The University of Calgary

Genetic Variability and Minimum Viable Populations in the Vancouver Island Marmot
(Marmota vancouverensis)

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ABSTRACT

Genetic variability and minimum viable populations in the Vancouver Island Marmot (*Marmota vancouverensis*)

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From 1987 through 1989 I studied four colonies of Vancouver Island marmots (*Marmota vancouverensis*) to assess genetic variability and population viability in this species.

Six family groups at two natural colonies remained remarkably stable throughout the study. Seven family groups at two logging-slash colonies displayed greater turnover of individuals, and comparatively short-term use of burrows. Females produced average litters of 3.2 young (n=13) every second year, although one bred in consecutive years. Litters of four were more common in "slash" colonies. *M. vancouverensis* appears to be essentially monogamous, and in other respects exhibits a social structure similar to that of *M. olympus*. Reproductive and survivorship rates varied dramatically with year, family group, and colony. Marmots using established burrow systems in natural habitats did comparatively well; marmots using new burrow complexes did either very well or very poorly. Most mortality apparently occurred during winter hibernation.

Sampled *M. vancouverensis* (n=44) were neither genetically destitute nor highly inbred. Electrophoresis revealed levels of genetic variability comparable to *M. flaviventris* and *M. monax* (n=22 scorable loci, estimated %polymorphic loci P=0.18, average expected heterozygosity H=0.073). Small but significant genetic differences were found between two colonies less than 20 kilometres apart, illustrating the importance of founder effects and infrequent dispersal. Effective population size N_e of the known population is close to 50 (estimates of 34.6 to 64.4).

M. vancouverensis is well-adapted to a "meta-population" lifestyle, in which a patchwork of colonies experience periodic extinctions and recolonizations. Small colonies of *M. vancouverensis* are vulnerable to extinction through random demographic and environmental events. Most known colonies are small. The entire population inhabits a geographically confined area, is insufficient to maintain long-term evolutionary potential (N_e=500), and is very close to the size necessary to prevent short-term loss of genetic variability through inbreeding and drift (N_e=50). The full effects of human-caused landscape alteration on marmots are not yet understood: I hypothesize that logging-slash may provide attractive summer habitat but poor conditions for successful hibernation, and may therefore act as a "sink" for dispersing marmots from higher-elevation natural colonies.

I conclude that the known population of *M. vancouverensis* is not "viable" using existing criteria. Long-term survival of *M. vancouverensis* requires that additional meta-populations be found or established, and that adequate gene flow between individual colonies be maintained. A three-pronged recovery plan is proposed. Objective #1 is to maintain current numbers and distribution, and to answer basic questions of population biology. Objective #2 is to establish a second meta-population of approximately 200 animals. At this time the species should be downlisted to "threatened" status. Objective #3 is to establish a third meta-population (of approximately 200 animals), at which time the species should be downlisted to "vulnerable" status. Additional research (on hibernacula, dispersal, and survivorship) and inventory efforts are needed. Discovery of new meta-populations could dramatically reduce the need for recovery efforts, but is unlikely.

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INTRODUCTION

The Vancouver Island Marmot

The Vancouver Island marmot (*Marmota vancouverensis*: Swarth) is the rarest and least studied of six *Marmota* species which inhabit North America. This gregarious and lively rodent lives only in the mountainous regions of Vancouver Island, British Columbia, and is one of three mammals that are endemic to Canada (Forsyth 1985). *Marmota vancouverensis* is a "good species" on the basis of karotype (Rausch and Rausch 1971), cranial-morphometric characteristics (Hoffman *et al.* 1979), and reproductive isolation from hoary (*M. caligata*) and Olympic (*M. Olympus*) marmots on the North American mainland. Recent surveys suggest a total population of 200 to 300 individuals; most known colonies are confined to a small area west of Nanaimo on Vancouver Island (Figure 1).

M. vancouverensis was listed as "endangered" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 1979, and the Province of British Columbia in 1980 (Munro *et al.* 1985). Reasons for designation included the late-1970s population estimate of 50 to 100 animals, lack of data concerning abundance and distribution, and unknown influence of human activities on marmot colonies. The taxonomy, history, present and historic distribution of *M. vancouverensis* is discussed in Appendix I.

Viable population theory

How many marmots are "enough" to ensure their long-term survival? In theory, for any population there is a threshold above which the risk of extinction falls below an established level of probability (i.e., becomes an "acceptable" risk: Shaffer 1981). The problem faced by wildlife managers is to identify <u>what</u> population size and distribution

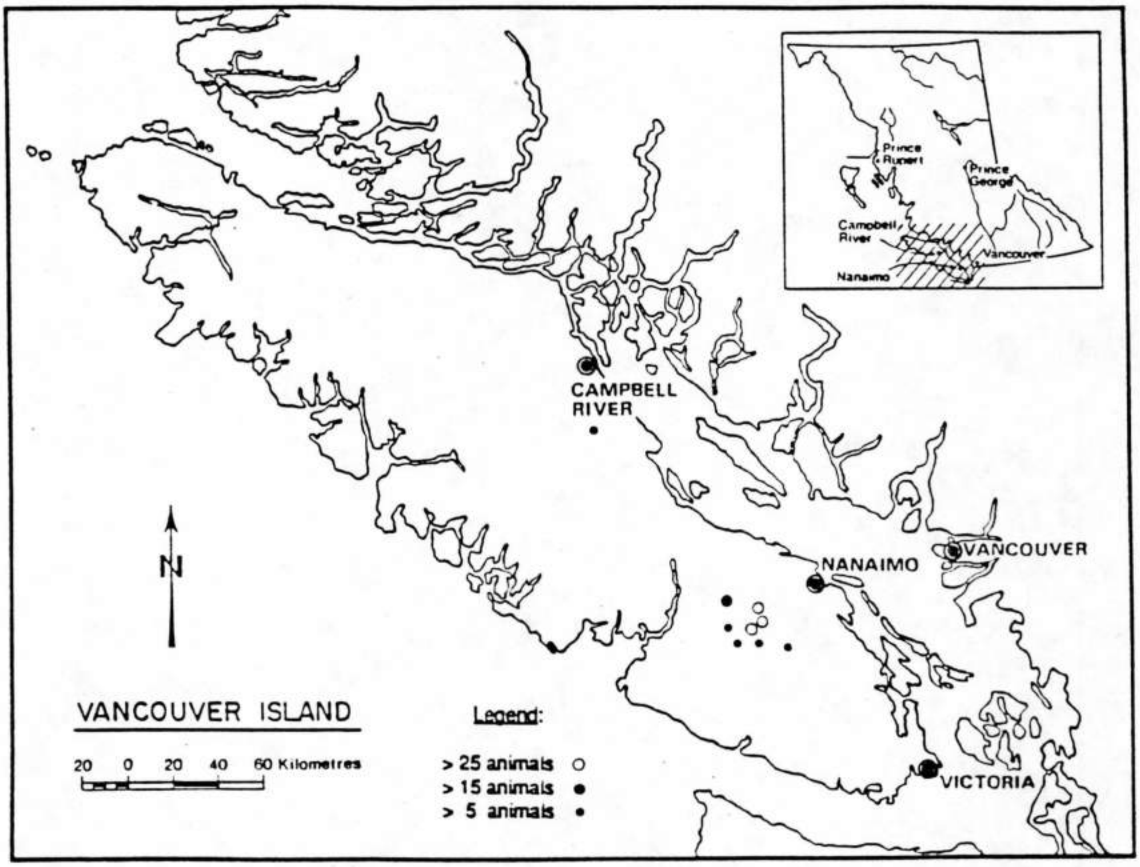

Figure 1: Size and distribution of known marmot colonies. Data are from Munro *et al.* (1985) and reflect 1984 conditions, the year of most comprehensive inventory effort.

provides a reasonable probability of survival despite deterministic or stochastic processes over time. The "minimum viable population" (MVP) concept was developed to help wildlife managers address this problem (reviews by Gilpin and Soulé 1986, Soulé 1987).

Early attempts to calculate MVP size were based on single criteria, i.e., the need to minimize inbreeding (Lacava and Hughes 1984), maintain long-term evolutionary potential (Franklin 1980) or survive random environmental or demographic events over time (Shaffer 1983). In each case, the intent was to estimate threshold population sizes, above which the chance of extinction through any one of these processes became an "acceptable" risk. However, as Soulé (1987) pointed out, there is no "magic number" or criteria that is universally valid. Extinction processes are often synergistic; several processes may act together to reduce the viability of a population. For example, persecution of prairie dogs (*Cynomys* spp.) led to reduced populations of black-footed ferrets (*Mustela nigripes*); remnant ferret colonies were more vulnerable to stochastic events such as the 1986 epizootic of canine distemper (Clark 1987). Similarly, population bottlenecks, and consequent loss of genetic variability through inbreeding, are thought to have reduced reproductive success and viability of cheetahs (*Acinonyx jubatus*) and lions (*Panthera leo*: O'Brien *et al.* 1985 and Wildt *et al.* 1987, respectively).

Gilpin (1989) suggested that MVP estimates based on single genetic, environmental or demographic criteria will be inadequate. The original concept of a viable population has evolved in recognition of this idea. Soulé (1987), amongst others, stressed that various extinction threats must be considered in a systems approach which emphasizes the interaction of factors. A useful synthesis of these ideas has been made available to wildlife managers in the form of "population vulnerability analysis" or PVA (Gilpin 1989, 1987). In Gilpin's model, the species in question is described by several population parameters. External environmental shocks may change these parameters and lead directly to extinction. In addition, changes in these parameters can set up feedback loops or "extinction vortices" (Gilpin and Soulé 1986) which may further reduce population viability (Figure 2).

The primary value of PVA is that each component of the model is amenable to empirical analysis. Techniques such as electrophoresis can be used to estimate genetic variability, and permit informed decisions concerning the danger of inbreeding depression or long-term loss of genetic variability (Wayne *et al.* 1986). Similarly, standard ecological techniques can be used to estimate other population parameters, and computer simulations can be used with these data to predict the effects of random environmental or demographic events on population persistance (Burgman *et al.* 1988). In essence, the idea is not to arrive at a single "magical" estimate of what constitutes a minimum viable population, but to give managers a better indication of which extinction threats are of most concern, and to provide target population objectives which, if achieved, will minimize such threats.

The PVA model, like all such models, is a tool for thinkers and not a crutch for the lazy. It is imperfect, particularly when applied to "real-world" examples where population parameters are estimated instead of known. It is an exercise in risk-assessment, and like all risk-assessments it is impossible to know whether the proverbial 100-year-flood will come tomorrow or much later. Despite this, PVA provides a coherent model for the design of management plans for rare or threatened species. Application of PVA to *M. vancouverensis* is the subject of this thesis.

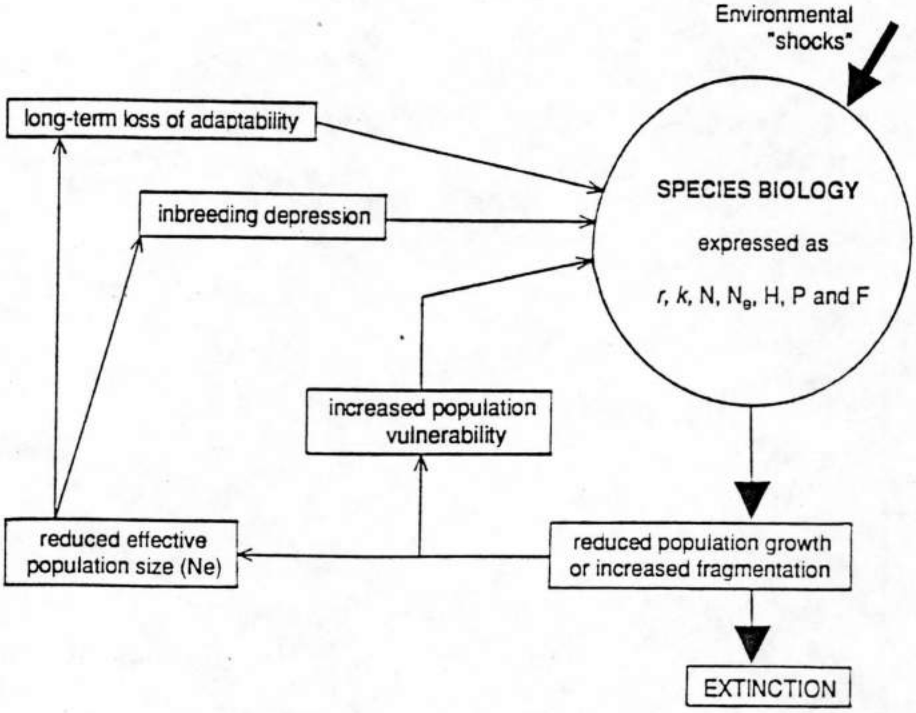

Figure 2: Population viability analysis. The species is described by several population parameters (intrinsic growth rate ***r***, carrying capacity *k*, total population size N_t, effective population size N_e average heterozygosity *H*, %polymorphism *P*, and fixation coefficients *F*). Environmental "shocks" may fragment or reduce growth of populations. This may lead directly to extinction or aggravate stochastic or genetic processes which further reduce population viability. The PVA model is an attempt to identify all factors which contribute to species extinction. Modified from Gilpin (1987).

Study objectives

The intent of this study was to conduct a population viability analysis for *Marmota vancouverensis*, and to design a recovery strategy such that the chances of future extinction are minimized. Specific objectives were to:

1) Determine levels of genetic variability in *M. vancouverensis*.
2) Evaluate the degree of "relatedness" between subpopulations and determine levels of inbreeding.
3) Determine reproductive and survivorship rates, and estimate population sizes necessary to survive random genetic, demographic and environmental events.
4) Design a recovery plan to attain these population objectives, and so permit the removal of *M. vancouverensis* from endangered status.

METHODS

Study areas

Locations of marmot colonies were obtained from the Nanaimo regional office of the B.C. Ministry of Environment (BCMOE). A subset of colonies was selected for analysis; selection was based on dispersion of colonies and consequent utility for testing genetic and ecological hypotheses (Figure 3). Other factors included ease of access and numbers of marmots. In 1987, 1988 and 1989, trapping was carried out at the Haley Lake Ecological Reserve (hereafter referred to as Haley Lake), the logging-slash colony below Haley Lake (hereafter referred to as Haley "slash"), and the colony located near the summit of Green Mountain. The project was expanded in 1988 and 1989 to include the Pat Lake "slash" colony near Mount Whymper.

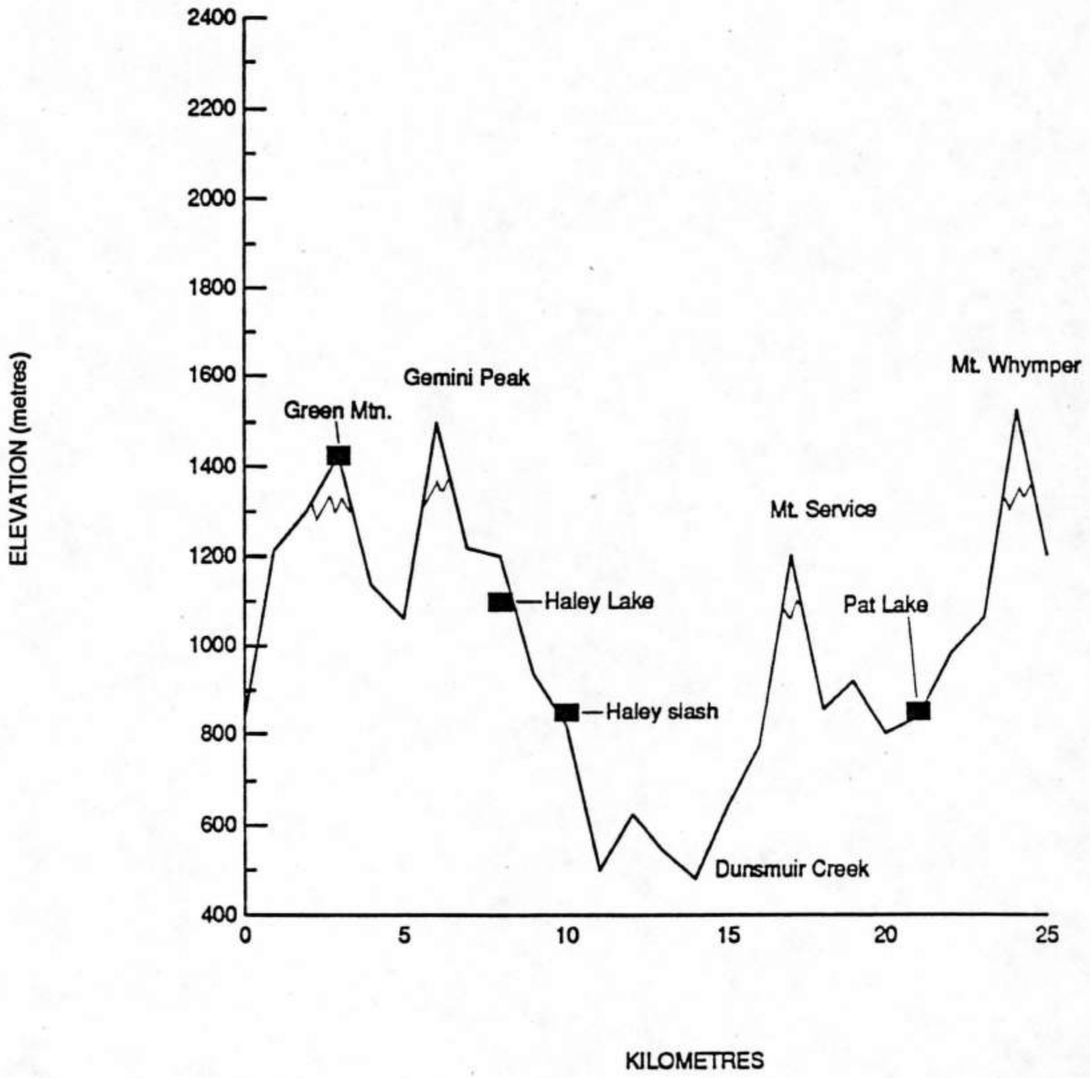

Figure 3: Spatial and topographic relationships between study colonies. Shown is the elevation gradient along a "bent-line" transect running south-southwest from Green Mountain to Haley Lake, and from there east-southeast to Mount Whymper. The total distance covered is about 25 kilometres.

No marmots were found at Mount Washington despite repeated visits in all years of the study. Additional areas visited included "P" Mountain, Mt. Strata, and Mt. Brooks in 1987, "P" Mountain, Sutton Pass, Mt. Whymper, and Douglas Peak in 1988, and Mount Todd, Jordan Meadows, Mount Arrowsmith, Marble Meadows, Flower Ridge and Victoria Peak (by helicopter) in 1989. No signs of recent marmot activity were found at these sites, with the exception of Mount Washington, where recent burrows were found, and "P" Mountain, where small numbers of marmots were seen. All known active marmot colonies are located in sub-alpine environments between 800 and 1500 metres elevation in the Georgia Depression Ecoregion of Vancouver Island (Demarchi 1987). Tree species characteristic of this zone include mountain hemlock *Tsuga mertensiana*, yellow cedar *Chamaecyparis nootkatensis*, subalpine fir *Abies lasiocarpa* and slide alder *Alnus sitchensis* (Brooke *et al.* 1970). Vegetation and terrain vary considerably between colonies.

The Haley Lake and Green Mountain sites are steep (30° to 45°) south or southwest-facing meadows kept free of trees by snow-creep and avalanches (1100 and 1420 metres elevation; Figures 4 and 5 respectively). A variety of forbs and grasses are found at these sites; common species include *Phlox diffusa*, *Castilleja* spp., *Erythronium grandiflorum*, *Saxifraga ferruginea* and *S. occidentalis*, *Anaphalis margaritacea*, *Aster foliaceus* and *Lupinus latifolius*. *Pteridium* ferns and dwarf *Vaccinium* spp. are occasionally dominant. Both sites have numerous boulders, rock outcrops and scattered krummholz. The lower portions of the Haley Lake Bowl site are dominated by thickets of *Alnus sitchensis*. The Green Mountain colony is adjacent to meadows created by ski-run development. The ski-hill was closed in the late 1970s, but abandoned buildings and debris remain. Haley Lake and Green Mountain colonies are about 8 kilometres apart, but connected by a ridge system which runs north-south. Marmot colonies occur along this ridge system at Bell Creek and Gemini Peak.

Figure 4: View of the Haley Lake study area. This site was designated as an ecological reserve in 1987. The immediate foreground shows the area used by the "Mom #2" family group, together with early-spring vegetation including *Phlox diffusa* (photo taken in early June, 1988).

Figure 5: View of the Green Mountain study area. This photograph portrays natural conditions; an abandoned ski-hill development is not visible in this view. The light-coloured rocks in the center of the picture conceal burrows used by the "Betsy" family group in 1987 and 1988 (photo taken in late July, 1987).

