Reproduction and persistence of Vancouver Island marmots (*Marmota vancouverensis*) in natural and logged habitats

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Abstract: I tagged and monitored Vancouver Island marmots (*Marmota vancouverensis*) to investigate demographic trends among colonies inhabiting natural subalpine meadows and recently logged habitats. *Marmota vancouverensis* exhibits low reproductive rates, with litter sizes of 2–5 ($\bar{x}$ = 3.36, SD = 0.83, n = 36). Females are capable of breeding at age 3, but most animals did not breed until age 4 ($\bar{x}$ = 4.00 years, SD = 0.82 years, n = 13), and displayed a nonreproductive interval of at least 1 year between litters ($\bar{x}$ = 1.83 years, SD = 0.76 years, n = 6). Persistence of marmots was higher at natural sites than in logged areas (65 versus 48%). Maximum female age was 9 years in natural habitats and 5 years in clearcuts. No adult female inhabiting a clearcut (n = 14) produced more than a single litter, while 5 of 14 females in natural habitats produced 11 litters. The net reproductive value of colonies in clearcut habitats was less than half that of natural colonies (0.25 versus 0.72). Recently logged habitats may act as a demographic "sink" by consuming more dispersers than they produce, and therefore impede the recolonization of distant natural habitats.

Résumé : J'ai marqué et suivi des Marmottes de l'île Vancouver (*Marmota vancouverensis*) pour étudier les tendances démographiques des colonies des prairies sub-alpines naturelles et de celles des forêts récemment coupées. Cette marmotte a un taux de reproduction faible et produit des portées de 2 à 5 petits ($\bar{x}$ = 3,36, écart type = 0,83, n = 36). Les femelles peuvent se reproduire à l'âge de 3 ans, mais la plupart ne le font qu'à l'âge de 4 ans ($\bar{x}$ = 4,00, écart type = 0,82 n = 13) et il y a un intervalle d'au moins 1 an entre les portées ($\bar{x}$ = 1,83, écart type = 0,76, n = 6). La fidélité des marmottes à un endroit est plus élevée aux sites naturels que dans les forêts coupées (65 versus 48%). L'âge maximal des femelles a été évalué à 9 ans dans les habitats naturels et à 5 ans dans les forêts coupées à blanc. Aucune femelle des forêts coupées à blanc (n = 14) n'a produit plus qu'une portée, alors que 5 des 14 femelles des milieux naturels ont produit 11 portées. Le coefficient net de reproduction des colonies des forêts coupées à blanc équivalait à moins de la moitié de celui estimé dans les colonies des milieux naturels (0,25 versus 0,72). Les forêts récemment exploitées servent peut-être de « bassins » démograhiques en absorbant plus d'individus non sédentaires qu'ils n'en produisent et ces milieux empêchent donc la recolonisation des milieux naturels éloignés.
[Traduit par la Rédaction]

Introduction

Solutions to many problems in wildlife management are hindered by a lack of demographic information with which to relate habitat conditions and population trends (Caughley 1977, 1994). This is particularly true for threatened or endangered species, because the usual difficulties involved in determining demographic rates are compounded by small populations and high per-sample costs (e.g., Wielgus et al. 1994; Forsman et al. 1984). In addition, relationships between habitat quality and population processes are often unclear. Pulliam (1988) suggested that population abundance in specific habitats may not necessarily reflect local demographics, and indeed, that a small number of high-quality "source" habitats could maintain much larger populations in adjacent "sinks." Despite this, many analyses of threatened populations continue to rely upon estimates of abundance in various habitats and ignore local demographics (e.g., Dupuis et al. 1995; Fimbel 1994). It may be dangerous to assume that because organisms occupy a variety of habitats, they must be equally successful in each. In this paper I consider habitat-specific demographic trends in a critically endangered mammal, the Vancouver Island marmot (*Marmota vancouverensis* Swarth, 1911).

Marmota vancouverensis differs from other marmots in karotype (Rausch and Rausch 1971), skull characteristics (Hoffman et al. 1979), pelage (Nagorsen 1987), and behavior (Heard 1977). The species is endemic to Vancouver Island. It is not known whether *M. vancouverensis* is a Pleistocene relict that survived the last glaciation in refugia or colonized Vancouver Island after the retreat of the Cordilleran Wisconsin glaciation, some 10 000 – 13 000 years ago (Nagorsen 1987; Hoffman et al. 1979).

Heard (1977) described *M. vancouverensis* as a highly social member of the genus *Marmota*. Mace and Shepard (1981) described a new anoplocephalid tapeworm species (*Diandrya vancouverensis*: Mace) found in a dead marmot. Milko (1984) characterized vegetation patterns at subalpine colonies and suggested that *M. vancouverensis* depends upon

Received April 12, 1995. Accepted October 24, 1995.

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meadow environments kept clear of trees by avalanches or snowcreep. Martell and Milko (1986) studied food habits using fecal analysis, and concluded that *M. vancouverensis* concentrates foraging effort upon few plant species. Bryant (1990) initiated a long-term mark–recapture study and reported that levels of electrophoretic genetic variability were similar to those of other marmot species.

Because of small known populations and the unknown impact of human activities, *M. vancouverensis* was listed as "endangered" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 1979), and by the Province of British Columbia in 1980 (Munro et al. 1985). A recovery team was established in 1988, and implementation of a recovery program began in 1993 (Bryant 1990; Janz et al. 1994). The current population is estimated at 100–200 individuals, with all but 1 colony situated within five adjacent watersheds on south-central Vancouver Island (Bryant and Janz 1996). Why marmots disappeared from some historic habitats remains unknown. During the early 1980s, Vancouver Island marmots colonized 11 habitats created by logging of forests between 730 and 1140 m elevation. The resulting population expansion was modest in size and extent, most colonizations occurring within 1 km of existing natural colonies.

