

Distribution and abundance of Vancouver Island marmots (*Marmota vancouverensis*)

Andrew A. Bryant and Doug W. Janz

Abstract: We analysed historic records and annual counts to assess the population status of Vancouver Island marmots (*Marmota vancouverensis*). Since 1972, marmots have been found at 47 sites on 15 mountains. All but 2 colonies were located within 5 adjacent watersheds on south-central Vancouver Island. Counts underestimated actual marmot abundance. For most site-year combinations, observers probably counted 66–78% of adults and 75–89% of juveniles. Reproductive colonies typically contained fewer than 5 adults ($\bar{x} = 3.86$, $SE = 0.61$, $n = 34$). Most animals were found at elevations above 1000 m (81%), on south- to west-facing slopes (74%). After 1981, marmots colonized 11 habitats created by logging of forests above 700 m. Numbers of adults were above average (134–147%) during the early 1980s and have been near or below average since 1990 (58–99%). The current (1995) population contains 100–200 animals, including 50–100 animals in logged habitats. *Marmota vancouverensis* is rare primarily because of the small size and patchy distribution of natural subalpine meadows on Vancouver Island. The species is apparently adapted to a metapopulation life-style, in which a network of small colonies exhibit population fluctuations, local extinctions, and recolonizations over time.

Résumé : Nous nous sommes basés sur des données historiques et sur les résultats d'inventaires annuels pour estimer la population de Marmottes de l'île Vancouver (*Marmota vancouverensis*). Depuis 1972, les marmottes ont été repérées à 47 endroits sur 15 montagnes. Toutes les colonies, sauf deux, ont été observées à l'intérieur des limites de cinq bassins hydrographiques adjacents dans le centre sud de l'île Vancouver. Les comptages avaient tendance à sous-estimer l'abondance réelle des marmottes. Dans la plupart des combinaisons endroit-année, les observateurs ont probablement compté 66–78% des adultes de 75–89% des juvéniles. Les colonies reproductrices contenaient généralement moins de 5 adultes ($\bar{x} = 3,86$, erreur standard = 0,61, $n = 34$). La plupart des marmottes ont été observées à des altitudes supérieures à 1000 m (81%), sur les versants sud, sud-ouest et ouest (74%). Après 1981, les marmottes ont colonisé 11 milieux créés par l'exploitation des forêts au-dessus de 700 m. Le nombre d'adultes était supérieur à la moyenne (134–147%) au début des années '80, et se maintient près de la moyenne ou sous la moyenne (58–99%) depuis 1990. La population actuelle (1995) compte de 100–200 animaux, dont 50–100 dans les forêts exploitées. *Marmota vancouverensis* est un animal rare surtout à cause de la petite taille et de la forte dispersion des prairies sub-alpines naturelles dans l'île. L'espèce semble avoir adopté un mode de vie de métapopulation au sein de laquelle un réseau de petites colonies subissent des fluctuations démographiques et disparaissent de certains endroits pour les recoloniser par la suite.
[Traduit par la Rédaction]

Introduction

The Vancouver Island marmot (*Marmota vancouverensis* Swarth, 1911) is endemic to Vancouver Island, British Columbia (Nagorsen 1987). It is listed as an endangered species by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 1979) and the Province of British Columbia (Munro et al. 1985). Prior to 1970, little was known about the distribution or ecology of this species. Heard (1977) conducted the first field research and described *M. vancouverensis* as a highly social member of the genus *Marmota*. Milko (1984) reported heavy use of *Anaphalis*–*Aster* wildflower meadows by marmots and concluded that they depend upon meadow environments kept clear of trees by avalanches or snowcreep. Bryant (1990) initiated mark–

recapture studies and reported on demographic and genetic characteristics.

This paper reports on the population status of *M. vancouverensis*. Our objectives were to (i) map historic location records for the species, (ii) describe current patterns of distribution, (iii) describe habitats used by this species, (iv) assess recent population trends, and (v) assess the reliability of count methods.

Methods

Location records

We compiled records of marmots at clearly identifiable times and places. Sources of data included museum specimens, photographs, newspaper accounts, reports of whistles or burrows, and descriptions of marmots or fresh burrows (see Acknowledgments). We rejected second-hand records, most reports of marmot whistles, and reports that were unconvincing because of location, habitat, or time of year. From each report we compiled location, number of marmots involved, and time of year. We coded sites as "active colony" (consecutive records of multiple marmots or young observed in apparently suitable habitat since 1990), "potential colony" (> 1 marmot observed in suitable habitat since 1990 but no evidence of reproduction), "inactive site" (unused burrows or

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A.A. Bryant. Andrew A. Bryant Services, 108 Fifth Street, Nanaimo, BC V9R 1N2, Canada (e-mail: abryant@island.net).

D.W. Janz. British Columbia Ministry of Environment, Lands and Parks, 2569 Kenworth Road, Nanaimo, BC V9T 4P7, Canada.

criteria as above, but with no record since 1990), or "solitary marmot" (no reoccurrence, and apparently unsuitable habitat below 700 m).

Population counts

Counts at colonies and potential colonies began in 1972. Observations were made by naturalists, government personnel, and researchers (see Acknowledgments). Field methods involved scanning meadows and cliffs with binoculars or spotting scopes, listening for marmot whistles, and searching for burrows and fresh scats or mud stains on rocks, stumps, or logs. Marmots were classified as adults or juveniles (young of the year) based on size and pelage. Juvenile *M. vanancouverensis* are readily identifiable by their small size and dark, almost black, pelage (Nagorsen 1987). For each site and year, we used maximum counts of adults and juveniles as measures of abundance. Counts of juveniles were considered relevant only if the count was made after July 1, when young first emerge from their natal burrows (Bryant 1990, 1996).