The Haley "slash" colony is located west of Haley Lake, approximately one kilometre away and 250 metres lower than the main colony, in an area that was clearcut between 1974 and 1978. Marmots were first observed here in 1985 (one) and 1986 (young observed: Fry *et al.* 1986). The topography is steep, with numerous talus slopes, boulders and eroded areas that are essentially bare of vegetation (Figure 6). Aspect of the colony is west-southwest, and the site is surrounded by steep hills to the east, north and west. Two small creeks flow through the site, and there are patches of *A. sitchensis* and regenerating conifers. An abandoned, badly eroded logging road (Vaughan road) runs through the site, and most marmot burrows have been constructed in the soft soil beneath the road cut. Logs and stumps provide sunning areas, and logging debris is abundant. Vegetation cover over much of the site consists of regenerating conifers, *Vaccinium* spp., *Berberis* and *Alnus sitchensis*. Many wildflower species found at Haley Lake do not occur in the "slash" area, although *Lupinus latifolius* and *Anaphalis margaritacea* are common.

The Pat Lake site is a steep north-facing bowl surrounding a shallow lake 16 kilometres southeast of Haley Lake Bowl and two kilometres northeast of Mount Whymper, where marmots are also known to occur (Figure 7). Elevation at Pat Lake is 820 metres. The site was clearcut between 1978 and 1979, and logging activites continue adjacent to the site. Marmots were first discovered here in 1985 (Smith 1985). As with the Haley "slash" colony, vegetation at this site is a complex of regenerating conifers, *Alnus* thickets, shrubs, grasses and *Lupinus* and *Anaphalis*-dominated communities. Talus slopes, eroded bare soil, boulders and rock outcrops are common. An abandoned logging road ("K3") surrounds the lake and provides easy access and easy burrowing for marmots. The Pat Lake/Mount Whymper complex is topographically isolated from the

Figure 6: View of the Haley "slash" study area, looking down from the "Tophat" burrow complex. The area most used by marmots is adjacent to the abandoned logging road (Vaughan Road) in the left-center of the photograph. The area was clearcut between 1974 and 1978; marmots were first observed here in 1985 (photo taken August, 1987).

Figure 7: View of the Pat Lake study site, looking south from the "Apex" burrow complex. Most marmot activity is concentrated along the abandoned logging road ("K3") in the immediate foreground. The colony was discovered in 1985, only four years after logging ceased (photo taken August, 1988).

Green Mountain/Haley Lake Bowl ridge system; mature lowland forests between the two areas have been almost completely removed by clearcutting.

Search and observation

Steep terrain and abbreviated daily activity rythyms make finding marmots difficult. Search techniques involved scanning slopes and cliffs with binoculars or spotting scope, listening for marmot whistles and searching for burrows, scats or mud-stains on likely lookout rocks. Although several weeks were devoted to the purpose, I did not succeed in finding any colonies not already known to BCMOE. One new "slash" colony near Mount Service was reported to me by MacMillan Bloedel personnel in 1989.

Marmot colonies were observed with binoculars or spotting scope. Typically, I used pre-selected vantage points and waited for marmots to emerge from their burrows. Normally I was "on-site" by 6:30 a.m. for morning sessions and 4:00 p.m. for evening sessions; this schedule was designed to coincide with the activity patterns identified by Heard (1977). Depending upon light conditions, ear-tags could sometimes be read at distances of more than 25 metres with a 60x ocular on a spotting scope. Some individuals would allow my approach close enough to read tags with binoculars; others were very shy and had to be trapped to ensure positive identification. At all sites I recorded numbers of marmots seen; on several occasions I conducted a "focal-animal" experiment and observed one individual throughout an entire day.

The essential unit of study for this project was family group rather than "colony". A family group was defined as one in which marmots were known to be related (nursing young) or consistently observed using the same set of burrows throughout at least one field season. Names given to family groups were based on the adult female present. All marmots observed were classified into one of several categories, as follows:

- Established families: those which consistently used the same burrow complexes from year to year. These were characterized by the presence of several sub-adults and yearlings, and a large number of nearby escape burrows and runways.

- New families: those formed of "new" or previously-identified marmots which constructed new burrows and reproduced successfully. These families were comprised exclusively of adults and young-of-the-year.

- Potential families: at least two adult marmots which consistently used one burrow complex but were not observed to reproduce.

- Transients: marmots of unknown origin, which resided only temporarily on site, or which were not observed with other marmots.

Trapping

Trap methods were tested on hoary marmots (*M. caligata*) at Whistler Mountain in early July of 1987. Havahart (Woodstream Corporation, Littitz, Pennsylvania) raccoon-sized Model 1079 single-door traps were used exclusively throughout the project; a double-door model was tested unsuccessfully at Pat Lake in 1988. Trapping of *Marmota vancouverensis* began on July 20th in 1987, on May 24th in 1988, and on June 8th in 1989. A variety of baits (including peanut butter, apples, carrots, honey, jam, bananas, lettuce, beansprouts, rosehips, fresh-cut grass and wildflowers) and trap placements were tested. In 1988 I used fishing net to fashion a marmot "corral" at Haley Lake but this was unsuccessful. Soft-catch leg-hold traps were considered but not used due to risk of possible injury to the animal.

One successful method involved placing the Havahart trap-door directly against a burrow entrance, and then securing burlap bags around the trap in such a way as to leave the animal no other exit. This only worked, obviously, if the burrow was occupied at the time. Often the animal would avoid capture by digging under the burlap or by simply staying in the burrow. Terrain features at several burrows precluded the use of this method, particularly in "slash" colonies where logging debris was abundant. The method is also labour-intensive; considerable time is required to confirm which burrows are used overnight, and traps must be placed and set before sunrise each morning. One advantage is that particular individuals can be targeted, and re-traps thus avoided. In 1987 and 1988, marmots became somewhat easier to trap after August. The traditional method of baiting with peanut butter and placing the traps on known runways was used after this date. Peanut butter proved to be an effective lure during the latter part of the season, and several animals became "trap-happy" and were re-captured on one or more occasions.

Marking, processing and blood sampling

Once trapped, marmots were transferred to a handling bag. This was a cone-shaped heavy canvas sock, open at both ends and equipped with a two-way zipper running lengthwise along its side. The large opening was placed around the Havahart trap and the door was opened, whereupon the marmot would usually run into the bag and be immobilized as the bag narrowed. The zipper could then be unfastened enough to grasp a hind-leg and administer an immobilizing injection. Occasionally animals would back into the handling bag, in which case the bag could be squeezed down and unzippered from the opposite end.

An intramuscular injection of 10% Ketamine/Ketaset (Rogets Pharmaceuticals, Vancouver) was used to immobilize marmots. Dosage was normally 0.5 ml/kg, which is somewhat less than that used on housecats by veterinarians (K. Langelier, Island Veterinary Hospital, Nanaimo, pers. com.). On young-of-the-year I used a slightly smaller dosage, and on large, highly perturbed males I used slightly more (0.35 ml/kg to

0.6 ml/kg respectively). The drug normally took effect within 5 minutes of injection and the animal could then be removed from the handling sock. A Bacitracin-Neomycin-Polymyxin opthalmic ointment was used to protect the animal's eyes during handling (Vatropelycin; Altana Inc., New York).

The following morphological data were recorded at time of capture: sex, weight, total length including 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. Sex determination was made by everting the genitalia, palpating for testes and/or by measuring the distance from anus to genital opening (Heard 1977). Determining sex of young-of-the-year proved to be difficult and I do not place much reliance on these data. Pelage characteristics, abundance of parasites, fat condition and any external characteristics, such as scars, which could aid in re-identification were noted. Marmots were categorized in one of five age classes at time of capture: young-of-the-year, yearling, sub-adult and adult and very old adult. Criteria used were:

- Young-of-the-year (0): small size, uniform dark colour with no moult pattern, observed nursing or initial emergence from burrow, weight less than 3.0 kg in late August.

- Yearling (1): recapture or very small size with moult pattern, weight less than 3.0 kg in late August, member of existing family unit.

- Sub-adult (2): moult pattern visible, weight between 3.0 - 5.0 kg, no evidence of reproduction, member of existing family unit in which adults are present.

- Adult (3+): weight greater than 5.0 kg early in season (non-lactating), reproductively active and/or well-defined family structure.

- Old Adult (4+): recapture or adult observed one year prior to initial capture. Extremely large size, grizzled appearance, many scars in early season. This classification was applied sparingly.

Marmots were equipped with ear-tags in both ears. I used either aluminum "rabbit-ear" tags or monel self-piercing tags (style #41 and #1005-3 respectively, both numbered sequentially; National Band and Tag Company, Newport, Kentucky). In 1987, I modified some rabbit-ear tags by making a coloured plastic washer from Dymo marking tape; the idea was to colour-code animals from different colonies. Curiously, the coloured tags were chewed off (presumably by other marmots) by spring of 1988, while the Green Mountain animals (with bare metal tags) were still intact. After 1987, all animals were equipped with monel self-piercing tags. Each tag, prior to installation, was coated with permanent black ink and sanded smooth such that embossed numerals were highlighted against the bare metal; this increased the distance at which the tag number could be read. Ear-tag loss was a problem throughout the study. After 1987, marmots were tattooed on their left ears using a "pliers" type tattoo kit with green ink (Ketchum Manufacturing Sales Ltd., Ottawa). Tattoos were given as a two character alphanumeric set such as "A1" or "B6".

A five to ten cubic centimetre blood sample was taken from the femoral vein using Monoject syringes with 20 gauge needles (Sherwood Medical, St. Louis, Mo.). Needle and syringe were coated with EDTA anticoagulant by "drawing and shooting" a tiny quantity; this prevents haemolysis of the blood sample. An elastic tourniquet made veins more visible. Hindlegs were sterilized with 80% isopropyl alcohol; pressure applied with a sterile cotton ball stopped bleeding. Blood was transferred from the syringe to a "purple-top" EDTA-treated Vacutainer (Becton-Dickonson Ltd., Vancouver). While in the field, samples were stored either in a portable cooler chilled with freezer packs or, more usually, in the nearest snowpack.

After processing, animals were returned to the Havahart trap to recover from the immobilizing agent. Marmots behave quite normally within 30 minutes of injection, but this is deceptive and prematurely-released animals could injure themselves as their motor coordination is still impaired. My policy was not to release any animal until at least an hour had passed. Particularly difficult animals (i.e., large adult males) were protected from injuring themselves by padding the interior of the Havahart trap with burlap bags or extra clothing.

Upon return to base camp, blood samples were centrifuged to separate plasma from red blood cells (RBCs). RBCs were washed with surgical 0.4 Molar saline solution and centrifuged three additional times. Samples were then frozen and transported to the Pacific Biological Station in Nanaimo, where they were stored at -80 C° until electrophoresis was performed. Glass vacutainers stored at this temperature sometimes cracked; after 1987 only plastic "cryogenic" sample tubes were used. Some 1987 and 1989 samples were transported whole and centrifuged at the Pacific Biological Station in Nanaimo. The maximum time that whole blood samples went unfrozen was 34 hours; in the majority of cases blood was spun and frozen within eight hours.

Electrophoresis

Experiments with 12 samples were carried out at the University of Calgary during the winter of 1987-1988; the purpose was to identify active systems and create a list of recipes for later analyses. Final electrophoretic analyses were performed under my supervision by Aqua-Life Biological Consultants (3217 Hammond Bay Road, Nanaimo). Choice of enzyme systems surveyed was based upon two criteria:

- enzymes found to be polymorphic in yellow-bellied marmots *M. flaviventris* by Schwartz and Armitage (1980) or *M. monax* by Wright *et al.* (1987).
- enzymes commonly polymorphic in a wide variety of mammalian species (Wayne *et al.* 1986).

Gel, buffer and stain recipes were taken from the literature; Harris and Hopkinson (1976), Selander *et al.* (1971) and Shaw and Prasad (1970) were particularly useful. R. Owen (U of Calgary, pers. com.) provided a recipe for Leucine aminopeptidase (LAP). A list of electrophoretic recipes is included as Appendix II.

Statistics

Calculation of average genetic heterozygosity H and fixation coefficients F_{it}, F_{is} and F_{st} were made using the formulae of Wright (1965). Significance of F_{st} values was tested with the procedure of Workman and Niswander (1970). Effective population size N_e was estimated using the formulae of Reed et al. (1986). Reproductive, survivorship and mark-recapture statistics were calculated as per standard practice (eg., Begon and Mortimer 1986). Descriptive statistics, regression analyses, Student T tests, Mann-Whitney U tests, chi-squared X^2 tests and N_e calculations were made using QUATTRO (Borland International 1987) or EXPLORE (Doane 1988) with an IBM-compatible personal computer. Significance was evaluated at the 95% confidence level unless otherwise noted.

RESULTS

Trapping success

A total of 48 individual marmots were captured during the study, including eight young-of-the-year, four yearlings and 36 adults or sub-adults. Nine animals were captured more than once, but recaptured animals were normally released without being tranquilized or measured in order to minimize handling stress. The reader is reminded that 48 marmots represent approximately 20% of the known population of this species (Munro *et al.* 1985).

Trapping success varied among study colonies (Figure 8). Ratio of captures/trap-day was 0.16 (56 trap-days) at Green Mountain, 0.15 (160 trap-days) at Haley Lake, 0.01 (130 trap-days) at Haley "slash", and 0.35 (78 trap-days) at Pat Lake. A trap-day is one trap used for one day; my definition differs from the norm in that traps were sometimes moved among several burrows during a single trapping day. Captures include animals caught more than once. Differences in captures/trap-day were significant (X^2=47.0, 3 df, $p<0.01$), although arguably my trap methods were not strictly "random".

Trapping success also varied with time of year; most captures were in June or August. This is partially the result of trapping effort; I was absent from the field in July of 1989. Figures 9 and 10 illustrate trapping success for male and female marmots, and "natural" and logging-slash colonies, plotted against number of days after emergence from hibernation (arbitrarily defined as May 1st). There was no obvious bias towards male or female marmots, or "natural" versus "slash" colonies, as a function of date-of-capture. I conclude that tests of differences between sexes or colonies are not biased by differences in capture date.

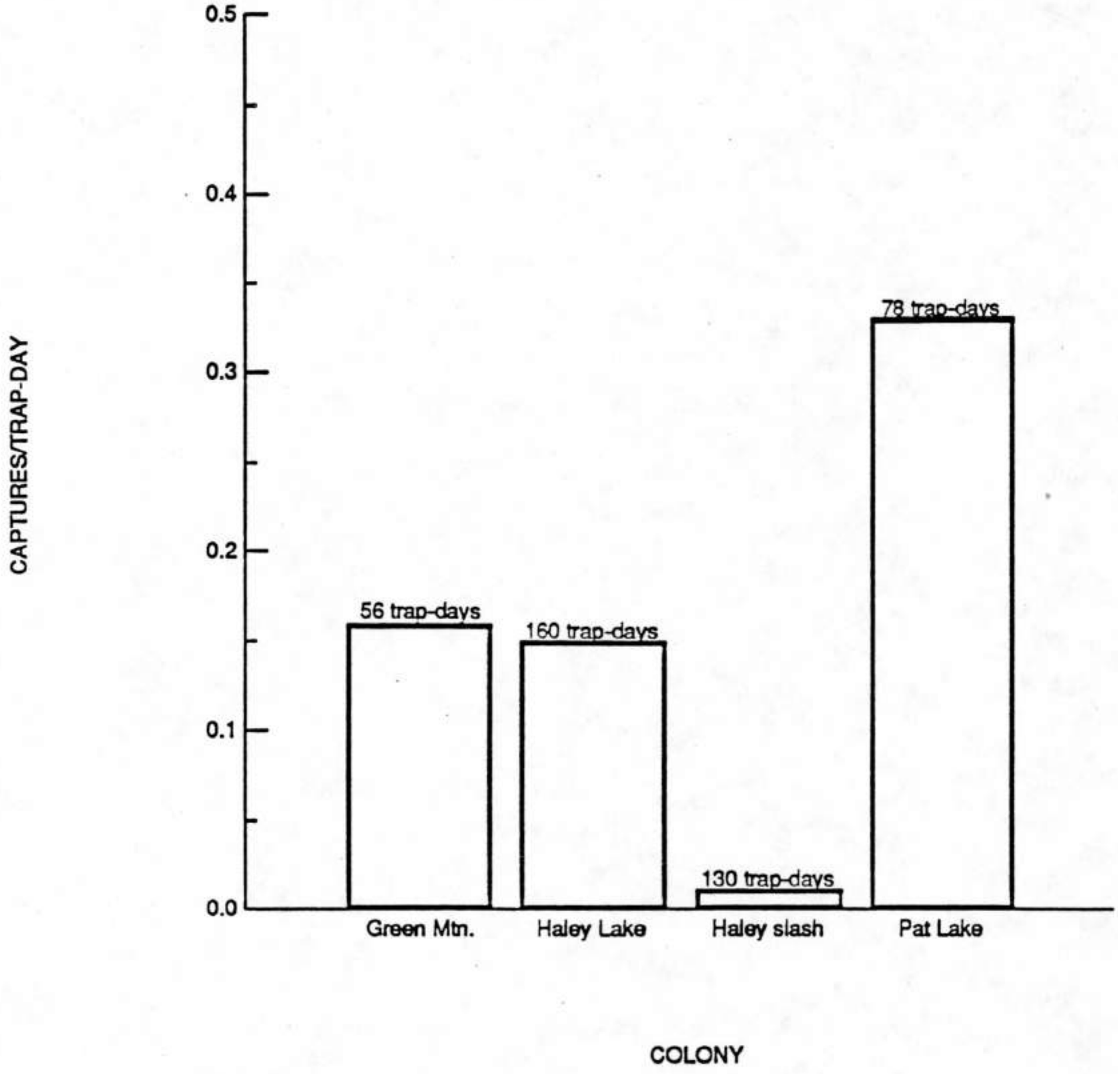

Figure 8: Trapping success #1: captures per trap-day at four study colonies. A trap-day is one trap used for one day; captures include recaptured animals. Differences in trapping success among colonies were highly significant.

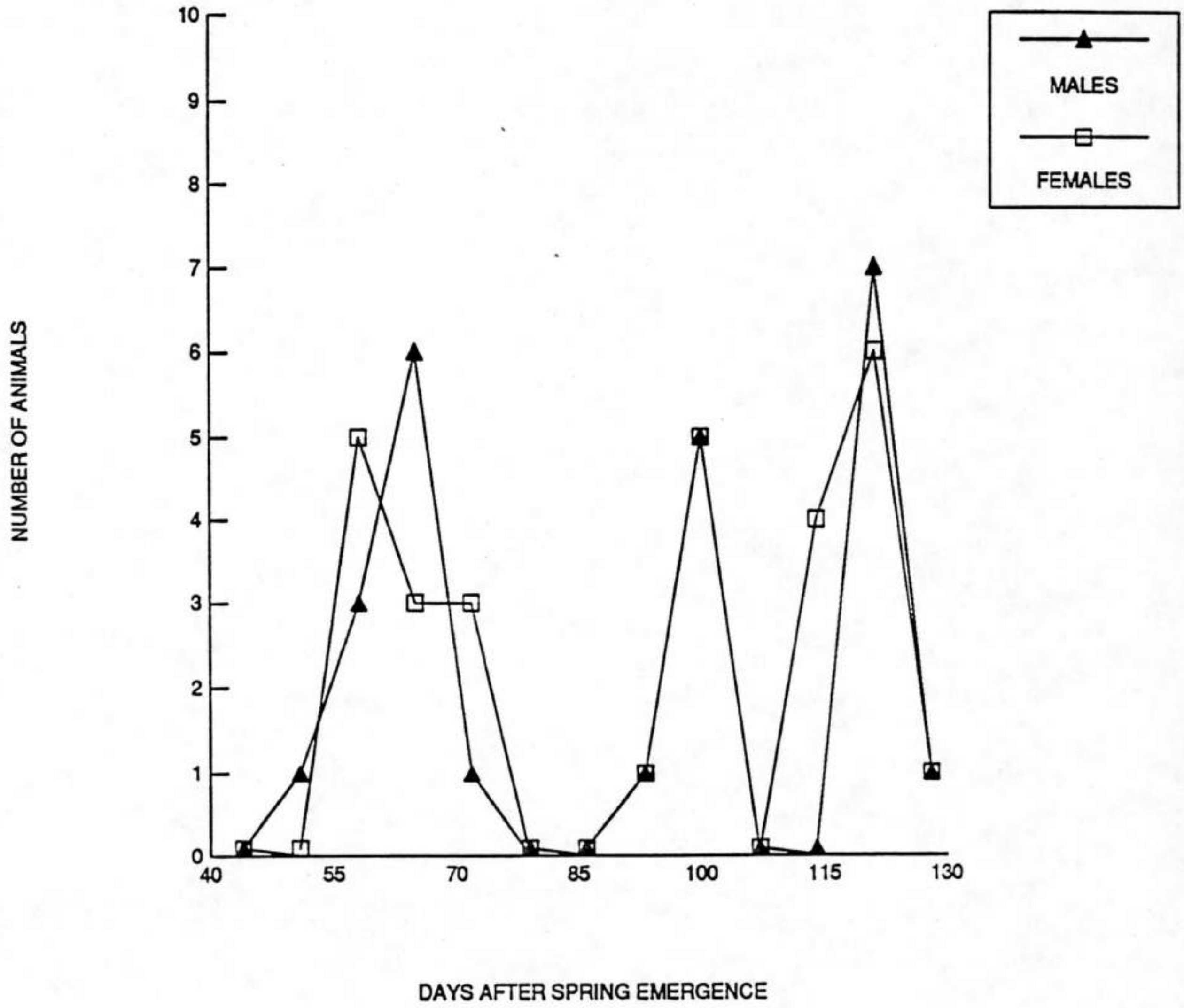

Figure 9: Trapping success #2: males versus females as a function of date. The x-axis refers to number of days after spring emergence (arbitrarily defined as May 1st). There was no correlation between sex and date-of-capture.