This study reports on *M. vancouverensis* demography within the present core area of distribution. My objectives were to (*i*) estimate reproductive and survival rates and their annual variability and (*ii*) compare demographic trends among populations in recently logged and natural subalpine meadow habitats.

Study areas

From 1987 to 1995, marmots were trapped at (*i*) Haley Lake Ecological Reserve "bowl" colony, (*ii*) the nearby clearcut colony at Vaughan Road, and (*iii*) the "top ski hill – southeast talus" colony located at the summit of Green Mountain. The project was expanded to include the (*iv*) Pat Lake clearcut colony in 1988 and (*v*) the Sherk Lake clearcut colony in 1992 (Fig. 1).

The Haley Lake and Green Mountain sites were steeply sloped (30°–45°) south- or southwest-facing meadows kept free of trees by snowcreep and avalanches at 1040 and 1420 m elevation, respectively. Common plant species included *Phlox diffusa*, *Castilleja* spp., *Erythronium grandiflorum*, *Saxifraga ferruginea*, *Saxifraga occidentalis*, *Anaphalis margaritacea*, *Aster foliaceus*, and *Lupinus latifolius* (Milko 1984). Both sites had numerous boulders, rock outcrops, and scattered Krummholz. 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 was located 1 km west of the Haley Lake natural colony, in an area that was logged between 1974 and 1978 (940 m elevation). Marmots were first observed there in 1983. The aspect is west-southwest and the site is surrounded by steep hills to the east and west. The Pat Lake site was a steep north-facing bowl surrounding a shallow lake 16 km southeast of the Haley Lake colony and 2 km northeast of Mount Whymper, where marmots also occur. Elevation at Pat Lake was 900 m. 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 have been reported in natural meadows. Vegetation at clearcut colonies was 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.

Methods

Trapping and mark–recapture

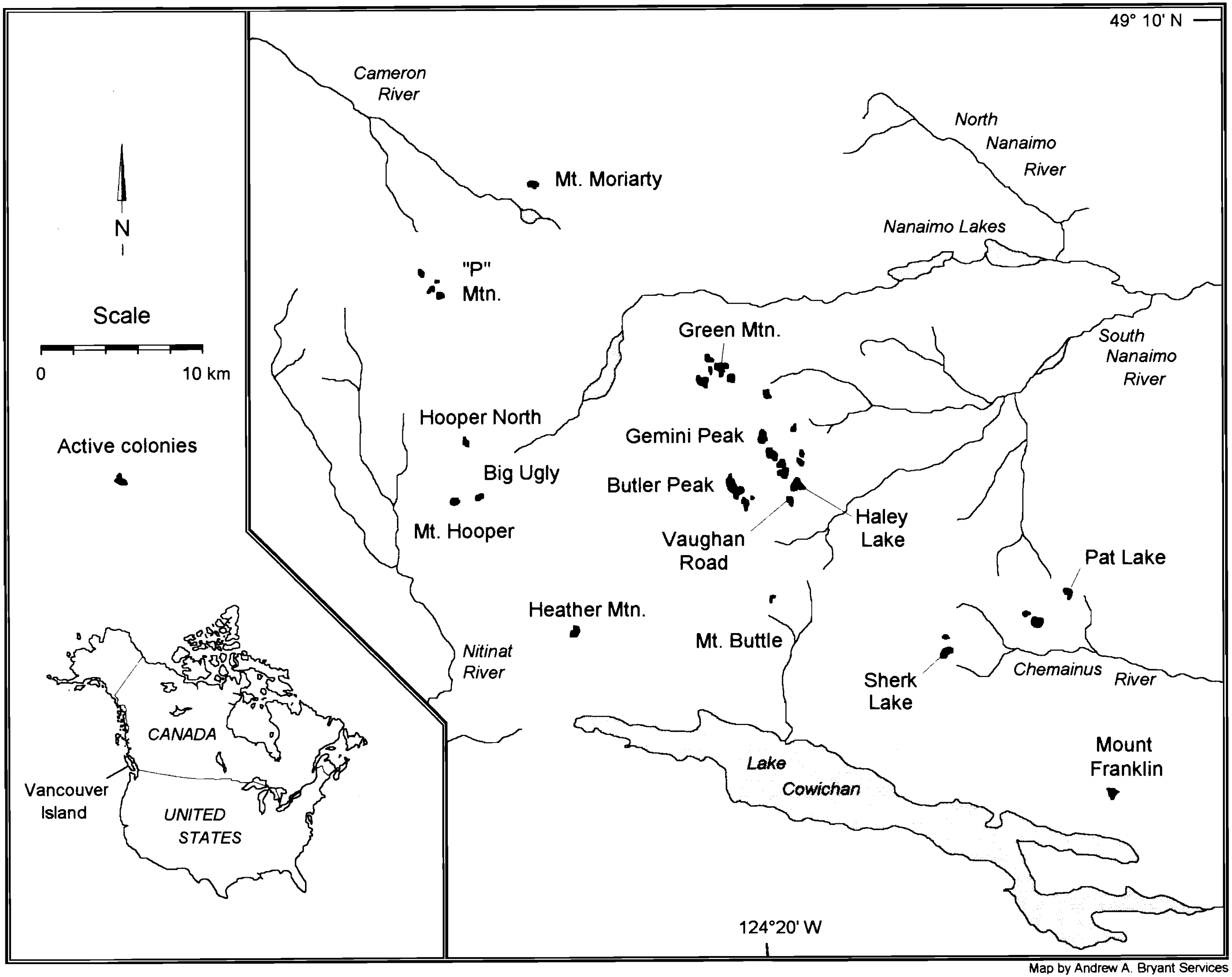
I trapped marmots using Havahart Model 1079 single-door traps (Woodstream Corporation, Lititz, Pa.) baited with peanut butter. Trap placements were not random but were usually made to capture particular individuals. Because *M. vancouverensis* is endangered, recaptures were avoided unless necessary to replace missing ear tags or verify reproductive status of females. All trapping was done with field personnel in attendance and traps were closed at the end of each trapping session. Trapped marmots were transferred to a canvas handling sock and an intramuscular injection of 10% Ketamine–Ketaset (Rogets Pharmaceuticals, Vancouver, B.C.) was used to immobilize them. Dosage was normally 0.2–0.4 mg/kg.