Most counts were conducted prior to 11:00 to coincide with known marmot activity rhythms (Heard 1977). Counts were usually repeated 2–4 times annually, although some sites were visited only once, and not every site was visited in each year. In addition, some sites were counted during periods of inclement weather, some sites were not visited early in the morning, and the number and experience level of observers varied from year to year. The most extensive surveys were conducted in 1979, 1982, 1984, 1986, 1993, 1994, and 1995. From 1987 to 1992, counts were primarily confined to 5 intensively studied colonies (see below). Data were therefore biased by differences in (i) survey coverage; (ii) site-specific observer effort; and (iii) day-specific differences in weather, level of observer experience, and time of day.

Intensively studied colonies

From 1987 to 1995, 123 individual marmots were ear-tagged and monitored at 5 colonies as part of a demographic study (Bryant 1996). Two colonies (Green Mountain and Haley Lake, at elevations of 1400 and 1100 m, respectively) were located in natural subalpine meadows kept clear of tree growth by snow movement. Both have presumably been occupied by marmots since their discovery in 1954 and 1915, respectively. Three colonies (Pat Lake, Sherk Lake, and Vaughan Road, at elevations of 830–1000 m) were located in previously forested habitats that were clear-cut in 1977, 1977, and 1976, respectively. At intensively studied sites, a large proportion of ear-tagged animals and numerous repeated visits provided relatively accurate population counts in some years. These data were used to provide benchmarks against which counts from other sites could be compared.

Habitat characteristics

Colonies and potential colonies were mapped (1:50 000 scale, National Topographic Series). Elevation and aspect were measured from maps or with an altimeter and compass in the field. Natural meadow and logging cutblock areas were measured from 1:20 000 scale aerial photographs using a random dot grid. Patch sizes of natural habitats were based on the dispersion of marmot sightings and the extent of meadows. Some sites were excluded from measurement because the extent of marmot use was unclear.

Statistical analysis

Analyses were restricted to the 47 known and potential colonies. The repeatability of adult count data was evaluated using intraclass correlation coefficients (Krebs 1989). The repeatability index (R) varies from 0 to 1.0 depending upon the similarity of repeated measurements. We used raw count data, in which the repeated measures were multiple counts made at a given site and year. We also divided count data into an "intensive" set (colonies with >5 repeated counts per year, and where at least 75% of marmots

were ear-tagged) and a "nonintensive" set (all other site-year combinations). This permitted comparison of repeatability indices from sites at which population sizes were known with some precision.

Because relatively few counts were made after emergence of young of the year in early July, we could not calculate the R index of count data for juveniles. Instead we used Kruskal–Wallis analysis of variance (ANOVA) and Mann–Whitney U tests to compare mean litter sizes derived from intensive versus nonintensive counts. To do this, we extracted counts from the nonintensive data for which numbers of both juveniles and litters had been recorded by field personnel.

Observations at intensively studied colonies were used to estimate how many counts are needed to accurately estimate population size. Each count was expressed as a proportion of the known population of ear-tagged marmots. For example, we made 6 counts at Green Mountain in 1987, producing counts of 4, 6, 5, 5, 6, and 2 adults. From tagging we identified 6 adults, so the "success" of each count was expressed as 0.66, 1.0, 0.83, 0.83, 1.0, and 0.33, respectively. We sampled the transformed count data, in random order, to generate an accumulated success curve, using linear regression and $\log_{10}$ -transformed x values (multiple y values for each x value; Sokal and Rohlf 1981). The same data were also used to test for seasonal effects, using single-factor ANOVA to determine whether the $\bar{x}$ success rate differed with time of year.

To describe habitats used by marmots, we weighted habitat data with the mean abundance of adults per year and tested for independence of observed frequencies using χ^2 methods. The relationship between habitat patch sizes and adult abundance was tested using Pearson's correlation statistics (Sokal and Rohlf 1981). To estimate the magnitude of population fluctuations, we calculated ratios of observed to expected numbers, annual expected numbers being calculated as the sum of the long-term averages, using only those sites actually surveyed in a given year. We used a mean successive difference test to evaluate autocorrelation among successive survey years (Zar 1974).

