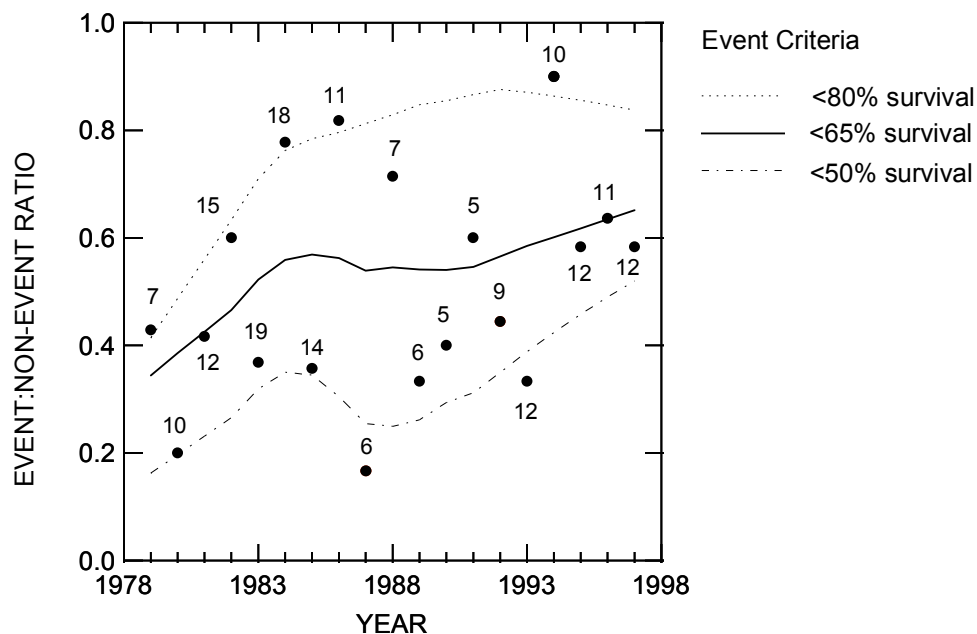
Figure 26: Incidence of high mortality events. Data points are event:non-event ratios using median annual survival (65%) as the event criterion. Lines are LOWESS regressions using three event criteria. Site-years with fewer than three marmots were excluded. Numbers of colonies in the sample are shown.

survival rate (65%), results suggest a gradual increase in the event:non-event ratio. Other event criteria produce different results. Using the high survival event criterion (<80%), results suggest that marmots have generally not experienced high survival since the mid 1980s. Of particular interest are the results based on a more stringent (<50%) event criterion.

Episodes of high mortality occurred often (39 events and 124 non-events; rate = 24%). In 10 years the event:non-event ratio was higher than this, and in 9 years it was lower than this. The lowest ratio occurred during the 1987-1991 period, but this is probably biased downward because sampling efforts were made at a few relatively stable colonies. The data suggest that most periods were characterized by an event:non-event ratio of between 20 and 25%. The ratio has been higher than 35% since 1994, and it was also higher than this during the 1984-1986 period. The early sampling period is interesting because it does not suggest high spatial correlation. Inspection of the data suggests that events occurred at widely separated colonies (e.g., Mount Whymper, "P" Mountain, Mount Buttle, Green Mountain) during the mid-1980s. It is also interesting that these

events went largely unnoticed by count crews, presumably because attention was focused on expanding clearcut colonies at that time.

The apparent increase in frequency of high mortality events is disturbing. Data from Haley Lake are again illustrative. At this colony, three of the four survival years since 1994 represented high mortality events and the fourth was borderline (survival = 50%). Given the natural history of *M. vancouverensis*, no colony could be expected to withstand the demise of 18 of 21 juveniles produced during a four-year period, and this was the fundamental cause of near-extinction at this site by 1998. Intriguingly, if the last four years of episodic mortality are excluded, median survival was increased (to 71%) to the extent that life-table analysis would suggest a relatively stable population ($R_O = 0.94$, $\lambda = 0.985$).

From these data I conclude that the frequency, magnitude and spatial correlation of episodes of high mortality have increased in recent years. These "crashes" are consistent with a hypothesis of disease outbreak or increased hunting effort by predators within a small geographic area.

DISCUSSION

Caughley and Gunn (1996) offered a straightforward model for managing endangered species. First, determine whether populations are declining or whether other evidence suggests that a problem exists. Second, learn about the ecology of the organism and use the accumulated knowledge to construct hypotheses about possible causal factors. Third, subject the resulting hypotheses to rigorous scientific testing, preferably under controlled experimental conditions. Finally, use the results to reverse the factors that are causing the problem.

Vancouver Island marmots illustrate many of the difficulties involved in trying to apply Caughley and Gunn's model to a "real-world" endangered species issue. Some difficulties are practical in nature. For example, despite over a decade of count efforts, at the beginning of this study there was no quantitative information about abundance or population trends because results had not been mapped, analyzed or tested for consistency. Demography was not well understood, and as recently as the early 1990s there was considerable uncertainty about whether marmot populations were increasing or declining (Janz et al. 1994). For these reasons much of my study was necessarily descriptive and designed to answer basic questions about population ecology. Other issues pose difficulties of a more philosophical nature. For example, neither marmot populations nor the landscape remained static during the study. The landscape became increasingly modified by forestry activities and the marmot population changed in abundance and structure. By definition there could therefore be no "control" or "treatment" groups with which to test hypotheses using a classical experimental approach (Popper 1968). For similar reasons we can never know why *M. vancouverensis* disappeared from central Vancouver Island. Empty burrows and unoccupied habitats provide few opportunities to identify causal mechanisms.

My approach was to test whether observed patterns were consistent with predictions made using a variety of hypotheses. Note that this approach can yield only "strong inference" and not "proof" of causal factors (Platt 1964). However, I suggest that given ~100 animals left in the world, it is the only possible approach. Recovering *M. vancouverensis* from the brink of extinction is fundamentally a management issue, and managers need to know not only what the problems are, but what the problems are not. The evidence suggests that Vancouver Island marmots are declining not because of one factor but because of several. Some factors are more important than others.

Habitat tracking

The environmental tracking hypothesis depends on issues of temporal scale. Over the long term, Vancouver Island marmots are presumably tracking climatic changes and associated vegetation patterns. Nagorsen et al. (1996) suggested that this could be inferred from finds of prehistoric bones well outside the core area of current distribution, and this interpretation is probably correct. Extra-limital finds of prehistoric marmot bones tell a similar story in other parts of the world (e.g., Preleuthner et al. 1995, Grayson 1987). Replacement of tundra parkland by forest has greatly reduced the quantity of marmot habitat available in the Pleistocene-Holocene prehistoric past. Tree-lines on mountains of western North America have changed substantially over the past 10,000 years in response to changing climate (Rochefort et al. 1994).

There is little evidence for habitat tracking in historical times. Within the past 100 years a warmer and drier climate has resulted in tree invasion of sub-alpine meadows in the Olympic (Fonda and Bliss 1969, Schreiner and Burger 1994) and Cascade mountains (Franklin et al. 1971). However, dendrochronological work at historic *M. vancouverensis* colonies north of Alberni Inlet does not support the hypothesis that similar processes caused recent marmot extinctions there. In western Strathcona Provincial Park, where marmots apparently disappeared some 10-30 years ago, most trees are more than 300 years of age and there is little evidence of recent forest succession (C. Laroque, University of Victoria, unpublished data).

Similarly, fire apparently plays a minor role in maintaining marmot habitat. Milko and Bell (1985) reported a distinct charcoal layer at Gemini Peak and suggested that an extensive fire created open meadow habitat at that site. Recent tree-ring analyses do not support this interpretation. Laroque (1998) determined a large range of tree ages at Gemini Peak and estimated a minimum disturbance interval of at least 250 years. This is congruent with results from Lertzman et al. (1998), who suggested that intervals between major fires were relatively short (<300 years) on southeastern Vancouver Island but substantially longer (700 - 3000 years) in western and central regions.

The evidence for environmental tracking in recent decades is weak, at least for marmots in natural habitats. Few of the predictions were strongly supported by the data.

Reproduction and survival will be chronically low at some natural colonies

A few natural colonies (e.g., Westerholm Basin, Meadow #1) had relatively low per capita birth rates and apparent survival compared to other sites. Low coefficients of variation suggest that these

patterns were "chronic", supporting the idea that habitats are gradually becoming unsuitable because of tree invasion or more subtle changes in vegetation. However, most natural colonies did not display similar trends. Colonies such as Hooper North, "P" Mountain, South Green or Gemini Peak exhibited relatively high survival and reproduction until catastrophic losses occurred. Extinctions happened abruptly and with no suggestion of a gradual decline in habitat suitability. I conclude that environmental tracking may be occurring at a small number of natural habitats but this process does not explain recent population trends.

Reproduction and survival will be associated with age of regenerating clearcuts.

Adult survival was weakly and negatively associated with clearcut age. The apparent reduction in survival among clearcuts coded as "young" or "old" (>10 years old) was also notable. It appears that marmots already living in regenerating clearcuts represent a special case of environmental tracking. However, the data are more suggestive of a threshold effect than of a gradual demographic response to forest succession. Clearcuts generally become unsuitable for marmots after the age of approximately 15 years, although site-specific conditions undoubtedly influence this timing.

Colonization of clearcuts will occur in proportion to their availability.

Colonization of clearcuts did not occur in spatial or temporal congruence to habitat availability. Marmots apparently did not colonize clearcuts until 1981, despite availability of nearby high elevation clearcuts during the mid 1960s. It appears that marmots are apparently not simply colonizing places when they become suitable, although they are clearly disappearing when these habitats become unsuitable.

Overall, the evidence for environmental tracking over the short term is weak. Data from natural habitats do not support a hypothesis of gradual vegetation change. Seral stage of regenerating clearcuts apparently represents a special case of environmental tracking. Marmots did not colonize clearcuts in temporal or spatial relation to their availability. Even allowing for substantial lag effects that might occur given the difficulty of finding and successfully colonizing clearcuts, the data are at odds with a fundamental prediction of the tracking hypothesis: marmots did not increase in numbers despite greatly increased habitat availability.

Weather hypothesis

Weather has been shown to have significant effects on other marmot species (e.g., Barash 1973, 1989, Van Vuren and Armitage 1991, 1994). My results support this interpretation but suggest that

weather effects are relatively modest. No prediction made under the weather hypothesis was strongly supported by the data.

Reproduction and survival will be associated with weather measurements.

Weather variables explained only small amounts of the variation in survival and birth rates. There was a consistent positive relationship between survival and the number of spring days with significant rainfall events, yet survival was negatively associated with cumulative spring rainfall. This result could reflect a threshold effect, in which too much rainfall results in poor survival conditions, but consistent moderate rainfall results in improved survival conditions. That marmots in all habitats responded consistently to these variables is particularly interesting, and could reflect nutritional factors or growth of parasites or disease.

Snowpack conditions were also important, but caution is needed in interpreting this result because local conditions probably differed considerably from those at snowpack measurement stations. However, the evidence from studies of other marmot species is compelling. Survival of *M. olympus* was positively associated with increasing snow depth, possibly because of increased insulation value of the snowpack (Barash 1973). Arnold's (1990*a*, 1990*b*, 1992, 1993) work on *M. marmota* suggested a possible physiological explanation for this. Indeed he suggested that a driving force behind the evolution of marmot sociality can be found in the physiological necessity for a thermally-stable environment in which to hibernate. Recent work on *M. marmota* lends additional credence to the snowpack-survival hypothesis (Farand et al. in prep.), but there has been no additional work concerning whether the mechanism is actually one of snowpack insulation. Specifically, the depth at which soils experience zero annual temperature amplitude (see Brown 1970) has not been related to the depth at which marmots hibernate, or to soil types. Van Vuren and Armitage (1991) suggested that the timing of snow melt, and not the depth of snowpack, may be the critical factor in determining marmot survival.

Reproduction and survival will be associated with habitat type or site characteristics such as elevation or aspect.

There was a weak association of survival with colony aspect, as would be predicted if snowpack effects were influenced by site exposure. Marmots inhabiting clearcut and natural habitats responded differently to weather conditions, which is not surprising given recent work on the nutritional and hibernation requirements of other marmot species. Physiological studies provide important clues regarding how short-term climatic variation could influence marmot survival during winter hibernation (Arnold et al. 1991). The laboratory study by Thorp et al. (1994) may also be

very relevant; in this study yellow-bellied marmots were fed diets containing high or low amounts of polyunsaturated fatty acids. Marmots supplied with a diet deficient in essential fatty acids showed identical weight gains during summer, but exhibited higher spontaneous arousal rates, shortened bouts of deep hibernation and higher overall metabolic expenditures. That this could lead to increased winter mortality is clear (Arnold 1993). It is likely that between-site soil characteristics and annual weather variation could influence both the availability and chemical composition of plants eaten by marmots (Sinclair et al. 1982, Walker et al. 1993).

Marmots inhabiting clearcuts do not have access to the same variety of food plants that they do in natural sub-alpine meadows. Reliance upon a small number of species (especially *Anaphalis margariticea*) could result in altered biochemistry or lack of essential nutrients in marmot diets, particularly if weather conditions such as drought produce important effects on these few plant species. Armitage (1994) found that a year of particularly low survival for *M. flaviventris* was associated with a short snow-free growing season, and with low rainfall during summer. Blumstein and Foggin (1997) determined that vegetation availability was strongly related to the probability that red marmots (*M. caudata*) successfully weaned juveniles in the following spring.

Weather had a marginal effect on the probability of reproducing in natural habitats. However, animals living in clearcuts were significantly influenced by rainfall and snowpack patterns and weather explained moderate amounts of the variation in reproductive status. Again there was a different response to rainfall magnitude and rainfall consistency, which could suggest nutrition or parasite/disease conditions that are influenced by moisture regimes.

Episodes of high mortality will occur randomly over time.

High mortality events did not occur randomly over time. Regardless of the event criteria used, the incidence of high mortality events systematically increased with time. This trend is inconsistent with a hypothesis of population response to random fluctuations in environmental conditions.

Ultimately, weather exerts significant effects upon marmots but does not appear to explain population trends. I conclude that recent population declines cannot be attributed to a succession of "bad" weather years.