Sex determination was made by everting male genitalia, palpating for testes, and measuring anus to genital slit distances (Armitage and Downhower 1974). I measured body mass to the nearest 100 g using a spring scale and measured total length and forearm length with a flexible tape. Lactating or postlactating females were distinguished from nonreproductive females by the presence of swollen nipples. External characteristics that could aid in reidentification (scars and molt patterns) were noted. Marmots were equipped with ear tags in both ears using either aluminum "rabbit-ear" tags or Monel self-piercing tags (Styles 41 and 1005-3, respectively, National Band and Tag Company, Newport, Ky.). Animals were normally released within 1 h of capture. Sampling effort was recorded in terms of field-days (a visit to a colony by 1 or more persons on 1 day), person-days (1 person on site during a morning or evening session in good weather), and trap-days (1 trap used at 1 site during 1 day, regardless of how many times the trap was moved among placements).

On each daily visit I recorded numbers of tagged and untagged adults, juveniles, and yearlings. Normally I did not recapture marmots to identify individuals, but read ear-tag numbers using a 60× spotting scope. Depending upon light conditions, and with experience, ear tags could be read from distances up to 20 m. *Marmota vancouverensis* juveniles emerge from their natal burrows in late June or early July and rarely stray far for several weeks (Heard 1977; Bryant 1990; Bryant and Janz 1996). Litter sizes were estimated by trapping and by counts of juveniles observed above ground near their natal burrows during the first 3 weeks of July. This produces minimum estimates of litter size, because some juveniles probably die prior to emergence (Allainé et al. 1994).

Known-age and presumed-age marmots

Life-table analysis requires accurate age-structured data (Caughley 1977). For marmots this is problematic, as there is no reliable method for aging adults. Other researchers (e.g., Barash 1973; Armitage and Downhower 1974) assigned ages to captured marmots using body mass alone, but this approach may be unreliable if growth rates vary among sites or years. I classified captured marmots into four age-classes at the time of first capture, using pelage, mass, and reproductive and behavioral characteristics, as follows. *Juveniles* (young of the year): small body size (length 30–47 cm excluding tail, forearm length 10.1–13.0 cm, mass 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 in relation to lactating adult



Map by Andrew A. Bryant Services

Fig. 1. Location of intensively studied Vancouver Island marmot colonies, 1987 – 1995. Recently active (1972 – 1995) colonies within the core area of distribution are also shown.

female(s). *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 length 12.0–15.5 cm, mass 2.0–4.75 kg). By late August, most yearlings are either in faded overall pelage or are in partial molt (unpublished data). *Subadults* (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 length 12.7–17.1 cm, mass 3.5–5.5 kg) but nonreproductive. 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 data). No female known to be 2 years of age reproduced during the study. *Adults* (3 years and older): Large-bodied males (body length >60 cm, forearm length >16 cm, mass >5.5 kg) and all reproductive females were initially classified as 3-year-olds. Molt patterns are unpredictable beyond the age of 2 years (unpublished data), but animals 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," and data from other animals were coded as "presumed age." My aging protocol was intentionally conservative, and undoubtedly underestimated the true age of some animals. The reverse is not true: it is unlikely that I overestimated marmot ages using the above criteria.

Statistics and life-table analysis

Population sizes were estimated from the cumulative number of animals known to be present at a given site–year combination (i.e., the known number of ear-tagged animals plus the maximum number of untagged animals observed at each colony in a given active season). These data include immigrants but exclude emigrants and deaths, and should therefore be interpreted as maximum colony numbers. The rate of ear-tag loss was calculated as the simple quotient of losses per tagged-animal-year. Because of small colony sizes, demographic trends may be greatly influenced by death, dispersal, or reproduction of particular individuals. To minimize this bias, all analyses employed pooled observations from Haley Lake and Green Mountain sites as "natural" data and pooled observations from Vaughan Road, Pat Lake, and Sherk Lake sites as "clearcut" data. I recognize that this could conceal site-specific demographic trends, but reasoned that pooling was justifiable, given my intention to characterize demographic trends among habitat types.

Mean litter sizes, birth rates, female lifetime reproductive success, and mean age at first reproduction were compared across habitats using Mann–Whitney U tests. Birth rates were expressed as the total number of young produced by females of reproductive age (defined as those 3 years and older) that were known to be alive. Lifetime female reproductive performance was calculated as the total number of juveniles produced by tagged females that subsequently disappeared. Animals known to be still alive in 1995 were excluded, as they could reproduce again. Juvenile sex ratios were tested against an expected 1:1 ratio using χ^2 goodness of fit and data for animals captured as juveniles or yearlings. Pearson's r statistics were used to test whether annual numbers of litters or juveniles were correlated across habitat types, after square-root transformation to standardize variance among populations of different size (Zar 1974).