Results

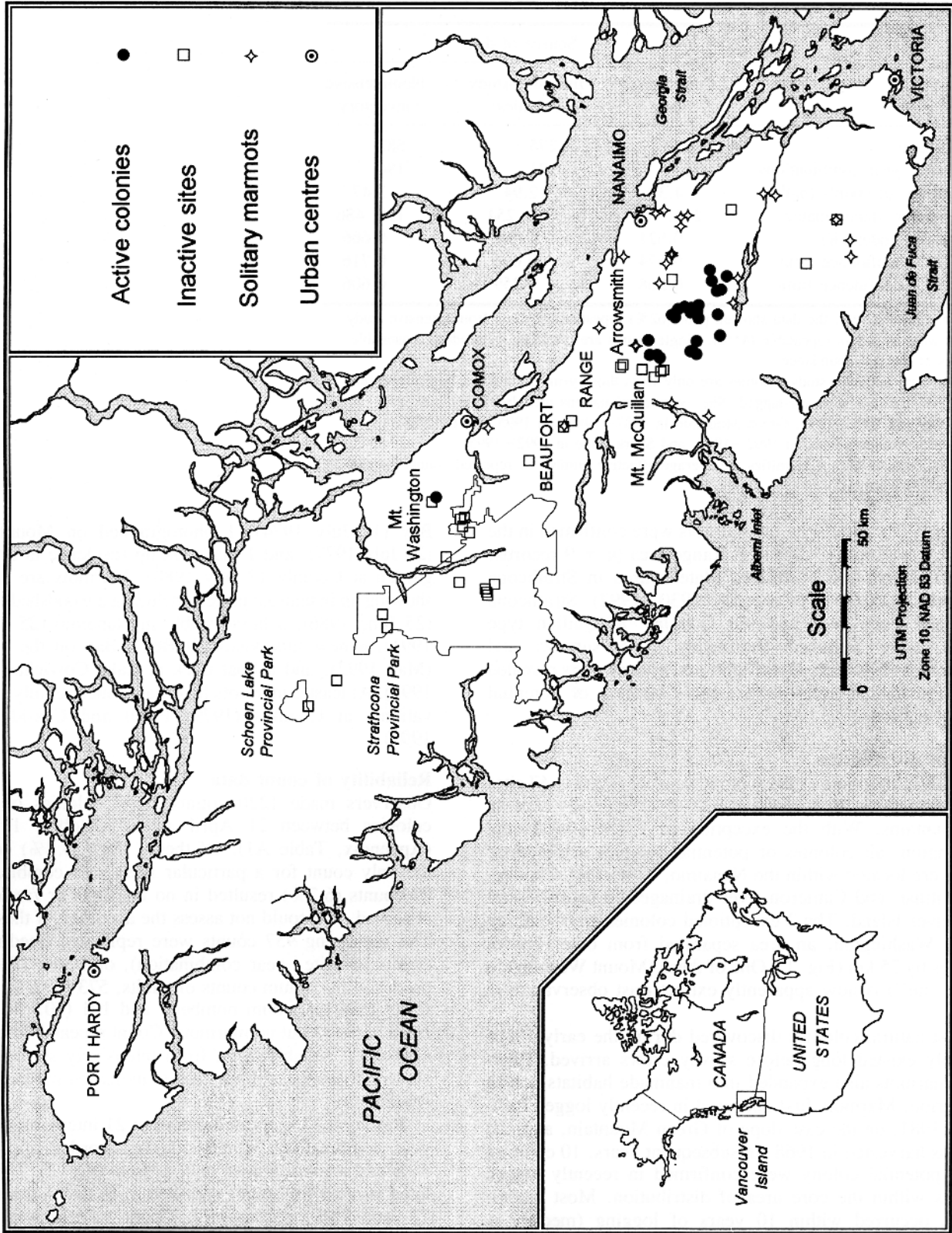
Historic distribution

Marmota vanancouverensis was apparently more widely distributed on Vancouver Island prior to 1970 than it is today. Between 1864 and 1969, marmots were recorded from a minimum of 28 sites on 25 mountains (Fig. 1). Most pre-1970 records are vague, and interpreting whether sightings referred to reproductive colonies or solitary individuals was difficult. One record mentioned "swarms of ground hogs" at the "head of Nitinat Valley" (*Victoria Times*, 7 September 1893), while another described a "brace" of marmots shot in the Beaufort Range (*Victoria Times*, 8 August 1922). Some indication of abundance can be drawn from the 11 adult specimens collected during a 21-day period near the Douglas Peak type locality (30 June to 19 July 1910; Swarth 1912) and from the 8 adult and juvenile specimens collected in 2 days at Haley Lake (22 June and 21 September 1931). Pre-historic bones have been found at 6 locations, all outside of the present core area of distribution (Nagorsen et al. 1996; Calvert and Crockford 1983).

Unsuccessful searches

All historic marmot locations have been ground-searched at least once since 1972, and most other mountain areas were inspected by helicopter. Several historic marmot locations appear to have no marmots at present, including the type locality at Douglas Peak, and nearby Mount McQuillan, where marmots were described as being "fairly abundant"

Fig. 1. Location records for *Marmota vancouverensis*, 1864 – 1995. Active colonies include those confirmed by inventory crews since 1990. Historic colonies were reported prior to this date. With the exception of a single colony on Mount Washington, the current population is concentrated within the headwaters of the Nanaimo, Cowichan, Chemainus, Cameron, and Nitinat rivers on southeastern Vancouver Island.



Map by Andrew A. Bryant Services

Table 1. Repeatability of adult marmot count data, 1972–1995.

	Source of data		
	Cumulative data	Intensive-study colonies ^a	Nonintensive inventory
No. of counts	957	275	682
No. of site–year combinations	217	21	196
Effective no. of counts (n_0) ^b	4.39	12.94	3.47
df (numerator, denominator)	216, 740	20, 254	195, 486
Repeatability index (R)	0.621	0.405	0.666
Upper 95% confidence limit	0.674	0.606	0.716
Lower 95% confidence limit	0.568	0.259	0.606

Note: Cumulatively, the data showed poor (62%) repeatability. Data from intensive study colonies were even less repeatable (41%). Single counts are not likely to produce reasonable estimates of marmot abundance.

^aData from intensive-study colonies are only from those years in which a high proportion (>75%) of marmots were ear-tagged. Site–year combinations included Haley Lake in 1988–1989 and 1992–1995, Green Mountain in 1987–1988 and 1995, Pat Lake in 1992–1995, Vaughan Road in 1992–1995, and Sherk Lake in 1992–1995.

^bAfter Krebs (1989); n_0 signifies the average effective number of repeated counts for each site–year combination.

(Swarth 1912). Similarly, no marmots were confirmed in the Mount Arrowsmith – Beaufort Range area ($n = 9$ records, 1922–1981) or the Forbidden Plateau area in Strathcona Provincial Park ($n = 14$ records, 1930–1992). Strathcona Provincial Park sites and the Douglas–McQuillan type locality were searched thoroughly (>5 surveys and >10 person-days/site). Overflights and ground visits revealed few large habitat areas or extensive clusters of potential marmot habitats.

Current distribution

Since 1972, marmots or fresh burrows were found at 47 sites on 15 mountains. Reproduction was observed at 34 sites on 14 mountains. With the exception of 2 sites on Mount Washington, all colonies or potential colonies active since 1972 were located within the Nanaimo, Cowichan, Chemainus, Nitinat, and Cameron river drainages on south-central Vancouver Island. The 2 exceptional colonies were both on Mount Washington, an area separated from other known colonies by 75 km (Fig. 1). One of these (Mount Washington “mine site”) is now apparently extinct (last observation in 1984).