Sink-connectivity

There is growing empirical evidence from a variety of taxa that some organisms are maintained in qualitatively heterogeneous "source-sink" metapopulations (e.g., Breininger et al. 1995, Donovan et al. 1995, Wauters and Dhondt 1990). There is also growing appreciation for the critical role that

dispersal or "connectivity" plays in maintaining metapopulations, and consequently for the effects that fragmentation may have (Fahrig and Merriam 1985, Hanski 1991, Dunning et al. 1992, Taylor et al. 1993, Fahrig 1997). Some organisms simply change their movement behavior in response to altered spatial distribution of habitats, seemingly with no effect on reproductive performance or survival (e.g., Taylor and Merriam 1995, Matthysen 1995). This appears not to be the case for Vancouver Island marmots. Most of the predictions of the sink-connectivity hypothesis were supported.

Reproduction and survival will be chronically low in clearcuts.

Mark-recapture results suggested that animals living in clearcuts experience a small (5-10%) but chronic reduction in annual survival. Population count results corroborated this finding for pups but were inadequate to evaluate adult survival because of the inability to distinguish survivors from immigrants. Despite a sample of tagged animals that represented 10-15% of the population, parametric estimates of survival were statistically insufficient to resolve the small observed habitat-specific or temporal differences.

Life-table analysis illustrates the biological importance that small changes in survival could have. Tagged females living in clearcuts produced only half as many offspring as their counterparts in natural meadows did, and these offspring themselves had a substantially reduced probability of reaching dispersal age. There are theoretical problems in using uncorrected estimates of net reproductive rate (R_o) as a measure of the degree to which populations may be increasing or decreasing (Gregory 1997). Specifically, this rate is valid only if the population in question exhibits constant birth and death rates (thereby yielding a stable age distribution), an assumption which is unlikely to be true for most wild populations and especially for Vancouver Island marmots. Despite such difficulties the data are consistent with a hypothesis of reduced survival in clearcuts and with observed population trends.

However it would be simplistic to conclude that natural habitats always acted as "sources" or that clearcuts always acted as "sinks". Although mortality appears to be concentrated in the clearcuts, some (e.g., Mount Franklin and Sherk Lake) showed high survival in some years, and some natural habitats also showed chronically poor performance. The fundamental difference between the two habitat types is of course temporal. Unlike natural meadows, clearcuts represent temporary habitats that have a brief "window" of perhaps 10 or 15 years during which they are capable of contributing dispersers to the overall metapopulation. This is a short period of time in terms of marmot generations, and represents a temporal habitat restriction that is novel for the

species. Because natural meadows do not change so quickly, *M. vancouverensis* has not had the opportunity to evolve appropriate behavioral responses to this process. Specifically, adults apparently do not move as clearcut habitats change with forest succession. In short, behavior that was adaptive during the past 10,000 years may be maladaptive in habitats created during the last 20 years.

Isolated colonies will show higher extinction rates.

Uncertainty over the timing of extinctions made it impossible to test for the influence of spatial isolation directly. However, a map of extinction events did not support the prediction that isolated colonies have a higher extinction probability. Some small and isolated natural colonies became extinct, but several large colonies near the center of the geographic range also became extinct.

Isolated colonies will show lower apparent survival due to reduced immigration.

Because of small colony sizes, Vancouver Island marmots are extremely vulnerable to random events. Most mountains apparently contain only 1 or 2 family groups (Bryant and Janz 1996), and the fate of single individuals causes important population effects. Local extinctions, lack of reproduction, and immigration "rescue effects" (Brown and Kodric-Brown 1977) were observed on several occasions that were apparently caused by the appearance or disappearance of single adults. Isolated colonies exhibited lower apparent adult survival, which is congruent with a hypothesis of reduced immigration and consequent reduced probability of "rescue effect" or recolonization of vacant habitat patches.

Colonizations of clearcuts will be spatially concentrated.

The evidence for reduced landscape connectivity is indirect but suggestive. Clearcuts were not colonized in proportion to their spatial availability. Colonizations appeared to be limited by the presence of nearby natural colonies at which numerous potential emigrants were produced. Colonization events were spatially clustered compared to clearcut habitats actually available. Few tagged marmots made long-distance dispersal movements and only one dispersing female is known to have eventually reproduced at a new site. All of these results are congruent with a hypothesis that colonization hinged on successful dispersal from a small number of "source" colonies, that dispersing marmots were "short-circuited" by the presence of nearby alternative habitats in which to settle, and that clearcuts consumed more marmots than they produced.

Dispersal is notoriously difficult to study in the wild. Simulation modeling indicates that metapopulations are extremely sensitive to changes in dispersal, and in particular to changes in rates

of long distance movements (e.g., Lindenmayer and Lacy 1995, Lamberson et al. 1992). Yet we still know relatively little about why real organisms disperse or how they respond to changes in the physical environment (e.g., Lidicker and Koenig 1997). Like other alpine-dwelling marmots, *M. vancouverensis* apparently exhibits presaturation dispersal (animals disperse at a wide range of population densities) and this may reflect the adaptive tendency of individuals to disperse when they approach reproductive age (e.g., Arnold 1990*a*, Barash 1989). However, in the case of *M. vancouverensis*, perhaps the question of what makes a marmot begin to move is less important than what makes it stop.

Apart from the obvious habitat cues furnished by newly available clearcuts, there may be behavioral issues to consider. Weddell (1991) determined that Columbian ground squirrels (*Spermophilus columbianus*) readily moved between habitat patches but invariably settled in habitats that contained other animals. For this reason recolonization of vacant habitat patches did not occur. It is tempting to interpret this idea to the highly social *M. vancouverensis* (Heard 1977), particularly since dispersing animals would commonly encounter other marmots in nearby clearcuts, and high mortality in these habitats could lead to unused burrows and therefore perhaps to "vacancies" in existing social groups.

The evidence for the sink-connectivity hypothesis is relatively compelling. Regenerating clearcuts in montane sites above 700 m in elevation resemble natural marmot sub-alpine meadow habitats for at least 10 to 20 years after harvest. This resemblance allowed marmots to colonize some clearcuts but population expansion was temporary and limited in geographic scope. Only a small proportion of available clearcuts were eventually colonized. By providing new alternative habitats in which to settle, forestry apparently changed natural dispersal patterns and probably reduced the rate at which animals were able to colonize distant habitats. The most important forestry effect was probably to concentrate the population and therefore exacerbate the "eggs in a small basket" problem, increasing the risk of mortality from processes that occur within a restricted geographic area.

Predators and prey

Marmota vancouverensis has evolved in the presence of wolves, cougars and eagles and exhibit a variety of typical anti-predator strategies that reduce predation risk. They appear to be no less vigilant than other marmots (D. Blumstein, University of Kansas, unpublished manuscript). To propose that predators have suddenly (in evolutionary terms) become of critical importance is not logical unless either predator abundance or hunting effort upon marmots has increased. The

evidence suggests that increased predator abundance is unlikely, but that increased hunting effort by predators is congruent with observed trends.

Most mortality will occur during summer.

In clearcut habitats, the timing of last observation of tagged marmots suggested that most mortality occurs during hibernation. In contrast, disappearances in natural habitats were more evenly distributed throughout the active season, which is consistent with the predator hypothesis. Cougars, wolves and eagles can and do exert significant impacts on marmots. Radio-telemetry and direct observation provided conclusive evidence of predator-kills, and several colonies declined after the loss of breeding-age animals. In addition, the frequency of losses to predators was substantial (16%) compared to the numbers of marmots equipped with radio-transmitters.

Survival will be associated with abundance of predators or alternative prey such as deer.

Merilees (1980) suggested that increasing golden eagle abundance may have had an impact upon marmots. Unfortunately, data with which to estimate golden eagle population trends in the Nanaimo Lakes region are non-existent. While it is interesting that the first confirmed nest record for that species on Vancouver Island was close to a historic marmot colony (Upper Campbell Lake in 1954; Campbell et al. 1990*b*), other sightings had been made well before that (Carl 1943) and it is perhaps significant that Swarth (1912) collected *M. vancouverensis* from a location known as "Golden Eagle Basin". In any case, the small number of observed predation incidents involving eagles makes me skeptical that marmot population trends could be attributed to changing eagle abundance.

Cougar and wolf abundance indices were poor predictors of marmot survival. However, I reiterate my concern that predator sightings or removals may not reflect true abundance. Annual indices fluctuated more dramatically than expected given the life-history characteristics of cougars and wolves. Certainly the available data cannot be interpreted to suggest significant changes in predator abundance during the study. It is therefore not surprising that predator indices showed no consistent relationship with marmot survival.

Predation pressure does not depend on predator abundance alone. Drastic declines in mule deer abundance raise the possibility that predators might be increasingly "switching" their hunting effort (Bergerud 1983) to *M. vancouverensis*. The significant but weak association between deer abundance and survival of marmot pups in natural habitats supports this idea, but the absence of similar relationships for adults or pups in clearcuts provides conflicting evidence.

Survival rates will be spatially correlated.

Changes in the hunting behavior of predators could also be important. Marmot survival rates were spatially correlated within an effects radii of several km, which is a predicted result if predators concentrate their hunting efforts at nearby colonies. Observations of predator tracks leading from colony to colony are consistent with that possibility, and with the idea that a small number of individual predators have become particularly adept at hunting *M. vancouverensis*.

Predator hunting behavior cannot be divorced from the landscape changes produced by forestry activities. It is possible that terrestrial predators may hunt more successfully in clearcuts because tree growth limits visibility, and predators may therefore be better able to stalk marmots while remaining undetected. The difference between survival in "young" and "old" clearcuts is congruent with that possibility. Logging roads could also function as corridors that provide easier movement to both predators and marmots, thereby increasing the frequency of interactions (e.g., Simberloff et al. 1992). Regardless of whether such ideas are correct, colonization of clearcuts had the effect of dramatically increasing marmot abundance in a small (40 km²) area, and this presumably increased the potential benefits of hunting within that area. The expected consequence would be to simultaneously increase predation pressure at nearby natural colonies, and this is consistent with the relatively rapid decline of marmots at natural colonies in the central portion of the Nanaimo Lakes region.

Disease

The potential importance of disease and parasites has long been recognized (Anderson and May 1979, May and Anderson 1979). There are several cases in which disease devastated populations on a continental scale (e.g., Dobson and May 1986, Geraci et al. 1982), and the risks for small or restricted populations are even more extreme. Canine distemper and black-footed ferrets (*Mustela nigripes*) must represent the classic case in this regard (Clark 1997), but there are undoubtedly others (Laurance et al. 1996).

The role of disease or parasites in regulating other species of marmots is not well understood. There is a large Eurasian literature concerning bubonic plague (*Yersinia pestis*) in marmots (the European "black death" of 1347-1348 may have originated from trade in marmot pelts; McEvedy 1988). Many other possible pathogens are carried by marmots, including Tularemia (Zykov and Dudkin 1996), Leptospirosis, Toxoplasmosis, Ricketsiosis, Listeriosis, Pseudotuberculosis=Yersiniosis, Salmonellosis and Powassan Encephalitus (Bibikov 1992). Woodchucks (*M. monax*) carry a virus similar to human hepatitis B (Summers et al. 1978).

External and internal parasite-loads have been studied in several species (e.g., Ageev and Pole 1996, Callait et al. 1996, Gortazar et al. 1996, Preleuthner et al. 1996). The consistent result of these studies is that while infections and infestations occur, there is no evidence to suggest that they have caused significant population declines (M. Callait, Université de Lyon, and S. Pole, Kazak Antiplague Research Institute, pers. comm.).

However, this does not mean that the risks disease or parasites are insignificant. What may be unimportant for a widespread or abundant species may be extremely important for a restricted population of Vancouver Island marmots. The evidence is generally consistent with a hypothesis of increased incidence of disease or parasitic infestation.

Survival will be density-dependent.

Disease and parasite problems are often considered to be density-dependent because the risks of infection are higher in high density populations (May and Anderson 1979). The data corroborated this prediction. Adult survival was negatively associated with observed/expected ratios. Survival of pups was not associated with relative density in linear fashion, although survival was visibly lower in colonies of high density (>150% of expected).

Survival rates will be spatially correlated.

Disease outbreaks would be expected to occur more frequently at nearby colonies. Marmot survival was spatially correlated, and in this case results are especially intriguing because the magnitude of spatial correlation increased substantially between the early (1981-1987) and late (1991-1997) sampling periods. The increase in spatial correlation occurred despite the marmot population becoming much less concentrated during the latter period.

The incidence of high mortality events will increase over time.

One possibility is that Vancouver Island marmots have been recently exposed to a novel pathogen to which they have no immunity. This presents a frightening scenario in which the infection would be expected to spread throughout the metapopulation, and in which the incidence of high mortality events would increase as a result. The evidence is consistent with this prediction. Episodes of high mortality apparently became more numerous in the 1991-97 period, and perhaps more disturbingly they became increasingly spatially correlated.

Most large colonies in the center of the geographic range suffered extremely high losses over short periods (e.g., Gemini Peak in 1986-87, Vaughan Road in 1988-89, Bell Creek in 1993-94, and Butler roads, Road K44A and Haley Lake in 1994-95). In these cases most disappearances

apparently occurred during hibernation, a period when marmots may be particularly vulnerable to infection. The negative evidence may also be relevant. During the late sampling period several isolated colonies (e.g., Big Ugly, Mount Franklin) apparently did not suffer similar episodes.

Whether an epizootic is responsible for the disappearance of *M. vancouverensis* from areas north of Alberni Inlet remains unknown and untestable. However it is apparent that catastrophic and abrupt losses from large, apparently healthy colonies contributed significantly to the overall decline of the Nanaimo Lakes metapopulation. I conclude that the threat of extinction from pathogens is real, and stress that epidemiological processes should not be viewed in isolation. For example, increased virulence in the bacterium *Y. enterocolitica* has been associated with unfavorable climatic conditions and poor nutrition (Zwart 1993, Blake et al. 1991). In addition, as with the predator hypothesis, increased density of marmots due to colonization of nearby clearcuts greatly increased the vulnerability of marmots by increasing the risk of infection.