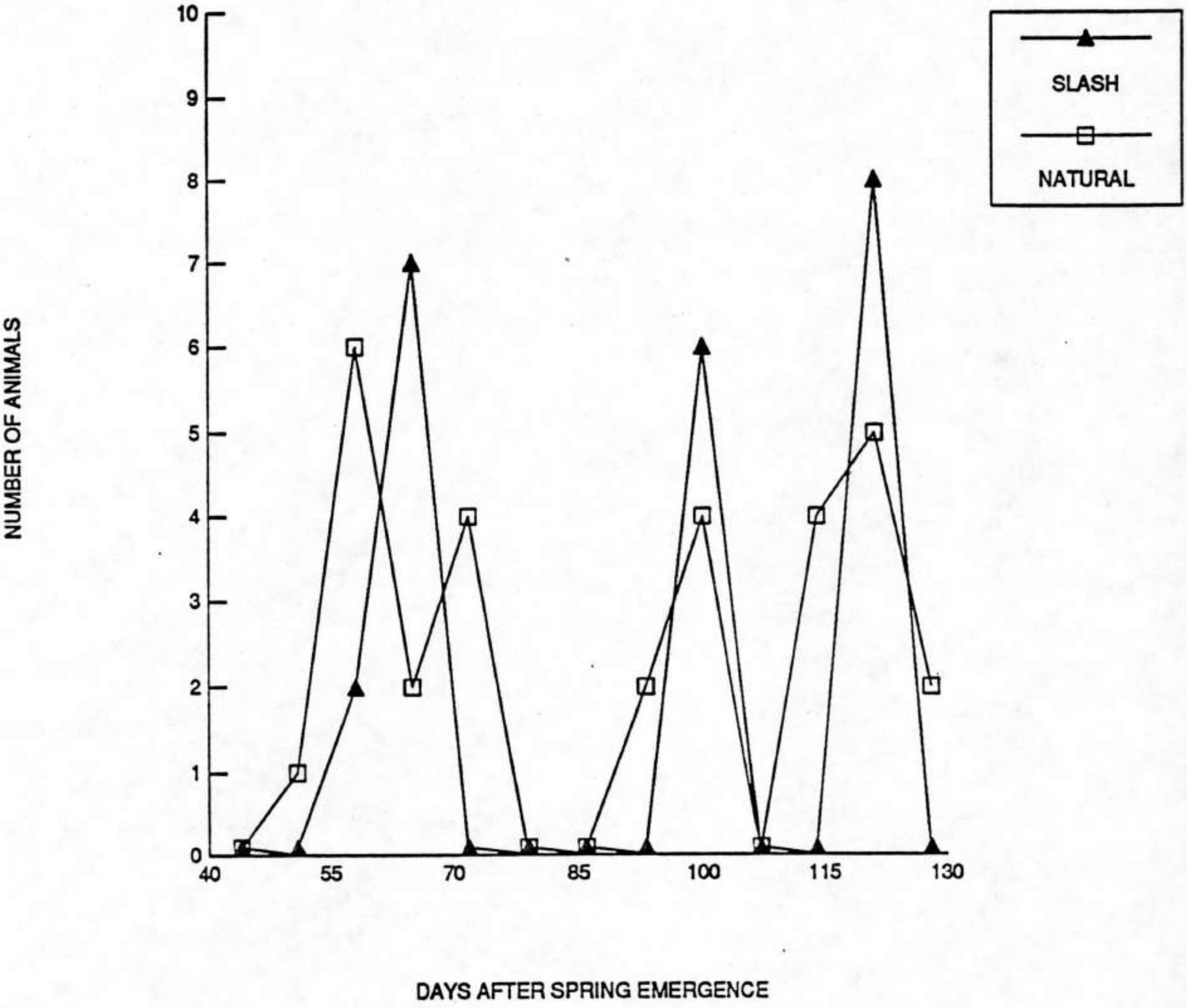

Figure 10: Trapping success #3: "natural" versus "slash" marmots as a function of date. The x-axis is as in Figure 9. Haley Lake samples are pooled with those from Green Mountain, and Haley slash with those from Pat Lake. I attempted to spread by trap efforts evenly between "natural" and "slash" colonies in order to facilitate inter-group comparison.

Morphology, sex ratio and age structure

Physical measurements were compared to determine whether *M. vancouverensis* is sexually dimorphic. Results of one-tailed Mann-Whitney U tests indicate that measured variables are not a reliable indication of sex (Table 1).

Among two-year-old marmots, forearm length was significantly longer in females ($U_{6,8}$=43, $p<0.01$). In older animals this relationship was reversed. Males had longer forearms when data for older animals were pooled ($U_{12,15}$=151, $p<0.01$), when data for three-year-olds alone were used ($U_{10,13}$=108, $p<0.01$), and when three-year-olds were analysed without lactating females ($U_{4,13}$=46, $p<0.05$). Three other variables (hindfoot length, total length and weight) were significantly different (Table 2) when age three and older animals were pooled; however, these differences disappeared when four-year-old marmots were removed from the data. Samples of young-of-the-year, yearlings and four-year-old marmots were too small to be tested. While forearm length might be used to sex bones (eg., museum specimens), I conclude that more direct methods (i.e., palpation for testes) are preferable if one has the animal in hand.

Linear regression was used to explore relationships between physical measurements and age. Because marmots grow rapidly during summer months (Heard 1977), regression of variables against age measured in years would be misleading. I therefore measured marmot age as presumed age-class+number-of-days after emergence from hibernation. Thus, for purposes of regression analysis, a presumed two-year-old marmot captured on June 28th is 2+(59 days/365)=2.16 years old, while one captured on August 26th is 2+(118/365)=2.32 years old. All variables showed incremental increase when plotted against age. Analysis of residuals indicate that linear regression is an appropriate analytical tool. Scattergrams of weight and forearm length are given in Figures 11 and 12; all other variables showed similar trends when plotted. However, regression does not

Table 1: Differences in physical measurements of marmots. Data are means ± s.d.

Measurement	males	females	U.	$U_{crit.}$	P-value
Infants					
Forearm length	12.5 ± 0.7	12.3 ± 0.6	6	16	>0.1
Hindfoot length	9.0 ± 0.1	8.6 ± 0.6	6	"	>0.1
Neck circumference	18.8 ± 3.3	18.0 ± 1.9	8	"	>0.1
Chest circumference	26.4 ± 2.8	24.2 ± 2.9	9	"	>0.1
Total length	54.7 ± 2.5	52.9 ± 2.5	5	"	>0.1
Tail length	15.4 ± 0.7	14.9 ± 1.3	9	"	>0.1
Weight	2.5 ± 0.5	2.6 ± 0.4	9	"	>0.1
n =	4	4			
Yearlings					
Forearm length	-	13.3 ± 1.4	-	-	-
Hindfoot length	-	8.8 ± 0.8	-	-	-
Neck circumference	-	21.5 ± 3.1	-	-	-
Chest circumference	-	28.5 ± 4.1	-	-	-
Total length	-	58.2 ± 5.9	-	-	-
Tail length	-	16.1 ± 1.6	-	-	-
Weight	-	3.1 ± 0.6	-	-	-
n =	0	4			
Sub-adults					
Forearm length	14.1 ± 0.6	14.6 ± 0.4	43	40	<0.01
Hindfoot length	9.4 ± 0.3	9.2 ± 0.6	22.5	"	>0.1
Neck circumference	24.3 ± 1.3	24.6 ± 1.5	27.5	"	>0.1
Chest circumference	31.9 ± 1.8	31.5 ± 1.5	23.5	"	>0.1
Total length	64.0 ± 2.6	66.1 ± 2.8	24.0	"	>0.1
Tail length	18.1 ± 0.9	18.2 ± 1.6	28.0	"	>0.1
Weight	4.3 ± 0.5	4.4 ± 0.6	27.5	"	>0.1
n =	8	6			
Adults					
Forearm length	16.1 ± 0.9	14.6 ± 0.7	151.0	131	<0.0025
Hindfoot length	9.7 ± 0.5	9.2 ± 0.4	137.0	"	<0.025
Neck circumference	26.9 ± 2.3	25.6 ± 2.7	121.0	"	>0.05
Chest circumference	35.5 ± 2.9	34.4 ± 2.5	106.0	"	>0.1
Total length	69.4 ± 4.3	65.6 ± 3.3	99.5	94	<0.025
Tail length	18.3 ± 2.5	17.4 ± 1.8	102.0	131	>0.1
Weight	5.4 ± 0.7	4.7 ± 0.9	133.0	"	<0.025
n =	12	15			

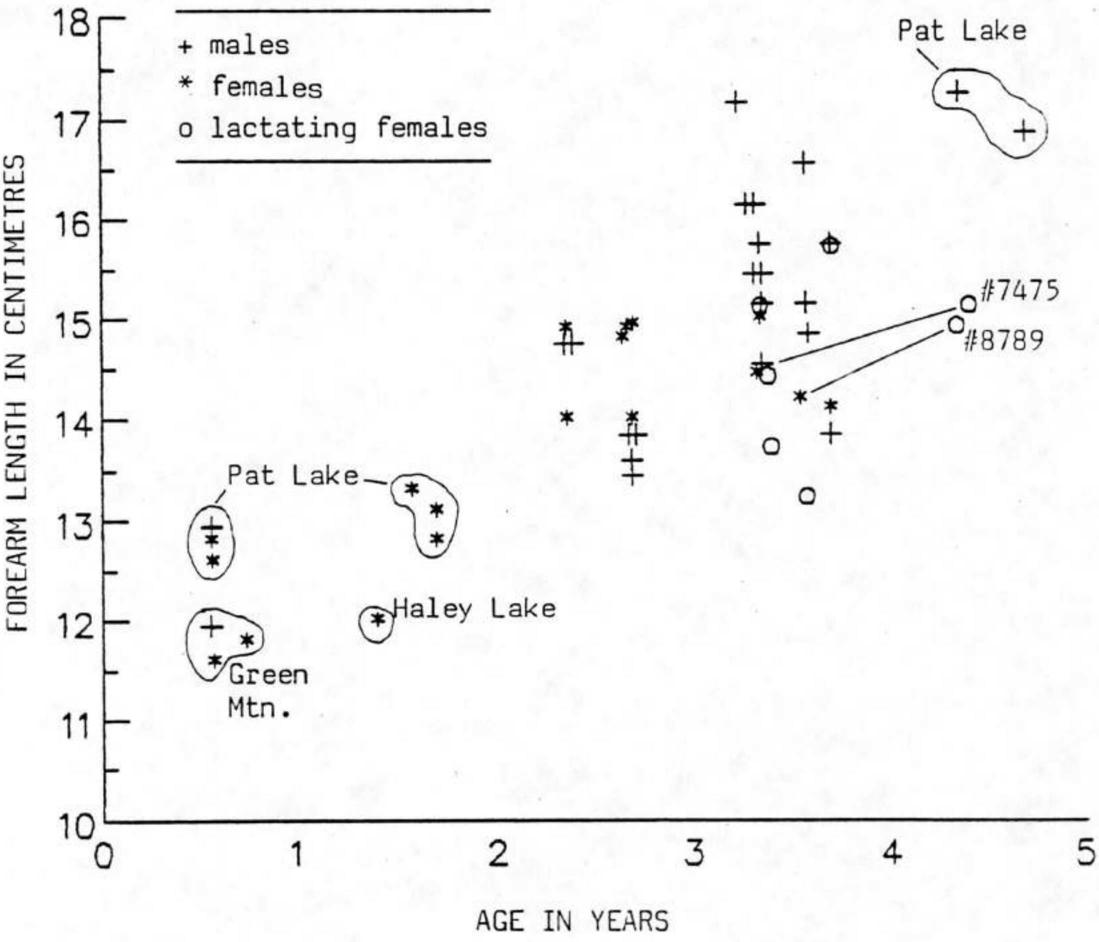

Figure 11: Forearm length as a function of marmot age. Other variables showed similar trends when plotted. The x-axis refers to presumed age-class plus number of days after emergence. Young animals from Pat Lake apparently grow faster, perhaps due to earlier emergence from hibernation. The two largest adult males ever taken were also from this colony.

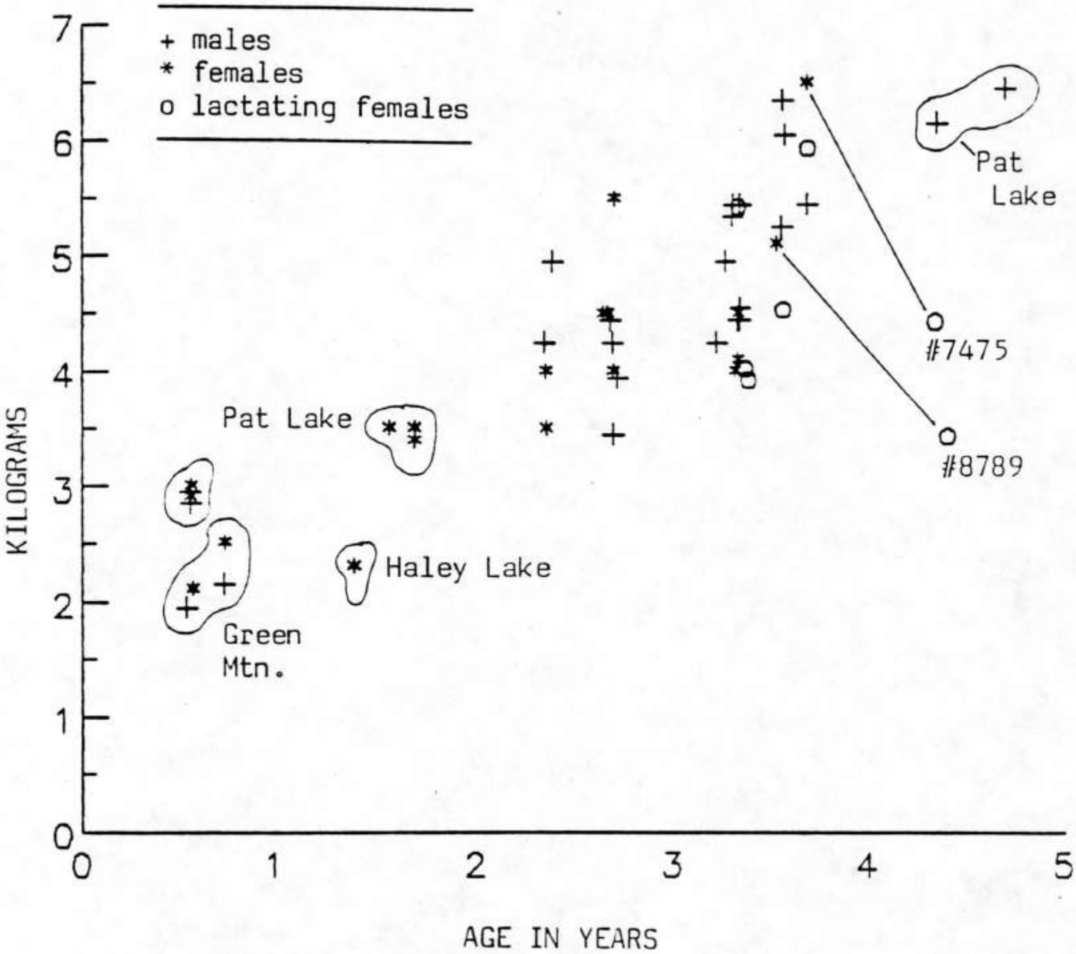

Figure 12: Weight as a function of marmot age. The x-axis is as in Figure 11. Note the apparently high cost of reproduction; lactating females were generally smaller than non-reproductive individuals. Marmot #7475 and #8789 showed large decreases in body weight shortly after breeding.

indicate that any single variable is an accurate indication of age (range of r^2 values=0.20 to 0.68; Table 2). In particular, my data do not support the crisp differentiation of adult and two-year-old marmots posited by Heard (1977) on the basis of body mass.

There were some interesting differences between animals from "slash" and "natural" colonies. Seven young marmots from Pat Lake (four young-of-the-year and three yearlings) appeared to grow faster and larger than five others from "natural" colonies, although sample sizes were too small to be tested for significance (Figures 11 and 12). The two largest adult marmots ever captured were also from Pat Lake. Among three-year-old marmots, "slash" animals were larger than those from "natural" colonies on the basis of forearm length ($U_{9,14}=104$, $p<0.01$), hindfoot length, ($U_{9,14}=120$, $p<0.01$), tail length ($U_{9,14}=95$, $p<0.05$), and total length ($U_{9,10}=66$, $p<0.05$). This may be a function of earlier emergence from hibernation at lower-elevation sites, although better nutrition or food availability in "slash" environments cannot be ruled out.

Also interesting is the apparently high physiological cost of breeding. Two females first captured as three-year-olds in late July and August (#8789 and #7475 respectively) were recaptured as lactating four-year-olds in early July one year later. Both had grown in bone structure (as measured by forearm and hindfoot length), but both also exhibited a dramatic decline in body weight (Figures 11 and 12). Overall, six lactating females captured at "natural" colonies during July averaged 4.2 kilograms (s.d.=0.42); two others from Pat Lake include a 5.5 kg. lactating female captured in late June (#955956) and a 6.0 kg. post-lactating female captured in late August (#919920). The latter can be largely explained by the two-month post-nursing period in which to recover lost body mass. The former marmot is anomolous and was either considerably older, or must lend credence to the possibility that food resources are more abundant or nutritious in logging-slash environments.

Table 2: Regression of physical measurements with sex and age classes. Because forearm length was found to be different between sexes, this variable was run for both classes. No single variable is a very reliable indicator of age.

	slope	y	s.e.	r^2	df	F
Forearm length (all animals)	0.98	12.0	0.8	0.64	49	85.7
Forearm length (males)	1.15	11.8	0.9	0.67	21	42.1
Forearm length (females)	0.79	12.2	0.7	0.63	26	44.0
Hindfoot length	0.25	8.7	0.5	0.20	49	12.4
Neck circumference	2.44	18.3	2.2	0.60	50	75.4
Chest circumference	3.15	24.5	2.5	0.68	50	105.4
Total length	4.34	53.7	4.0	0.60	42	64.2
Tail length	0.83	15.4	1.9	0.20	50	12.5
Weight	0.80	2.4	0.7	0.64	51	89.4

Sex ratio of 40 adult, sub-adult and yearling marmots was exactly equal when animals from all colonies were pooled. Ratio of adult (age 3+) males:females was 4:4 at Haley Lake and 2:2 at Green Mountain. At Pat Lake the ratio was considerably higher (8:2). However, observed differences in sex ratio between pooled "natural" and "slash" colonies were not significant for either age three-or-older marmots (X^2=2.12, 1 df) or age two-or-older marmots (X^2=4.0, 3 df). Sex ratio of eight young-of-the-year was 4:4, although these animals were very difficult to sex. Age structure of all captured marmots is presented as Figure 13.

Family group structure and persistance

Because of overlap in habitat use by individuals, it is difficult to define "colony" boundaries. The basic unit of understanding is therefore the family group, which is defined by consistent use of a particular home burrow complex. Observations suggest that *M. vancouverensis* conforms to the "egalitarian" model of sociality described by Michener (1983). Males do not aggressively dominate females, interactions between females are mostly non-aggressive or even amicable, juveniles from adjacent litters associate together after weaning, and adult females do not discriminate between young from different litters. In these respects, *M. vancouverensis* exhibits a social structure similar to that of *M. olympus* (Barash 1973).