Most natural colonies discovered during the early 1980s probably existed long before survey crews arrived. However, marmots also expanded into manmade habitats during this period. Marmots first appeared in recently logged habitats in 1981, on the east slope of Green Mountain, at a site that was harvested in 1968. In subsequent years, 10 colonies and 1 potential colony were confirmed in recently logged habitats within the core area of distribution. Most colonizations occurred within 10 years of logging (median = 8.5 years, range = 1–15 years, $n = 11$) and within 1 km of existing natural colonies (median = 0.82 km, range = 0.4–4.5 km, $n = 11$). Marmots also colonized ski runs and an abandoned mine site on Mount Washington during this period.

Solitary marmots

We compiled 22 records of solitary marmots during 1972–1995, including 1 found “wandering” on the beach at Union

Bay (12 July 1974), 1 photographed on Mount Demers (25 July 1977), and 1 that took up residence in a vegetable garden at Coombs (7 July 1980). Marmots are capable of showing up in unusual places, including a woodshed in Youbou (25 June 1986), a horse stable in Nanaimo (25 September 1991), a new subdivision at Bell’s Bay on the west coast (May 1992), and a boat dock at Lake Cowichan (18 May 1993). At least 2 marmots hibernated successfully at low elevations, at Coombs (1979–1980) and Cassidy (1991–1992).

Reliability of count data

Observers made 1220 counts at 47 colonies or potential colonies between 21 April and 7 October, 1972–1995 (Appendix, Table A1). Of these, 181 (14.8%) constituted the only count for a particular site–year combination and 82 counts (6.7%) resulted in no marmots or fresh burrows observed. We could not assess the accuracy of these counts. The remaining 957 counts were replicated (median = 3.0 counts per site–year combination), of which 283 (29.6%) produced maximum counts of adults, 573 (59.9%) recorded fewer than maximum numbers, and 101 (10.6%) recorded fresh burrows but no marmots. Count repeatability was poor (Table 1). Notably, data from intensively studied colonies showed low repeatability despite increased numbers of measurements.

Based on 275 repeated counts at 21 intensive-study site–year combinations, single counts recorded approximately 54% of the adults known to be present (Fig. 2). The accumulated success for counts repeated 2, 3, and 4 times was 66, 73, and 78%, respectively. Count success was generally higher in May, June, and July than in August (Fig. 3). This suggests that either (i) adults are easier to count when vegetation cover is still low or (ii) numbers decline during summer, as dispersers leave the colony and predation losses accumulate, or (iii) both factors apply.

A total of 746 counts were made after 1 July, yielding 255 (34.2%) counts of juveniles and 491 (65.8%) counts with no juveniles observed. Excluding repeated counts of the same litters, 111 litters were recorded during nonintensive counts,

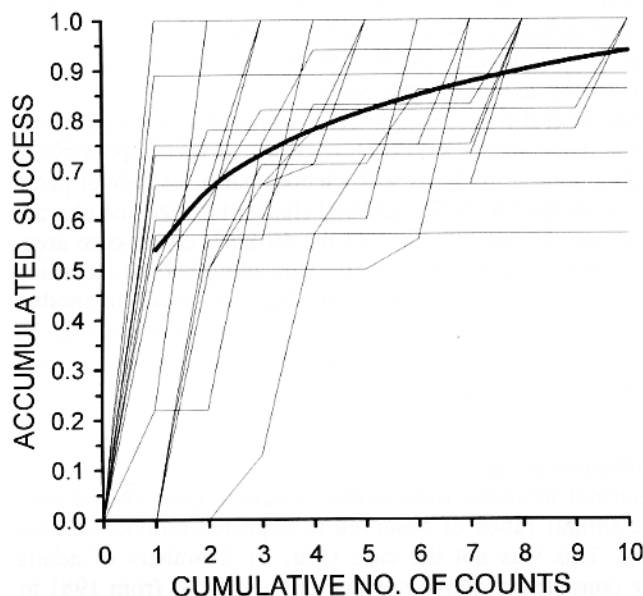
Table 2. Comparison of mean litter sizes estimated by inventory and intensive mark-recapture work at five colonies.

	Source of data			ANOVA ^a	df	P
	Intensive study (July counts)	July counts	Post-July counts			
No. of litters	36	77	34			
$\bar{x}$	3.36	3.01	2.53	10.79	2	0.005
SE	0.14	0.13	0.22			
Frequency distribution						
1 YOY	0	6	8			
2 YOY	3	21	10			
3 YOY	22	24	10			
4 YOY	6	20	3			
5 YOY	5	4	2			
6 YOY	0	2	1			

Note: Inventory efforts underestimate production of young of the year (YOY), and the degree of underestimation is increased if counts are conducted after July.

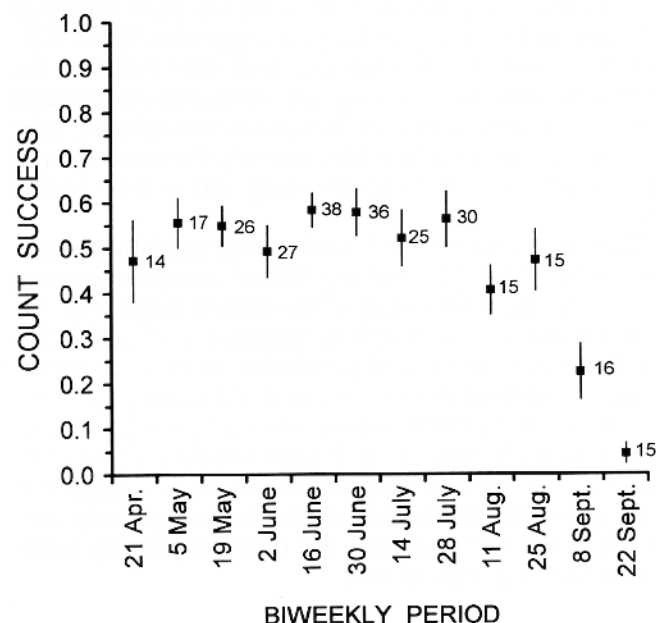
^aKruskal-Wallis ANOVA. Pairwise comparisons using Mann-Whitney *U* tests determined significantly different mean litter sizes based on intensive-study colonies versus post-July counts ($U_{(36,34)} = 882$, $P = 0.001$), but found no difference between intensive and nonintensive July data ($U_{(36,77)} = 1133.5$, $P = 0.103$).