Determination of survival was based on resightings of tagged animals in their original colony. This resulted in data that excluded dispersers and therefore underestimate actual survival. For this reason I use "persistence" in lieu of "survival." For the same reason I excluded resighting data from the few animals known to have dispersed to other locations. Inclusion of these data would bias results, since other animals probably dispersed but were never found. Because age- and sex-specific sample sizes were small, I used χ^2 methods to test for differences in persistence of two classes: (*i*) young of the year, using frequencies of all juveniles that disappeared or yearlings that were observed at the site 1 year later, and (*ii*) all ear-tagged animals, using frequencies of animals that disappeared or were observed 1 year later.

Mean annual persistence rates were calculated for juveniles, yearlings, and older males and females using annual probabilities of persistence weighted by the count of animals in that age-class and year. Weighting was necessary to reduce bias caused by small numbers of surviving or disappearing animals in particular years. I also calculated age-specific residence times using the minimum number of days that a tagged animal stayed at the site. Persistence rates and residence times were compared across habitat types using Mann–Whitney U tests (Zar 1974). I did not use parametric tests because persistence rates were based on count data and because residence times were not strictly continuous (animals that died in midwinter would be classified as disappearing in late summer, when they were last seen). Annual variation in reproductive or persistence rates was expressed as a coefficient of variation (CV) calculated from annual means if more than 5 years of data were available.

I used standard methods and nomenclature to construct life tables (Caughley 1977, method 2). All rates were calculated from frequencies of sex- and age-specific disappearences. To verify that the tagged marmot cohort reasonably reflected actual trends, I recalculated life tables using (*i*) tagged juvenile data alone, (*ii*) all juvenile data, including observations of surviving but untagged yearlings, (*iii*) fecundity estimated using the observed ratio of female to male juveniles, and (*iv*) fecundity estimated assuming a 1:1 sex ratio at birth. No smoothing was employed (Krebs 1989) and I did not test for differences in survivorship curve shape (e.g., Pyke and Thompson 1986) because age-specific samples were small.

Finally, most analyses resulted in tests with low statistical power (Zar 1974). I employed a conventional ($\alpha = 0.05$) decision rule to accept or reject null hypotheses, but included probability (P) values for all tests so that readers may judge for themselves whether observed differences might be biologically significant despite a lack of statistical significance (Krebs 1989).

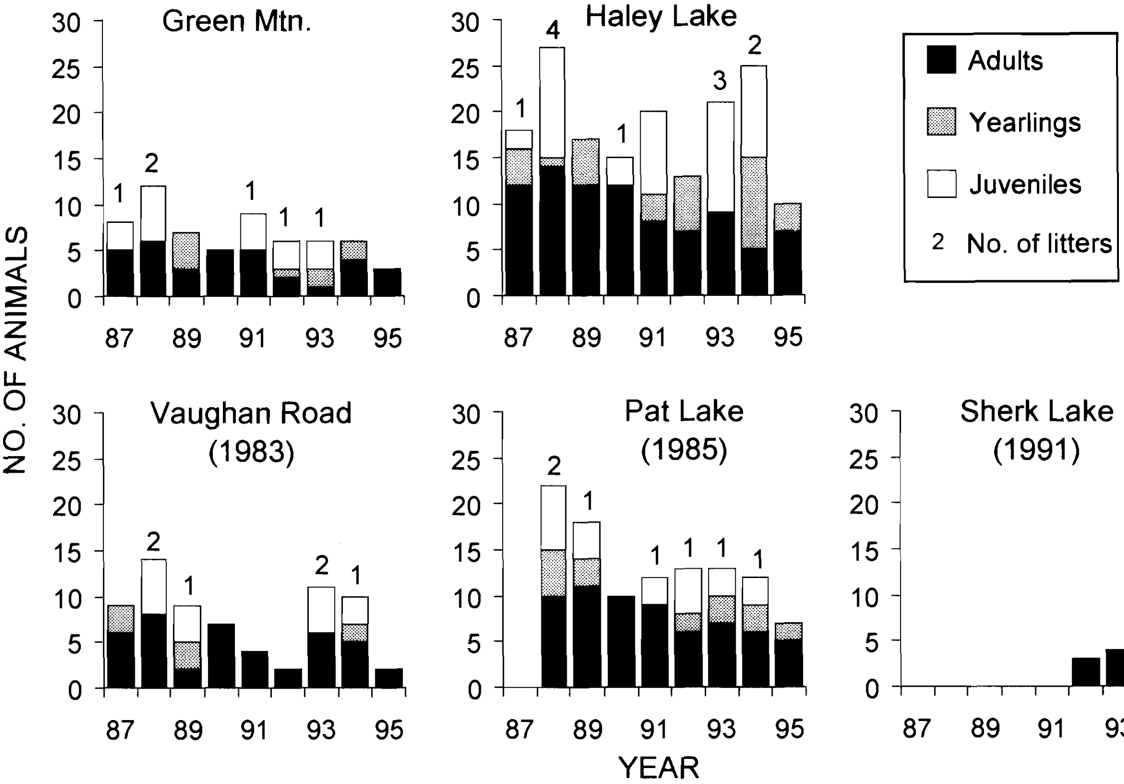
Results

Sampling effort and ear-tag loss

Field effort was not consistent across years. Efforts were greatest in 1987–1988 and 1992–1995. I attempted to spread field effort equally among colonies, but in practice spent more time at clearcut colonies (362 person-days and 530 trap-days) than at natural colonies (259 person-days and 447 trap-days). In total, 262 captures, involving 127 individuals, were made during the study. Most marmots observed at study colonies from 1987 to 1995 were eventually ear-tagged (mean annual tagging success = 61%, SD = 19%).