Converging lines of evidence

Vancouver Island marmots live in a complex world. There is no *a priori* reason to imagine that a single factor is responsible for recent population dynamics, or that the same suite of factors acted uniformly across time or space. *M. vancouverensis* is and will continue to be influenced by a multitude of mortality factors including unsuccessful hibernation, predators, and disease. In many respects it therefore represents an organism caught in the "vortices of extinction" (Gilpin and Soulé 1986), and its story is not dissimilar to that of the heath hen (*Tymphanuchus cupido*), which became extinct after disease, predators and wildfires had taken their toll on an already depleted population (Caughley and Gunn 1996).

South of Alberni Inlet, forestry appears to be the principal factor behind recent marmot population trends. Logging reduced the ability of marmots to re-colonize or "rescue" isolated natural colonies by the simple mechanism of creating large amounts of nearby alternative habitat. Animals living in clearcuts produced fewer than half the number of potential dispersers than did their counterparts in natural meadows. The fast pace of forest regeneration after clearcut logging posed new challenges for animals that are not adapted to take advantage of habitats that change over a period of several years. Both the colonization pattern and the lack of long-term expansion are consistent with a hypothesis of source-sink regulation, although it appears that clearcuts are not necessarily sinks, or sinks in all years.

The most important impact of forestry was to increase population concentration, thereby making individual colonies more vulnerable to predators and disease. Sweitzer et al. (1997) documented near extinction of porcupines (*Erithizon dorsatum*) from a 15 km² area in Nevada due to cougar predation and suggested that reduced deer populations were the proximate cause. Beier (1995) observed that cougars will readily use dirt roads and trails. Observations of marmots and predators travelling along roads makes it logical to suggest that road networks increased the frequency of marmot-predator interactions. The growing rate of high mortality events is consistent with a disease outbreak, and again the implications are made more severe because of population concentration. Finally, recent population trends in the Nanaimo Lakes metapopulation are disturbing because most animals occupy habitats that will become unsuitable in a few short years. This structural problem is not easily resolved except that over time forest regeneration will occur and sites will become unattractive to marmots. Road networks may well act as a more permanent structural change, at least as they pertain to facilitating movements of predators and prey.

It remains unknown why marmots disappeared from areas north of Alberni Inlet. Predators, weather, disease and demographic stochasticity probably all played a role. Landscape connectivity may have changed for several reasons. Tree invasion may have occurred at important "stepping stone" colonies such as those that apparently existed on Mount Arrowsmith and in the Beaufort range prior to the 1980s. Another possible factor may relate to construction of Strathcona Dam at the north end of Buttle Lake. This dam, completed in 1957, raised the water level by 9 metres, and increased the area of the lake substantially (it inundated nearly 90% of the lake's tributary stream spawning areas; Hyntka 1990). The reservoir could have acted as a new barrier and influenced dispersal and metapopulation dynamics. Evidence from the Nanaimo Lakes metapopulation indicates how important dispersal processes are in maintaining colonies, and the timing of dam construction would seem to be congruent with probable marmot disappearances after the 1950s. Finally, Nagorsen et al. (1996) documented prehistoric marmot hunting by humans, possibly significant hunting events also occurred in modern times.

It seems unlikely that we will ever definitively answer the question of why marmots disappeared from central Vancouver Island. Historical marmot population data simply do not exist with which to test the relative importance of various environmental effects. However, perhaps focusing on this question would be less useful than focusing on an essential dichotomy. Specifically, while several plausible mechanisms can be invoked to explain disappearances, few can be raised to support the idea that marmots might re-colonize such habitats on their own. There are several sites in western

and eastern Strathcona Provincial Park where abandoned burrows and vegetation conditions suggest that potential natural habitats are still available. Unfortunately, geography and natural and landscape changes make it unlikely that marmots could successfully re-colonize these sites if left to their own devices.

Lessons from marmots

Most alpine-dwelling marmots exhibit metapopulation structure (they are colonial, inhabit discrete habitat patches that suffer local extinctions and recolonizations, and are connected by dispersing individuals within an ecological time scale). However, with a few notable exceptions (e.g., Armitage and Downhower 1974, Schwartz et al. 1998) marmots have been largely ignored by students of metapopulation and landscape ecology. This trend is unfortunate. The same attributes that make marmots such useful organisms for students of evolution, sociobiology, and demography also make them good candidates for metapopulation studies (specifically: they are diurnal, large enough to be easily seen, respond well to capture and marking, and exhibit generally predictable habitat-affinities and activity-rhythms: see Armitage 1992). Most importantly, there are 14 species that display a wide range of colony sizes, social assemblages, densities and distributions with which to test ideas about landscape connectivity and population persistence. Comparative studies among threatened and non-threatened marmots could indeed build a useful bridge between what Caughley (1994) termed the "small population paradigm" (what happens to small populations) and the "declining population paradigm" (what causes populations to become small?")

The source-sink concept has important ramifications for conservation biology, principally because it suggests that organisms may not necessarily be most numerous in habitats where they are most successful in demographic terms (Pulliam 1988, Wauters and Dhondt 1990). Metapopulation processes that involve changes in landscape connectivity or fragmentation complicate the issue. Many habitats may be unoccupied not because they are unsuitable but because organisms can't get there (Dunning et al. 1992, Fahrig 1997). For many species it is therefore extremely dangerous to equate high abundance with habitat quality, or to equate low abundance with habitat unsuitability. Unfortunately, measures of relative abundance still form the basis of many management and land-use decisions involving threatened species, perhaps because of the mistaken belief that relative abundance is all that can be measured given practical field difficulties or intrinsic rarity of the organism in question. The *M. vancouverensis* experience suggests that such beliefs may be unwarranted.

This study found close congruence among demographic estimates from marked and unmarked segments of the study population. Admittedly, marmots represent an unusual case (because

juveniles, yearlings and adults are easily distinguished it is possible to estimate birth and survival rates). However the point remains: carefully designed and tested count methods may be a valuable adjunct to more intensive (and expensive) monitoring techniques if the basic biology of the organism is understood. Conversely, unadjusted population counts or estimates of abundance based on "detection rates" have the potential to provide highly misleading impressions about demographic performance or population trends if the basic biology is poorly understood.

Recent advances in technology (such as implantable radio-transmitters) and theory (such as Cormack-Jolly-Seber modeling of survival) are welcome but I caution that there will be inevitable trade-offs between intensively sampling a small population using such techniques and sampling a larger population using less intensive methods. Results from *M. vancouverensis* illustrate the problem well. Even robust scientific methods may be inadequate to resolve small but potentially significant changes in demographic rates if only a hundred or so animals exist. For this reason I believe that much more work is needed to determine valid measures of demographic success for rare species and to integrate the results of "intensive" and "non-intensive" research methods.

Questions of spatial and temporal scale are critical. I wish to add my name to the long list of authors who stressed the value of long-term research (e.g., Armitage 1991, Schwartz et al. 1998) conducted on a geographic scale large enough to address the problem (e.g., Pimm 1991, Caughley and Gunn 1996). In the case of *M. vancouverensis*, a study of typical duration for graduate students (2-5 years) and involving only a few colonies would have produced very different impressions about what was happening to marmots.

Rarity has been described as the inevitable result of a limited niche pattern (Gaston 1994). Under this interpretation, niche pattern consists of niche breadth (the range of environmental conditions in which organisms can survive and reproduce) and niche position (the spatial and temporal availability of these resources and population abundance). There is no evidence to suggest that Vancouver Island marmots have a particularly narrow niche breadth. They live and reproduce in a variety of habitats and exploit a wide variety of food resources. The small amount of comparative work done with *M. vancouverensis* and other species suggests that they are not dissimilar to other alpine-dwelling marmots in antipredator behavior (D. Blumstein, University of Kansas, pers. comm.) or sociality (Heard 1977).

There is strong evidence for limited niche position. Vancouver Island marmots inhabit a spatially patchy environment in which the size of available meadows is small compared to the

surrounding matrix. However, limited niche position is not a new phenomena. Low rates of natural disturbance (Lertzman et al. 1996) suggest that niche position has remained essentially unchanged for at least the last several thousand years. Some habitat losses undoubtedly occurred from forest succession and some gains occurred after fire or avalanches, but in general there is little support for the idea that habitat quality or quantity have systematically changed over a temporal scale measured in centuries. Vancouver Island marmot abundance and distribution in the mid 1900s were probably quite similar to what they were several hundred years ago.

Hence the paradox of *M. vancouverensis*. Marmot persistence at particular sites has been quite remarkable and yet they disappeared from about two thirds of their apparent recent geographic range within the past 50 years. They successfully colonized some clearcuts and greatly increased numbers within a few years yet did not expand in proportion to habitat availability. It is difficult to reconcile recent population trends in the severely human-modified environment on private lands south of Alberni Inlet with the loss of marmots from seemingly pristine sites on central Vancouver Island. Or at least it is difficult if one searches for a single causal factor. Perhaps the recognition that there are many is the most important result of this study.

Given rejection of the tracking and weather hypotheses there seems little reason to expect that population trends might suddenly reverse themselves. An aggressive program of captive-breeding combined with reintroduction appears to offer the only realistic hope of preventing extinction of this species. Fortunately, marmot captive-breeding programs have achieved success both in Russia (with *M. bobac, M. baibacina* and *M. menzbieri*) and the United States (with *M. monax, M. broweri* and *M. flaviventris*). There would appear to be no particular technical difficulties associated with maintaining and breeding marmots in captivity (e.g., Tokarsky 1996, Rymalov 1996, Concannon et al. 1989). Similarly, reintroductions of *M. marmota* and *M. bobac* have been successful in western Europe (Ramousse et al. 1992, Dmitriev et al. 1994). In particular, alpine marmots (*M. marmota*) disappeared from portions of the Alps (Preleuthner et al. 1995) and from the Pyrenees during historical times. As is the case for *M. vancouverensis*, causes of disappearance remained unknown but reintroduction was spectacularly successful despite this lack of knowledge. Reintroduction of several groups of wild-captured *M. marmota* in the 1960s has resulted in an apparently stable population of several hundred animals (Herrero et al. 1994). In the Alps, substantial portions of the extant population is thought to have been derived from transplants that occurred since the 1940s (Preleuthner et al. 1995, Ramousse et al. 1992). There appears to be no reason why reintroduction

could not be equally successful on Vancouver Island, provided that sufficient reintroduction habitat still exists.

Additional research is required in several broad areas of study. Much more work is required in the field of epidemiology, with the objective of identifying pathogens of relevance to *M. vancouverensis*. Emphasis must be placed on developing diagnostic tools and effective treatments. Further work involving spatial patterns of survival could provide important clues about possible modes of transmission (e.g., Mantel 1967, Rossi et al. 1992). The idea that hibernation success could depend on the nutritional composition of food plants also needs to be tested, particularly as it relates to dietary differences among habitat types and possible weather effects (e.g., Thorp et al. 1994). Finally, more work is needed to identify and prioritize reintroduction habitats on Vancouver Island, and to test for the possibility of systematic environmental change either through tree invasion or more subtle vegetation change in natural sub-alpine meadows (e.g., Walker et al. 1993).

Successful management of endangered species requires an understanding of the biology of the organism and the processes that shape its environment (Caughley and Gunn 1996). For many years little progress was made towards understanding *M. vancouverensis*, largely because of a lack of carefully framed and tested hypotheses. Much speculation was therefore published about the supposed effects of ski-hill development, all-terrain vehicles, people or dogs (e.g., Dearden and Hall 1983). Conjectures of natural population regulation from weather or natural processes of vegetation change were accepted with little or no supporting evidence (Milko 1984). Severe population crashes were sometimes discounted because they were presumed to be something that "just happened". Conversely, the relationship between forestry and marmots remained unexplored because population counts suggested that marmots were increasing in clearcut habitats. The result of these impressions was to convince many people that either no problem existed, that the problem was somehow unsolvable, or that the problem could be solved by creation of small protected areas (e.g., the 127 ha Haley Lake Ecological Reserve).

In their assessment of wildlife reintroductions, Griffiths et al. (1989) suggested that the possibility of success is highest when animals are taken from donor populations that are expanding. However they ruefully noted that such conditions "are the ones that tend to make endangered species biologists relax". This is an apt description of much of the recent human history involving Vancouver Island marmots. The tragedy is that populations declined precipitously while the causes of decline remained untested and mis-understood. While I remain convinced that full recovery of this species is ecologically feasible, recovery will be a more lengthy and expensive process as a result.

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Appendix 1: Active season temperature and rainfall trends [a]

Year	May-June avg. midday temperature	May-June average rainfall (mm)	May-June days with >5 mm of rain	July-August avg. midday temperature	July-August average rainfall (mm)	July-August days with rainfall >5mm
1973	-	-	-	-	-	-
1974	14.9	3.8	13	21.2	1.8	7
1975	15.3	2.0	9	21.1	3.5	8
1976	14.4	2.9	12	18.2	3.1	10
1977	15.6	2.2	10	23.2	1.4	6
1978	16.9	3.0	14	22.6	2.7	6
1979	15.3	1.0	4	21.0	1.2	4
1980	16.0	1.9	9	21.5	0.8	2
1981	11.9	2.7	10	20.9	0.8	6
1982	16.8	1.5	3	18.5	1.1	2
1983	14.3	2.3	8	18.9	2.0	7
1984	-	-	-	-	-	-
1985	15.0	1.5	8	24.2	0.3	1
1986	14.2	4.2	13	20.2	1.0	5
1987	15.2	3.1	13	18.9	0.9	4
1988	11.5	3.8	14	19.2	0.9	5
1989	14.6	1.0	3	16.7	1.0	5
1990	12.4	3.0	14	21.6	0.7	3
1991	12.1	1.4	7	18.6	3.7	9
1992	17.0	1.3	6	19.9	2.2	7
1993	13.4	3.1	13	16.5	1.7	8
1994	13.0	2.1	6	21.6	0.4	3
1995	16.1	2.6	10	16.8	2.2	6
1996	10.9	3.5	12	20.5	0.8	4
mean	**14.4**	**2.4**	**9.6**	**20.1**	**1.5**	**5.4**
SD	*1.8*	*0.9*	*3.6*	*2.1*	*1.0*	*2.4*
CV	12%	38%	38%	10%	63%	44%

Notes:

[a] Raw data are from the Copper Canyon weather station (#210, at 840 m) maintained by MacMillan Bloedel Limited and compiled by the B.C. Ministry of Forests (Victoria).