Fig. 2. Count success based on data from sites with known numbers of adults. Transformed count data were randomly resampled to create 100 trials of 10 counts each (for clarity, results from only 25 trials are shown). The cumulative success curve (heavy line) was fitted using linear regression (log-transformed x values, slope = 0.397 and constant = 0.540). On average, 2 counts resulted in detection of 66% of the adults actually present, but 9 counts were needed to account for >90%.



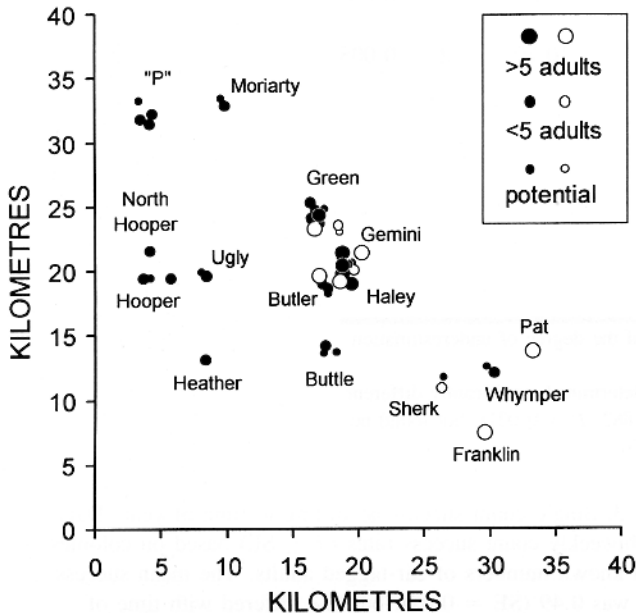
of which 77 were counted in July and 34 after July. Non-intensive counts generally underestimated numbers of juveniles (Table 2). Litter size estimated from July counts was not significantly different from that estimated at the intensively studied colonies, although it was approximately 10% lower (3.01 versus 3.36 young/litter). Litter size based on counts made after July significantly underestimated litter size (2.53 young/litter).

Fig. 3. Single count success according to time of year. Data are biweekly count success rates ($\bar{x} \pm SE$) based on colonies with known numbers of ear-tagged adults. The mean success rate was 0.49 (SE = 0.02), but this differed with time of year ($F = 6.41$ with 11,263 df, $n = 275$, $P < 0.001$). Count success was relatively constant from May through July (49–58%) but declined in August and September (5–47%).



Results suggest that >9 repeated visits are necessary to obtain accurate population data, but that 2 or 3 counts provide a reasonable index of marmot use. For sites and years with single visits, observers probably counted 40–60% of the adults actually present, depending upon time of year. For most site-year combinations (2 or more visits in June and July), observers probably counted 66–78% of adults and 75–89% of young present.

Fig. 4. The core area of current *M. vancouverensis* distribution. Colonies in natural (solid circles) and clearcut habitats (open circles) are shown. Data are based on mean annual numbers of adults observed since 1972. At least 67% of the current population is found in the central 40 km² of the current range. Marmots colonized only a small fraction of the newly logged habitat above 700 m elevation.



Colony size and spatial distribution

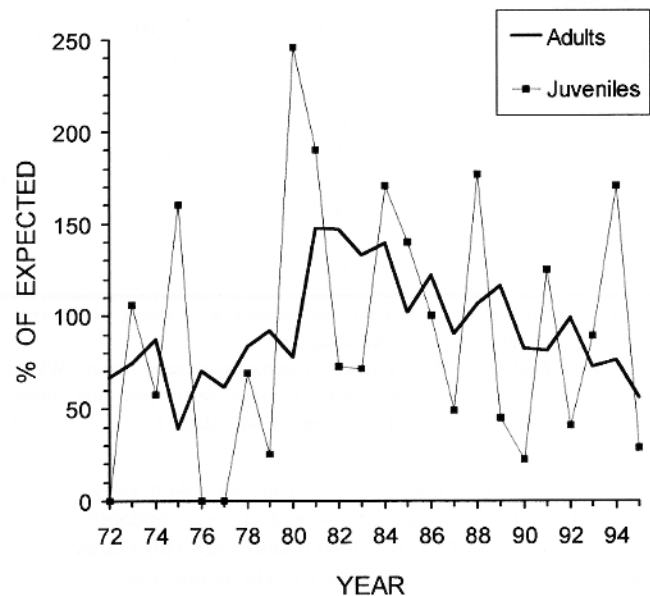
Using average numbers for the 47 known sites over 24 years, the "expected" population of *M. vancouverensis* contained 145 adults and 50 young of the year (Appendix, Table A2). That these numbers are underestimates does not alter the essential fact that most colonies are small and concentrated in small geographic areas. Of 34 reproductive colonies, only 2 contained more than 10 adults and only 9 contained more than 5 adults ($\bar{x} = 3.86$ adults/colony, $SE = 0.61$ adults/only).

Most large colonies (>5 adults) were spatially concentrated, with all but 2 located in a 40-km² area encompassing four mountains in the center of the current range (Fig. 4). Most colonies on the periphery averaged 2–5 adults and contributed little to the total population. Finally, 13 nonreproductive potential colonies averaged <2 adults ($\bar{x} = 1.05$, $SE = 0.19$). A typical *M. vancouverensis* family group consists of an adult male, 1 or 2 adult females, 2-year-olds, yearlings, and young of the year (Heard 1977). Even allowing for count underestimation, most colonies apparently contain only 1 or 2 family groups, and there are probably fewer than 50 family groups in total.