Trapping success at study colonies improved with time, increased effort, and experience (from 34% in 1987 to 97% in 1995). Ear-tag loss was a problem when aluminum "rabbit-ear" tags were used, and I discontinued using them after 1987. Tag losses also occurred using self-piercing tags, but losses were few (23 cases, 318 animal-years) and seldom involved both tags simultaneously ($n = 4$, of which 3 animals were eventually retagged). On average, approximately 13% of the known population of this species was tagged in any given year (range 5–22%; population estimates from Bryant and Janz 1996).

Fig. 2. Population trends at 5 study colonies, 1987–1995. Data are based on maximum daily counts and the cumulative annual number of ear-tagged individuals. They therefore represent maximum numbers before mortality or dispersal, but include immigrants in any given year. The names of clearcut colonies are followed by their probable date of colonization. All colonies fluctuated in size during the study (24–154% of average numbers), but changes were caused mostly by highly variable reproductive rates (0–333% of average numbers of juveniles).



Population trends

All colonies fluctuated in size during the study, mostly as a result of changing numbers of juveniles and yearlings (Fig. 2). One clearcut colony (Sherk Lake) was apparently colonized in 1991 and produced young for the first time in 1994. Other colonies were either stable (Green Mountain) or showed a gradual decline after 1988 (Pat Lake and Haley Lake). The Vaughan Road clearcut showed a decline followed by a wave of immigrants in 1993, followed by another decline. Production of juveniles and litters was not highly correlated among habitat types ($r = 0.53$ and 0.55, respectively; $n = 9$, $0.10 > P > 0.05$). However, reproduction in some years was high (23–31 juveniles in 1988, 1993, and 1994) and low in others (0–8 juveniles in 1989, 1990, 1992, and 1995).

Reproductive trends

I counted 121 juveniles at study colonies from 1987 to 1995 ($\bar{x} = 3.36$ juveniles/litter, SD = 0.83 juveniles/litter, $n = 36$ litters). The earliest day that juveniles were seen was 22 June 1988, but most (29 of 36) litters emerged between 1 and 7 July in any year. Litters of 3 were most common ($n = 22$), but litters of 4 ($n = 6$), 5 ($n = 5$), and 2 ($n = 3$) also occurred. Litter sizes, births per adult-female-year, proportions of breeding females, and juvenile sex ratios did not differ between natural and clearcut habitats (Table 1). The sex ratio of 69 animals initially captured as juveniles or yearlings was skewed towards females (41:28), but this ratio was not significantly different from 1:1 (goodness-of-fit $\chi^2 = 2.45$ with 1 df, $0.25 > P > 0.10$). Juvenile *M. vancouverensis* are difficult to sex compared with yearlings or adults, but 25 animals first captured as yearlings showed a similar sex ratio (15:10).

Only 3 females tagged as juveniles eventually reproduced (at 5, 5, and 4 years of age). The mean age at first reproduction for 13 animals tagged as juveniles, yearlings, or presumed 2-year-olds was 4.00 years (SD = 0.82 years, range = 3–5 years). This estimate was not significantly different among habitat types, although small sample sizes make me cautious about discounting the possibility of earlier reproduction in clearcut habitats. *Marmota vancouverensis* is physiologically capable of producing litters in consecutive years, although this occurred only twice, both times in natural habitats (Green Mountain, presumed-age adult in 1987–1988, and Haley Lake, animal known to be 5–6 years old in 1990–1991).

Five of 14 females in natural habitats produced at least 2 litters, including 1 that produced 3 litters during the study. Cumulatively, these 5 females produced 59% ($n = 37$) of all juveniles observed at the natural sites. No female produced more than 1 litter in a clearcut site, but the apparent difference in mean lifetime reproductive success among habitat types was not significant (Table 1). Fecundity appeared to be relatively stable with increasing age, and values for natural and clearcut habitats were similar for animals of equal age (Fig. 3).

I could not identify male parents, but behavior and small

Table 1. Reproductive traits of female *Marmota vancouverensis* living in natural and clearcut habitats.

	Natural habitats					Clearcut habitats					
Variable	N^a	$\bar{x}$	SD	Range	CV (%)	N^a	$\bar{x}$	SD	Range	CV (%)	P value
Litter size[b]	20 (7)	3.35	0.93	2–5	24	16 (6)	3.38	0.72	2–5	22	0.636
Births per adult-female-year[c]	49 (9)	1.27	1.77	0–5	94	29 (8)	1.28	1.73	0–5	83	0.919
Age at first reproduction[d]	6	4.33	0.33	3–5	—	7	3.71	0.76	3–5	—	0.173
Lifetime reproductive success[e]	10	4.40	3.54	0–11	—	11	2.27	1.90	0–5	—	0.213
No. of years between litters	6	1.83	0.76	1–3	—	0	—	—	—	—	—
Ratio of breeders to nonbreeders	49	18:31	—	—	—	29	11:18	—	—	—	>0.900
Ratio of female to male juveniles[f]	33	20:13	—	—	—	36	21:15	—	—	—	>0.750

[a] Coefficients of variation were calculated from annual means. Numbers in parentheses show the number of years. Tests were Mann–Whitney U comparisons of means except for sex and breeder to nonbreeder ratios (χ^2 test).

[b] Including 8 litters produced by untagged females.

[c] Including juveniles of both sexes produced by ear-tagged females known or presumed to be age 3 or older.

[d] Including known-age females (originally captured as juveniles or yearlings) and presumed 2-year-olds.

[e] Excluding 10 adult females which remained alive in 1995, and could reproduce again.

[f] Including 25 animals (15 females and 10 males) first captured as yearlings.