Appendix 2: Snowpack trends [a]

Year	Jan.	Feb.	March	April	May	June	Early snow (Jan-Feb)	Late snow (June)
1973	-	231.0	181.5	250.7	236.0	163.0	-	163.0
1974	-	290.0	523.0	450.5	-	442.0	-	442.0
1975	-	205.5	306.0	346.0	315.0	310.0	-	310.0
1976	135.0	206.0	336.0	404.0	334.7	317.0	170.5	317.0
1977	15.0	13.0	52.7	167.7	119.7	97.0	14.0	97.0
1978	122.0	165.0	138.7	151.7	153.3	152.0	143.5	152.0
1979	132.0	142.0	260.0	200.3	199.3	144.0	137.0	144.0
1980	100.0	152.0	122.7	186.0	150.0	97.0	126.0	97.0
1981	0.0	27.0	41.7	98.5	81.7	29.0	13.5	29.0
1982	184.0	302.0	313.0	325.0	345.7	324.0	243.0	324.0
1983	221.0	253.0	250.0	249.3	226.0	200.0	237.0	200.0
1984	189.0	166.0	243.3	194.7	241.0	299.0	177.5	299.0
1985	188.0	160.0	173.7	212.0	189.7	149.0	174.0	149.0
1986	116.0	139.5	125.7	115.7	146.3	108.0	127.8	108.0
1987	127.0	274.0	196.7	184.3	165.0	117.0	200.5	117.0
1988	158.0	177.0	198.5	262.7	233.3	226.0	167.5	226.0
1989	130.0	169.0	187.0	284.7	233.7	180.0	149.5	180.0
1990	30.0	141.0	223.3	221.3	131.7	88.0	85.5	88.0
1991	108.0	140.0	81.0	122.7	117.0	91.0	124.0	91.0
1992	78.0	151.0	138.0	105.0	62.5	0.0	114.5	0.0
1993	128.0	154.0	119.5	154.0	167.0	77.0	141.0	77.0
1994	75.0	64.0	217.0	225.5	150.5	89.0	69.5	89.0
1995	232.0	260.0	227.0	269.0	258.0	128.0	246.0	128.0
1996	69.0	128.0	161.0	129.5	130.0	98.0	98.5	98.0
mean	120.8	171.3	200.7	221.3	190.7	163.5	141.0	163.5
SD	62.7	74.2	103.3	92.3	76.3	106.6	64.1	106.6
CV	52%	43%	51%	42%	40%	65%	45%	65%

Notes:

[a] Data are snow depths (in centimetres) averaged across three sampling stations: Sno-bird Lake (1400 m), Mount Cokely (1190 m), and Heather Mountain (1170 m). Unpublished file data, B.C. Ministry of Environment, Lands and Parks (Victoria).

Appendix 3: Measures of landscape change [a]

Year	Mature forest remaining (ha)	Area logged below 700 m (ha)	Area logged above 700 m (ha)	Regenerating forests (ha)	Road density (linear km per square km)	Natural marmot habitat (ha)	Water and non-forested lands
1972	51,491.8	19,775.8	5,435.5	32,275.4	1.18	118.3	9,089.5
1973	49,858.0	19,575.8	5,815.6	33,729.2	1.32	assumed to be invariant	
1974	48,349.9	19,989.5	6,334.6	34,304.5	1.32	-	-
1975	46,192.8	18,917.0	6,581.5	37,287.3	1.34	-	-
1976	45,039.0	18,484.1	7,373.6	38,081.8	1.39	-	-
1977	43,339.6	18,052.5	8,195.7	39,390.7	1.46	-	-
1978	41,352.3	17,707.1	9,273.2	40,645.8	1.53	-	-
1979	39,323.2	17,361.1	10,151.4	42,142.9	1.61	-	-
1980	37,463.2	16,431.5	11,320.9	43,762.9	1.69	-	-
1981	34,973.1	15,951.9	12,035.1	46,018.4	1.77	-	-
1982	33,216.1	14,937.1	12,813.9	48,011.4	1.86	-	-
1983	31,717.0	13,008.8	12,521.0	51,731.7	1.96	-	-
1984	30,817.6	12,291.7	13,244.2	52,624.9	2.05	-	-
1985	29,544.6	11,145.4	13,119.6	55,168.9	2.10	-	-
1986	28,629.0	10,507.0	13,009.5	56,833.1	2.12	-	-
1987	27,975.3	9,617.3	13,043.8	58,342.0	2.16	-	-
1988	27,196.9	8,864.0	13,391.5	59,526.1	2.21	-	-
1989	26,094.4	7,621.1	13,199.8	62,063.2	2.25	-	-
1990	25,371.9	7,061.7	13,281.2	63,263.7	2.25	-	-
1991	24,696.1	6,524.3	12,934.0	64,824.2	2.30	-	-
1992	23,881.4	5,758.0	12,214.9	67,124.2	2.34	-	-
1993	23,379.4	5,140.7	11,347.4	69,110.9	2.39	-	-
1994	22,835.0	4,601.0	10,617.6	70,924.8	2.44	-	-
1995	22,244.6	3,881.8	9,362.8	73,489.3	2.48	-	-
1996	21,728.5	3,117.0	8,370.6	75,762.4	2.53	-	-
mean	32,717.5	12,323.1	10,921.0	52,539.2	1.93	118.3	9,089.5
SD	9017.8	5436.9	2533.3	12467.9	0.40		
CV	28%	44%	23%	24%	21%		

Notes:

[a] Raw data were obtained from digital and hard copy maps provided by MacMillan Bloedel Limited, Pacific Forest Products, TimberWest Forests, and the Ministry of Environment, Lands and Parks. Size of the study coverage was 106,000 hectares.

Appendix 4: Deer population trends in Management Unit 1-5. [a]

Year	Copper Canyon	Nanaimo River Camp	Nanaimo Lakes	Northwest Bay	N of areas in sample	% of expected [b]
1976		7.50			1	78%
1977		9.90			1	103%
1978		17.40			1	182%
1979		19.60	5.90		2	131%
1980		19.10	7.90		2	137%
1981		16.90	7.50		2	124%
1982		15.20	10.00		2	127%
1983		11.80	13.30		2	125%
1984		10.80	11.40		2	111%
1985		9.60	12.79		2	111%
1986	12.33	8.70	13.20		3	111%
1987	12.31	9.70	13.12		3	114%
1988	11.99	11.50	12.40		3	117%
1989	13.02	11.36	11.50		3	117%
1990	15.29	9.00	12.56	7.06	4	116%
1991	17.40	9.80	8.20	6.90	4	112%
1992	9.50	7.20	6.70	12.50	4	105%
1993	8.60	6.80		7.90	3	91%
1994	6.80	5.40		5.40	3	68%
1995	8.40	4.50		2.70	3	56%
1996		4.10		3.10	2	45%
1997		5.20			1	54%
1998	2.20	3.50			2	29%
1999		2.80			1	29%
2000		2.10			1	22%
mean	10.71	9.58	10.46	6.51		97%
SD	4.21	5.00	2.69	3.31		39%
CV	0.39	0.52	0.26	0.51		41%

Summary:
Estimates from the sub-units were not strongly correlated. Significant Pearson correlations are in bold type.

Sub-unit	Copper Canyon	Nanaimo River Camp	Nanaimo Lakes	Northwest Bay	N
Copper Canyon	-				
Nanaimo River Camp	0.819	-			11
Nanaimo Lakes	0.048	-0.552	-		7, 14
Northwest Bay	0.103	0.562	-0.680	-	6, 7, 3

Notes:
[a] Raw data are numbers of deer seen per kilometre during March and April counts. Unpublished file data, B.C. Ministry of Environment, Lands and Parks, Nanaimo.
[b] Observed numbers over the sub-unit average, calculated using only those areas counted in any given year. Abundance estimates based on a single sub-unit were excluded from analyses.

Appendix 5: Terrestrial predator trends in Management Unit 1-5. [a]

Year	Cougars seen per 100 hunter days	Wolves seen per 100 hunter days	Predators seen per 100 hunter days	Cougars removed [a]	Wolves removed [a]	Predators removed
1976	-	0.820	-	6	-	-
1977	-	0.590	-	12	-	-
1978	-	0.353	-	17	-	-
1979	0.746	0.714	1.46	6	-	-
1980	-	-	-	3	5	8
1981	0.361	1.265	1.63	8	1	9
1982	0.611	3.599	4.21	7	2	9
1983	0.539	3.183	3.72	6	1	7
1984	0.475	2.431	2.91	16	3	19
1985	0.736	2.160	2.90	11	24	35
1986	0.339	2.910	3.25	5	7	12
1987	0.888	1.037	1.92	10	5	15
1988	3.151	1.688	4.84	20	9	29
1989	0.197	0.983	1.18	11	3	14
1990	0.109	0.473	0.58	6	6	12
1991	1.307	1.139	2.45	7	4	11
1992	1.807	1.236	3.04	10	7	17
1993	1.404	1.872	3.28	14	3	17
1994	2.662	2.814	5.48	13	2	15
1995	1.384	0.874	2.26	12	1	13
1996	3.836	2.995	6.83	17	3	20
1997	3.917	6.617	10.53	12	9	21
1998				5	5	10
1999						
mean	1.04	1.59	2.82	10.33	5.06	15.41
SD	0.87	0.99	1.33	4.62	5.41	7.36
CV	84%	63%	47%	45%	107%	48%

Notes:

[a] Raw data are numbers of predators seen by deer hunters in autumn. Unpublished file data, B.C. Ministry of Environment, Lands and Parks, Nanaimo.

[a] Including hunter kills, animal control kills, and incidental kills.

Appendix 6: Survey effort and probable count success. [a]

Year	Number of colonies counted	Total N of counts	N of juvenile counts [b]	Effective N of counts [c]	Probable count success [d]	Correction factor [e]
1972	2	4	4	2.0	0.66	-
1973	6	11	9	1.8	0.64	1.55
1974	7	19	12	2.7	0.71	1.40
1975	1	1	1	1.0	0.54	-
1976	3	3	2	1.0	0.54	-
1977	2	3	3	1.5	0.61	-
1978	4	5	5	1.3	0.58	-
1979	14	20	4	1.4	0.60	1.66
1980	18	41	35	2.3	0.68	1.47
1981	19	50	27	2.6	0.71	1.41
1982	30	99	58	3.3	0.75	1.34
1983	30	80	47	2.7	0.71	1.41
1984	37	101	73	2.7	0.71	1.40
1985	25	38	14	1.5	0.61	1.63
1986	34	113	73	3.3	0.75	1.34
1987	17	35	15	1.2	0.57	1.74
1988	16	47	22	1.6	0.62	1.61
1989	15	41	17	1.1	0.55	1.80
1990	9	18	18	1.0	0.54	1.85
1991	7	24	21	1.3	0.59	1.69
1992	18	64	51	1.5	0.61	1.63
1993	34	126	84	1.6	0.62	1.60
1994	33	130	81	2.1	0.67	1.50
1995	43	162	75	2.5	0.70	1.43
1996	43	234	117	4.1	0.78	1.28
1997	36	242	109	4.2	0.79	1.27
1998	40	227	117	3.9	0.78	1.29
mean	20.8	74.4	41.9	2.1	0.7	1.5
SD	13.8	73.7	37.9	1.0	0.1	0.2
CV	66%	99%	90%	47%	12%	11%

Notes:

[a] Not including visits to the 5 intensively-studied colonies, or days with inclement weather.

[b] Counts made after July 1st.

[c] Average number of counts per colony.

[d] According to the regression formula: LOG(effective number of counts)*0.397+0.540

[e] 1/count success rate. Years in which 5 or fewer colonies were counted were excluded.

Appendix 7: Age-sex structure at 5 intensively studied colonies.

Green Mountain (natural)	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	sum	mean	SD
Tagged Males														
Young-of-the-year	1	1										2		
Yearlings			1								1	2		
2 year-old				1					1			2		
3 year-old	2				1					1		4		
4 year-old		2										2		
5 year-old			1									1		
6 year old												0		
7 year-old												0		
8 year-old												0		
9 year-old												0		
10 year-old												0		
Tagged Females														
Young-of-the-year	1	1										2		
Yearlings			1				1					2		
2 year-old	1			1				1				3		
3 year-old	1	1			1				1			4		
4 year-old		1	1			1						3		
5 year-old			1	1				1				3		
6 year old				1	1			1				3		
7 year-old									1			1		
8 year-old												0		
9 year-old												0		
10 year-old												0		
Untagged animals														
adults	1	2	0	1	2	1	0	2	1	2	2	14		
yearlings	0	0	2	0	0	1	1	2	0	0	2	8		
young-of-the-year	1	4	0	0	4	3	3	0	0	3	0	18		
TOTALS														
Total adults	5	6	3	5	5	2	1	4	4	3	2	40	3.6	1.6
Total yearlings	0	0	4	0	0	1	2	2	0	0	3	12	1.1	1.4
Total young-of-the-year	3	6	0	0	4	3	3	0	0	3	0	22	2.0	2.1
Immigrants		2	0	0	0	0	1	0	1	0	0	4	0.4	0.7
N of litters (n of breeders)	1	2	0	0	1	1	1	0	0	1	0	7	0.6	0.7

Haley Lake (natural)	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	sum	mean	SD
Tagged Males														
Young-of-the-year				1	2		2	1		2	2	10		
Yearlings	1				1			5	1			9		
2 year-old	1	3		1		1	1		1			8		
3 year-old		3	2	1	1	1				1		9		
4 year-old			2	1	1			1			1	6		
5 year-old					1			1				2		
6 year old												0		
7 year-old												0		
8 year-old												0		
9 year-old												0		
10 year-old												0		
Tagged Females														
Young-of-the-year				1	1		4	5		2	1	14		
Yearlings	1	1			2	2		5	2			13		
2 year-old	1	2	4			2	3		3			15		
3 year-old	1	4	1	3			1	1		1		12		
4 year-old		1	3	1	3			1	1		1	11		
5 year-old				2	1	1			1	1		6		
6 year old					1	1	1			1	1	5		
7 year-old						1	1	1				3		
8 year-old								1	1			2		
9 year-old								1		1		2		
10 year-old											1	1		
Untagged animals														
adults	9	1	0	3	0	0	0	0	0	0	0	13		
yearlings	2	0	5	0	0	3	0	0	0	0	0	10		
young-of-the-year	2	12	0	1	6	0	6	4	0	3	1	35		
TOTALS														
Total adults	12	14	12	12	8	7	9	5	7	5	4	95	8.6	3.4
Total yearlings	4	1	5	0	3	6	0	10	3	0	0	32	2.9	3.2
Total young-of-the-year	2	12	0	3	9	0	12	10	0	7	4	59	5.4	4.8
Immigrants		0	3	0	0	2	1	1	2	0	0	9	0.9	1.1
N of litters (n of breeders)	1	4	0	1	3	0	3	2	0	2	1	17	1.5	1.4

Appendix 7 continued...