Habitat conditions

Most (81% of expected) marmots were found at elevations between 1000 and 1400 m. Colonies in clearcut habitats were generally at lower elevations (median = 990 m, range = 730–1140 m) than natural subalpine meadows (median = 1240 m, range = 1040–1450 m). Most marmots were found on south- to west-facing slopes (74%). This trend was not strong in clearcut habitats at 800–1000 m, where northwest- to southeast-facing slopes were all used by more marmots

Fig. 5. Ratios of observed to expected numbers of adults and young, 1972–1995. Observed and expected frequencies were significantly different among years for both adults ($\chi^2 = 69.5$ with 23 df, $P < 0.001$) and young ($\chi^2 = 100.1$ with 23 df, $P < 0.001$). There were few years in which expected numbers of young were produced. Reproduction is largely synchronous among colonies, suggesting that environmental factors produce good and poor years for reproduction.



than expected, and south- to west-facing slopes were used by fewer than expected. Slope aspect was not independent of colony type ($\chi^2 = 50.4$ with 14 df, $P < 0.001$). However, analysis was complicated by local topography. Most colonies in clearcut habitats were in sheltered "bowl" habitats where local microclimatic conditions may not be accurately reflected by average aspect data.

For natural sites, abundance of adults was correlated with habitat patch size ($r = 0.609$, $n = 28$). It was impossible to conduct similar analyses with clearcut sites, as habitat patch sizes were hard to define and had changed in size and character during the last 20 years. In the 40-km² central core area, there were 16 patches of natural meadow habitat, totalling 34.5 ha, and 7 colonies in clearcut habitats, totalling another 20–25 ha at peak colony size. By 1979, 1560 of the 3625 ha above 700 m elevation (43%) had been harvested, yet only a fraction of this area (<2%) was colonized.

Population trends

If marmot numbers were stable, annual counts should produce similar ratios of observed to expected numbers across years. This was not the case (Fig. 5). Numbers of adults were consistently above average (134–147%) from 1981 to 1984 and near or below average (58–99%) from 1990 to 1995. The magnitude of annual change was generally small (mean absolute change = 19.7%, $SD = 15.9\%$). Adult abundance was autocorrelated with values in the preceding year (mean square successive difference test, $C = 0.63$, $P < 0.0005$). Juvenile numbers fluctuated dramatically from 1972 to 1995 (0–231%). The magnitude of annual change was much higher than for adults (mean absolute change =

79.9%, SD = 50.3%). Production of young was serially random and not influenced by numbers in preceding years ($C = 0.01$, $P > 0.05$). There were few years with expected reproductive success.

Individual marmot colonies fluctuated in size and the incidence of occupied habitats varied, particularly between 1980 and 1995. For example, the Butler Peak "west roads" site was logged during 1976–1980, was apparently colonized by 2 marmots in 1982, and contained at least 28 adults in 1989. By late 1992 it contained only 17 adults, and by 1995 this had been reduced to 13 adults, despite production of 24 juveniles in the previous year. The history of 6 other clearcut colonies is similar, showing expansion during the mid-1980s, and decline or extinction in more recent years (Road D15, Road D, Road G2C, Road K44, Pat Lake, Vaughan Road).

Natural colonies showed similar patterns. Colonizations of natural habitats were generally restricted to habitat patches in the central core area, where small numbers of adults formed potential colonies or produced occasional litters during the early 1980s (Green Mountain Heart Lake basin, Gemini meadows 1 and 2). Photographic evidence exists that at least 2 marmots reached the Mount McQuillan type locality and produced a litter in 1991 (5 km west of natural colonies on P Mountain), but this dispersal did not lead to the establishment of a colony. At least 8 extinctions or near extinctions occurred at natural sites in the 1990s (Heather, Hooper north, Gemini Peak south slope, Westerholm basin, P Mountain southeast basin and northwest ridge, south Green, and elk meadow). Ultimately, increased numbers of marmots during the 1980s did not lead to an expanded geographic range, with the exception of the currently declining Pat Lake colony and the new Sherk Lake (1994) and Mount Franklin (1992) colonies.

Discussion

Historic records preclude assessment of the extent of habitats previously occupied by *M. vancouverensis*, or of pre-1970 population levels. Negative search results and historic location records suggest that Vancouver Island marmots are confined to a smaller geographic range than they were several decades ago. Marmots no longer inhabit several locations that appear to offer pristine habitat conditions in natural subalpine meadows above 1000 m in elevation. Colonies presently occur on 15 mountains, with all but 1 located within 5 adjacent watersheds on south-central Vancouver Island. Given the publicity surrounding *M. vancouverensis*, the popularity of back-country recreation, and the recent discovery of old burrows and prehistoric bones in remote locations by untrained personnel, we doubt that significant new marmot populations will be found north of Alberni Inlet.

Our count methods undoubtedly underestimated true marmot abundance. For most years and sites, observers probably counted 66–78% of adults and 75–89% of young. Because of differences in survey coverage and experience of personnel, we have not attempted to place confidence intervals on population estimates, or to test for population changes using parametric statistics. However, resulting count data were internally consistent, showing annually autocorrelated adult counts, a predicted result given probable marmot longevity (Bryant 1990). As expected, peaks in reproductive perfor-

mance were generally followed by higher counts of adults in following years. Indeed, any other result would invalidate our reliance on annual counts.

We believe that marmot numbers increased to 250–350 during the mid-1980s and have declined to 100–200 animals since then. Of the current population, 67% of animals are found within an area of 40 km². Vancouver Island marmots are both extremely rare and localized. To place these results in context, Barash (1989) estimated the total population of Olympic marmots (*Marmota olympus*) at fewer than 2000 individuals. Mainini et al. (1993) estimated that there were approximately 1000 alpine marmots (*Marmota marmota*) in a 7-km² area in the Bernese Oberland of Switzerland.