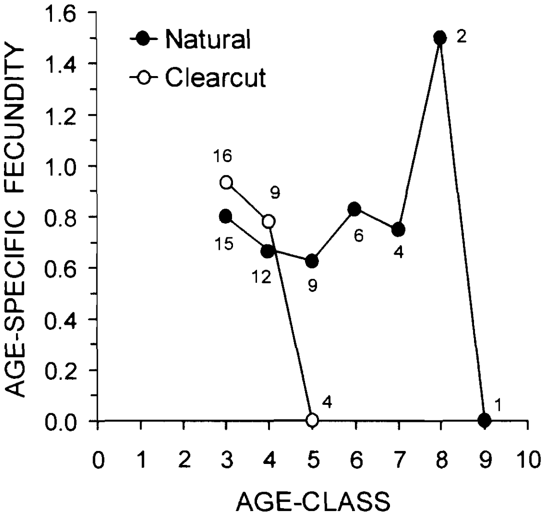
numbers of animals permitted some inferences about the mating system. Although numbers of adults were apparently biased towards females, in most years and for most colonies, numbers of males were sufficient for me to suspect single male – single female breeding groups. However, on three occasions, multiple litters were produced at colonies which contained only a single adult male, suggesting that polygamy does occur in this species. Single males apparently sired 2 litters in 1988 at Green Mountain, 2 litters in 1994 at Haley Lake, and 3 litters in 1994 at the newly colonized Sherk Lake site.

Persistence

At least 58 of 121 juveniles (48%) survived their first winter and were observed as yearlings. This is a minimum estimate, as most (n = 77) juveniles were never captured; however, the rate obtained from tagged juveniles was identical (at least 21 of 44 animals survived; 48%). Persistence of tagged yearlings was generally higher than that of juveniles. At least 24 of 37 yearlings (65%) survived their second winter and persisted at the site during their second active season, although observations characteristically showed expanding use of habitats and daily foraging movements. Adults showed similar persistence (persistence:disappearence ratio = 89:63; persistence rate = 59%)

Marmot persistence was sex-biased, suggesting differential mortality or dispersal or both (persistence:disappearence ratio = 42:49 for males and 92:50 for females; χ^2 = 7.88 with 1 df, $P < 0.005$). The difference was enhanced when juveniles and yearlings were removed from the data (24:33 for males and 65:30 for females; χ^2 = 10.72 with 1 df, $P < 0.001$), suggesting that sex-specific differences in persistence are concentrated in older age-classes, as might be the case if adult males are more likely to disperse. Males older than yearlings rarely persisted longer than one active season at a given site (mean residence time = 0.83 years, SD = 1.04 years, n = 26 individuals). Females older than yearlings were more likely to persist for several years, (mean residence time = 1.87 years, SD = 1.79 years, n = 28 individuals, Mann–Whitney U = 226.0, P = 0.015).

Fig. 3. Age-specific fecundity for female *Marmota vancouverensis* in natural and clearcut habitats. Data were calculated from counts of juveniles born to ear-tagged marmots, 1987–1995, assuming an equal sex ratio for juveniles. Sample sizes are shown. Discounting one high value caused by a single reproductive 8-year-old, fecundity rates were apparently stable with age. The major difference among habitat types was reduced persistence of adult females in clearcuts.



Tagged marmots in clearcuts showed lower persistence (48%) than those living in natural meadows (65%; persistence:disappearence ratios = 50:54 and 84:45, respectively; χ^2 = 6.84 with 1 df, $P < 0.01$). Juvenile persistence was lower in clearcuts (39%) than in natural habitats (55%), but the difference was not significant (persistence:disappearence ratios = 21:33 and 37:30, respectively; χ^2 = 3.19 with 1 df, $0.10 > P > 0.05$). Annual persistence and residence times were lower in clearcut habitats than in natural habitats (Table 2). However, observed differences were significant only in some sex and age classes, and results differed depending upon whether annual persistence or residence times were

Table 2. Annual persistence and minimum residence times of *Marmota vancouverensis* living in natural and clearcut habitats.

	Natural habitats				Clearcut habitats				
Sex–age class	*n*	$\bar{x}$	SD	CV (%)	*n*	$\bar{x}$	SD	CV (%)	P^a
Annual persistence rate									
Juveniles (both sexes)	7 (21)	0.62	0.42	68	3 (23)	0.35	0.11	31	0.012
Yearlings (both sexes)	7 (21)	0.62	0.34	55	5 (16)	0.69	0.32	46	0.873
Females >1 year old	8 (59)	0.73	0.14	19	7 (36)	0.61	0.26	43	0.001
Males >1 year old	8 (28)	0.54	0.38	70	8 (29)	0.31	0.27	87	0.070
All tagged animals	8 (129)	0.65	0.30	46	8 (104)	0.48	0.29	60	<0.001
Residence time (years)									
Juveniles (both sexes)	21	1.21	1.77		23	0.60	0.98		0.075
Yearlings (both sexes)	11	0.92	0.65		12	1.24	1.11		0.538
Females >1 year old	14	2.44	2.20		14	1.29	1.02		0.213
Males >1 year old	10	1.22	1.06		16	0.58	0.99		0.028
All tagged animals	56	1.46	1.70		65	0.86	1.05		0.018

Note: Data are from 121 individuals tagged between 1987 and 1994 and monitored through 1995. Annual persistence was calculated from annual means. Residence times are based on the date of initial capture and the last recorded observation. Two animals that died from "unnatural" causes were excluded (see the text).

[a] Tests were Mann–Whitney *U* comparisons of means. Raw annual persistence rates were weighted by the count of animals in each sex–age class which could have survived in that year (the total number of animal-years is shown in parentheses).

used. Small sample sizes precluded testing for age-specific differences among older age-classes, and cumulative adult persistence rates hid some interesting trends.