Vaughan Rd. (clearcut)	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	sum	mean	SD
Tagged Males														
Young-of-the-year								1				1		
Yearlings								1				1		
2 year-old	1			1								2		
3 year-old							1					1		
4 year-old								1				1		
5 year-old												0		
6 year old												0		
7 year-old												0		
8 year-old												0		
9 year-old												0		
10 year-old												0		
Tagged Females														
Young-of-the-year								1				1		
Yearlings								1				1		
2 year-old							2		1			3		
3 year-old							1	2				3		
4 year-old								1				1		
5 year-old									1			1		
6 year old												0		
7 year-old												0		
8 year-old												0		
9 year-old												0		
10 year-old												0		
Untagged animals														
adults	5	8	2	6	4	2	2	1	0	0	0	30		
yearlings	3	0	3	0	0	0	0	0	0	0	0	6		
young-of-the-year	0	6	4	0	0	0	5	1	0	0	0	16		
TOTALS														
Total adults	6	8	2	7	4	2	6	5	2	0	0	42	3.8	2.8
Total yearlings	3	0	3	0	0	0	0	2	0	0	0	8	0.7	1.3
Total young-of-the-year	0	6	4	0	0	0	5	3	0	0	0	18	1.6	2.4
Immigrants		4	0	2	0	0	4	0	1	0	0	11	1.1	1.7
N of litters (*n* of breeders)	0	2	1	0	0	0	2	1	0			6	0.7	0.9

Pat Lake (clearcut)	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	sum	mean	SD
Tagged Males													
Young-of-the-year	3				1		1				5		
Yearlings	2	2				1	2	1			8		
2 year-old	2	6	2	2			1	1			14		
3 year-old	1	2	1	1		1			1		7		
4 year-old			1				1				2		
5 year-old				1				1			2		
6 year old					1				1		2		
7 year-old											0		
8 year-old											0		
9 year-old											0		
10 year-old											0		
Tagged Females													
Young-of-the-year	1				3		2				6		
Yearlings	3	1			2	1		1			8		
2 year-old		1	3		1	2	1				8		
3 year-old	1	1	1	1	2	2	1	1			10		
4 year-old				1		2	1	1	1		6		
5 year-old							1		1	1	3		
6 year old											0		
7 year-old											0		
8 year-old											0		
9 year-old											0		
10 year-old											0		
Untagged animals													
adults	6	1	2	3	2	0	0	0	1	0	15		
yearlings	0	0	0	0	0	1	1	0	0	0	2		
young-of-the-year	3	4	0	3	1	3	0	0	0	0	14		
TOTALS													
Total adults	10	11	10	9	6	7	6	4	5	1	69	6.9	3.1
Total yearlings	5	3	0	0	2	3	3	2	0	0	18	1.8	1.8
Total young-of-the-year	7	4	0	3	5	3	3	0	0	0	25	2.5	2.5
Immigrants		3	2	2	2	2	0	0	0	0	11	1.2	1.2
N of litters (*n* of breeders)	2	1	0	1	1	1	1	0	0	0	7	0.7	0.7

Appendix 7 continued...

Sherk Lake (clearcut)	1992	1993	1994	1995	1996	1997	sum	mean	SD
Tagged Males									
Young-of-the-year			4		3		7		
Yearlings						4	4		
2 year-old				2		1	3		
3 year-old		1			1		2		
4 year-old			1				1		
5 year-old							0		
6 year old							0		
7 year-old							0		
8 year-old							0		
9 year-old							0		
10 year-old							0		
Tagged Females									
Young-of-the-year			6		2		8		
Yearlings				3		2	5		
2 year-old	2				3		5		
3 year-old		3					3		
4 year-old			3				3		
5 year-old				2			2		
6 year old					2		2		
7 year-old						2	2		
8 year-old							0		
9 year-old							0		
10 year-old							0		
Untagged animals									
adults	1	0	0	0	1	1	3		
yearlings	0	0	0	0	0	1	1		
young-of-the-year	0	0	1	0	3	0	4		
TOTALS									
Total adults	3	4	4	4	7	4	26	4.3	1.4
Total yearlings	0	0	0	3	0	7	10	1.7	2.9
Total young-of-the-year	0	0	11	0	8	0	19	3.2	5.0
Immigrants	3	1	0	2	1	2	9	1.5	1.0
N of litters (*n* of breeders)	0	0	3	0	3	0	6	1.0	1.5

Summary:
Cumulative age-sex ratio of ear-tagged animals at 5 intensively studied colonies. [a]

A) Natural colonies   B) Clearcut colonies
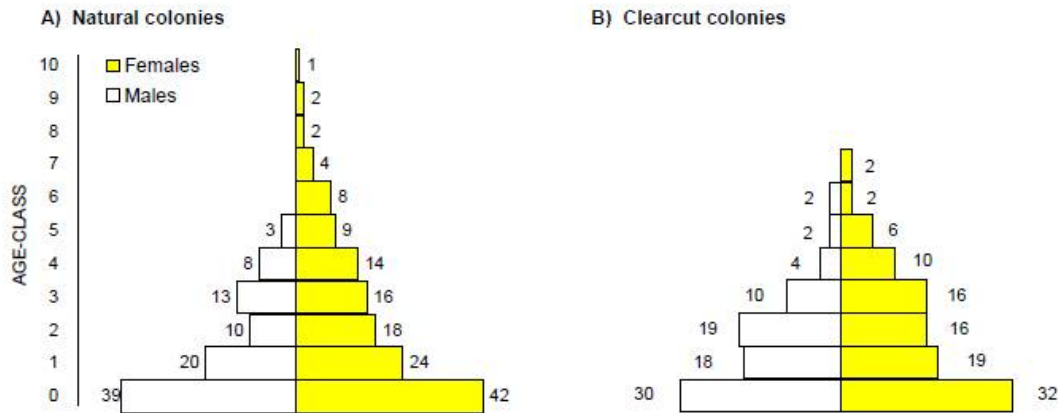
Notes:
[a] Sex ratio of all captured juveniles did not differ from 1:1 (54 females: 39 males, $\chi^2 = 2.42$, 1 df, $P = 0.12$
The age-sex structured figures assume equal sex ratio of untagged juveniles and yearlings. Older
untagged animals were excluded as they generally comprised less than 10% of the overall population.

Appendix 8: Tagging success and ear-tag loss rates.

Estimated tagging success

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	mean	SD	N
Intensive colonies														
N of tagged animals	12	30	30	24	23	22	34	55	28	25	18			
Observed pop. size	35	75	51	37	45	37	55	68	29	38	25			
Cumulative *n* tagged	12	36	48	55	61	77	93	123	127	144	166			
Annual tagging success	*0.34*	*0.40*	*0.59*	*0.65*	*0.51*	*0.59*	*0.62*	*0.81*	*0.97*	*0.66*	*0.72*	62.3%	17.5%	11
All colonies														
PROBABLE total pop. [a]	209	295	252	185	226	215	194	249	141	134	125	209.9	53.7	11
Probable tagging success	0.06	0.10	0.12	0.13	0.10	0.10	0.18	0.22	0.20	0.19	0.14	14.0%	5.0%	11

Ear-tag-loss rate [b]

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	mean	SD	N
losses of single tags		16	1	3	1	1	4	6	2	7	3			
tag replacements		3	0	3	1	0	4	4	2	5	2			
N of tags (usually 2/animal)	24	60	60	48	46	44	68	109	56	49	35			
Annual tag loss rate	*0.67*	*0.02*	*0.05*	*0.02*	*0.02*	*0.09*	*0.09*	*0.02*	*0.13*	*0.06*		5.5%	3.9%	9
Net loss rate after replacements		0.02	0.00	0.00	0.02	0.00	0.03	0.00	0.04	0.02		1.4%	1.4%	9

Notes:

[a] Population estimates are from Appendix 11.

[b] Type of ear-tags was changed in 1988, as few of the original "rabbit-ear" tags persisted (Bryant 1990). Accordingly, tag-loss data from 1987 are excluded from summary statistics.

Appendix 9: Raw and adjusted population estimates. [a]

Year	N of colonies with counts	Observed N of adults	Percent of expected [b]	Probable N of adults	N of colonies with juvenile counts [c]	Observed N of juveniles	Percent of expected	Probable N of juveniles
1972	2	13	70.9		2	0	0.0	
1973	6	18	77.9	100.4	6	8	106.6	32.1
1974	7	35	93.0	110.9	5	7	59.7	18.5
1975	1	5	41.3		1	8	156.1	
1976	3	11	74.5		2	0	0.0	
1977	2	12	65.5		2	0	0.0	
1978	4	19	80.0	117.1	4	7	68.7	21.2
1979	14	51	99.1	140.2	4	2	26.6	8.1
1980	18	63	99.3	125.0	15	41	204.4	63.6
1981	19	105	154.0	200.1	15	34	199.4	65.8
1982	30	148	157.7	225.9	28	24	83.1	33.7
1983	30	140	146.3	228.1	23	23	79.3	33.6
1984	37	167	151.2	254.4	36	68	190.9	92.6
1985	25	108	108.8	228.7	11	31	156.8	80.1
1986	34	150	130.3	223.5	34	40	109.3	55.6
1987	17	57	96.1	183.1	5	5	49.3	25.6
1988	16	69	114.3	197.3	14	36	186.0	99.3
1989	15	97	125.9	221.3	10	13	54.9	28.8
1990	9	48	85.5	169.0	9	5	21.6	12.4
1991	7	38	87.5	150.5	6	18	130.8	64.6
1992	18	90	105.3	187.7	16	11	40.2	23.5
1993	34	86	77.0	136.4	31	34	92.9	52.7
1994	33	97	82.4	144.9	29	64	174.8	88.2
1995	43	86	64.5	114.9	41	19	42.7	23.9
1996	43	72	54.1	86.8	39	30	71.9	35.5
1997	36	69	53.2	79.5	30	31	84.4	37.9
mean	20.0	73.6	97.0	164.8	16.6	22.4	95.6	45.3
SD	13.5	46.2	32.7	52.7	13.1	18.6	63.4	27.1

Summary:

Mean Successive Difference Test (see Zar 1974) [d]

	Adults	Juveniles
N of years	20	20
variance	2667.16	761.39
S*	881.60	824.88
Maximum	254.41	99.29
Minimum	79.51	8.14

	adults	juveniles
Test statistic C	0.67	-0.08

Adult abundance index was autocorrelated among successive years.
Juvenile abundance index was not autocorrelated among succesive years.

Notes:
[a] Including animals at the 5 "intensively-studied" colonies.
[b] N of observed animals divided by the long-term average abundance, using only those sites actually counted.
[c] Counts made after July 1st.
[d] The mean successive difference test was made using probable numbers of adults and juveniles.

Appendix 10: Colony-specific habitat conditions. [a]

Code	Mountain	Colony	Habitat	Elev. (m)	Aspect (°)	Size (ha)	Year of discovery	Year colonized	Year extinct	Status
1.1	Green	Top ski hill/SE talus	natural	1420	250	2.3	1954	-	-	colony
1.2	Green	NW Ridge	natural	1400	245	0.5	1979	-	-	colony
1.3	Green	West Green	natural	1169	210	0.1	1980	-	1987	potential
1.4	Green	South slope	natural	1220	215	6.6	1980	-	1986	colony
1.5	Green	Road D15/D16	clearcut	730	350		1981	1981	1987	colony
1.6	Green	Elk Meadow	natural	1138	250	0.1	1983	-	1988	colony
1.7	Green	Road D	clearcut	861	100		1983	1984	1993	colony
1.8	Green	Road K44A/K30	clearcut	1138	210		1983	1981	-	colony
1.9	Green	Heart Lake basin	natural	1076	60	0.4	1985	-	1986	potential
2.1	Gemini	South slope	natural	1450	180	2.4	1973	-	1992	colony
2.2	Gemini	Westerholm	natural	1169	160	3.6	1979	-	1988	colony
2.3	Gemini	Meadow #1	natural	1230	180	0.6	1982	-	1989	colony
2.4	Gemini	Meadow #2	natural	1261	170	0.6	1982	-	1984	potential
2.5	Gemini	Bell Creek North	natural	1353	260	1.0	1982	-	1987	potential
2.6	Gemini	Road G2C	clearcut	991	120		1982	1982	1993	colony
2.7	Gemini	Road D13E/W4	clearcut	861	140		1984	1984	-	colony
3.1	Haley	Bowl	natural	1040	185	6.9	1915	-	-	colony
3.2	Haley	Bell Creek	natural	1258	225	4.2	1973	-	-	colony
3.3	Haley	Vaughan Road	clearcut	941	260		1983	1983	1996	colony
4.1	Butler	West face	natural	1385	280	0.6	1928	-	-	colony
4.2	Butler	East alder slide	natural	1292	120	0.4	1980	-	-	colony
4.3	Butler	Above Road V7	natural	1138	110		1982	-	-	potential
4.4	Butler	West roads	clearcut	1076	240		1982	1982	-	colony
4.5	Butler	Third step	natural	1100	45		1996	-	-	potential
5.1	Mt. Buttle	Top meadow	natural	1323	120	0.2	1980	-	-	colony
5.2	Mt. Buttle	South pocket	natural	1240	75	0.2	1984	-	1994	potential
6.1	Whymper	South basin/burn	natural	1400	180		1979	-	1996	colony
6.2	Whymper	West basin	natural	1323	230		1983	-	1993	potential
6.3	Whymper	Pat Lake basin	clearcut	900	45		1985	1984	1997	colony
7.1	Landalt	Lomas Lake	natural	1243	100		1984	-	-	potential
7.2	Landalt	Sherk Lake	clearcut	980	160	2.0	1991	1992	-	colony
8.1	Heather	S. alder meadow	natural	1076	200	1.6	1973	-	-	colony
9.1	Hooper	SW basin	natural	1415	260	1.2	1979	-	-	colony
9.2	Hooper	SE side	natural	1450	170	0.4	1982	-	1995	potential
9.3	Hooper	West Shaw Creek	natural	1160	100		1980	-	1995	colony
10.1	Hooper N.	Hooper North	natural	1384	140	0.6	1982	-	1993	colony
11.1	P Mtn.	NW meadow	natural	1230	320	0.6	1978	-	-	colony
11.2	P Mtn.	SE basin	natural	1140	165	6.4	1980	-	1988	colony
11.3	P Mtn.	NW ridge	natural	1065	255	0.8	1982	-	1988	potential
11.4	P Mtn.	West areas	natural	1120	270	0.8	1982	-	1987	colony
12.1	Moriarty	SW aspect	natural	1300	215		1992	-	-	colony
12.2	Moriarty	NE aspect	natural	1300	44		1992	-	-	colony
12.3	Moriarty	Meadow above Br146	natural	1290	355		1996	-	-	potential
13.1	Franklin	S. summit	clearcut	1060	160		1990	1990	-	colony
14.1	Washington	West basin/ski-runs	clearcut	1446	260		1943	-	-	colony
14.2	Washington	Minesite	clearcut	1353	90		1984	1984	1986	colony
14.3	Washington	Quad runs	clearcut	1300	SW		1996	-	-	potential
15.1	Big Ugly	SE face	natural	1300	170	1.1	1985	-	-	colony
15.2	Big Ugly	N avalanche track	natural	1200	330	0.8	1993	-	-	potential