Vancouver Island marmots are rare primarily because their natural habitat patches are small and scattered. Milko (1984) suggested that populations declined because of natural processes during the past 10 000 years. Climate change and forest succession following the most recent glacial period left only patches of grass-forb meadow habitat, typically in avalanche bowls or adjacent to talus slopes (Franklin et al. 1971; Kuramoto and Bliss 1970). Thus, for most of its evolutionary history, *M. vancouverensis* has faced a metapopulation life-style (Hanski and Gilpin 1991), the entire population consisting of small colonies located in a matrix of unsuitable forest or alpine habitat. Presumably some behavioral attributes of *M. vancouverensis*, including its high level of sociality (Heard 1977) and ability to make long-distance dispersal movements, are the inevitable result of this metapopulation existence.

Hanski (1991) suggested that two kinds of random events influence metapopulations. "Immigration-emigration stochasticity" consists of chance births and deaths that influence individual subpopulations, and "regional stochasticity" consists of environmental factors acting on a number of subpopulations simultaneously. Both processes probably play a critical role in regulating numbers of *M. vancouverensis*. With some mountains containing only 1 or 2 family groups, the fate of single individuals (predation, over-winter mortality, dispersal, successful immigration) could cause important population effects. Immigration of a single male into the previously nonreproductive Sherk Lake site in 1993 led to successful production of 3 litters in 1994, converting this "potential colony" into an active colony. Despite the loss of most juveniles in the subsequent winter, together with a female and the single male, "rescue effects" (Brown and Kodric-Brown 1977) continue to occur. Two untagged adult males immigrated into the colony in 1995, providing some possibility of future reproduction at that site.

Regional stochasticity also appears to be important. Our results suggest that reproduction was spatially correlated (among colonies and within years) but temporally variable (there were only a few years with high reproductive success between 1972 and 1995). Because most colonies are small and individual females seldom reproduce in consecutive years (Bryant 1990), colony reproductive performance will inevitably vary. However, if variance in individual female reproduction is the key factor in regulating individual colonies, one would expect some colonies to be reproductive, while others are not, in any given year. Overall, the peaks and lows among colonies should tend to cancel each other out, and one should expect no large departure from expected

numbers. In fact, the data suggest quite the opposite. We suspect that regional weather patterns (regional stochasticity) produce good and poor reproductive years for marmots, although we are unsure which environmental patterns are important.

For yellow-bellied marmots (*Marmota flaviventris*), the timing of snowmelt is significantly associated with reproductive performance, and with over-winter survival of juveniles (Armitage 1991; Van Vuren and Armitage 1991; Armitage and Downhower 1974). Armitage (1994) also suggested that marmot body mass is lower in years of low rainfall, and that this may translate into reduced over-winter survival. Given the confined geographic range of *M. vancouverensis*, regional stochasticity could have important ramifications for the entire metapopulation.

Logging of forests above 700 m during the 1960s, 1970s, and 1980s created a form of ecological release for Vancouver Island marmots, in which thousands of hectares of habitat were created, much of which offered good soil for burrowing, a variety of grasses and forbs to eat, and abundant logs, stumps, and boulders to serve as lookout spots. This, possibly combined with regional weather trends that promoted good reproduction and survival, allowed marmots to colonize new areas in both natural and clearcut habitats during the early 1980s. However, the resulting population expansion was modest in scale and geographic scope. For many sites the expansion was temporary, and recent years have seen a decline in marmot numbers and in the incidence of occupied habitats.

Thomas (1994) argued that many rare species track environmental conditions, becoming locally extinct where conditions are no longer suitable and colonizing sites where conditions improve. However, this does not fully explain recent population trends in Vancouver Island marmots. Apparently suitable habitat patches exist on some mountains of northern and western Vancouver Island, including the type locality for the species and other sites that harbored marmots until recent decades. We do not know why marmots disappeared from these habitats, although regional weather patterns, hunting by aboriginal peoples, predation, and sheer chance were all probably important. Similarly, we do not understand why marmots colonized only a fraction of new clearcut habitats, although thermoregulation and heat stress probably influence marmot habitat selection (Türk and Arnold 1988; Webb 1980).

Early metapopulation models were characterized as a series of habitat patches of uniform quality and irrelevant spatial structure, in which the only functional variables were extinction and recolonization rates (Levins 1970). More recent papers have stressed that consideration of individual patch dynamics, together with the "landscape matrix" in which occupied patches are embedded, may be vital in understanding how metapopulations are maintained in nature (Taylor et al. 1993; Fahrig and Merriam 1985). Further work is needed to determine whether climatic variables are correlated with birth and death rates, and how habitat quality relates to marmot persistence.

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Appendix

Table A1. Vancouver Island marmot counts by year, 1972–1995.

Year	No. of counts	No. of sites counted	Maximum adult count	Maximum infant count	Total no. of marmots
1972	4 (4)	2 (2)	13	0	13
1973	11 (9)	6 (6)	18	8	26
1974	19 (12)	7 (5)	35	7	42
1975	1 (1)	1 (1)	5	8	13
1976	3 (2)	3 (2)	11	0	11
1977	3 (3)	2 (2)	12	0	12
1978	5 (5)	4 (4)	19	7	26
1979	20 (4)	14 (4)	51	2	53
1980	41 (35)	18 (15)	54	52	106
1981	50 (27)	19 (15)	105	34	139
1982	99 (58)	29 (27)	148	24	172
1983	80 (47)	30 (23)	140	23	163
1984	101 (73)	37 (36)	167	68	235
1985	38 (14)	25 (12)	108	31	139
1986	113 (73)	34 (34)	150	40	190
1987	35 (15)	17 (5)	57	5	62
1988	47 (22)	16 (14)	69	36	105
1989	41 (17)	15 (10)	95	13	108
1990	18 (18)	9 (9)	48	5	53
1991	24 (21)	7 (6)	38	18	56
1992	64 (51)	18 (16)	90	11	101
1993	127 (84)	35 (32)	86	34	120
1994	130 (81)	34 (30)	98	64	162
1995	164 (93)	44 (42)	86	19	105

Note: Numbers in parentheses refer to counts conducted after emergence of young (July 1). Analyses were based on data current to 15 August, 1995.