Family groups normally included one adult male for each adult female. In no case was polygamy documented, although I remain uncertain of the male parentage of several families. In particular, one adult male (#2522) at Green Mountain could have been responsible for two litters in 1988. Apart from that possible exception, *M. vancouverensis* does not appear to form polygynous harems within a single reproductive season, as does *M. flaviventris* (Anderson *et al.* 1976). In this respect it more closely

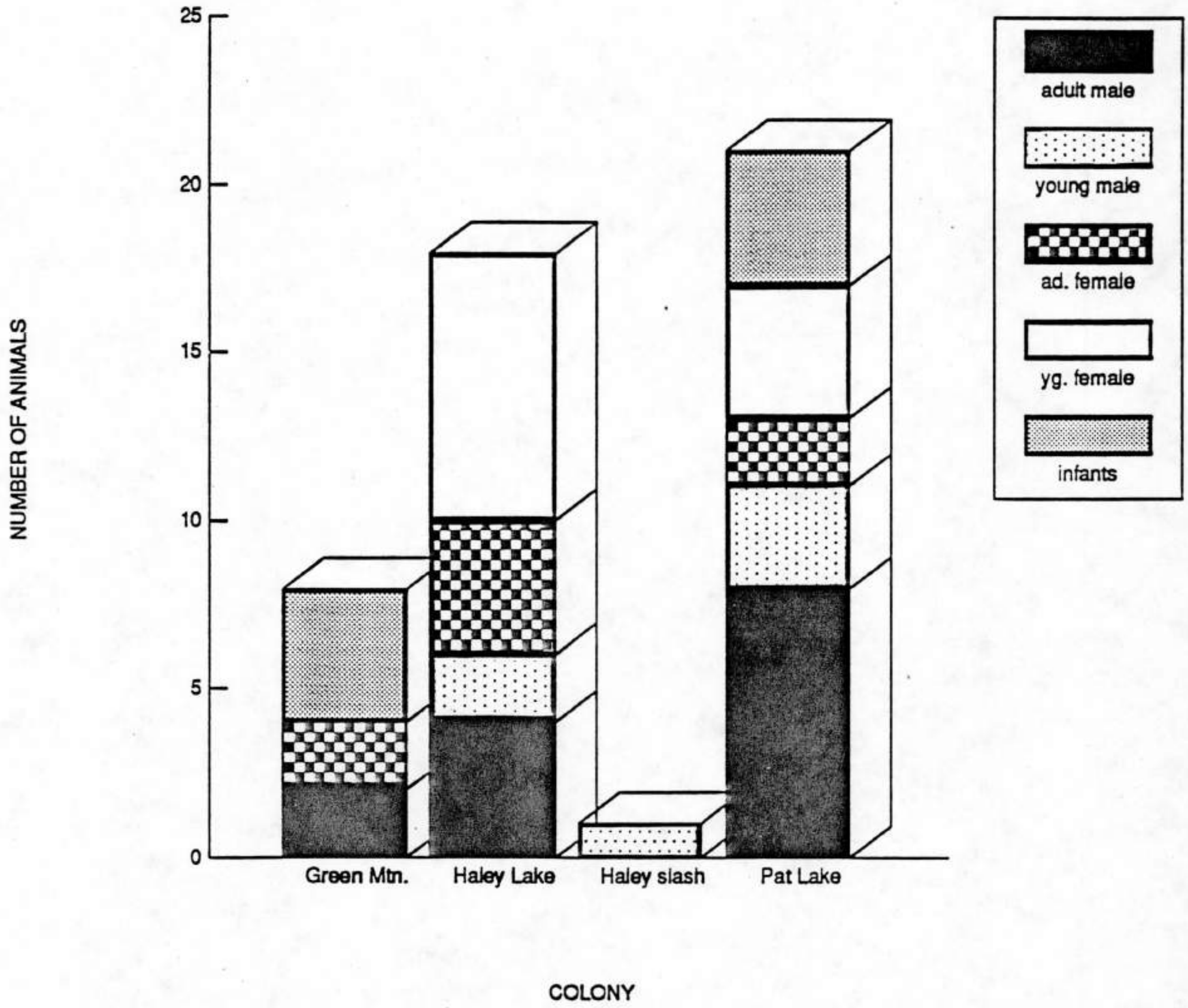

Figure 13: Sex and age structure of captured marmots. When all data were pooled, sex ratio was exactly equal (1:1). Sex ratio of "natural" and "slash" colonies was not significantly different.

resembles Alaskan populations of *M. caligata* studied by Holmes (1984). The description of *M. vancouverensis* family groups by Heard (1977) is biased towards what I call "established" families. Often no sub-adults share a set of burrows with older animals; I observed five cases in which family groups were comprised of adults and young-of-the-year exclusively, usually in logging-slash habitats. I interpret this to be the result of a newly formed family group. Occasionally I observed solitary "transient" marmots (usually sub-adults) or a pair of marmots with no young (a "potential" family).

Six family groups at "natural" colonies were remarkably stable. At Green Mountain, two established families were identified (Figure 14: "Betsy" and "Rocky Raccoon"); both used the same burrows over the course of the project. At Haley Lake, two established groups (Figure 15: "Tonto" and "Mom #2") also used the same burrows throughout the project. At the latter site, one new family ("Mom #1") established itself in 1988 and remained stable through 1989. Another new family ("Mom #3") was identified in 1988 but disappeared by 1989. Several "transient" marmots were observed or captured in 1988 and 1989, and two solitary sub-adults used burrows consistently in 1988 and 1989.

The situation in logging-slash colonies was noticeably different. At the Haley "slash" colony, two new families (Figure 16: "Red-tail" and "Menza") were identified in 1988. The "Menza" group disappeared by 1989, but "Red-tail" used the same burrow complex as in 1988. The "Tophat" potential family was abandoned by 1988, and the 1988 "Apex" and "Patches" (transient) burrows were not used in 1989. Several "new" marmots (possibly yearlings from "Menza" or "Red-tail") established a new burrow complex 150 metres south of the "Red-tail" complex. Unfortunately, Haley "slash" data are confounded by extremely poor trapping success (*n*=1), and my consequent inability to positively identify marmots from year-to-year.

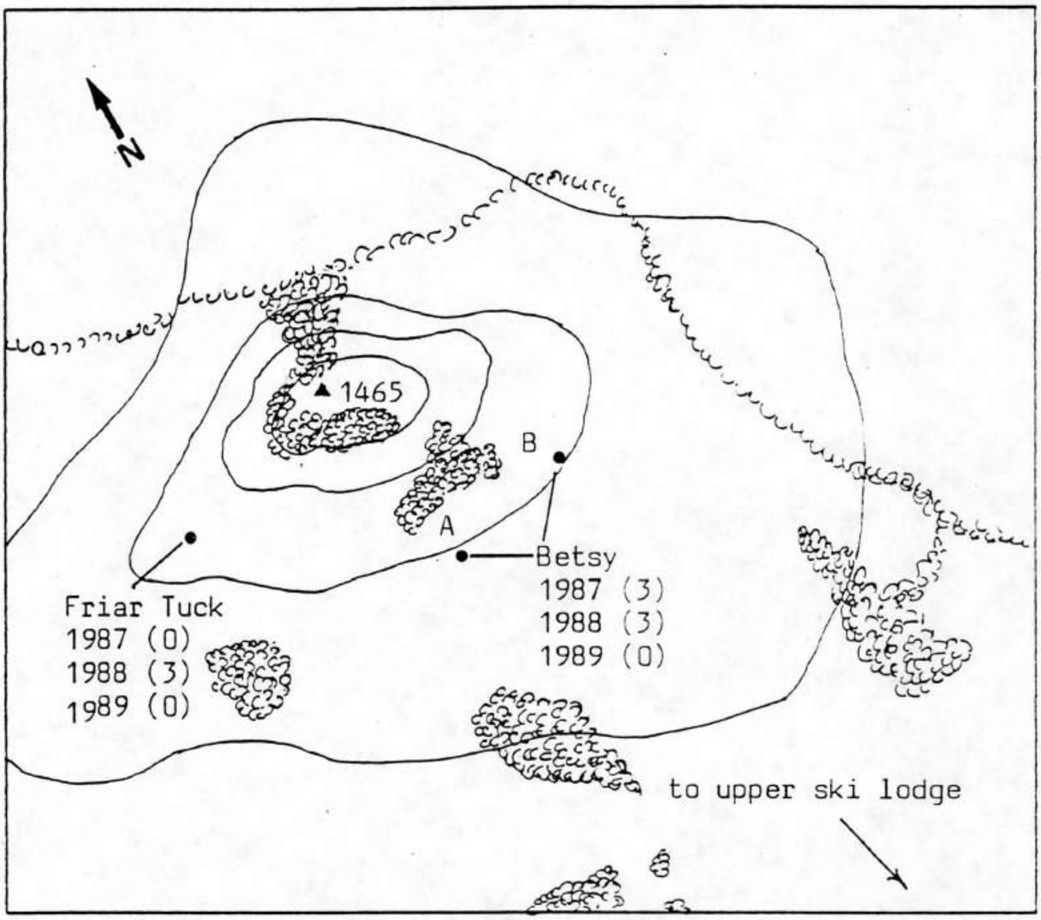

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Figure 14: Family groups and reproduction at Green Mountain, 1987-1989. Numbers in parentheses are numbers of young produced. This small colony remained very stable throughout the study period. The "Betsy" group moved from site A to B in 1988. The adult female present (#1820) remains the only marmot known to have produced litters in consecutive years.

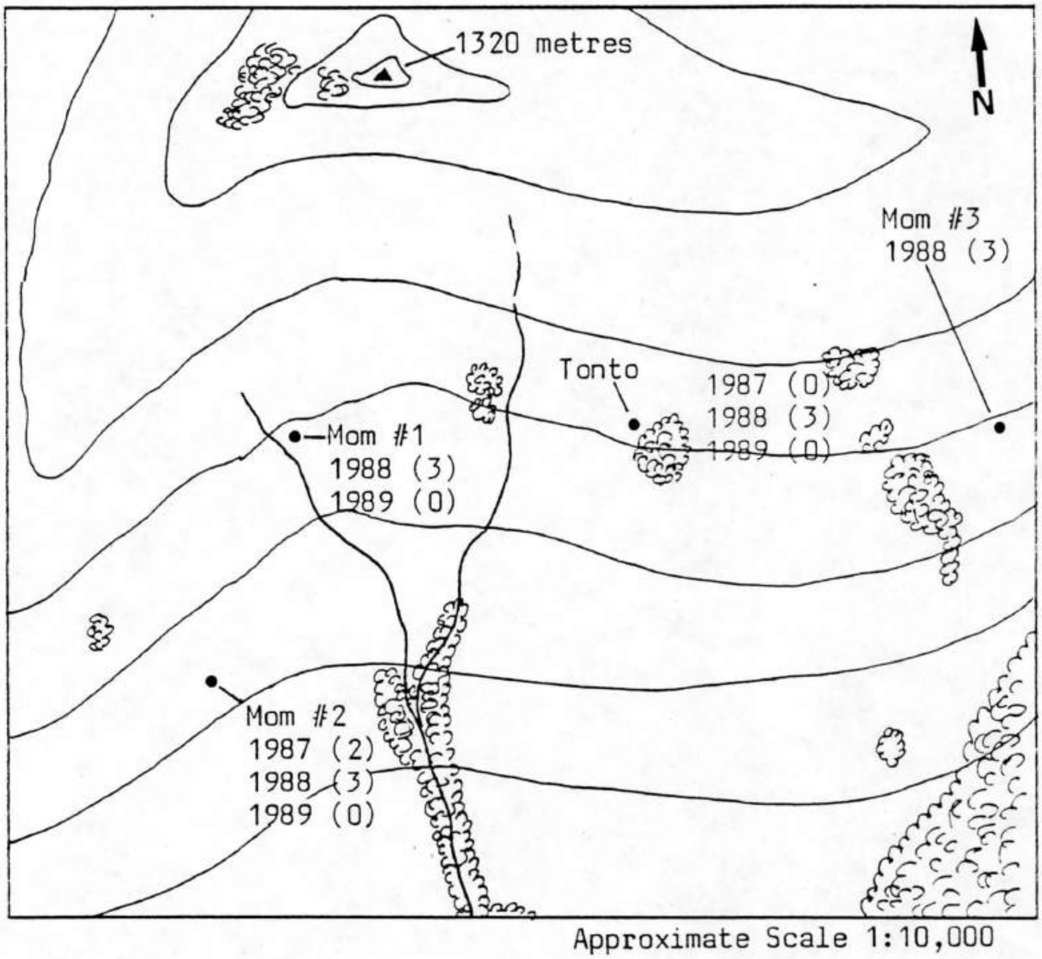

Figure 15: Family groups and reproduction at Haley Lake, 1987-1989. The "Tonto" and "Mom #2" groups used burrows consistently in all years. The "Mom #1" family was new in 1988 and remained stable through 1989. "Mom #3" was new in 1988 and disappeared that winter.

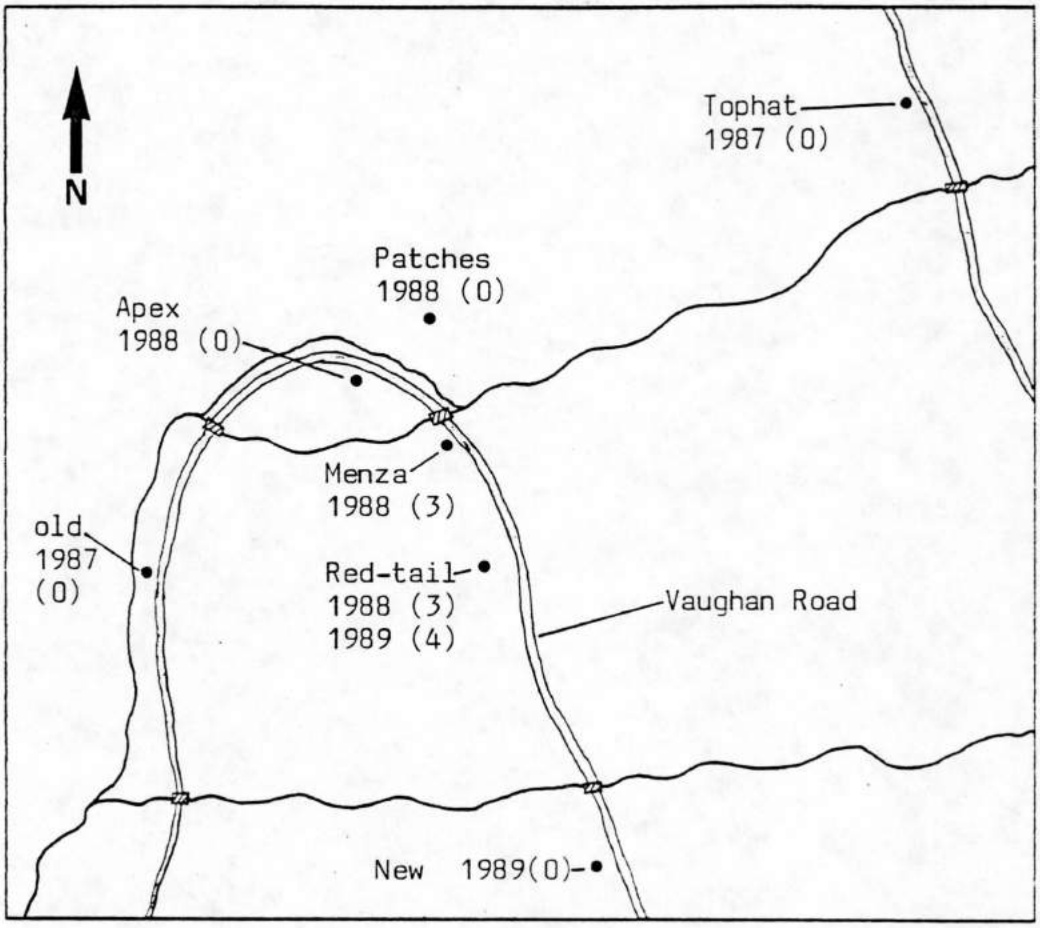

Figure 16: Family groups and reproduction at Haley "slash", 1987-1989. Poor trapping success made it impossible to identify most individual marmots from year-to-year, but use of burrows was not stable. "Tophat" and "Old" burrow complexes were not used after 1987. "Apex", "Patches" and "Menza" were new in 1988 but abandoned by 1989. Only the "Red-tail" burrow complex was used in consecutive years.

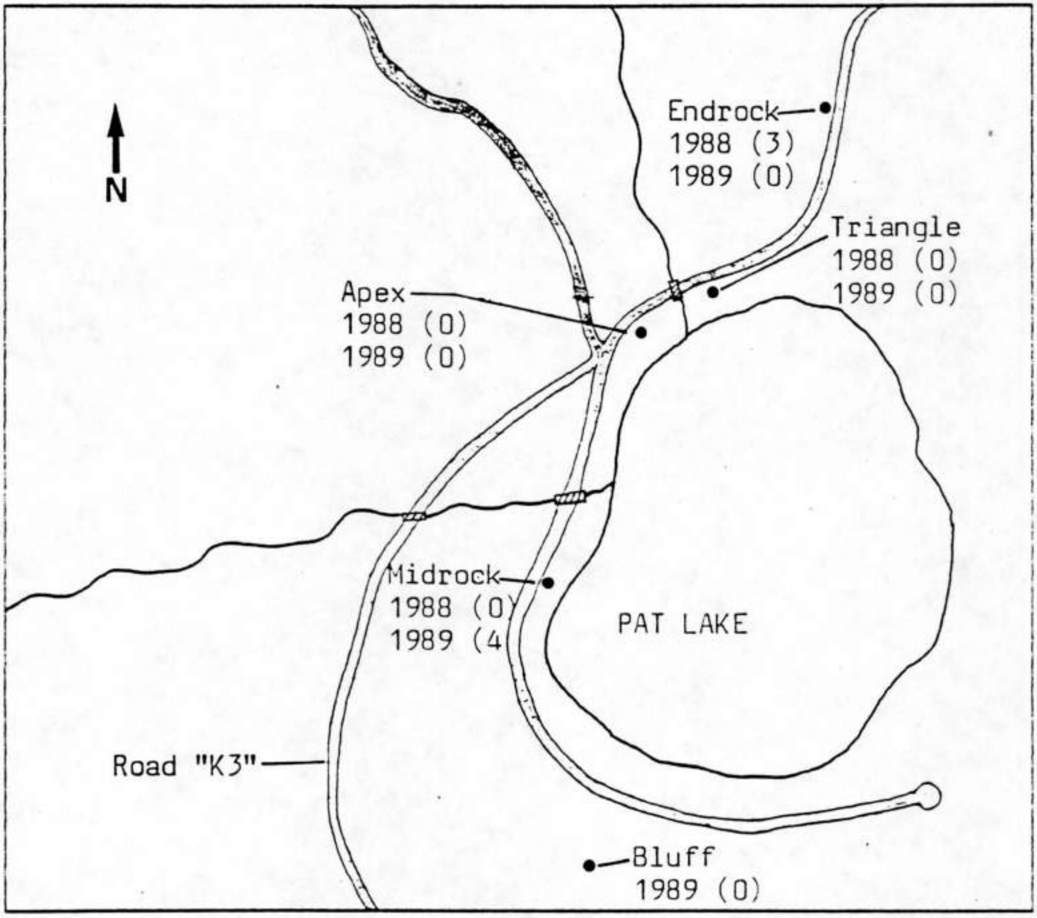

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Figure 17: Family groups and reproduction at Pat Lake, 1988-1989. This site was not observed in 1987. "Endrock", "Midrock", "Apex" and "Triangle Rock" were all used by marmots in 1988 and 1989, but individual turnover was high. Most 1988 marmots disappeared, but were replaced by "new" marmots in 1989.

At Pat Lake, turnover rates were also high, although no 1988 burrows were abandoned and one additional complex was constructed in 1989. The four established "Endrock", "Midrock", "Apex" and "Triangle Rock" burrows were all used again in 1989, but most surviving adults and yearlings were captured or positively identified some distance from their 1988 burrows (Figure 17). Adult male #928929 moved from "Endrock" to "Midrock" and apparently replaced an existing adult at that site. Two yearlings (#901902 and #903904) from "Apex" were observed at the new "Sidehill" complex in 1989, approximately 300 metres from the 1988 site. A surprising feature of the Pat Lake colony was the disappearance of most 1988 adults, and apparent influx of "new" adults in 1989.

I tested for differences in family persistance between "natural" and "slash" sites in the following manner. A "turnover" was defined as a) abandonment of a "home" burrow complex by known reproductive-age adults one year after initial observation, b) movement to a new "home" burrow complex by known reproductive-age adults one year after initial observation, or c) use of an existing "home" burrow complex by "new" (previously unobserved) adults one year after initial observation. Conversely, use of the same burrow complex by the same adults, one year later, was defined as "persistance". Note that although ear-tags were often lost, tattoos, torn ears and/or holes made it easy to distinguish "old" from "new" marmots.

Ratio of turnovers/persistance was 1:3 at Green Mountain, 1:5 at Haley Lake, 4:1 at Haley "slash" and 4:0 at Pat Lake. Pooled data for "natural" and "slash" groups indicate significantly higher turnover rates for "slash" marmots (X^2=6.43, 1 df, $p<0.025$). This may be the result of higher overwintering mortality in "slash" habitats, or may indicate movement. Whatever the cause, use of burrows in "slash" appears to be more ephemeral than in "natural" sites.

Reproduction

For 12 families with known female parents, I observed 13 reproductive events over the course of the project. Number of young-of-the-year appearing aboveground by direct count totalled 41, for a mean litter size of 3.2 (range=2.0 to 4.0). Litter sizes of up to six have been reported (G.W. Smith, BCMOE, and B. McKinnon, Cowichan Valley Naturalists', pers. com.) but parentage in those cases is unconfirmed. In no case did I observe reproduction of a known two-year-old; *M. vancouverensis* apparently exhibits delayed sexual maturity.

Average litter size was slightly larger in logging-slash environments than at "natural" colonies (Table 3; $U_{5,8}=33$, $p<0.05$). Average fecundity (expressed as total young produced/total adult-female-years, in which an adult-female-year is an age three-or-older female alive in one year) was higher at logging-slash sites; however, this is partially a sampling artifact. Poor trapping success at the Haley "slash" colony, combined with the high turnover of adults at the Pat Lake site, made it virtually impossible to document the presence of non-breeding adult females from previous years. Almost all adult-female-years in "slash" colonies were based on breeding events, which inflates this statistic.

Marmots did not breed consistently during the three years of this study. The Haley Lake colony produced one litter in 1987, four in 1988 and none in 1989. The associated Haley "slash" colony produced none, two and one during the same period. The Green Mountain colony produced one litter in 1987, two in 1988 and none in 1989. At Pat Lake (which was not visited in 1987), one litter was identified with certainty in both 1988 and 1989, although the comparitively short periods of time spent at this site mean that some reproductive events may have been missed.

Table 3: Reproductive rates of *M. vancouverensis* at "natural" and "slash" colonies. Only litters with known female parents are included.

	n of litters	mean litter size	range	mean fecundity[a]	s.e.
"Natural" colonies	8	2.88[b]	2 - 3	0.67	0.36
"Slash" colonies	5	3.60[b]	3 - 4	1.50	0.78
All colonies	13	3.15	2 - 4	0.89	0.60

[a] Mean fecundity is expressed as average number of young produced/adult-female-year, defined as a reproductive-age female alive in one year.