Notes:

[a] As determined from GIS compilation. Dates of discovery, colonization and extinction are derived from the long-term inventory database (this study).

Appendix 11: Ear-tagged and apparent juvenile survival at 5 colonies.

Site	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	N	mean	SD
Green Mountain (natural)													
Total young-of-the-year [a]	3	6	0	0	4	3	3	0	0	3	22		
Apparent survivors [a,b]	0	4	-	-	1	2	2	-	-	3	12		
APPARENT SURVIVAL	1.00	0.67			0.25	0.67	1.00			1.00	6	0.76	0.30
Tagged young-of-the-year	2	2	0	0	0	0	0	0	0	0	4		
Tagged yearlings	0	2	-	-	-	-	-	-	-	-	2		
TAGGED SURVIVAL	0.00	1.00									2	0.50	0.71
Haley Lake (natural)													
Total young-of-the-year	2	12	0	3	9	0	12	10	0	7	55		
Apparent survivors	1	7	-	3	6	-	10	3	-	0	30		
APPARENT SURVIVAL	0.50	0.58		1.00	0.67		0.83	0.30		0.00	7	0.55	0.33
Tagged young-of-the-year	0	0	0	2	3	0	6	6	0	7	24		
Tagged yearlings	-	-	-	2	0	-	6	3	-	0	11		
TAGGED SURVIVAL				1.00	0.00		1.00	0.50		0.00	5	0.50	0.50
Vaughan Road (clearcut)													
Total young-of-the-year	0	6	4	0	0	0	5	3	0	0	18		
Apparent survivors	-	3	0	-	-	-	2	0	-	-	5		
APPARENT SURVIVAL		0.50	1.00				0.40	0.00			4	0.48	0.41
Tagged young-of-the-year	0	0	0	0	0	0	0	2	0	0	2		
Tagged yearlings	-	-	-	-	-	-	-	0	-	-	0		
TAGGED SURVIVAL								0.00			1	-	-
Pat Lake (clearcut)													
Total young-of-the-year	-	7	4	0	3	5	3	3	0	0	25		
Apparent survivors	-	3	0	-	2	3	3	2	-	-	13		
APPARENT SURVIVAL		0.43	0.00		0.67	0.60	1.00	0.67			6	0.56	0.33
Tagged young-of-the-year	-	4	0	0	0	4	0	3	0	0	11		
Tagged yearlings	-	2	-	-	-	3	-	2	-	-	7		
TAGGED SURVIVAL		0.50				0.75		0.67			3	0.64	0.13
Sherk Lake (clearcut)													
Total young-of-the-year	-	-	-	-	-	0	0	11	0	8	19		
Apparent survivors	-	-	-	-	-	-	-	3	-	7	10		
APPARENT SURVIVAL								0.27		0.88	2	0.57	0.43
Tagged young-of-the-year	-	-	-	-	-	0	0	10	0	7	17		
Tagged yearlings	-	-	-	-	-	-	-	2	-	6	8		
TAGGED SURVIVAL								0.20		0.86	5	0.53	0.46

Notes:

[a] Including tagged individuals.

[b] Minimum number of yearlings observed in the subsequent year.

Appendix 12: Ear-tagged and apparent adult survival at 5 colonies.

Site	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	N	mean	SD
Green Mountain (natural)													
Adults and yearlings	5	6	7	5	5	3	3	6	4	3	47		
Apparent survivors [a]	6	3	5	5	2	1	4	4	3	2	35		
APPARENT SURVIVAL [b]	1.00	0.50	0.71	1.00	0.40	0.33	1.00	0.67	0.75	0.67	10	0.70	0.24
Apparent immigration	(1.20)						(1.33)						
Tagged adults+yearlings	4	4	4	4	3	1	2	2	3	1	28		
Surviving adults	4	3	4	3	1	1	2	2	1	0	21		
Immigrants	-	2	0	0	0	0	1	0	1	0	4		
TAGGED SURVIVAL	1.00	0.75	1.00	0.75	0.33	1.00	1.00	1.00	0.33	0.00	10	0.72	0.37
Haley Lake (natural)													
Adults+yearlings	16	15	17	12	11	13	9	15	10	5	123		
Apparent survivors	14	12	12	8	7	9	5	7	5	4	83		
APPARENT SURVIVAL	0.88	0.80	0.71	0.67	0.64	0.69	0.56	0.47	0.50	0.80	10	0.67	0.13
Apparent immigration													
Tagged adults+yearlings	3	13	12	9	11	10	9	15	10	5	97		
Surviving adults	3	8	9	8	5	8	4	10	5	4	64		
Immigrants	-	0	3	0	0	2	1	1	2	0	9		
TAGGED SURVIVAL	1.00	0.62	0.75	0.89	0.45	0.80	0.44	0.67	0.50	0.80	10	0.69	0.19
Vaughan Road (clearcut)													
Adults+yearlings	9	8	5	7	4	2	6	7	2	0	50		
Apparent survivors	8	2	7	4	2	6	5	2	0	-	36		
APPARENT SURVIVAL	0.89	0.25	1.00	0.57	0.50	1.00	0.83	0.29	0.00		9	0.59	0.36
Apparent immigration			(1.40)			(3.00)							
Tagged adults+yearlings	1	0	0	1	0	0	4	6	2	0	14		
Surviving adults	0	-	-	0	-	-	4	2	0	-	6		
Immigrants	-	4	0	2	0	0	4	0	1	0	11		
TAGGED SURVIVAL	0.00			0.00			1.00	0.33	0.00		5	0.27	0.43
Pat Lake (clearcut)													
Adults+yearlings	-	15	14	10	9	8	10	9	6	5	86		
Apparent survivors	-	11	10	9	6	7	6	4	5	1	59		
APPARENT SURVIVAL	-	0.73	0.71	0.90	0.67	0.88	0.60	0.44	0.83	0.20	9	0.66	0.22
Apparent immigration													
Tagged adults+yearlings	-	9	14	8	6	6	9	8	7	3	70		
Surviving adults	-	6	14	4	1	5	6	4	3	1	44		
Immigrants		-	3	2	2	2	2	0	0	0	11		
TAGGED SURVIVAL		0.67	0.43	0.50	0.17	0.83	0.67	0.50	0.43	0.33	9	0.50	0.20
Sherk Lake (clearcut)													
Adults+yearlings	-	-	-	-	-	3	4	4	7	7	25		
Apparent survivors	-	-	-	-	-	4	4	4	7	4	23		
APPARENT SURVIVAL	-	-	-	-	-	1.00	1.00	1.00	1.00	0.57	5	0.91	0.19
Apparent immigration						(1.33)							
Tagged adults+yearlings	-	-	-	-	-	3	4	4	7	6	24		
Surviving adults	-	-	-	-	-	3	4	2	6	3	18		
Immigrants						3	1	0	2	1	7		
TAGGED SURVIVAL						1.00	1.00	0.50	0.86	0.50	5	0.77	0.25

Notes:

[a] Minimum number of adults (excluding yearlings) counted in the subsequent season.

[b] N of adults/(adults+yearlings in the previous year). For correlation analysis, maximum survival was assumed to be 1.00. Higher rates (probably due to immigration) are shown in parentheses as "apparent immigration".

Appendix 13: Birth rates and fecundity at 5 colonies.

Site	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	N	mean	SD
Green Mountain (natural)														
Adults excluding yearlings	5	6	3	5	5	2	1	4	4	3	2	40		
All births	3	6	0	0	4	3	3	0	0	3	0	22		
N of litters	1	2	0	0	1	1	1	0	0	1	0	7		
PER CAPITA BIRTHS [a]	0.6	1.0	0.0	0.0	0.8	1.5	3.0	0.0	0.0	1.0	0.0	11	0.72	0.93
Adult female-years	2	2	2	3	2	1	1	2	2	0	0	17		
Births from tagged females	3	6	0	3	1	1	2	2	1	-	-	19		
N of litters	1	2	0	0	0	0	1	0	1	-	-	5		
FECUNDITY [b]	1.5	3.0	0.0	1.0	0.5	1.0	2.0	1.0	0.5			9	1.17	0.90
Haley Lake (natural)														
Adults excluding yearlings	12	14	12	12	8	7	9	5	7	5	4	95		
All births	2	12	0	3	9	0	12	10	0	7	4	59		
N of litters	1	4	0	1	3	0	3	2	0	2	1	17		
PER CAPITA BIRTHS	0.2	0.9	0.0	0.3	1.1	0.0	1.3	2.0	0.0	1.4	1.0	11	0.74	0.69
Adult female-years	2	7	8	6	5	5	7	4	6	4	3	57		
Births from tagged females	0	12	0	3	9	0	12	10	0	7	1	54		
N of litters	0	4	0	1	3	0	3	2	0	2	1	16		
FECUNDITY	0.0	1.7	0.0	0.5	1.8	0.0	1.7	2.5	0.0	1.8	0.3	11	0.94	0.96
Vaughan Road (clearcut)														
Adults excluding yearlings	6	8	2	7	4	2	6	4	2	0	0	41		
All births	0	6	4	0	0	0	5	3	0	-	-	18		
N of litters	0	2	1	0	0	0	2	1	0	-	-	6		
PER CAPITA BIRTHS	0.0	0.8	2.0	0.0	0.0	0.0	0.8	0.8	0.0			9	0.48	0.68
Adult female-years	0	0	0	0	0	0	3	3	2	0	0	8		
Births from tagged females	-	-	-	-	-	-	2	2	0	-	-	4		
N of litters	-	-	-	-	-	-	1	0	1	-	-	2		
FECUNDITY							0.7	0.7	0.0			3	0.44	0.38
Pat Lake (clearcut)														
Adults excluding yearlings	-	10	11	10	9	6	7	6	5	3	1	68		
All births	-	7	4	0	3	5	3	3	0	0	0	25		
N of litters	-	2	1	0	1	1	1	1	0	0	0	7		
PER CAPITA BIRTHS		0.7	0.4	0.0	0.3	0.8	0.4	0.5	0.0	0.0	0.0	10	0.32	0.31
Adult female-years	-	1	2	4	2	3	6	4	2	2	1	27		
Births from tagged females	-	4	4	0	3	5	3	3	0	0	0	22		
N of litters	-	1	1	0	1	1	1	1	0	0	0	6		
FECUNDITY		4.0	2.0	0.0	1.5	1.7	0.5	0.8	0.0	0.0	0.0	10	1.04	1.29
Sherk Lake (clearcut)														
Adults excluding yearlings	-	-	-	-	-	3	4	4	4	7	4	26		
All births	-	-	-	-	-	0	0	11	0	8	0	19		
N of litters	-	-	-	-	-	0	0	3	0	3	0	6		
PER CAPITA BIRTHS						0.0	0.0	2.8	0.0	1.1	0.0	6	0.65	1.13
Adult female-years	-	-	-	-	-	3	3	3	2	5	2	18		
Births from tagged females	-	-	-	-	-	0	0	11	0	8	0	19		
N of litters	-	-	-	-	-	0	0	3	0	3	0	6		
FECUNDITY						0.0	0.0	3.7	0.0	1.6	0.0	6	0.88	1.51

Notes:

[a] Total number of births divided by number of adults (excluding yearlings).