Table A2. Observed marmot abundance by site, 1972–1995.

Site	Adult counts (all counts)					Infant counts (after July 1)					Colony status
	Years counted	No. of counts	Mean no. of adults	SD	Range	Years counted	No. of counts	Mean no. of infants	SD	Range	
Green Mountain											
Top of ski hill	19	96	6.16	3.15	3–15	18	59	2.94	3.90	0–16	Colony
Northwest ridge	10	22	3.30	2.63	0–8	8	11	1.75	1.98	0–4	Colony
West Green	10	27	2.70	2.75	0–8	8	16	0.50	1.41	0–4	Colony
South slope	10	25	2.70	2.36	0–7	8	15	0.75	1.16	0–3	Colony
Road D15	7	13	0.71	0.95	0–2	3	7	0.67	1.15	0–2	Colony ^a
Elk Meadow	9	21	0.89	0.93	0–2	6	11	0.67	1.63	0–4	Colony
Road D	7	13	1.57	1.51	0–3	5	8	1.00	1.41	0–3	Colony ^a
Road K44A/K30	14	45	5.86	4.17	1–17	10	23	1.70	2.91	0–8	Colony ^a
Heart Lake	2	2	1.00	1.41	0–2	1	1	0.00	—		Potential ^a
Gemini Peak											
South-facing slope	14	31	6.86	7.08	0–20	12	21	1.92	2.87	0–9	Colony
Westerholm basin	10	26	5.80	4.18	0–13	7	14	0.86	1.21	0–3	Colony
Meadow 1	8	15	1.13	1.13	0–3	5	9	0.40	0.89	0–2	Colony
Meadow 2	7	13	0.57	0.98	0–2	5	9	0.00	0.00		Potential
Bell Creek north	6	10	1.50	2.35	0–6	6	8	0.00	0.00		Potential
Road G2C/W4	9	19	1.00	1.00	0–3	4	9	1.00	2.00	0–4	Colony ^a
Road D13E	10	27	7.10	3.25	2–12	9	17	3.67	3.64	1–12	Colony ^a
Haley Lake											
Bowl	24	139	12.75	3.79	5–19	23	80	5.04	4.70	0–14	Colony
Bell Creek	21	61	6.67	3.07	1–12	16	33	1.88	1.93	0–6	Colony
Vaughan Road	13	94	4.92	2.60	1–9	12	46	1.75	2.30	0–6	Colony ^a
Butler Peak											
West face	10	22	4.40	2.67	1–9	9	13	1.89	1.69	0–4	Colony
East alder slide	10	17	2.30	2.06	0–6	9	11	1.00	2.12	0–6	Colony
Above road V7	7	12	1.14	1.21	0–3	7	9	0.00	0.00		Potential
West roads	10	35	15.40	7.62	2–28	10	20	4.80	7.83	0–24	Colony ^a
Mount Butte											
Top meadow	9	14	2.11	1.90	0–5	8	12	0.63	0.92	0–2	Colony
South pocket	4	6	1.00	1.41	0–3	4	6	0.00	0.00		Potential
Road NM 50	3	5	0.00	0.00		3	5	0.00	0.00		Potential ^a
Mount Whymper											
South Basin	11	20	2.82	3.79	0–11	8	13	0.38	0.74	0–2	Colony
West Basin	6	10	0.67	1.21	0–3	6	8	0.00	0.00		Potential
Pat Lake Basin	10	103	9.50	2.95	6–15	10	67	2.70	2.31	0–7	Colony ^a
Mount Landalt											
Top east meadow	5	6	1.80	0.45	1–2	5	6	0.00	0.00		Potential
Sherk Lake	5	55	3.60	2.51	0–7	5	32	2.20	4.92	0–11	Colony ^a
Heather Mountain											
South alder meadow	15	26	1.73	1.75	0–5	11	18	0.36	0.92	0–3	Colony
Mount Hooper											
Southwest basin	7	10	2.43	1.51	0–4	5	7	1.80	1.79	0–4	Colony
Southeast side	2	3	2.50	0.71	2–3	2	3	0.00	0.00		Potential
West Shaw Creek	2	2	0.50	0.71	0–1	1	1	3.00	—	3–3	Colony
Hooper north	4	7	1.25	1.89	0–4	4	7	0.75	1.50	0–3	Colony
P Mountain											
Northwest meadow	13	27	2.85	2.79	0–8	11	18	0.45	1.21	0–4	Colony
Southeast basin	11	21	1.91	2.12	0–5	9	12	0.33	1.00	0–3	Colony
Northwest ridge	8	9	1.25	1.16	0–3	5	5	0.00	0.00		Potential
North areas	9	13	0.78	1.09	0–4	6	8	0.33	0.82	0–2	Colony
Mount Moriarty											
Southwest aspect	8	11	1.25	1.28	0–3	8	11	0.00	0.00		Potential
Northeast aspect	7	8	1.00	1.00	0–2	7	8	0.14	0.38	0–1	Colony

Table A2 (concluded).

Site	Adult counts (all counts)					Infant counts (after July 1)					Colony status
	Years counted	No. of counts	Mean no. of adults	SD	Range	Years counted	No. of counts	Mean no. of infants	SD	Range	
Mount Franklin											
Southeast summit	5	17	6.80	1.92	5–10	5	10	2.20	2.05	0–4	Colony ^a
Mount Washington											
West basin, ski runs	19	41	1.05	0.97	0–3	15	29	0.13	0.52	0–2	Colony
Mine site	9	15	0.56	1.13	0–3	7	11	0.43	1.13	0–3	Colony ^a
Big Ugly											
Southeast face	4	5	1.00	0.82	0–2	3	3	0.00	0.00		Potential
North avalanche track	1	1	0.00	—		1	1	0.00	—		Potential
Total		1220	144.77				751	50.02			

^aClearcut sites.