[b] Mean litter size was significantly larger in "slash" colonies as determined by Mann-Whitney U-test (U=33, p<0.05).

Variability of marmot reproductive rates are shown for Haley Lake and Green Mountain in Figure 18. Data were compiled from Heard (1977), surveys carried out by the Vancouver Island Marmot Protection Committee (Routledge and Merilees 1980, Routledge 1982, 1981), BCMOE surveys (Fry *et al.* 1986, Smith 1985, Smith *et al.* 1984, Heinsalu and Smith 1983, 1982,) and this study (1987 through 1989). Milko (1984) hypothesized that poor reproductive success was due to late snow-melt. I attempted to test this using snowpack data collected by BCMOE from Sno-bird lake, which is 0.5 kilometre south of the Green Mountain colony and at a similar elevation (1400 metres). Correlation analysis revealed no significant relationship between total reproductive success and April 1st snow depth (r=0.043, t=0.14, 10 df). There is also no obvious "threshold effect" between snow-depth and reproductive success, with the possible exceptions of 1974 and 1989, when large snowpacks occurred in years of low reproductive success.

Survivorship

All captured marmots were observed days or weeks after release; I have no evidence that capture or handling contributed to mortality. Virtually all disappearances occurred between years rather than from month to month, suggesting that most mortality or dispersal occurs either during hibernation, or very shortly after spring emergence.

A summary of mark-recapture data is included as Table 4: raw data are included in Appendix III. Results indicate higher mortality rates for younger age classes, as is true for most species. Only seven of 21 (33%) "natural", and two of 10 (20%) "slash" young-of-the-year were confirmed as having survived their first hibernation period. The difference between "natural" and "slash" rates was not significant (X^2=0.33, 1 df). Yearlings also have a low survival rate (one of four; 25%), but disappearances may suggest dispersal rather than mortality. Survivorship of age two-and-older marmots is

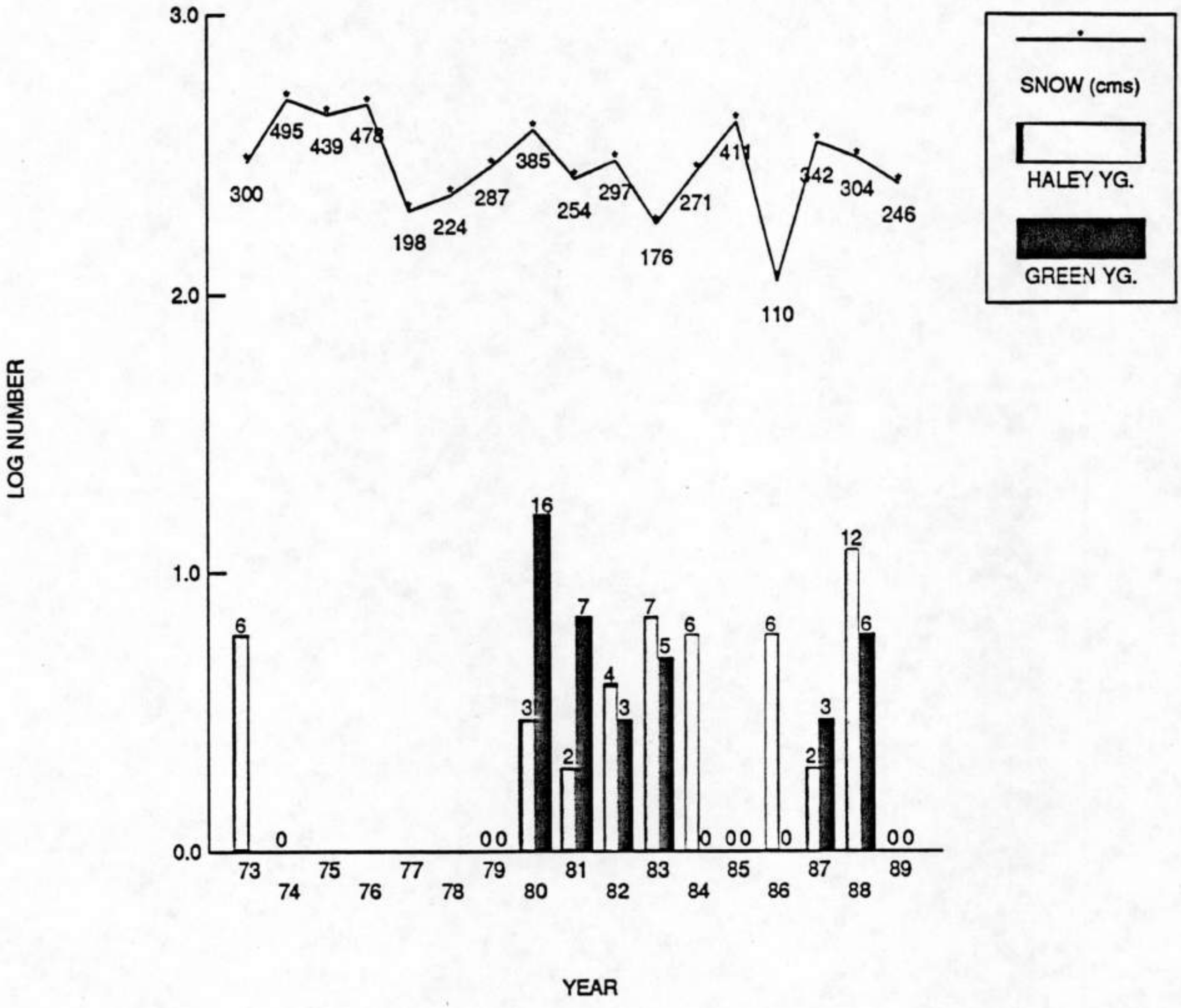

Figure 18: Reproductive variability and snowpack conditions at two colonies. Haley Lake and Green Mountain reproductive data are from Heard (1977), BCMOE-sponsored surveys (1979-1986) and this study. April 1st snowpack depths are from BCMOE observations from a site <1 kilometre north and slightly higher (1400 metres elevation) than the Green Mountain colony. There is no significant correlation between overall reproductive success and early-spring snowpack conditions.

Table 4: Mark-recapture data for *M. vancouverensis*, 1987-1989.

Sex and estimated age at 1st capture	*n* [a]	estimated age at time of recapture[b] 1-2	2-3	3-4	4-5	5-6
"natural" colonies[c]						
young-of-the-year	21	7				
yearling	1					
2-year-old	7(4)[d]			5(2)	2(1)	
3-year-old+	10(4)				8(3)	4(1)
"slash" colonies						
young-of-the-year	10	2				
yearling	3		1			
2-year-old	3(2)			2(1)		
3-year-old+	4(3)					

[a] Animals which were "first-time" captures in 1989 are not included in these data.

[b] Not all young-of-the-year were captured. Older animals were often "recaptured" with spotting scope only. Given ear-tag loss and possible dispersal, these represent minimum survivorship rates.

[c] "Natural" colonies refer to pooled Haley Lake/Green Mountain data; "Slash" colonies are pooled Pat Lake/Haley "slash" data.

[d] Numbers in parentheses refer to males.

comparitively high, particularly at established colonies in "natural" habitats (13 of 17; 76%). Comparatively few (two of seven; 28%) adults were observed from year to year in logging-slash environments; the difference between "natural" and "slash" rates was not significant (X^2=1.30, 1 df). Again, it is not clear whether "disappearances" represent mortality or dispersal.

Only three clear-cut cases of mortality were documented during the project. A jawbone was found at the entrance of a burrow at Haley Lake in 1988. A skull with dried fur was found amidst trees adjacent to Haley Lake in June of 1989, and a presumed golden eagle (*Aquila chrysaetos*) pellet was found to contain marmot bones in August at that site. None of these were known to represent ear-tagged individuals. No cases of predation were actually observed, although golden eagles were commonly seen at Green Mountain and Haley Lake. Wolves (*Canis lupus*) were known to use the road leading to Haley Lake (observed scat), and one observation was made of a wolf digging at the entrance of a marmot burrow in October of 1989 (G.W. Smith, BCMOE, pers. com.). D. Nagorsen (Royal B.C. Museum, pers. com.) has reported finding marmot fur in wolf scat on Gemini Peak. While marmots may be taken by a variety of predators, I have no evidence that predation exerted a significant population effect at any colony.

Movement

Throughout this study, no ear-tagged marmot was captured or observed more than 0.5 kilometre from site of original capture. However, there were several cases in which longer movements were suggested by circumstantial evidence. In mid-June of 1987 and again in 1989, marmot tracks leading away from Haley Lake were found in snow at that site. One marmot had apparently followed the ridge north to Gemini Peak, while at least two others had descended into the Haley "slash" colony. Similarly, in 1987 and 1988, a fairly large influx of marmots (>5 adults) was observed at the Haley "slash" colony for a period of several days during early July. These animals were not seen after this period, and presumably were dispersing. Similarly, four adult females which had not been previously observed were captured at the Haley Lake colony in early August of 1989.

My limited data suggest that *M. vancouverensis* disperse at roughly the same time of year as other marmot species; i.e., between mid-June and mid-July (as in *M. flaviventris*; Brody and Armitage 1985). Data are insufficient to determine which sex or age-class make up the bulk of dispersing individuals. That all four yearlings captured were females may suggest that yearling males are more prone to dispersal, or may be a sampling artifact. Similarly, the disappearance of 70% of 1988 adults from Pat Lake could be interpreted as dispersal, i.e., that animals colonize a site for a summer and then disperse to new areas.

Individual daily movements of *M. vancouverensis* can be extensive. "Focal-animal" observations of individuals at Haley Lake, Haley "slash" and Pat Lake from sunup to sundown showed that adults of both sexes forage widely and may use escape burrows distributed throughout a given study colony. However, foraging marmots do not use "home" burrows belonging to other marmot families; this was illustrated dramatically when I captured a "transient" adult female (#980981) near the Mom #2 burrow complex on August 20th of 1989. When released, this animal sought shelter in the Mom #2 burrow complex; much hissing and whistling ensued and the intruder was quickly ejected. Defense of "home" burrows appears to be the only time that aggressive territorial behavior is elicited in *M. vancouverensis*; most other interactions, even those including adult males, are non-violent in the extreme.

Hibernacula

Five hibernacula were identified by the presence of emergence tunnels through the snowpack in spring (Figure 19), or by burrow entrances plugged by grasses in late fall. Unfortunately, fiscal constraints precluded observations before early May or after late September. Most hibernacula were therefore identified at higher-elevation "natural" colonies, at which snow cover persists longer. My initial supposition that marmots should choose hibernacula in sites which shed snow cover early in the spring was wrong. Instead, marmots appear to choose hibernacula where snow cover persists the longest, i.e., in "snow-bowls" below steep slopes. In retrospect this makes sense, because such sites would offer the most thermodynamically stable environments for hibernation. Similar trends have been reported for other species, eg., grizzly bears *Ursus arctos* (Vroom *et al.* 1980).

At Green Mountain, three hibernacula were identified by the presence of tunnels up through the snowpack in May or early June, or by burrow entrances plugged by vegetation in November. The hibernacula exit illustrated in Figure 19 was still covered by approximately two metres of snow in early June; this particular hibernacula was used in all years of the project. Observations of marmots at this site indicate increased use of the area in late August. At Haley Lake, two hibernacula were identified in areas of high snow accumulation and again, increased use of these areas by marmots was observed in late August. At logging-slash colonies, lack of snow cover precluded positive identification of hibernacula. However, based on late-summer observations of marmot activity, I suspect that the "Patches" and "Red-tail" sites were used as hibernacula at Haley "slash" in 1988. In general, observations tend to support the conclusion that *M. vancouverensis* is a colonial hibernator, at least insofar as adult females and family groups are concerned. Large numbers of marmots observed using particular burrows in late summer, together with limited numbers of hibernacula, offer no other explanation.

Figure 19: Hibernacula exit, Green Mountain, June 1987. Shown is G.W. Smith (BCMOE) with one hibernacula that was used in all years of the study. Observations suggest that *M. vancouverensis* is a colonial hibernator, and normally select sites in similar "snow-bowl" environments.

Genetic variability

Electrophoresis of 44 marmot plasma and red blood cell (RBC) samples revealed activity in 20 enzyme systems. Scorable resolution was obtained at 22 loci in 15 of these systems. Note that four blood samples from Pat Lake were not used; I judged that the added cost of running two gels instead of one for each system was unjustifiable. The single animal sampled from the Haley "slash" colony was pooled with Haley Lake samples for analysis. Appendix II describes recipes, results and scoring criteria used in electrophoresis.

Of 22 scorable loci, 18 showed no variation and four were polymorphic. Polymorphic loci included the most anodal Lactate dehydrogenase loci (LDH), the most cathodal Esterase loci (EST), and two Peptidases acting on leucyl-proline and leucyl-glycerine substrates (PEP-pp and PEP-lgg respectively). Phosphoglucose mutase (PGM) was possibly variable but unscorable for all samples. My estimate of P (%polymorphic loci) for *M. vancouverensis* is thus 4/22 or 0.18. While the significance of this estimate is directly untestable, 0.18 is less than that found in *M. flaviventris* (0.4; Schwartz and Armitage 1980) or *M. monax* (0.25; Wright *et al.* 1987). Average expected heterozygosity H was calculated as $(1-p_i^2)/n$ of loci, where p_i is the frequency of the *i*th allele at each locus: Hartl 1981). My estimate of $H=0.073$ for *M. vancouverensis* is similar to values found in other marmots (*M. flaviventris*; 0.075 and *M. monax*; 0.054: Schwartz and Armitage 1981 and Wright *et al.* 1987 respectively).

Expected and observed allele frequencies were calculated for each of the three sampled subpopulations. Because expected frequencies were sometimes <5, I tested for conformance to Hardy-Wienberg expectations using the log-likelihood G test (Zar 1974). Results indicate that patterns of genetic variation within the three sampled subpopulations were very close to those expected under Hardy-Weinberg assumptions

(Table 5). Variation within colonies is distributed in a manner congruent with random mating between marmots. I conclude that close inbreeding or genetic drift has not caused genetic differentiation of social units (family groups) within any of the three subpopulations. However, differences were found in genetic structure among subpopulations. Animals from Pat Lake were fixed for the fast *A* allele at the LDH loci, while slow *a* alleles were found in Hardy-Weinberg proportions at Green Mountain and Haley Lake.

Polymorphic loci were used to calculate Wright's fixation coefficients (F_{is}, F_{it} and F_{st}; Wright 1965). F_{is} is an inbreeding coefficient which measures the reduction of individual heterozygosity due to inbreeding within a subpopulation. F_{st} is a fixation coefficient which indicates reduction of heterozygosity within a subpopulation due to random genetic drift, and F_{it} is a composite index which measures reduction of heterozygosity due to both processes (Hartl 1981). Positive values for F_{is} and F_{it} are found in populations for which conditions promote genetic fixation (increased homozygosity); negative values occur when conditions promote an excess of heterozygotes (Schwartz and Armitage 1980). Values for F_{st} range from 0 to 1, with values of 0 to 0.05 indicating "little" genetic differentiation, values of 0.05 to 0.15 indicating "moderate" differentiation, and values >0.15 indicating "great" differentiation (Hartl 1981). Significance of F_{st} values was determined using the chi-squared test $X^2=F_{st}2N_t$, where N_t is the total population size (Workman and Niswander 1970).

Fixation statistics for each locus are given in Table 6. The EST, PEP-PP and PEP-LGG loci indicate no differentiation among colonies (non-significant F_{st} values) and general avoidance of close inbreeding (negative F_{is} and F_{it} values). However, the LDH locus showed significant differentiation ($F_{st}=0.144$, $X^2=12.7$, 1 df, $p<0.05$) and positive

Table 5: Expected and observed allele frequencies in marmots from three colonies. Within colonies, patterns of variation do not differ from those expected under Hardy-Weinberg assumptions.

LDH	*AA*		*Aa*		*aa*		*G*	P-value
Green Mountain (n=8)	4	(3.8)[a]	3	(3.4)	1	(0.8)	0.146	0.85
Haley Lake (n=15)	13	(12.1)	1	(2.7)	1	(0.1)	3.564	0.07
Pat Lake (n=21)	21	(21.0)	0	(0.0)	0	(0.0)	0.0	1.00
EST-1								
Green Mountain (n=8)	4	(4.3)	4	(3.0)	0	(0.5)	1.723	0.20
Haley Lake (n=15)	7	(7.3)	7	(6.3)	1	(1.3)	0.191	0.87
Pat Lake (n=21)	8	(8.1)	10	(9.9)	3	(3.0)	0.062	0.95
PEP-pp								
Green Mountain (n=8)	4	(4.5)	4	(3.0)	0	(0.3)	1.359	0.25
Haley Lake (n=15)	6	(6.7)	8	(6.7)	1	(1.6)	0.573	0.45
Pat Lake (n=21)	8	(7.8)	9	(10.0)	4	(3.2)	0.426	0.55
PEP-lgg								
Green Mountain (n=8)	2	(2.5)	5	(3.9)	1	(1.5)	0.781	0.40
Haley Lake (n=15)	4	(4.3)	9	(7.4)	1	(2.9)	0.781	0.40
Pat Lake (n=21)	5	(4.8)	10	(10.5)	6	(5.9)	0.365	0.63

[a] Expected frequencies (in parentheses) are those expected under Hardy-Weinberg ($A^2+2Aa+a^2=1$) conditions. *G* values refer to the log-likelihood test of goodness-of-fit (Hartl 1981). Number of df.=1 in all cases.

Table 6: Fixation F_{is}, F_{it} and F_{st} coefficients among three marmot sub-populations.

enzyme	range[a]	mean	X^2	F_{st}	F_{is}	F_{it}
LDH	0.68-1.0	0.86	12.7[b]	0.144	0.275	0.380
EST-1	0.62-0.75	0.69	1.2	0.014	-0.140	-0.124
PEP-pp	0.61-0.75	0.68	1.4	0.016	-0.130	-0.112
PEP-lgg	0.44-0.56	0.53	0.5	0.006	-0.145	-0.138
Cumulative X^2 (8 d.f.)			15.8[b]			
Mean F statistics				0.045	-0.035	0.001

[a] Range of frequencies of the most common allele among the three sampled subpopulations.

[b] Significant ($p<0.05$) fixation (F_{st}) among colonies as determined by the test of Workman and Niswander (1970).

F_{is} and F_{it} (inbreeding and drift). Cumulative F_{st}, F_{is} and F_{it} values for *Marmota vancouverensis* were 0.045, -0.035 and 0.001 respectively, with overall differentiation among colonies being "little" but significant (X^2=15.85, 8 df, $p<0.05$). To provide a basis for comparison, the equivilent F_{st}, F_{is} and F_{it} values for nine colonies of yellow-bellied marmots in Colorado were calculated as 0.07, -0.09, and -0.07 respectively (Schwartz and Armitage 1980).

My interpretation of genetic data is that Vancouver Island marmots are neither genetically destitute nor highly inbred. Differentiation among colonies is limited to fixation of the LDH *A* allele at Pat Lake, which is probably the result of "founder effects" (i.e., rapid population increase from a small "founding" population which did not happen to carry the alternate allele). This is consistent with anecdotal observations showing a "boom or bust" lifestyle in which small marmot colonies expand rapidly from a relatively tiny "seed source" (Fry *et al.* 1986). Results also suggest that close inbreeding is avoided in this species. However, significant overall differentiation among colonies suggests that genetic exchange (dispersal) occurs infrequently between Pat Lake and the Haley/Green complex.

In four cases, genetic analysis provided an independent test of field observations. Alleles from four young-of-the-year and their female parents from Green Mountain were passed along in conformance to Mendelian expectations. However, according to my genetic results, adult male #2726 ("Opportunity Knox") could not have fathered "Betsy's" (#1820) litter of 1987 or 1988, or "Rocky Raccoon's" (#8789) litter of 1988, as I assumed on the basis of behavioral observations. In this case, "Friar Tuck" (#2522) was possibly the culprit; he remains the only adult male whom I suspect may have sired two litters in the same year.

Effective population size

Effective population size was defined by Wright (1969) as "whatever must be substituted for *N*" whenever a population fails to meet the genetic ideals of random mating, monogamy, equal survivorship of sexes, uniform reproduction by all individuals, and non-overlapping generations. Because these ideals are commonly violated by real organisms, N_e is generally a fraction of the total census population N_t. For grizzly bears (*Ursus arctos*), the ratio of N_e:N_t has been estimated at 0.26 to 0.31 (Harris and Allendorf 1989), for moose (*Alces alces*) at 0.20 to 0.36 (Ryman *et al.* 1981), and for bison (*Bison bison*) at 0.08 to 0.30 (Shull and Tipton 1987).

Genetic variation is lost through genetic drift and inbreeding at a rate proportional to N_e and not N_t (Hartl 1981). For small populations this may be of considerable importance, and calculation of N_e is thus an integral component of the PVA process (Gilpin 1987). There are currently two rules-of-thumb for what constitutes a "viable" population on genetic grounds; one designed to ensure that inbreeding levels are kept below 1% per generation (N_e=50), the other designed to ensure the maintainance of virtually all genetic variability (evolutionary potential) over the long-term (N_e=500: see review by Lande and Barraclough 1987). Numerous formulae are available with which to calculate N_e. Unfortunately, most require detailed population data that is often unavailable (see comparison of methods by Harris and Allendorf 1989). Reed *et al.* (1986) presented one formula, given by:

$$1/N_e = 1/[(4N_{bm}*L_m*I_m)+(4N_{bf}*L_f*I_f)] \quad \text{in which:}$$

N_e = effective population size.