[b] Including juveniles of both sexes. Sex ratio of captured juveniles did not differ from 1:1 (Appendix 1)

Appendix 14: Variation in female reproductive performance. [a]

n	Ear-tags	Name	Age at first capture	Site	First capture	Adult-years [b]	Lifetime reproduction	N of litters
1	2930	Tweedledum	2	Haley	20-Aug-89	9	11	3
2	947948	Oprah	2	Haley	26-Aug-87	8	11	3
3	7172	Live-wire	2	Haley	30-Jun-88	6	8	2
4	8789	R. Raccoon	2	Green	30-Jul-87	5	7	2
5	923924	Delilah	0	Green	1-Sep-88	6	6	2
6	1820	Betsy	3	Green	5-Aug-87	4	6	2
7	2276	Meanie	0	Haley	19-Sep-90	5	5	1
8	910	Canada One	3	Pat Lake	1-Jul-92	2	5	1
9	78	Curly	2	Sherk	14-Jul-92	3	4	1
10	955956	Midrock	3	Pat Lake	27-Jun-89	1	4	1
11	1360	Canada Two	1	Pat Lake	1-Jul-92	4	3	1
12	5354	Mom #1	3	Haley	27-Jun-88	3	3	1
13	7475	Tonto	3	Haley	25-Aug-87	2	3	1
14	6970	Mom #2	3	Haley	3-Jul-88	2	3	1
15	963964	Iris	1	Pat Lake	29-Jun-89	2	3	1
16	5857	Big Momma	3	Pat Lake	5-Jul-93	2	3	1
17	3334	Sparbabe	2	Vaughan	22-Jul-93	2	3	1
18	7879	Mom #3	3	Haley	6-Jul-88	1	3	1
19	919920	Lady	3	Pat Lake	26-Aug-88	1	3	1
20	6768	Redsonia	3	Vaughan	15-Jul-93	3	2	1
21	343344	Hera	3	Butler	15-Jun-96	1	2	1
22	907908	Cher	1	Pat Lake	4-Aug-88	3	0	0
23	909910	Luna	2	Haley	17-Aug-89	3	0	0
24	978979	Alice	2	Haley	20-Aug-89	3	0	0
25	983984	Barbara	3	Pat Lake	9-Aug-92	3	0	0
26	985986	Happy	2	Pat Lake	2-Aug-92	2	0	0
27	251252	SparGirl	2	Vaughan	21-Jul-93	2	0	0
28	201202	Imelda	1	Green	30-Jul-93	2	0	0
29	9192	Pleasure	1	Haley	15-Jun-94	2	0	0
30	8384	Fredegunda	1	Vaughan	4-Jul-94	2	0	0
31	5758	Blackie	1	Haley	25-Aug-87	1	0	0
32	980981	Tweedledee	2	Haley	20-Aug-89	1	0	0
33	943944	Apex	2	Pat Lake	6-Aug-90	1	0	0
34	945946	Goldilocks	2	Pat Lake	9-Aug-90	1	0	0
35	971972	Xavier	1	Haley	5-Sep-91	1	0	0
36	12	Dopey	1	Pat Lake	3-Jul-92	1	0	0
37	939940	Donna	1	Haley	13-Jul-92	1	0	0
38	5354	Sophie	1	Haley	31-Aug-92	1	0	0
39	3536	Mottley	3	Haley	16-Jul-93	1	0	0
40	241242	Bader	0	Sherk	20-Aug-94	1	0	0
41	375374	Livia	0	Sherk	9-May-95	1	0	0
42	371372	Sif	1	Haley	22-May-95	1	0	0
					TOTALS	106	98	29

Summary: Mann-Whitney U test of lifetime performance based on females that reproduced at least once.

	N	Mean	SD	U	P
Natural lifetime performance	11	6.00	3.03	87.5	0.02
Clearcut lifetime performance	10	3.20	0.92		

Notes:

[a] Excluding tagged females that were still alive at the end of 1997, and could reproduce again.

[b] N of years during which the animal was age 2 or older.

Appendix 15: Estimates of minimum dispersal distances.

A) Ear-tagged dispersers and known movements

#	Movement	Age and sex class	Year	Date [a]	minimum distance
1	Haley - Bell Creek	Adult male #4 (Heard 1977)	1974	mid-June	0.92
2	Pat Lake - Franklin	913914 "Betty" female not seen as yearling, but probably dispersed at age 2	1990?	-	7.4
3	Pat Lake - Franklin	959960 "Franklin" male dispersed at age 2	1990	late June	7.4
4	Vaughan - Green	8182 "Misty" male dispersed at age 2	1995	4-May	5.9
5	McQuillam -	347346 "Volsung", yearling male dispersed after being transplanted, killed by predator	1996	early July	5.7
				mean distance	5.4
				SD	2.6
				CV	49%

B) Probable dispersers and minimum distance to nearest active colony

#	Locale	Notes and observer	Year	Date [a]	minimum [b] distance	nearest colony
1	Mount Demers	Photographed near road L6510 (D. Berry)	1977	25-Jul	44.0	Whymper
2	Coombs	Hibernated successfully (J. Allen)	1980	7-Jul	17.9	Moriarty
3	Nanoose	On road adjacent to lot 117 (G. Rolph)	1980	2-Jul	27.4	Green
4	Mount Moriarty	NW Bay road 143-52 (G. Gott)	1980	12-Sep	6.0	Moriarty
5	Nanaimo Lakes	100 m from main road (J. Wilson)	1981	7-Oct	14.1	Gemini
6	Mount Whymper	At end of road R12 (N. Fagnello)	1981	4-Oct	2.2	Whymper
7	Cassidy	Spruston Rd. (J. Lampman)	1981	10-Sep	17.0	Whymper
8	Nanaimo Lakes	On road 1.6 km east of gate (H. Langin)	1981	2-Sep	13.4	Whymper
9	Nanaimo River	On Nanaimo River bridge (A. Wilson)	1982	aug	13.0	Whymper
10	Green Mountain	K44A road (L. Woodbury)	1982	16-Jul	0.1	Green
11	Green Mountain	West Green clearcut (G.W. Smith)	1982	4-Jun	0.8	Green
12	Mount Moriarty	On SE slope in basin (A. Collier)	1983	5-Sep	0.3	Moriarty
13	Youbou	5 km W. of Youbou (R. Erskine)	1986	25-Jun	6.9	Landalt
14	Green Mountain	Adult and 2 young (?) on road (A. Deboon)	1988	2-Jul	2.2	Green
15	Mount Franklin	Photographed (C. Macknak)	1990	30-May	4.4	Whymper
16	Cedar	Built burrow, but not seen in spring (T. Oster)	1991	25-Sep	25.6	Pat Lake
17	Cassidy	Carmichael Rd. (G. Van Reewyk)	1991	20-Jun	19.7	Pat Lake
18	Bell's Bay	In new subdivison (J. Bell)	1992	May	20.6	P Mtn.
19	Mount Moriarty	NW Bay Road 143-20 (R. Patten)	1992	19-Sep	6.0	Moriarty
20	Cassidy	Hibernated successfully (B. Jensen)	1991	10-Jun	19.9	Pat Lake
21	Youbou	Photographed on boat dock (R. Nott)	1993	18-May	4.6	Franklin
22	Mount Franklin	At end of road F12 (T. Stein)	1994	1-Aug	1.5	Franklin
23	Jump Lake	S. of dam entrance road (D. Judson)	1994	27-May	6.5	Gemini
24	Bell Creek	Ear-tagged, but not read (A. Bryant)	1995	18-May	0.9	Haley
25	Youbou	On road 8 km W. of Youbou (G. Shillito)	1995	24-Jun	5.2	Buttle
26	S. Nanaimo River	In new clearcut on road R22C (T. Stein)	1995	10-May	5.4	Pat Lake
27	Coronation Lake	Photographed on power line (Pete Maus)	1996	15-May	11.7	Pat Lake
28	Mt. Holmes	Ear-tagged, but not read (P. Olsen)	1996	15-Jun	2.8	Franklin
				mean minimum dispersal distance	10.7	
				SD	10.4	
				CV	97%	

Notes:

[a] For A), this refers to date of disappearance. For B), it refers to date first seen at new location.

[b] Minimum distance (km) to the nearest colony active at the time of observation. I make no assumptions that nearest colony was actually the source, but such records do represent minimum dispersal movements.

Appendix 16: Fate of radio-telemetered marmots. [a]

n	Ear-tags	Name	Site	age	sex	Implant date	Fate of animal and transmitter
1	910	Canada One	Pat Lake	3	f	9-Aug-92	survived, transmitter failed in winter
2	983984	Barbara	Pat Lake	3	f	9-Aug-92	survived
3	1920	Arnold	Haley	3	m	16-Aug-92	survived, transmitter failed in winter
4	991992	Whitey	Pat Lake	0	m	27-Aug-92	survived, transmitter failed in summer
5	2122	Max	Haley	2	m	29-Aug-92	died, hyperthermia, research
6	939940	Donna	Haley	1	f	29-Aug-92	survived, transmitter failed in summer
7	5354	Sophie	Haley	1	f	31-Aug-92	survived, transmitter failed in winter
8	5857	Big Momma	Pat Lake	3	f	13-Jul-93	survived
9	983984	Barbara	Pat Lake	4	f	13-Jul-93	survived
10	6162	Tiger	Vaughan Rd.	3	m	14-Jul-93	survived
11	2930	Tweedledum	Haley	6	f	16-Jul-93	survived, transmitter failed in winter
12	56	Meanie	Haley	3	f	16-Jul-93	survived, transmitter failed in winter
13	19300	Arnold	Haley	4	m	16-Jul-93	survived
14	6768	Redsonia	Vaughan Rd.	3	f	18-Jul-93	survived
15	993994	Tough gal	Pat Lake	1	f	24-Aug-93	survived, dispersed and returned
16	991992	Whitey	Pat Lake	1	m	24-Aug-93	survived, dispersed and returned
17	255256	Runt	Haley	0	m	26-Aug-93	survived
18	277278	Robin	Haley	0	f	26-Aug-93	survived
19	259260	Tapedeck	Haley	0	f	26-Aug-93	survived
20	253254	Hillary	Haley	0	f	26-Aug-93	survived
21	983984	Barbara	Pat Lake	5	f	29-Jun-94	died, predator kill
22	19232	Arnold	Haley	5	m	30-Jun-94	died, predator kill
23	2276	Meanie	Haley	4	f	30-Jun-94	survived
24	1360	Canada Two	Pat Lake	3	f	11-Aug-94	survived
25	2930	Tweedledum	Haley	7	f	13-Aug-94	survived
26	7980	Chekmate	Haley	3	f	13-Aug-94	survived
27	9332	Liberace	Sherk	4	m	16-Aug-94	died, predator kill
28	237238	Fluffy	Sherk	0	f	16-Aug-94	unknown, transmitter failed in winter
29	241242	Bader	Sherk	0	f	20-Aug-94	survived
30	989224	Moe	Sherk	5	f	16-Jun-95	survived
31	303304	Steven	Sherk	3	m	23-Jun-95	unknown, transmitter failed in winter
32	9596	Canuck	Pat Lake	2	m	21-Jul-95	survived
33	279296	Repeat	Pat Lake	1	f	21-Jul-95	unknown, transmitter failed in winter
34	347346	Volsung	Franklin	1	m	5-Jun-96	died, predator kill, transplanted
35	307308	Sally Ride	Franklin	4	f	5-Jun-96	died, hibernation/disease, transplanted
36	315316	Cheyenne	Franklin	1	f	7-Jun-96	died, hibernation/disease, transplanted
37	349350	Freya	Franklin	1	f	8-Jun-96	died, hibernation/disease, transplanted
38	481878	no-name	Washington	3	m	8-Aug-97	survived
39	485482	no-name	Washington	1	m	15-Aug-97	died, predator kill in 1998
40	325326	Athena	K44A	1	f	7-Jul-98	died, predator kill
41	461462	Conrad	K44A	1	m	8-Jul-98	survived
42	401402	Cadby	K44A	1	f	8-Jul-98	died, predator kill
43	409410	Hedwig	K44A	1	m	8-Jul-98	survived

Summary:

Fate of telemetered marmots by transmitter type. [a]

Transmitter type	N	died	survived	unknown
Custom Telemetry [b]	28	3	22	3
Telonics [c]	14	7	6	0
Totals	42	10	28	3

Overwintering transmitter performance by type.

Transmitter type	N	failed	persist
Custom Telemetry [b]	28	10	18
Telonics [c]	14	0	14
Totals	42	10	32

Notes:

[a] Survival was based on both telemetry and ear-tagged observations.

[b] Excluding animals with unknown fate and 1 research mortality, gross annual survival was 28/38 = 74%.

Appendix 17: Habitat-specific life-tables for *M. vancouverensis* .[a]

	MALES					FEMALES						
	f(x)	dx	qx	k	Lx	f(x)	dx	qx	k	Lx	bx	lx*bx
Natural meadows												
Juveniles [b]	82	38	0.46	1.00	1000	82	38	0.46	1.00	1000	0.00	0.00
Yearlings	12	5	0.42	0.54	537	17	6	0.35	0.54	537	0.00	0.00
2 year-olds	10	2	0.20	0.58	313	18	7	0.39	0.65	347	0.00	0.00
3 year-olds	13	4	0.31	0.80	250	16	2	0.13	0.61	212	0.79	0.17
4 year-olds	9	5	0.56	0.69	173	14	3	0.21	0.88	186	0.86	0.16
5 year-olds	3	3	1.00	0.44	77	9	1	0.11	0.79	146	0.77	0.11
6 year-olds	0	0	0.00	0.00	0	8	4	0.50	0.89	130	0.65	0.08
7 year-olds	0	0	0.00	0.00	0	4	2	0.50	0.50	65	0.72	0.05
8 year-olds	0	0	0.00	0.00	0	2	0	0.00	0.50	32	1.44	0.05
9 year-olds	0	0	0.00	0.00	0	2	1	0.50	1.00	32	1.15	0.04
10 year-olds	0	0	0.00	0.00	0	1	1	1.00	0.50	16	0.00	0.00
											R_o =	0.65
											λ =	0.94
Clearcuts												
Juveniles [b]	62	35	0.56	1.00	1000	62	35	0.56	1.00	1000	0.00	0.00
Yearlings	13	4	0.31	0.44	435	14	4	0.29	0.44	435	0.00	0.00
2 year-olds	20	12	0.60	0.69	301	16	6	0.38	0.71	311	0.14	0.04
3 year-olds	12	8	0.67	0.40	121	19	6	0.32	0.63	194	0.91	0.18
4 year-olds	4	2	0.50	0.33	40	12	4	0.33	0.68	133	0.43	0.06
5 year-olds	3	0	0.00	0.50	20	7	4	0.57	0.67	89	0.33	0.03
6 year-olds	3	2	0.67	1.00	20	2	0	0.00	0.43	38	1.15	0.04
7 year-olds	1	0	0.00	0.33	7	2	0	0.00	1.00	38	0.00	0.00
8 year-olds	1	0	0.00	1.00	7	2	1	0.50	1.00	38	0.00	0.00
9 year-olds	1	0	0.00	1.00	7	1	0	0.00	0.50	19	0.00	0.00
10 year-olds	1	1	1.00	1.00	7	0	0	0.00	0.00	0	0.00	0.00
											R_o =	0.35
											λ =	0.80

Notes:

[a] Life-table nomenclature and calculations followed Caughley (1977; Method 2).