Females inhabiting natural meadows were confirmed alive in 4 age-classes that contained no females from clearcut habitats (i.e., at ages 6, 7, 8, and 9; Table 3). At least 4 female juveniles or yearlings captured at natural colonies became resident there and eventually reproduced. A single yearling eventually reproduced in a clearcut. The essential arithmetic is that the colony net reproductive rate in clearcut habitats was less than half that observed at natural sites (R_0 = 0.25 and 0.72, respectively).

Mortality and dispersal

It was generally impossible to ascertain causes of mortality. In the course of 607 field-days, 3 cases of predation by golden eagles (*Aquila chrysaetos*) were observed, all apparently involving juveniles or yearlings. Many unsuccessful attacks by golden or bald eagles (*Haliaeetus leucocephalus*) were also seen. A single research mortality occurred in 1992, after an adult male overheated while being moved prior to implantation of a radio transmitter. A yearling male was killed in 1994 after a trap was set and left open by unknown visitors to the site. Heard (1977) described a probable instance of predation by cougar (*Felis concolor*), and there are 2 corroborative instances based on observations of cougars "stalking" marmots (D. Janz, B.C. Environment, personal communication, and this study). Marmot fur has been found in wolf (*Canis lupus*) scat, and at least 3 marmots have been shot by vandals (Janz et al. 1994). Of 7 animals equipped with radio transmitters in 1994, 3 were confirmed to have been killed by terrestrial predators. I could not identify the predator species, although it was likely cougar or wolf.

Mortality during winter hibernation is often cited as a limiting factor for marmot populations (Barash 1989), but is difficult to document from field observations. On 8 occasions I observed the disappearance of entire family groups including juveniles. In all cases, animals were observed using particular burrows in late August. When I returned in the following spring, burrows showed no evidence of use by marmots whatsoever, or were occupied by new, untagged adults exclusively (7 cases in clearcuts and 1 case in a natural colony). Low juvenile survival was particularly evident in 1989–1990 (13 of 31 animals), 1990–1991 (0 of 8), and 1994–1995 (8 of 27). Relatively high juvenile survival was observed in 1991–1992 (10 of 16) and 1993–1994 (17 of 23). My data do not exclude the possibility that some disappearing juveniles dispersed, although I consider this to be unlikely.

At least 5 ear-tagged marmots dispersed from study colonies. Two animals were seen outside their original colony only briefly, and ear-tag numbers were not recorded. Their origin and eventual fate remain unknown. Two animals moved from the Pat Lake clearcut colony to the Mount Franklin clearcut colony in 1992 or earlier, and another made the identical movement in 1995. This represents a dispersal movement of 7.4 km. Two males dispersed as 2-year-olds and 1 female probably dispersed at that age. The female produced a litter in 1993 and persisted through 1994, but was absent in spring of 1995. One male was still resident on Mount Franklin in late summer of 1995 and remains the oldest male recorded during the study (presumed age 8).

Discussion

In most respects *M. vancouverensis* is a typical alpine-dwelling marmot, showing slow maturation, a relatively long life-span, and a complex degree of social organization. Although age-specific sample sizes were small, some demographic trends identified in other marmots (e.g., Armitage

Table 3. Life tables for *Marmota vancouverensis* in natural and clearcut habitats.

	Males					Females						
	f_x	d_x	q_x	p_x	L_x	f_x	d_x	q_x	p_x	L_x	$b_x{}^a$	l_xb_x
Natural habitats												
Juveniles[b]	8 (67)	3 (30)	0.38	1.00	1000	13 (67)	5 (30)	0.38	1.00	1000	0.00	0.00
Yearlings	8	4	0.50	0.63	625	13	4	0.31	0.62	615	0.00	0.00
2-year-olds	7	2	0.29	0.50	313	13	5	0.38	0.69	426	0.00	0.00
3-year-olds	11	4	0.36	0.71	223	14	2	0.14	0.62	262	0.80	0.21
4-year-olds	7	4	0.57	0.64	142	12	3	0.25	0.86	225	0.67	0.15
5-year-olds	3	3	1.00	0.43	61	8	1	0.13	0.75	169	0.56	0.09
6-year-olds	0	0	0.00	0.00	0	7	3	0.43	0.88	147	0.83	0.12
7-year-olds	0	0	0.00	0.00	0	3	1	0.33	0.57	84	0.75	0.06
8-year-olds	0	0	0.00	0.00	0	1	0	0.00	0.67	56	1.50	0.08
9-year-olds	0	0	0.00	0.00	0	1	1	1.00	1.00	56	0.00	0.00
Clearcut habitats												
Juveniles[b]	10 (54)	6 (33)	0.60	1.00	1000	13 (54)	9 (33)	0.69	1.00	1000	0.00	0.00
Yearlings	8	3	0.38	0.40	400	8	2	0.25	0.31	308	0.00	0.00
2-year-olds	15	13	0.87	0.63	250	11	3	0.27	0.75	231	0.00	0.00
3-year-olds	8	4	0.50	0.13	33	13	4	0.31	0.73	168	0.94	0.16
4-year-olds	4	2	0.50	0.50	17	10	5	0.50	0.69	116	0.78	0.09
5-year-olds	1	0	0.00	0.50	8	2	2	1.00	0.50	58	0.00	0.00
6-year-olds	1	1	1.00	1.00	8	0	0	0.00	0.00	0	0.00	0.00

Note: The colony net reproductive rate, R_0, was 0.72 in natural habitats and 0.25 in clearcut habitats. 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_xb_x, age-specific reproductive value; R_0, net reproductive rate.

[a] Fecundity was calculated using the observed (26:18) juvenile sex ratio. Assumption of a 1:1 ratio at birth reduced R_0 to 0.67 in natural habitats and 0.21 in clearcuts.