N_b = number of breeding animals.

L = generation length (mean age of reproductive animals).

I = probability of survival to age L and breeding.

and "$_m$" and "$_f$" subscripts refer to males and females respectively.

As population parameters remain poorly understood for *M. vancouverensis*, I made several assumptions, as follows, to arrive at a "basic" estimate of current N_e:

1) The population is neither increasing nor declining (either trend would influence N_e), so use 1984 data (most extensive survey) to estimate average population parameters. Total population N_t=234 (Munro *et al.* 1985).

2) There is a stable annual recruitment rate of 68 young/year (Munro *et al.* 1985). Division by mean litter size of 3.15 yields 22 reproductive pairs.

3) *M. vancouverensis* is essentially monogamous, so *n* of reproductive males=*n* of reproductive females N_{bm}=N_{bf}=22.

4) There is no variance in reproductive potential, i.e., <u>every</u> reproductive pair produces 3.15 young with equal sex ratio of progeny; therefore k_m=k_f=3.15.

5) Average generation length is equal for males and females. *M. vancouverensis* is not known to breed before age three. *M. flaviventris* in a similar high-altitude environment (O. Schwartz, University of Northern Iowa, pers. com.) may live to age 11, but the average age of reproductive adults is five. As a first approximation, let L_m=L_f=5.

6) Males and females have an equal probability of surviving to reproductive age <u>and</u> reproducing. The probability that male *M. flaviventris* lives to age five is 0.035, for females it is 0.078 (O. Schwartz, University of Northern Iowa, pers. com.). As a first approximation, let l_m=l_f=0.05.

7) All known colonies are "connected" through dispersal of at least one reproductive-age adult each generation.

Given these assumptions, the known population has an effective size N_e=34.6. To determine how various factors influence N_e, I modified the "basic" case as follows:

A) If males and females have differential survivorship rates (as might be the case if males disperse preferentially), let l_m=0.04 and l_f=0.08: then N_e=36.9.

B) If average breeding-age marmots are younger, let L_m=L_f=4 years and assume consequently higher survivorship of males (l_m=0.05) and females (l_f=0.12) to this age: then N_e=39.0.

C) If males disperse preferentially but live to breed elsewhere, assume equal generation length (L_m=L_f=4 years) and more similar male/female survivorship values (l_m=0.08 and l_f=0.12): then N_e=53.2.

D) If males breed earlier than females, assume shorter generation length L_m=3, L_f=4, and higher survivorship to this age (l_m=0.15, l_f=0.12): then N_e=64.4.

Using these assumptions, N_e:N_t varies from approximately 0.15 to 0.28. This suggests that the known population is extremely close to the effective size necessary to avoid loss of genetic variability over the short term (N_e=50), and is an order-of-magnitude smaller than that necessary to preserve all genetic variability (evolutionary potential) over the long-term (N_e=500). Polygamy, variance in lifetime reproductive success among individuals, and unequal sex ratio of progeny would reduce N_e:N_t still further (Harris and Allendorf 1989). Non-reproduction of some surviving animals, as would occur if dispersing animals did not find a mate, would also reduce N_e. Finally, genetic isolation of any marmot colonies would necessitate calculation of (much smaller) N_e values for each sub-population. Conversely, uniform dispersal of males would increase N_e because close inbreeding would be avoided, and gene flow between family groups and colonies would be maximized.

DISCUSSION

Population structure

The known population of *Marmota vancouverensis* consists of clusters of social units (colonies) inhabiting patches of sub-alpine habitat kept treeless by natural processes or logging. The species conforms to the "meta-population" model described by Gilpin (1987), in which a total population consists of smaller sub-populations which may be periodically extinguished or re-colonized. Dispersal is a key ingredient of the meta-population model; it may "buttress" existing colonies, provide a "rescue effect" for colonies which are not doing well, or provide "seed" for re-colonization. The meta-population view of Vancouver Island marmots is supported by existing data.

High observed variability in reproductive success, family group persistance, and individual survivorship indicates that a small, isolated colony of *M. vancouverensis* is not likely to persist without either expanding or quickly becoming extinct. Several colonies have indeed exhibited "boom or bust" population trends in recent times, for example at Green Mountain, Hooper North, "P" Mountain and Mount Washington (Smith 1982, Munro *et al.* 1985, this study). The observed influx of "new" marmots at Haley Lake, Haley "slash" and Pat Lake sites demonstrates how rapid expansion could occur at a given site, and suggests that dispersal is an integral aspect of *M. vancouverensis* behavior. Finally, the appearance of solitary marmots in unusual habitats (Comox and Coombs records; Munro *et al.* 1985) indicates that *M. vancouverensis* is capable of dispersing through extensive stretches of forested habitat, and reinforces the view that this species is adapted to a lifestyle involving local extinctions and re-colonization.

The meta-population structure of *M. vancouverensis* is not new. Since the most recent glacial period more than 10,000 years ago, *M. vancouverensis* has been confined to patches of sub-alpine habitat kept clear of trees by soil-structure, snow-creep, avalanches and fire (Heard 1977, Milko 1984). Expansive areas of suitable natural habitat are rare. Few sub-alpine meadows on Vancouver Island compare in size with those at Haley Lake, Douglas Peak or "P" Mountain. Indeed, results of BCMOE surveys suggest that many, if not most, marmot colonies are comprised of one to three family units inhabiting smaller habitat patches. A fundamental conclusion must be that marmots have survived, to date, largely through their ability to disperse and re-colonize a mosaic of small habitat patches (i.e., to live in meta-populations).

Given this logic, records of individual marmots or small colonies indicate that nearby sources of dispersal exist, or existed recently. The historic evidence (Appendix I) therefore suggests that in recent times there were at least three meta-populations on Vancouver Island; one centered around the Douglas Peak type locality, one centered in the Nanaimo Lakes/River watersheds, and another in the Strathcona Park/Forbidden Plateau region. This interpretation is supported by the number of adult marmots collected in 1910 at Douglas Peak (Swarth 1912) and by various records from the Strathcona Park region (BCMOE files). Records from intermediate areas (eg., Mount Joan and Mount Arrowsmith) may indicate that in recent times the entire population constituted a single, large, meta-population.

M. vancouverensis apparently no longer inhabits portions of its historic range. Observations suggest that the Douglas Peak and Forbidden Plateau meta-populations are extinct or near extinction. The Mount Washington colony (if it still exists) is either a remnant of the Forbidden Plateau meta-population or, less probably, suggests that nearby colonies remain undiscovered. In contrast, the Nanaimo meta-population is doing comparatively well, and appears to be stable in "natural" habitats, and stable or increasing in "slash" areas. The meta-population structure of *M. vancouverensis* suggests an important conservation principle. Rather than focusing on attempts to "protect" individual marmot colonies from extinction, wildlife managers must provide for a mosaic of occupied habitats, close enough together to facilitate re-colonization if and when local extinctions occur.

Sociality and ecology

M. vancouverensis is among the most social of marmots (Heard 1977). I believe this to be the logical result of its evolutionary history and population structure. Michener (1983) classified several *Marmota* species on a gradient from "asocial" types, characterized by male dominance and territoriality (eg., *M. monax*), to highly social "egalitarian" species in which dominance relationships and territoriality are essentially absent (eg., *M. olympus*). Michener hypothesized that the prime forces determining trends in social structure are avoidance of predation, and avoidance of inbreeding. Anderson *et al.* (1976), working with *M. flaviventris*, proposed that limited resource availability (hibernacula) promoted increased social tolerance and organization. I find no conflict between these points of view, since both are directly linked to the size of marmot colonies.

Compared to other *Marmota*, *M. vancouverensis* inhabits smaller habitat patches, and presumably has done so for much of its evolutionary history (Milko 1984). Assuming Michener's (1983) viewpoint, a highly social, but monogamous, population structure would be advantagous for *M. vancouverensis* since both inbreeding and chances of predation would be minimized. The limited-resource hypothesis of Anderson *et al.* (1976) would also suggest that *M. vancouverensis* display little territoriality, and share communal hibernacula. My data tend to confirm these expectations. Behavioral observations and genetics suggest that *M. vancouverensis* is essentially monogamous within any given reproductive season. Males apparently do not form harems, which would reduce effective population size. Data are insufficient to assess year-to-year pair-bonding; the observed persistance of several pairs may reflect a dearth of breeding-age marmots rather than a purely behavioral trend. Communal hibernation is suggested by the small number of hibernacula found, and by late-summer observations of numbers of marmots using these burrows. Obvious dominance behavior (eg., chasing or lunging) was rarely observed, and young from different litters were seen to mingle freely.

Marmota vancouverensis does not appear to reproduce before its third spring. Delayed maturity is presumably the result of a short growth season combined with the need to attain a relatively large body size before first reproduction (Heard 1977). Morphological data suggest that the physiological cost of reproduction to females is high, which supports this idea. The single female which produced litters in consecutive years was exceptional; generally a biennial (if not longer) interval between reproductive events appears to be the rule for females. Cumulatively, these factors suggest a fairly low lifelong reproductive potential for *M. vancouverensis*, although this is obviously contingent upon maximum age. Several animals are known to be at least 5 years old; unfortunately I was unable to find a reliable formula for determining age of *M. vancouverensis* from morphological characteristics. Continued mark-recapture work is needed to establish maximum age, lifelong reproductive potential and average survivorship rates. My data do not rule out the possibility that adult males breed annually. However, observations do not support the hypothesis that an "average" family unit consists of an adult male and two reproductive-age females which breed in alternate years, as is the case in *M. olympus* (Barash 1973). If this were true of *M. vancouverensis*, colony reproductive rates should be more stable from year-to-year.

Differences between "slash" and "natural" marmots probably result from several factors acting in concert. Larger average litter sizes in "slash" environments may reflect better nutritional resources, earlier emergence from hibernation, response to an unoccupied habitat or a combination of these. Although sample sizes are small, Pat Lake "slash" animals apparently grow faster and larger than those from "natural" sites, which lends credence to this possibility. Similar results were reported for "satellite" colonies in *M. flaviventris* by Armitage and Downhower (1974). Differences in turnover rates between "slash" and "natural" sites were unexpected; if "slash" animals truly inhabit a more "optimal" environment (as suggested by larger body mass and larger litters), one should also expect them to exhibit increased persistance at their "home" burrows. This was not the case.

It is possible that my turnover data from "slash" colonies reflect dispersal rather than mortality. However, I can offer no explanation as to why an adult marmot, having reproduced successfully in a "slash" burrow and grown large and fat, would then abandon the site and disperse from the immediate area. Certainly this behavior was not observed in marmots from "natural" sites. In evolutionary terms, such "continuous dispersal" behavior would dramatically increase the possibility of dispersal-related mortality, which is already likely higher than it is for sedentary individuals (Smith 1987). Thus, I believe the alternate hypothesis (higher overwintering mortality in "slash" colonies) to be more likely correct, despite my inability to demonstrate this using very limited survivorship data.

Türk and Arnold (1988) hypothesized that distribution of Alpine marmots (*M. marmota*) is limited by thermoregulation. They suggest that high ambient temperatures at low elevation habitats force marmots to curtail daily foraging behavior, and therefore prevent marmots from obtaining fat reserves sufficient to survive winter hibernation. Morphometic data from Pat Lake animals do not support this idea; if anything, Pat Lake animals were larger than their counterparts from "natural" sites. However, Türk and

Arnold's hypothesis should not be rejected out of hand. Avoidance of high ambient temperatures at low elevations could explain the observed distribution of "slash" colonies; many face northwest to northeast, or are partially shielded from direct morning or afternoon sunlight by topographic features (Fry *et al.* 1986, this study). The negative evidence may also be important; vast areas of logging-slash at 800 to 1400 metre elevations have not been colonized by *M. vancouverensis*, which suggests some form of microclimatic limitation.

A possible limiting factor involves elevation and hibernacula suitability. Presumably the same mechanisms which could allow earlier emergence from hibernation in "slash" environments (i.e., earlier snow-melt and vegetation growth) could also restrict the availability of thermally stable hibernacula. More variable (although not necessarily warmer) temperatures caused by reduced snow-pack insulation could increase the rate of spontaneous natural arousals, increase hibernation-related metabolic expenditures, or both (B.M. Barnes, University of Alaska Fairbanks, pers. com.). This would have obvious repercussions upon overwintering survival. Indeed, Barash (1973) reported that mortality of *M. Olympus* appeared to correlate inversely with snow cover. This hypothesis could and should be tested, possibly using the microclimate methods of Barnes (1989) or, more directly, by excavating suspected hibernacula in "slash" areas to search for skeletal remains.

Deterministic environmental change

The historic rarity of *M. vancouverensis* is largely explained by its habitat requirements. Pronounced climatic change and forest succession following the most recent glacial period left only patches of habitat available for this species (Milko 1984, Franklin *et al* 1971, Kuramoto and Bliss 1970). This, however, does not explain the comparatively recent disappearance of marmots from other areas such as the Douglas

Peak type locality or the Strathcona Park region, where much apparently suitable habitat remains unoccupied.

During the 1970s and early 1980s there was considerable public concern that *M. vancouverensis* suffered from habitat changes caused by forestry or ski-hill development (Munro *et al.* 1985, Deardren 1983). Data concerning the impact of ski-hills are ambiguous. At Mount Washington and Green Mountain, removal of trees and creation of ski runs was followed by increased marmot numbers and distribution through the early 1980s (Munro *et al.* 1985). My observations indicate that the Mount Washington colony is now extinct or at an extremely low population level, and Green Mountain animals no longer occupy several burrow complexes located in ski-run areas. Similarly, several recent reports exist from the Mount Arrowsmith ski hill area, but no active burrows have been found on that mountain since 1938. It would be premature to conclude that ski-hills exert either a negative or positive effect; however, the limited number of ski-hills essentially makes this a "non-issue" in terms of overall population viability.

Logging has indisputably created new marmot habitat at several sites surrounding the Green Mountain/Gemini Peak/Haley Lake area, and at Mount Whymper and Mount Service. In 1984 fully 1/3 of the censused population was found in "slash" sites (Munro *et al.* 1985). Marmots have established colonies and reproduced successfully at these sites, and some colonies have survived for almost a decade. (However, higher marmot turnover rates at both "slash" sites studied suggests important differences between these colonies and those occupying higher elevation "natural" habitats.) Logging-slash habitats have also been described as "ephemeral" because reforestation will eventually make them unsuitable for marmots (Munro *et al.* 1985). This is arguable; I suspect that some "slash" sites (eg., the one at Road D13) may resist forest succession for as long as some "natural" sites. The point is probably moot. As logging is a principal component of the

Vancouver Island economy, there is little danger that logging-slash will ever be in short supply.

Other effects of logging-slash, particularly on dispersal and colony formation, are not understood. I. McTaggart-Cowan and D. Heard (cited in Munro *et al.* 1985) suggested that removal of forest cover would enhance dispersal and recolonization of mountain sites. I believe the reverse may be true; i.e., that creation of new habitats at the base of mountain colonies decreases long-distance dispersal movements, and thus reduces the probability that animals find a mate and establish a colony at a distant mountain. Dispersing pikas (*Ochotona princeps*), which exhibit a meta-population structure similar to *M. vancouverensis*, generally attempt to colonize the first suitable patch of habitat which they encounter (Smith 1987). I suspect this is also true in *M. vancouverensis*, since long-distance dispersers would encounter increased probability of death from predation or thermal stress.

In effect, dispersing marmots could be "short-circuited" by nearby, expansive and attractive areas of new "slash" habitat; this would reduce the probability that dispersing marmots "buttress" or "rescue" colonies farther away. This would be particularly true if "slash" animals incur higher overwintering mortality, and themselves produce fewer dispersers. Although speculative, this hypothesis would explain observed genetic patterns (showing little gene flow between Pat Lake and the Haley Lake/Green Mountain complex), and recent population trends (with marmots doing well in the greater Nanaimo River/Lakes watershed and more poorly at outlying, peripheral colonies). My data are insufficient to test these competing hypotheses.

It has been suggested that logging, mining and ski-hill development may create problems associated with human visitation and harrassment by providing easy access to marmot colonies. Deardren (1983) listed a number of possibly deleterious actions, including trampling of vegetation, snow compaction, wildlife photography, disturbance from dogs, noise from gunshots or all-terrain vehicles, and vandalism. Apart from two known cases of marmots being shot by vandals (Munro *et al.* 1985), there is no evidence that any of these factors have had a significant effect on marmots. Many colonies are protected by inaccessability (the Nanaimo River watershed is closed to the public during the period of marmot activity, except during the autumn hunting season) and through lack of specific information as to their location (members of the public are generally directed to Green Mountain only). In addition, *M. vancouverensis* appears to be very tolerant of human presence. Heinsalu and Smith (1983) described marmots living amidst the noise and dust of log-yarding activities on Butler Peak. Both Heard (1977) and I believe that our daily intrusion into marmot habitats did not produce lasting impacts or impinge upon reproductive success. In both studies, no mortality occurred as a result of capture; four animals from this study produced young one year after capture.

I conclude that *M. vancouverensis* has not suffered population "shock" due to habitat loss caused by logging or ski-hill development, except in a positive sense. Levels of human visitation or harrassment are low and likely insignificant. Management of such influences should not constitute a major component of recovery efforts. The effects of logging-slash upon marmot survivorship, dispersal patterns and colony formation are not yet clear but may be of major importance; this question urgently requires additional research.

Demographic and environmental stochasticity

Random demographic or environmental events are probably of major importance to *M. vancouverensis* colonies. Data from Milko (1984), Heard (1977) and this study illustrate the variable reproductive success at Haley Lake in recent years. Smith (1982) reported a substantial population increase at Green Mountain colony from the 1950s to the early 1980s. In contrast, Hooper North (Heinsalu and Smith 1983), Mount Washington and "P" Mountain colonies (this study) have declined within the past few years. Such population fluctuations may be related to yearly climate patterns, although my data do not demonstrate a statistical association.

Smith (1982) attributed increased marmot numbers and distribution during the late 1970s to a period of mild winters. Milko (1984) thought that annual differences in reproductive success were related to variation in winter snow-depths and the timing of spring snow-melt. Similar trends exist in other marmots (eg., *M. flaviventris*; Armitage and Downhower 1974) and certainly the sub-alpine regions of Vancouver Island exhibit highly variable weather conditions. Page (1987) postulated the existence of an 18-year cycle in Vancouver Island snowfall, with decades of comparatively mild winters followed by periods of more extreme winters. Such patterns could have enormous implications for marmot survival, particularly at small colonies with marginal hibernacula or food resources.

Circumstantial evidence suggests that predation can have important effects on small colonies. Nagorsen (1988a) attributed 13 partial skeletons found in a limestone cave near Sutton Pass to an entire colony that was extirpated by human hunters 2500 years ago. Similarly, no marmots have been found at Douglas Peak since Swarth's scientific collecting in 1910. These observations suggest that single predation events could exert a catastrophic effect on small marmot colonies. In addition, predation events should not be considered in isolation from social structure. Halpin (1987) found that the shooting-death of several adult males from a colony of black-tailed prairie dogs (*Cynomys ludovicianus*) was followed by severe population effects. Young animals continued to disperse and did not replace lost adults; the population was thus left with a dearth of breeding males and declined. For such reasons, observations of wolf-scat containing marmot fur (D.W. Nagorsen, Royal B.C. Museum, pers. com.), presumed cougar predation (Heard 1977) and presumed golden eagle predation (this study) should not be discounted lightly. Clearly a single predator can exert a severe population effect upon a colony which consists of one or a few family units. Despite such examples, I cannot conclude that predation is now, or has been in recent times, an important limiting factor for *M. vancouverensis*.

No disease or parasite-induced mortality is known in *M. vancouverensis*. Infestation with fleas (*Thrassis spenceri*) is often heavy, but I have no evidence that it contributes to mortality. Other known parasites include an unidentified *Ixodes* tick (Heard 1977), the helminth *Diandrya vancouverensis* described only from this marmot, the nematode *Baylisascaris laevis* (Mace and Shepard 1981), and several as yet unidentified ear-mites (this study). *Eimeria* sp., the Anoplocephaline tapeworm *Dianandrya composita*, and ascarid eggs have been found in marmot scats collected at Haley Lake (K. Langelier, Island Veterinary Hospital, Nanaimo, pers. com.). I have no evidence that any of these parasites are important, in a population sense, for *M. vancouverensis*.

Marmot pathology is poorly understood. Woodchucks (*M. monax*) are chronic carriers of woodchuck hepatitus virus (WHV) in several eastern states, but this infection has not been recorded in western populations (Summers *et al.* 1978). Armitage and Downhower (1974) found no disease-related mortality in *M. flaviventris*. However, lack of information concerning possible disease threats to *M. vancouverensis* does not mean that none exist. Indeed, compact distribution of known Vancouver Island marmot colonies suggests that infection could spread rapidly if an epizootic occurred. The risk is aggravated by the recent expansion of introduced Eastern cottontails (*Sylvilagus floridanus*) into the Nanaimo watershed region. These rabbits could act as a new vector for existing diseases, or could themselves introduce new diseases such as Tularemia (*Francisella tularensis*).