[b] Including juveniles of both sexes, and based on counts of juveniles and surviving yearlings. Calculations for other age-classes relied upon ear-tagged animals at all colonies. Sex ratio of tagged juveniles was 50:37 in favour of females, and this figure was used to derive fecundity (bx) rates.

Appendix 18: Colony-specific juvenile abundance and apparent survival. [a]

Code	Mountain	Colony	Years with counts	N of counts	Max. YOY	Mean YOY	SD	Survival years	Animals in sample	Apparent survival	CV (%)
1.1	Green	Ski hill/SE talus	20	102	16	2.95	3.69	9	55	0.48	70%
1.2	Green	NW Ridge	9	12	4	1.56	1.94	2	14	-	-
1.3	Green	West Green	10	21	0	0.00	-	0	0	-	-
1.4	Green	South slope	9	18	3	0.67	1.12	2	6	-	-
1.5	Green	Road D15/D16	3	7	2	0.67	1.15	0	2	-	-
1.6	Green	Elk Meadow	8	14	4	0.50	1.41	0	4	-	-
1.7	Green	Road D	6	9	3	0.83	1.33	1	5	-	-
1.8	Green	Road K44A/K30	12	51	8	1.42	2.71	2	34	-	-
1.9	Green	Heart Lake basin	1	1	0	0.00	-	0	0	-	-
2.1	Gemini	South slope	14	23	6	1.43	2.17	2	20	-	-
2.2	Gemini	Westerholm	9	16	3	0.56	1.13	1	5	-	-
2.3	Gemini	Meadow #1	6	10	2	0.33	0.82	0	2	-	-
2.4	Gemini	Meadow #2	6	10	0	0.00	-	0	0	-	-
2.5	Gemini	Bell Creek North	6	8	0	0.00	-	0	0	-	-
2.6	Gemini	Road G2C	5	10	4	0.80	1.79	0	4	-	-
2.7	Gemini	Road D13E/W4	11	28	12	3.27	3.38	4	35	0.81	46%
3.1	Haley	Bowl	25	109	14	4.92	4.64	12	127	0.49	62%
3.2	Haley	Bell Creek	18	42	6	1.56	1.95	4	28	0.54	77%
3.3	Haley	Vaughan Road	14	54	6	1.50	2.21	5	21	0.38	109%
4.1	Butler	West face	11	22	4	1.45	1.75	2	18	-	-
4.2	Butler	East alder slide	10	20	6	0.90	2.02	0	9	-	-
4.3	Butler	Above Road V7	8	11	0	0.00	-	0	0	-	-
4.4	Butler	West roads	12	43	24	4.33	7.18	6	54	0.36	93%
4.5	Butler	Third step	2	5	0	0.00	-	0	0	-	-
5.1	Buttle	Top meadow	10	19	2	0.50	0.85	1	5	-	-
5.2	Buttle	South pocket	5	7	0	0.00	-	0	0	-	-
6.1	Whymper	South basin	10	18	2	0.30	0.67	0	3	-	-
6.2	Whymper	West basin	6	8	0	0.00	-	0	0	-	-
6.3	Whymper	Pat Lake basin	12	87	7	2.25	2.34	7	27	0.62	55%
7.1	Landalt	Lomas Lake	5	6	0	0.00	-	0	0	-	
7.2	Landalt	Sherk Lake	7	74	11	3.71	4.79	2	18	-	
8.1	Heather	S. alder meadow	13	23	3	0.46	0.97	1	6	-	-
9.1	Hooper	SW Basin	8	11	4	1.13	1.64	2	10	-	-
9.2	Hooper	SE side	5	8	0	0.00	-	0	0	-	-
9.3	Hooper	West Shaw Cree	3	3	3	1.00	1.73	0	3	-	-
10.1	Hooper N.	Hooper North	6	9	3	0.50	1.22	0	3	-	-
11.1	P Mtn.	NW meadow	13	24	4	0.38	1.12	0	5	-	-
11.2	P Mtn.	SE basin	11	14	3	0.27	0.90	1	3	-	-
11.3	P Mtn.	NW ridge	6	7	0	0.00	-	0	0	-	-
11.4	P Mtn.	West areas	7	9	2	0.29	0.76	0	2	-	-
12.1	Moriarty	SW aspect	10	14	0	0.10	0.32	1	1	-	-
12.2	Moriarty	NE aspect	7	7	1	0.14	0.38	1	1	-	-
12.3	Moriarty	Br146 meadow	2	10	0	0.00	-	0	6	-	-
13.1	Franklin	South summit	7	27	7	2.57	2.51	4	22	0.48	88%
15.1	Big Ugly	SE face	5	11	0	1.40	2.19	2	15	-	-
					average	1.27				0.52	75%
					SD	1.25				0.14	21%

Notes:

[a] Juvenile (young-of-the-year) abundance is derived from the long-term inventory database (this study). No correction factors were applied. Apparent survival was calculated from consecutive annual counts if more than three years of data were available. "Survival years" are those with consecutive counts. Data from Mount Washington were excluded.

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Appendix 19: Colony-specific adult abundance and apparent survival. [a]

Code	Mountain	Colony	Years with counts	N of counts	Max. adults	Mean adults	SD	Survival years	Animals in sample	Apparent survival	CV (%)
1.1	Green	Ski hill/SE talus	21	141	15	6.05	3.07	18	130	0.73	36%
1.2	Green	NW Ridge	12	22	8	2.92	2.57	7	35	0.59	62%
1.3	Green	West Green	12	34	8	2.58	2.78	6	31	0.56	63%
1.4	Green	South slope	12	30	7	2.33	2.31	6	28	0.43	94%
1.5	Green	Road D15/D16	7	13	2	0.71	0.95	1	5	-	-
1.6	Green	Elk Meadow	11	26	2	0.73	0.90	4	8	-	-
1.7	Green	Road D	8	13	3	1.38	1.51	2	11	-	-
1.8	Green	Road K44A/K30	16	68	17	5.56	3.97	10	102	0.73	43%
1.9	Green	Heart Lake basin	3	2	2	0.67	1.15	0	2	-	-
2.1	Gemini	South slope	16	31	20	6.19	7.09	5	99	0.86	22%
2.2	Gemini	Westerholm	12	27	13	4.83	4.41	5	58	0.49	83%
2.3	Gemini	Meadow #1	9	15	3	1.00	1.12	2	9	-	-
2.4	Gemini	Meadow #2	8	13	2	0.50	0.93	1	4	-	-
2.5	Gemini	Bell Creek North	6	9	6	1.50	2.35	0	9	-	-
2.6	Gemini	Road G2C	10	19	3	0.90	0.99	3	9	-	-
2.7	Gemini	Road D13E/W4	12	37	12	7.00	2.95	5	86	0.57	32%
3.1	Haley	Bowl	26	162	19	12.12	4.27	20	317	0.67	37%
3.2	Haley	Bell Creek	23	70	12	6.22	3.30	13	143	0.61	55%
3.3	Haley	Vaughan Road	15	95	9	4.20	2.91	13	63	0.65	53%
4.1	Butler	West face	12	28	9	4.00	2.73	8	48	0.66	62%
4.2	Butler	East alder slide	11	26	6	2.55	1.81	6	28	-	57%
4.3	Butler	Above Road V7	8	14	3	1.13	1.13	3	9	-	-
4.4	Butler	West roads	12	62	28	13.67	8.09	9	165	0.64	58%
4.5	Butler	Third step	2	8	0	1.00	1.41	1	2	-	-
5.1	Buttle	Top meadow	11	21	5	1.91	1.76	4	20	-	-
5.2	Buttle	South pocket	6	7	3	0.67	1.21	1	4	-	-
6.1	Whymper	South basin	13	23	11	2.38	3.62	6	31	0.56	89%
6.2	Whymper	West basin	6	8	3	0.67	1.21	1	4	-	-
6.3	Whymper	Pat Lake basin	12	116	15	8.25	3.98	10	99	0.66	28%
7.1	Landalt	Lomas Lake	5	6	2	1.80	0.45	2	9	-	
7.2	Landalt	Sherk Lake	7	88	7	5.00	3.46	6	44	0.86	23%
8.1	Heather	S. alder meadow	17	28	5	1.65	1.66	7	28	0.49	103%
9.1	Hooper	SW Basin	10	13	4	1.90	1.60	4	19	-	-
9.2	Hooper	SE side	5	7	3	1.00	1.41	0	5	-	-
9.3	Hooper	West Shaw Cree	4	3	1	0.25	0.50	0	1	-	-
10.1	Hooper N.	Hooper North	6	8	4	0.83	1.60	0	5	-	-
11.1	P Mtn.	NW meadow	15	32	8	2.73	2.63	9	42	0.66	64%
11.2	P Mtn.	SE basin	13	21	5	1.62	2.06	4	22	-	-
11.3	P Mtn.	NW ridge	9	9	3	1.11	1.17	2	10	-	-
11.4	P Mtn.	West areas	10	11	3	0.70	1.06	1	7	-	-
12.1	Moriarty	SW aspect	10	14	3	1.20	1.23	4	14	-	-
12.2	Moriarty	NE aspect	7	6	2	1.00	1.00	2	7	-	-
12.3	Moriarty	Br146 meadow	2	10	0	2.50	0.71	2	8	-	-
13.1	Franklin	South summit	7	48	10	6.57	2.37	6	49	0.65	53%
15.1	Big Ugly	SE face	6	11	5	3.50	2.43	4	26	-	-
15.2	Big Ugly	N avalanche trac	3	4	0	0.33	0.58	1	1	-	
					average	2.98				0.63	57%
					SD	2.99				0.11	24%

Notes:

[a] Adult abundance is derived from the long-term inventory database (this study). No correction factors were applied. Apparent survival was calculated from consecutive annual counts if more than 4 years of data were available. "Survival years" are those with consecutive counts. Data from Mount Washington animals were excluded.

Appendix 20: Colony-specific birth rates. [a]

Code	Mountain	Colony	Years with counts	N of counts	Max. YOY	Per capita births	CV (%)	Per capita litters	CV (%)
1.1	Green	Ski hill/SE talus	21	89	16	0.44	129%	0.13	117%
1.2	Green	NW Ridge	7	11	4	1.43	128%	0.38	118%
1.3	Green	West Green	6	20	0	0.00	0%	0.00	0%
1.4	Green	South slope	6	18	3	0.36	166%	0.15	134%
1.5	Green	Road D15/D16	2	7	2	-	-	-	-
1.6	Green	Elk Meadow	3	12	4	-	-	-	-
1.7	Green	Road D	4	8	3	-	-	-	-
1.8	Green	Road K44A/K30	13	53	8	0.45	216%	0.12	185%
1.9	Green	Heart Lake basin	0	1	0	-	-	-	-
2.1	Gemini	South slope	8	25	6	0.66	205%	0.15	238%
2.2	Gemini	Westerholm	6	16	3	0.08	155%	0.03	159%
2.3	Gemini	Meadow #1	3	10	2	-	-	-	-
2.4	Gemini	Meadow #2	1	10	0	-	-	-	-
2.5	Gemini	Bell Creek North	3	8	0	-	-	-	-
2.6	Gemini	Road G2C	3	10	4	-	-	-	-
2.7	Gemini	Road D13E/W4	12	39	12	0.44	75%	0.24	67%
3.1	Haley	Bowl	26	99	14	0.46	104%	0.11	120%
3.2	Haley	Bell Creek	18	40	6	0.26	182%	0.09	183%
3.3	Haley	Vaughan Road	12	53	6	0.28	130%	0.05	199%
4.1	Butler	West face	11	22	4	0.71	167%	0.23	142%
4.2	Butler	East alder slide	10	17	6	0.20	211%	0.07	211%
4.3	Butler	Above Road V7	5	11	0	0.00	0%	0.00	0%
4.4	Butler	West roads	13	38	24	0.40	144%	0.14	134%
4.5	Butler	Third step	1	3	0	-	-	-	-
5.1	Buttle	Top meadow	7	17	2	0.19	126%	0.13	147%
5.2	Buttle	South pocket	2	7	0	-	-	-	-
6.1	Whymper	South basin	8	17	2	0.10	190%	0.07	188%
6.2	Whymper	West basin	2	8	0	-	-	-	-
6.3	Whymper	Pat Lake basin	12	82	7	0.22	97%	0.06	108%
7.1	Landalt	Lomas Lake	5	6	0	0.00	0%	0.00	0%
7.2	Landalt	Sherk Lake	7	63	11	0.56	189%	0.18	175%
8.1	Heather	S. alder meadow	10	23	3	0.30	214%	0.15	211%
9.1	Hooper	SW Basin	5	13	4	1.25	126%	0.45	82%
9.2	Hooper	SE side	2	10	0	-	-	-	-
9.3	Hooper	West Shaw Cree	1	3	3	-	-	-	-
10.1	Hooper N.	Hooper North	2	9	3	-	-	-	-
11.1	P Mtn.	NW meadow	12	23	4	0.14	279%	0.06	234%
11.2	P Mtn.	SE basin	6	15	3	0.25	245%	0.08	245%
11.3	P Mtn.	NW ridge	2	7	0	-	-	-	-
11.4	P Mtn.	West areas	2	9	2	-	-	-	-
12.1	Moriarty	SW aspect	7	16	0	0.07	265%	0.08	245%
12.2	Moriarty	NE aspect	4	7	1	-	-	-	-
12.3	Moriarty	Br146 meadow	3	17	0	-	-	-	-
13.1	Franklin	South summit	8	29	7	0.55	110%	0.14	98%
15.1	Big Ugly	SE face	6	16	0	0.45	116%	0.12	120%
15.2	Big Ugly	N avalanche trac	1	5	0	-		-	
					average	0.44	163%	0.14	159%
					SD	0.34	55%	0.10	53%

Notes:

[a] Per capita birth rates were calculated as juveniles (young-of-the-year) over non-juveniles (all yearling and adult marmots). No correction factors were applied. Data from Mount Washington colonies were excluded.