[b] Disappearance rates were calculated from tagged juveniles. The use of untagged juveniles and disappearing yearlings of both sexes (numbers in parentheses) reduced R_0 in natural habitats to 0.60 and increased R_0 in clearcuts to 0.27.

1991; Barash 1989) were visible in the data. In older age-classes, females showed greater persistence than males. Disappearance rates were generally higher for juveniles, suggesting the importance of predation and overwintering mortality. Once sexual maturity was reached, age-specific fecundity was relatively stable and females continued to produce juveniles as long as they remained alive. Yearlings generally remained at their natal colony until they reached age 2 or older, after which some dispersed.

The most intriguing feature of *M. vancouverensis* ecology concerns their ability to persist despite a small and fragmented natural habitat base (Bryant and Janz 1996) and their response to a human-modified landscape (this study). There is no obvious reason why Vancouver Island marmots cannot successfully inhabit clearcut habitats. At least in the short term, resource availability in newly logged sites is sufficient to sustain marmots and permit reproductive rates equivalent to those observed in natural habitats. Despite this, the relationship between marmots and forestry remains paradoxical. Clear-cut logging created thousands of hectares of potential habitat during the 1960s, 1970s, and 1980s, of which 11 sites and <50 ha were colonized during the 1980s and 1990s (Bryant and Janz 1996). During the same period some natural habitats were colonized, while others within apparent dispersal distance remained vacant. The total population increased during the 1980s but declined in the 1990s despite the availability of large amounts of potential new habitat.

My results indicate reduced persistence of marmots inhabiting clearcuts. No tagged juvenile, and only a single yearling, persisted long enough to reproduce in a clearcut habitat. No female inhabiting a clearcut site persisted long enough to produce more than a single litter, and only 4 females reached age 5. These data contrast with results from yellow-bellied (*Marmota flaviventris*), Olympic (*Marmota olympus*), hoary (*Marmota caligata*) and alpine (*Marmota marmota*) marmots, in which 20–75% of females did not disperse, but were eventually recruited into their natal colonies (Armitage 1991; Arnold 1990; Barash 1973, 1989). Indeed, this typical sciurid pattern (Michener 1983) was observed at natural study colonies, where 4 females became resident and reproduced at least once and matriarchal lineages could be traced over more than one generation.

Reduced persistence of marmots in clearcuts was not concentrated within particular age or sex classes. Rather, the data suggest a 10–25% reduction in persistence for males and females of all ages. Although methods precluded identification of the eventual fate of most disappearing animals, I suggest that this trend is more likely due to increased mortality than dispersal, particularly for the all-important adult females. There is no evidence that adult female hoary, Olympic, or alpine marmots disperse after reproducing at a given site (Barash 1973, 1989; Arnold 1990). In the long-term (32 years, 1860 tagged animals) study of yellow-bellied marmots in Colorado, a "few" females dispersed after reproducing (Van Vuren and Armitage 1994). My data corroborate this finding. Females that survived long enough to reproduce were essentially sedentary, and a few animals in good habitats produced a disproportionate number of offspring.

Confirmed predator kills, together with disappearances immediately after reproduction, tend to support the hypothesis of increased mortality. If these trends are real and not sampling artifacts, the essential conclusion must be that clearcut habitats do not allow female *M. vancouverensis* to attain the same lifetime reproductive performance that their counterparts in natural habitats exhibit, and colony net reproductive rates will remain low. Clearcut colonies could be maintained only by continued immigration of new females and would function as demographic ''sinks'' (Pulliam 1988).

I believe that creation of new clearcut habitats within the landscape inhibits normal dispersal movements, simply by providing dispersers with closer alternative sites in which to settle (Bryant 1990). If these new sites are ''sinks'' that consume more dispersers than they provide, the result would be a reduced probability of colonizing distant natural habitats. This hypothesis would explain recent population trends, with marmots doing comparatively well in the center of their geographic range but disappearing from some natural habitats on the periphery of their historic range. The alternative explanation (that marmots which colonize clearcuts alter their behavior and adopt a nomadic life-style) would in many respects be more interesting, as it would force reconsideration of current ideas about the evolution of marmot behavior and sociality (Armitage 1991; Arnold 1992). Resolution of these competing hypotheses awaits either confirmation of successful reproduction at multiple sites by individual females or identification of the mechanism(s) that cause increased mortality of animals inhabiting clearcut sites.

Acknowledgments

I thank D. Milne, J. Voller, and especially L. Dyck, who provided extremely capable assistance in the field. D.W. Janz, W.T. Munro, S. Herrero, D. Eastman, and the Vancouver Island Marmot Recovery Team provided unflagging support for research and management of *M. vancouverensis*. Project funding was provided in various years by the B.C. Habitat Conservation Fund, B.C. Ministry of Environment, Lands and Parks, World Wildlife Fund (Canada), Forest Alliance of B.C., and Cowichan Valley Field Naturalists Society. MacMillan Bloedel Limited and Timber West allowed unrestricted access to private property. The Ecological Reserves Unit of B.C. Parks permitted me to trap marmots in the Haley Lake Ecological Reserve. While at Calgary (1987–1989) I was partially supported by a Province of Alberta Graduate Scholarship, University of Calgary Thesis Research Grant, and a Canadian Wildlife Service Research Grant. While at Victoria (1992–present) I was partially supported by a King–Platt Memorial Award, Franc Joubin Graduate Bursary in Environmental Science, and University of Victoria (Biology) graduate award. D.W. Nagorsen and K.B. Armitage provided helpful comments on an earlier draft of the manuscript. G.W. Smith showed me my first marmot and freely shared his files and ideas. This paper is dedicated to the memory of B. McKinnon, who did so much to inspire interest in Vancouver Island marmots.

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