Available data for *M. vancouverensis* indicates that colony extinction is a normal and fairly common occurence. Anecdotal evidence and reproductive data support the general rule that small colonies are more vulnerable to random extinction than larger ones. Large "colony-complexes" such as the Green Mountain/Gemin Peak/Haley Lake colonies undoubtedly fulfill an important role in facilitating the re-colonization of smaller colonies; these should be protected to the extent possible. Efforts to control parasites or predators are currently unwarranted. The risk of catastrophic disease is real given recent introduction of a possible new disease vector (*Sylvilagus floridanus*), concentration of known marmot colonies in a limited geographic area, and an evolutionary history which has isolated *M. vancouverensis* from mainland marmots and diseases .

Inbreeding depression

Inbreeding leads to loss of genetic variability and expression of deleterious recessive alleles, a phenomenon known as inbreeding depression. Inbreeding depression has been documented in a wide variety of mammals (Wayne *et al.* 1986); it may involve reduced reproductive success (Wildt *et al.* 1987), increased juvenile mortality (Ralls *et al.* 1988), or increased susceptability to disease (O'Brien *et al.* 1985). Alternately, inbreeding can "purge" populations of deleterious genetic traits, and some highly inbred captive populations have survived for many generations (white lab rats being the classic example). In most natural populations, strong behavioral traits, such as dispersal of juveniles, tend to prevent close inbreeding (Ralls *et al.* 1986). Inbreeding depression is therefore most common in zoo populations where such behavioral traits cannot operate (Wayne *et al.* 1986).

Recent studies suggest that inbreeding depression may be of concern for wild populations that are small or increasingly fragmented by human activities (Gilpin and Soulé 1986). For example, Chesser (1983) found genetic differences between colonies of black-tailed prairie-dogs (*Cynomys ludovicianus*) that were extreme given the short geographic distances between colonies. He suggested that human-caused habitat changes had altered normal dispersal patterns to the point where inbreeding was aggravated. In contrast, close inbreeding is unknown in *M. flaviventris* (Schwartz and Armitage 1981, 1980). Rates of dispersal between colonies, together with behavioral traits, evidently prevent inbreeding depression in that species.

There is no evidence for inbreeding depression in *M. vancouverensis*. Although my data show slight genetic differences between colonies, results are more suggestive of founder effects and a small overall gene pool than a tendency towards close inbreeding. Blood samples from additional colonies would be helpful; in particular, from a geographically-distant site such as Mount Washington. Theory dictates that a small isolated colony of marmots, such as that thought to have existed at that site since the 1940s, must be inbred by definition. Blood samples from the Mount Washington colony, if it still exists, could provide an important test of whether my samples describe "normal" levels of genetic variability and inbreeding in this species.

The current effective population size of *M. vancouverensis* is disturbingly close to that which must, under panmictic conditions, yield an inbreeding level of 1%/generation (the level considered "acceptable" by most animal breeders: Lande and Barraclough 1987). In addition, genetic data suggest some differentiation among the sampled sub-populations; it is likely that more peripheral colonies (eg., Heather Mountain, Mount Hooper) are also partially isolated. If this is the case, my estimate of N_e must be reduced far below the commonly-accepted N_e=50 criteria. However, it is also possible that a history of population "bottlenecks" has purged most deleterious alleles from *M. vancouverensis*, and that this species may be less influenced by inbreeding than other mammals. In fact I think this likely given its meta-population structure, and paleoecological evidence suggesting a long history of survival in limited habitat patches (Milko 1984). Indeed, one interpretation of the unique dark pelage of *M. vancouverensis* suggests that it was a melanistic form that became fixed during just such a "bottleneck" (Hoffman *et al.* 1979). Ultimately, current genetic data, together with observed reproductive rates, do not immediately dictate either a captive-breeding program, or translocation between colonies, as a genetic management tool.

Long-term evolutionary potential

While inbreeding depression has measurable effects upon reproductive success or other population parameters, long-term loss of genetic variability may confer evolutionary disadvantages which do not become apparent for generations (Frankel and Soulé 1981). Unfortunately, for obvious reasons there exist few empirical data which suggest how much genetic variability is "enough". This places wildlife managers in a difficult situation, particularly if no information is available concerning "normal" levels of genetic variability in a particular species.

Franklin (1980) argued that an effective population N_e of 500 would balance the conflicting forces of mutation and genetic drift, and would be sufficient to preserve genetic variability over the long term. Substitution into Reed *et al.*'s (1986) formula suggests that this would require over 2000 *M. vancouverensis*. This is not a realistic possibility; it is unlikely that existing natural habitats on Vancouver Island could ever support such a large population. Moreover, the N_e=500 rule-of-thumb assumes a single effective population and does not consider behavioural traits that counterbalance inbreeding (as suggested for *M. vancouverensis* by negative F_{is} and F_{it} values).

My data do not suggest that *M. vancouvensis* is in any immediate danger of becoming genetically monotypic or less evolutionarily-fit than other mammal species. This statement must be qualified; as stated earlier, by my sampling of *M. vancouverensis* from the single meta-population which is stable or increasing (or even, to be blunt, demonstrably extant). I believe that the current small effective population size of *M. vancouverensis* is not adequate to ensure evolutionary potential over time; however, population objectives must by necessity be based more upon practical considerations (available habitat) than a simplistic "N_e=500" or similar rule.

Population viability

In the words of McTaggert-Cowan (1980), *Marmota vancouverensis* is currently undergoing "a very difficult stage in its evolutionary history". Population viability analysis (PVA) using genetic, demographic and distribution data indicates that current populations are not "viable" given current scientific opinion as to what that word means.

Stochastic demographic and environmental events (bad winters, predation, disease, poor reproduction and/or survivorship in consecutive years, etc.) currently pose the largest threat of extinction to this species. This is the inevitable result of small and semi-isolated colonies, chronic low survivorship of young marmots, and present "eggs-in-one-basket" geographic distribution. The known population is barely large enough to prevent short-term loss of genetic variability due to genetic drift or inbreeding, and insufficient to maintain long-term evolutionary potential if one assumes the current "N_e=500" rule-of-thumb to be valid for an island species. Because *M. vancouverensis* may already have been "purged" of deleterious alleles through a succesion of population bottlenecks, I consider genetic issues to be a secondary issue. Or, as Lande and Barraclough (1987) put it, "genetic variation is not important if the population becomes extinct".

The present situation is largely attributable to deterministic environmental change. Past patterns of *M. vancouverensis* distribution and abundance were certainly dictated by climate change, and consequent forest succession, between the time that *Marmota* first colonized Vancouver Island and modern times. Given current paleoecological evidence, it is virtually certain that Vancouver Island marmot habitat has shrunk dramatically in the past 10,000 years due to trees growing where glaciers once scoured. Recent conversion of Vancouver Island from a mostly forested environment to a patchwork of clearcuts has complicated the marmot equation. Minimal data are available to relate colony dynamics with these changes. The conflicting hypotheses of McTaggart-Cowan and Heard (Munro *et al.* 1985) and myself require testing, as dispersal is central to understanding why, when and how marmots establish new colonies or reinforce existing ones. The essential question has been efficiently posed by W.T. Munro (BCMOE, pers. com.) as follows: does logging-slash act as a marmot "sink" which truncates normal dispersal patterns, or does it function as a "reservoir" which is still in the process of being filled?

If the latter is true, expansion of "slash" colonies will be accompanied by an overall increasing range as now empty natural habitats are re-occupied. If the former, then continued drainage of dispersing animals from natural colonies into logging-slash will occur at the expense of more peripheral colonies, and wildlife managers will be faced with a shrinking "basket" centered around the Green/Gemini/Haley Lake complex. My data do not eliminate either possibility. Logging-slash colonies are known to become established soon after an area is clearcut, several "slash" colonies have survived for almost a decade, and females produce slightly larger litters in "slash" than in natural colonies. All these things are consistent with a species encountering a new, unoccupied ecological niche or "reservoir". In contrast, genetic differentiation between nearby colonies, high turnover of individuals, family units and burrow complexes in logging-slash, together with an overall declining range in historical times, all tend to support the "sink" hypothesis.

Marmota vancouverensis currently occupies a precarious position. Because colonies within the greater Nanaimo watershed are mostly stable or increasing, the threat of imminent extinction is low. However, geographically confined distribution, small effective population size, and high susceptibility of colonies to random events all suggest that fears of extinction are not unfounded. Ultimately, long-term survival of *Marmota vancouverensis* will require additional meta-populations, larger overall population size, and maintenance of reasonable levels of gene flow between individual colonies.

THE RECOVERY PLAN

Note to the reader

A formal Vancouver Island Marmot Recovery Team was established by BCMOE in August of 1988; team members are listed in the Acknowledgments. I wrote the draft recovery plan under contract to BCMOE in January of 1989; the initial draft has been modified after extensive consultation with the Recovery Team, and incorporation of new research results. I anticipate that a slightly revised version of the following will be released as the "official" plan in late 1990.

Establishing objectives

Establishing recovery objectives for *M. vancouverensis* is difficult because mechanisms of colony extinction have not been conclusively identified. Wildlife managers are thus placed in the unfortunate position of trying to "recover" *M. vancouverensis* without knowing, with any degree of certainty, why the species is "endangered". The situation is complicated by a lack of information on historical distribution and abundance, which makes it difficult to establish what "recovery" should entail. Despite this, population viability analysis suggests that direct management is required to reduce the vulnerability of this species to extinction. PVA, in concert with historic data, also offers a clear direction for recovery efforts.

Criteria for downlisting species from "endangered" status have been produced by COSEWIC (Committee on the Status of Endangered Wildlife in Canada, Ottawa). These criteria were followed with modifications in accordance with the Vancouver Island environment and the biology of *M. vancouverensis*. The proposed population objectives for this species are to:

1) Maintain the existing population of 200-300 animals (N_e=effective population size of about 50) within the area of current distribution.

2) Establish a second population (N_e=50) with a center of distribution not less than 50 km away from the centre of distribution of the existing population.

3) Establish a third population (N_e=50) if sufficient habitat is available.

In this context, "population" means "meta-population", here defined as a set of local colonies or sub-populations (Gilpin 1987). Meta-populations should include approximately 200 marmots each, for a total population of about 600 animals throughout Vancouver Island. My results suggest that each of the these three meta-populations would be sufficient to maintain genetic variability over the forseeable future, and large enough to survive the effects of demographic or environmental stochasticity. The provision of three distinct meta-populations is justified on the basis of historic evidence, and on the simple desire to prevent an "eggs-in-one-basket" scenario involving existing colonies in the Nanaimo River/Nanaimo Lakes watersheds.

Downlisting of *M. vancouverensis* from "endangered" to "threatened" status should occur when population objective #2 is met. Downlisting from "threatened" to "vulnerable" status should occur when population objective #3 is attained. Because *M. vancouverensis* is confined to Vancouver Island, complete de-listing from "vulnerable" status is not recommended. Attainment of population objectives require the following actions:

Objective #1: Maintain existing meta-population.

a) Determine survival and dispersal of radio-collared animals including use of hibernacula at both natural and "slash" colonies.

b) Monitor existing core populations annually for numbers and reproduction.

c) Protect existing habitat from disturbance through designating Crown lands as Wildlife Management Areas, increasing the size of the Haley Lake Ecological Reserve, and obtaining agreements with private landowners.

d) Conduct literature review on potential diseases.

Objective #2: Establish a second meta-population.

a) Compile a systematic inventory of populations and potential habitats. This will require the mapping of all marmot sightings and additional marmot surveys.
b) Review translocation literature.
c) Develop a transplant plan including methods, costs and timetable.
d) Initiate transplant and monitoring program.

Objective #3: Establish a third meta-population.

a) No actions to be taken until Objective #2 is achieved.

Inventory

Additional surveys are required to determine present habitat suitability and marmot population status throughout Vancouver Island. Discovery of new colonies could modify the nature of recovery efforts, notably concerning the need for transplants. Although I think it unlikely, discovery of additional meta-populations could drastically reduce the need for other "recovery" activities. Towards this end, all possible marmot sightings from northern and western Vancouver Island should be investigated, and systematic surveys of potential habitats must be undertaken. Particular attention should be given to historical sites in the Douglas Peak (type locality) and Forbidden Plateau regions.

Research and monitoring

Limited understanding of *M. vancouverensis* ecology dictates that research and monitoring activities be integral components of recovery efforts. I propose that several priorities be established, as follows:

1) Survivorship and reproduction: The existing data base on Haley Lake, Green Mountain and Pat Lake colonies should be maintained. This will serve to provide early warning if population trends turn downward, and will augment, at minimal cost, basic biological knowledge concerning age structure, survivorship, reproductive potential and social characteristics. I propose that the established mark/recapture experiment established during this study be continued for a minimum of five years.

2) Dispersal: Because dispersal is central to understanding how marmot metapopulations function, research is needed to determine rates and magnitude of marmot movements. Emphasis should be placed on determining the influence of land-use changes (i.e., logging slash) upon dispersal movements, and learning which age and sex classes disperse. The experiment should utilize radio-telemetry and surgically-implanted transmitters; tests are necessary to determine their practicality in a remote, Vancouver Island environment.

3) Hibernacula: Additional research is required to characterize *M. vancouverensis* hibernacula. This is particularly important given my suggestive but inconclusive data concerning burrow use, family group turnover, and individual survivorship in "natural" versus "slash" habitats. This would be best accomplished with a system of remote microclimate

monitoring stations. As above, tests are needed to determine the feasibility of using such equipment on Vancouver Island.

4) Translocation: It is important that appropriate methods be developed for transplanting marmots. In a "best-case" scenerio, transplant technology may provide an ace-in-the-sleeve that allows remnant populations (Mt. Washington?) to grow quickly. In a "worse-case" scenario (epizootic at Haley Lake?), transplant technology may be be the only card left to play. I propose that an experimental transplant involving one or two family groups be carried out early in the recovery program.

Habitat acquisition and management

There is much habitat available for *M. vancouverensis* on Vancouver Island, most of which is either owned outright or leased by private forest companies. Given marmot predilection for steeply-sloped, treeless areas, most sites are not likely to be threatened by intensive resource extraction or urban development. Tourism and recreation development may become important issues at some existing or potential marmot colonies. However, given limited funds and the history of successful landowner agreements with companies owning marmot sites, outright purchase of *M. vancouverensis* habitat is not recommended. However, it is important that BCMOE secure control over public access at transplant and reintroduction sites; I propose the following:

1) BCMOE should aquire (purchase) the sub-alpine meadows known locally as "Grassy Mountain" near the Douglas Peak type locality and designate same as a wildlife management area (WMA).

2) BCMOE should consult with B.C. Parks to determine which portions of the Strathcona Park ecosystem might be "posted" as a marmot "recovery area", in which public access would be controlled.

3) BCMOE should continue efforts to expand the Haley Lake "marmot" reserve as originally proposed by Heard (1977). Functionally, the Haley Lake/Gemini Peak/Green Mountain ridge system is the "epicentre" of marmot activity. Although nothing along this ridge system is likely to provoke a "jobs versus marmots" scenario in the near future, prudence dictates that essential habitats be secured now.

Translocation and reintroduction

Unless large new colonies of *M. vancouverensis* are discovered, translocation will become the most effective means of achieving recovery objectives. Intuitively, animals should be removed from colonies where there is a "surplus", and transplanted to areas where there is a "shortage". Wherever possible, transplanted animals should be taken from "slash" colonies because access will be easier for trappers, and because the risk of disturbing social structures at natural colonies is minimized.

The timing, sex, age, number of animals and the degree of preparation required at reintroduction sites in order to successfully establish marmot colonies is presently unknown. This study suggests that trapping success will likely be highest during August, but this would leave little time for animals to become habituated to their new environs. Similarly, there is little point in attempting transplants if hibernacula are not available at the new site, yet little information exists on what constitutes a suitable hibernacula. For these reasons, the timing, scale and methods involved in reintroduction are research questions of the highest priority. A prototype reintroduction, involving the transplant of one or two families to one site, would provide much-needed information regarding specific techniques that work. Due to the small size of the available reservoir population, reintroduction efforts must focus initially on the establishment of only one additional colony. Having proven the reliability of translocation techniques, reintroduction can then proceed on a larger scale.

Captive breeding

There is currently no justification for the establishment of a captive-breeding colony of *Marmota vancouverensis*. Apart from the high costs involved, there is no evidence to suggest that a captive marmot colony would assist recovery efforts. Captive *M. vancouverensis* at the Okanagan Game Farm changed their seasonal and daily activity patterns (Dyer 1982). This, together with possible exposure to pathogens foreign to Vancouver Island, produced animals that were not suitable candidates for reintroduction, even had the colony flourished.

This should not preclude the establishment of a captive marmot colony for other purposes such as public education or research; however, the goals of such a program must be carefully established, and permission should be granted only if these will not detract from the success of recovery efforts. Furthermore, captive colonies should be maintained, if at all, in suitable habitat on Vancouver Island.

Public education and liaison

BCMOE should continue to promote a high public profile for both marmots and the recovery plan. Several specific activities should be carried out, including:

1) <u>Maintain the Vancouver Island Marmot Liaison Committee</u>: This committee, comprised of members of government, non-government organizations and the general public, is an effective forum through which many issues can be, and have been, addressed. The committee has also performed a fund-raising function and this should be encouraged. Particularly given the large scale of recovery efforts, the Liaison Committee should be used to channel funds or volunteer labour from non-government sources into the recovery effort.

2) Provide signs encouraging the public to report marmots: Signs are already in place on the access roads to the Nanaimo Lakes and River watersheds. Additional signs are needed near Forbidden Plateau in Strathcona Provincial Park, at the entrance to Mount Arrowsmith Regional Park, on the Port Alberni/Bamfield road just outside of the city limits and on the Island Highway just outside of Woss. Posters requesting marmot information should be placed in all BCMOE offices on Vancouver Island. Signs and posters should be designed by BCMOE in concert with the Interpretation section of B.C. Parks.

3) Develop marmot-viewing potential at one site: Wildlife-viewing and wildlife-related tourism are growth industries of the 1990s. Reid *et al.* (1988) determined that more British Columbians are interested in endangered species than in ungulates, songbirds or waterfowl. One marmot colony should be developed for marmot-viewing; this would have two beneficial results. First, a public able to see marmots would be more prone to supporting the costs of recovery efforts. Second, by planning ahead, managers can control and confine impacts to one site. It is better to be "pro-active" than be forced to react to tourism-development activities that will likely happen anyway. Green Mountain is probably most suitable for development, but further study is required regarding the intensity and management of development.

Fund-raising and management of disbursements

Because the scale and direction of recovery efforts will likely change as a result of inventory and research results, only a three-year budget is proposed here. The recovery plan should be reviewed and updated annually by the Recovery Team. Funding should be sought through RENEW and other non-government agencies. Disbursement of funds shall be made through a special marmot recovery fund to be managed by a non-profit organization (yet to be established). B.C. government funds will be disbursed through existing channels such as the Habitat Conservation Fund (HCF).

Timetable and budget

Year 1

1) Determine survival and dispersal of animals including use of hibernacula	$35,000
2) Inventory -map all marmot sightings	$1,000
3) Monitor existing populations	$10,000
4) Habitat management and protection	$1,500
5) Review disease and chemical hazards	$500
Total	$48,000

Year 2

1) Continue dispersal research	$20,000
2) Inventory -survey possible habitats	$30,000
3) Monitor existing populations	$10,000
4) Develop transplant plan	$5,000
5) Habitat management and protection	$1,500
Total	$66,000

Year 3

1) Monitor existing populations	$10,000
2) Continue inventory if required	$20,000
3) Carry out transplant	$20,000
4) Habitat protection and management	$1,500
Total	$51,500

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APPENDIX I: the Vancouver Island Marmot

Taxonomy

Marmota vancouverensis was described in 1911 from 11 specimens shot near Douglas Peak in west-central Vancouver Island (Swarth 1911, 1912). The species is endemic to Vancouver Island and is the only member of the genus *Marmota* that occurs there (Nagorsen 1987). Placed in the *caligata* group by Hoffman *et al.* (1979), *M. vancouverensis* differs from the closely-related Hoary marmot *M. caligata* and Olympic marmot *M. olympus* in its overall dark brown pelage, cranial morphology (Hoffman *et al.* 1979), karotype (Rausch and Rausch 1971) and behavioral traits (Heard 1977). It is reproductively isolated from other marmot species, although no one has tested interbreeding with *M. caligata* or other species.

History

Prior to 1970, little was known about the distribution or biology of *M. vancouverensis* (Janz 1982). Swarth (1912) described it as locally abundant near Douglas Peak but did not encounter it elsewhere on Vancouver Island. K. Racey collected specimens from Haley Lake in 1931 (Munro *et al.* 1985), Carl (1944) described a colony from Mount Washington and Hardy (1955) listed records from Forbidden Plateau near Strathcona Provincial Park. Rausch and Rausch (1971) collected an adult female from Mount Washington in 1968. Nanaimo hunters inspired the first (Finkelstein and Darling 1973) attempt to inventory marmot colonies, and sponsored the establishment of an unofficial "marmot reserve" surrounding Haley Lake (Janz 1982).

Heard (1977) conducted the first field investigations of *M. vancouverensis*; he compiled ecological and population data which established the basis for all later investigations. His work also enhanced public interest in Vancouver Island marmots, and the late 1970s saw considerable effort directed towards defining their status. Carson (1978) compiled historical records, and members of the public established a public-interest group which became known as the Vancouver Island Marmot Preservation Committee (Routledge and Merilees 1980, Routledge 1981, 1982). From 1979 through 1986, surveys were conducted at known or suspected marmot colonies by either the above group or BCMOE. The Canadian Wildlife Service (CWS) sponsored a survey in 1981 (Fry 1981). In 1984, Milko (1984) completed a botanical analysis of Haley Lake; he later collaborated with CWS in a study of marmot food habits at that site (Martell and Milko 1986).

In 1980 an adult marmot was found living in a garden near the hamlet of Coombs, captured and sent to the Okanagan Game Farm near Penticton. Four additional animals from the Green Mountain area were later added. Despite successful reproduction in captivity, escapes and mishaps led to the functional extirpation of this colony (a single animal remains alive). In 1987, a portion of the Haley Lake site was donated by MacMillan Bloedel and designated as an Ecological Reserve for marmots. The present study also began in that year. In 1988, BCMOE took the lead in establishing a formal Recovery Team; the draft recovery plan was written by myself in early 1989.

Historic distribution and abundance

There exists only an incomplete picture of the past status of *M. vancouverensis*. The distribution of all records is included as Figure 20. Swarth (1912) discovered Vancouver Island Marmots in the basins, meadows and ridges in the vicinity of Douglas Peak and Mount McQuillan, where he described them as "fairly abundant" and "vigilant and unapproachable". That his party could collect 11 adults over the course of two weeks suggests a sizeable population in the region (indeed, he mentions others which escaped

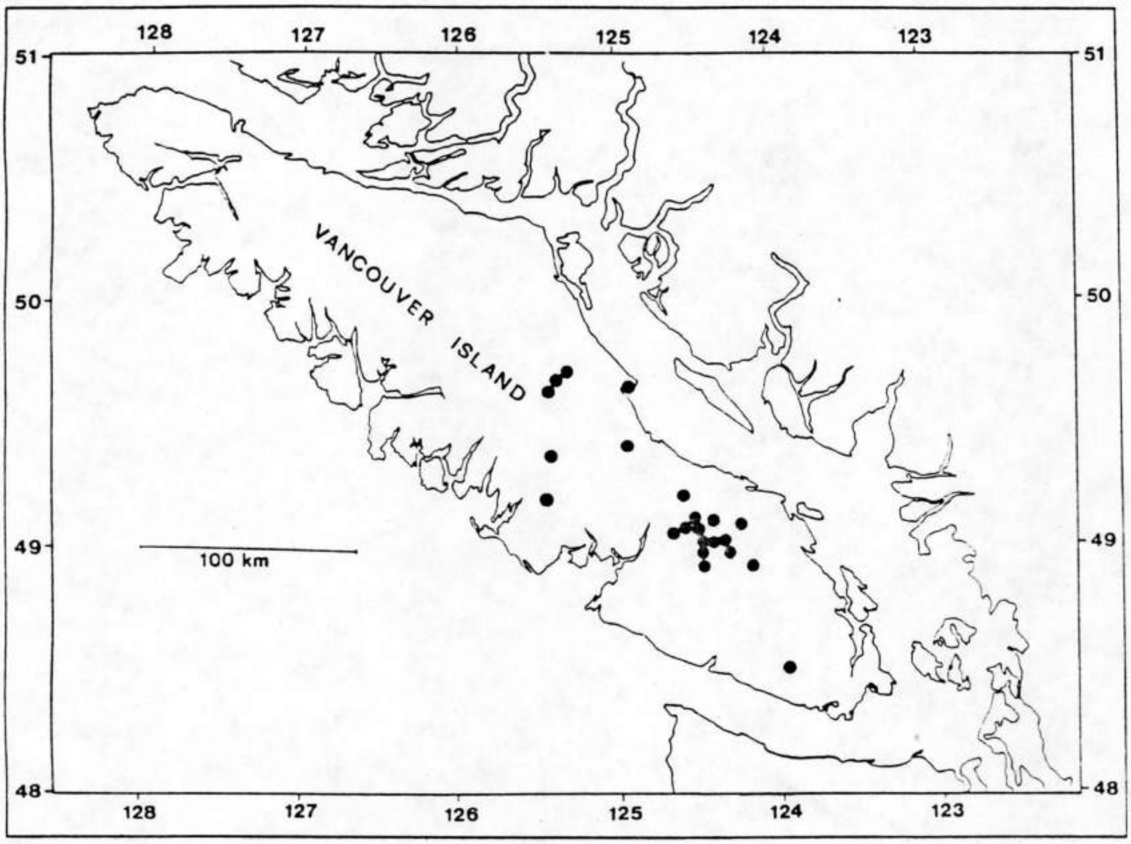


Figure 20: Distribution of historical records for *M. vancouvenensis*. Modified from Nagorsen (1987).

into their burrows "in every instance" after being shot with hard-point bullets). Swarth's work is also intriguing for what he did not find; he ascended Mount Arrowsmith and explored the mountains north of Great Central Lake without finding marmots.

A. Peake collected an adult female from Mount Buttle in 1929. K. Racey collected eight adult specimens from Haley Lake in 1931 (Nagorsen 1988b). In 1938, I. McTaggert-Cowan reported burrows and marmots on the northeast slopes of Mount Arrowsmith (Munro *et al.* 1985). A small colony on Mount Washington and a single animal on Mt. Strata were reported in 1942 by Hardy (1955). Carl (1944) confirmed *M. vancouverensis* from Mount Washington but did not give estimates of population size. More recent reports from the Strathcona Park region include a marmot jawbone of indeterminate age from the Golden Hinde in 1976 and fresh burrows and scats near the summit of Mount Jutland in 1983 (BCMOE files). Two old burrows and a "trial burrow" were found just west of the south end of Buttle Lake by Wildlife Branch personnel in 1982 but no fresh sign was observed (Heinsalu and Smith 1982).

Carl (1944) described marmots from the head of Shaw Creek and Jordan Meadows, which is the most southern record for this species. A 1930 specimen in the Royal B.C. Provincial Museum which was labelled "Jordan River" may in fact be from Jordan Meadows. In 1982, B. Hazeldine forwarded a marmot skull which had been collected from Mount Joan, in the Beaufort Range, in 1968 (Nagorsen 1988b). Prehistoric marmot remains have been found at two sites; Shoemaker Bay (Calvert and Crockford 1983) and Sutton Pass (Nagorsen 1988a). Living marmots are not known from either of these sites; there is a report of marmot whistles heard near the latter site in 1988 (on Nahmint Mountain; G.W. Smith, BCMOE, pers. com.).

On the strength of museum specimens, sight records and interviews, Carson (1978) suggested a historical distribution of some 25 colonies throughout Vancouver Island. Her analysis included the important *caveat* that some records are uncertain and may be based on solitary (dispersing) individuals. Additional records compiled since 1978 suggest a slightly more widespread historical distribution of *M. vancouverensis*, but Carson's *caveat* still holds true. There is no evidence that *M. vancouverensis* was abundant on Vancouver Island in the recent past.

Current distribution and abundance

Early inventory efforts suggested a small (<100 animals) and extremely local population (Routledge 1982, 1981, Routledge and Merilees 1980). Later surveys by BCMOE found several additional colonies (Fry *et al.* 1986, Smith 1985, Smith *et al.* 1984, Heinsalu and Smith 1983, 1982). Surveys in 1982 and 1983 were designed to inventory habitats used by marmots and not to count individuals (Munro *et al.* 1985). In 1984 and 1986, surveys were more intensive and involved repeated visits to colonies; they provide a better estimate of population size. The 1984 effort resulted in a minimum count of 234 individuals, including 68 young, at 42 colonies or potential colonies in nine distinct areas (Munro *et al.* 1985). Fry *et al.* (1986) found 188 marmots including 40 young in 1986, but several areas surveyed in 1984 were not included in this survey. After 1986 no methodical surveys have been carried out, although I monitored numbers at study colonies and searched unsuccessfully for marmots at historical sites (see methods).

Populations of *M. vancouverensis* have increased in the Nanaimo Lakes-Nanaimo River watersheds since the early 1970s (Munro *et al.* 1985). Most of this increase has occurred in logging-slash environments near Haley Lake, Pat Lake and Mount Butler. Other colonies have apparently declined. The Mount Washington colony, if it still exists at all, survives at a very low population level, and no animals are known from the Forbidden Plateau/Strathcona Park region. The "P" Mountain colony appears to be at a low ebb and few recent records exist for the type locality region around Douglas Peak.

Caution must be used in interpreting the distribution data. Large portions of Vancouver Island have never been searched for *M. vancouverensis* and many sites have been only cursorily inspected. Promising leads exist for areas in northern and western Vancouver Island which have never been followed up (G.W. Smith, BCMOE, pers. com.). Given the wide variety of habitats used and reclusive nature of the species, it is likely that additional colonies remain undiscovered. However, recent decades have seen both increased backcountry access from logging roads, and growing public interest in wildlife and Vancouver Island marmots. It is therefore difficult to imagine that large colonies remain undiscovered. As it stands, *Marmota vancouverensis* must be considered one of the world's rarest mammals. The known population numbers only a few hundred, and is concentrated in a relatively small portion of Vancouver Island.

Appendix II: Recipes used in electrophoresis

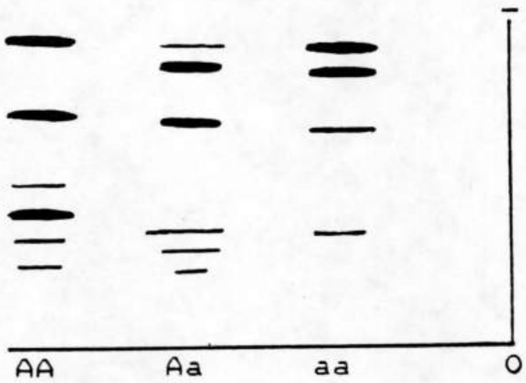
#	Enzyme		tissue	loci	gel	ph	Ref.^{a}
1.	ACP	Acid phosphatase	both	-	all	7-8.0	1.
2.	ADA	Adenosine deaminase	RBCs	1	AC	7.0	1.
3.	ALD	Aldalase	both	-	all	7-9.0	1.
4.	EST	Esterase	plasma	4	RW	7-9.0	2.
5.	GP	General protein	plasma	1?	RW	7-9.0	2.
6.	GOT	Glutamic oxacetic transaminase	both	-	all	7-9.0	1.
7.	GPI	Glucose phosphate isomerase	both	1	RW		3.
8.	IDH	Isocitrate dehydrogenase	plasma	1	AC	7.0	1.
9.	LAP	Leucine aminopeptidase	both	-	all	7-9.0	4.
10.	LDH	Lactate dehydrogenase	RBCs	3	RW		2.
11.	MDH	Malate dehydrogenase	RBCs	1	AC	7.0	1.
12.	ME	Malic enzyme	RBCs	1	AC	7.0	1.
13.	PEPA	LGG-peptidase	plasma	2	MF	?	1.
14.	PEPB	LT-peptidase	plasma	1	MF	?	1.
15.	PEPC	PP-peptidase	plasma	1	MF	8.0	1.
16.	PEPD	GL-peptidase	plasma	1	MF	8.0	1.
17.	PGI	Phosphoglucose isomerase	plasma	1	RW	?	2.
11.	G6PD	Phosphogluconate dehydrogenase	RBCs	1	AC	7.0	1.
18.	PGM	Phosphoglucomutase	plasma	1	AC		3.
19.	SOD	Superoxide dismutase	RBCs	1	RW	?	1.
20.	SDH	Sorbitol dehydrogenase	both	-	all	7-9.0	1.

^{a} References:

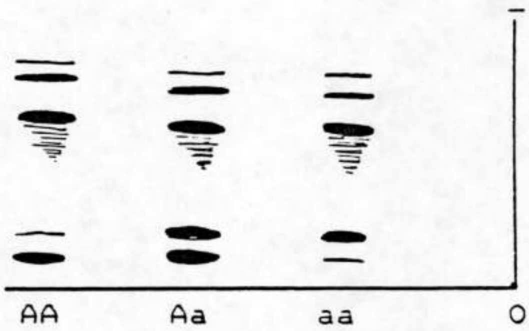
1) Harris and Hopkinson (1976)
2) Selander *et al.* (1971)
3) Shaw and Prasad (1970)
4) R. Owen, University of Calgary (pers. com.).

Appendix II continued: Scoring patterns

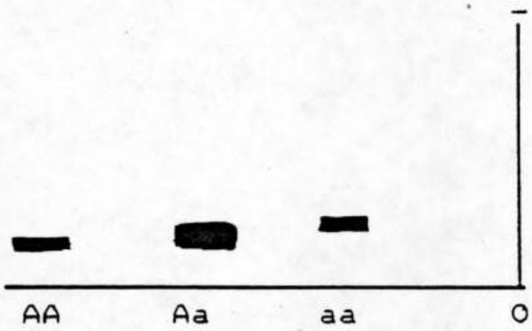
LDH Lactate dehydrogenase



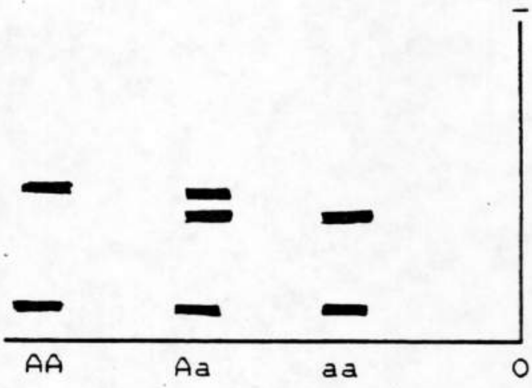
EST-1 Esterase



PEP-pp Peptidase



PEP-lgg Peptidase



Appendix III: Survivorship of marmots at four colonies, 1987 - 1989.

An "o" denotes initial capture; "+" denotes positive identification either by recapture or reading of ear-tags. "x" denotes young-of-the year which were not captured but where location of birth was certain. A question mark ("?") denotes non-positive identification because of ear-tag loss or damage. In several cases, animals were identified before capture from pelage characteristics, scars etc., in these cases an "*" precedes the initial capture "o". Finally, "-" denotes no later observation of the previously-observed marmot.

Green Mountain

Family unit	tags	sex	Age at 1st capture	1987	Year 1988	1989	Name
Betsy	1820	f	3	o	+	+	Betsy
" "	2726	m	3	o	+	-	Opportunity Knox
" "	1514	?	0	o	-	-	
" "	1617	?	0	o	-	-	
" "		-	0	x	-	-	
" "		-	0		x	+	
" "		-	0		x	-	
" "		-	0		x	-	
Rocky	1312	f	3	o	+	+	Rocky Raccoon
" "	2522	m	3	o	+	+	Friar Tuck
" "	923924	f	0		o	+	
" "	926927	m	0		o	+	
" "		-	0		x	-	

Total adults identified	4	4	4
Total young identified	3	6	0
n of reproductive incidents	1	2	0

Haley Lake Bowl

Family unit	tags	sex	Age at 1st capture	Year			Name
				1987	1988	1989	
Triangle	3334	f	3	o	+	+	Tonto
" "	6162	m	3	*	o	-	Oscar
" "	2829	m	2	o	+	+?	Haley's Comet
" "	3132	f	2	o	+	-	Blackie
" "	3536	f	2	o	+	+?	Oprah
" "	3738	m	2	o	-	+?	Boss
" "	-	?	0		x	+	
" "	-	?	0		x	-	
" "	-	?	0		x	-	
Mom #1	5354	f	3		o	+	Mom #1
" "	4748	m	3	*	o	+	Cardinal
" "	-	?	0		x	+	
" "	-	?	0		x	-	
" "	-	?	0		x	-	
Mom #2	6970	f	3		o	+	Mom #2
" "	4950	m	2		o	-	
" "	7172	f	2	*	o	+	Live-wire
" "	6364	m	2	*	o	+	Newfie
" "	-	?	0	x	-	-	
" "	8586	f	1	x	o	-	yearling #1
" "	-	?	0		x	+	
" "	-	?	0		x	+	
" "	-	?	0		x	-	
Mom #3	7879	f	3		o	-	Mom #3
" "	-	?	0		x	-	
" "	-	?	0		x	-	
" "	-	?	0		x	-	
Transient	909910	f	2			o	Luna
" "	976977	f	2			o	Tweedledum
" "	978979	f	2			o	
" "	980981	f	2			o	Tweedledee

Total adults identified	9	11	9
Total young identified	2	12	0
n of reproductive incidents	1	4	0

Pat Lake

Family unit	tags	sex	Age at 1st capture	1987	Year 1988	1989	Name
Endrock	919920	f	3		o	-	
" "	901902	f	0		o	+	
" "	903904	m	0		o	+	
" "	905906	m	0		o	-	
" "	913914	f	0		o	-	
" "	957958	m	4			o	
" "	959960	m	3			o	
" "	961962	m	3			o	
" "	963964	f	2			o	
Midrock	955966	f	3			o	
" "	911912	m	3		o	-	
" "	915916	m	2		o	+	
" "			0			x	
" "			0			x	
" "			0			x	
" "			0			x	
Triangle	907908	f	1		o	+	
" "	932933	f	1		o	-	
" "	934935	f	1		o	-	
" "	928929	f	2		o	+	
" "	917918	m	3		o	-	
" "	921922	m	4		o	-	
" "	951952	m	2			o	
" "	953954	m	3			o	
" "	930931	m	3			o	

	1988	1989
Total adults identified	9	10
Total young identified	4+	4
n of reproductive incidents	2+	1

Haley Slash

Family unit	tags	sex	Age at 1st capture	1987	Year 1988	1989	Name
Tophat	4243	m	2	o	-	-	Sylvester
" "			2	+	-	-	Eyebrows
Patches		m	3		*	+	Patches
Red-tail		f	3		*	+	Red-tail
" "			1		*	-	Apex
" "			0		x	+?	
" "			0		x	+?	
" "			0		x	-	
" "			0			x	
" "			0			x	
" "			0			x	
" "			0			x	
Menza		f	3		*	-	Menza
" "			0		x	-	
" "			0		x	-	
" "			0		x	-	

	1987	1988	1989
Total adults identified	2	4	4
Total young identified	0	6	4
n of reproductive incidents	0	2	1

Appendix III continued: Physical measurements

date	site	age	sex	tags	tatt	FA	HF	neck	chest	total	tail	wght	name
09/01/88	Green	0	f	926927	E7			15	23.5		15	2.2	
07/30/87	Green	0	f	1514								2	
08/03/88	Pat Lake	0	f	905906	F0	13	9.1	20.5	26.8	56.5	16.2	2.9	
08/02/88	Pat Lake	0	f	903904	E0	12	9	21	29	53	15	3	
09/01/88	Green	0	m	923924	A6	11.8	8.4	18.5	23.9	51.5	14	2.5	
08/04/87	Green	0	m	1617		11.6	7.9	15.2	20.2		14.2	2.1	
08/03/88	Pat Lake	0	m	913914	E9	12.6	9	19.5	26.5	51.5	14.8	3	
08/02/88	Pat Lake	0	m	901902	D6	12.8	9.1	19	26.3	55.8	16.8	2.9	
07/06/88	Haley	1	m	8586	C4	12	8.1	17	22.5	50	15	2.3	
08/25/88	Pat Lake	1	m	932933	05	12.8	8.4	23.5	31.2	59	15.5	3.4	
08/25/88	Pat Lake	1	m	934935	07	13.1	10	22	29.2	60	18.5	3.5	
08/04/88	Pat Lake	1	m	907908	F7	13.3	8.9	23.5	31	64	15.5	3.5	
07/05/88	Haley	2	f	6364	F3	14.8	9.4	26	34.2	64	19.6	5	Newfie
08/23/87	Haley	2	f	2928		13.9	8.8	25.3	30.3	64.6	17.7	4.5	Haley's Comet
08/29/87	H. slash	2	f	4342		13.9	9.5	22.8	33	65.9	17.7	4	Sylvester
06/28/89	Pat Lake	2	f	951952	C3	14.8	9.5	24.7	33	66	18	4.3	
08/26/88	Pat Lake	2	f	915916	F6	13.5	9.3	24	29.8	59.5	18.8	3.5	
08/25/88	Pat Lake	2	f	928929	03	13.5	9.8	23	31		17	4.3	
08/20/89	Haley	2	m	976977	F1	14.9	9.4	24.5	33	64	20.8	4.5	Tweedledum
08/20/89	Haley	2	m	978979	D3	14.9	9.7	22	30	71	18.2	4.5	
08/20/89	Haley	2	m	980981	G1	14.9	10	25.5	33	67	18.5	4.5	Tweedledee
08/17/89	Haley	2	m	909910	D2	14.8	9.1	24.1	32.8	67	19.1	4.5	Luna
06/30/88	Haley	2	m	7172	E4	14	8.7	25	31.5	62	15.6	3.5	Live-wire
08/26/87	Haley	2	m	3635		14.9	8.2	26.9	33.2	65.9	16.5	5.5	Oprah
08/25/87	Haley	2	m	3132		14	9.2	25.3	32.9		19	4	Blackie
06/29/89	Pat Lake	2	m	963964	G2	14.9	9.6	23.5	29.5	66	18.3	4	
08/07/87	Green	3	f	2726		14.9	8.9	30.5	35.5	70.9	16.4	6.1	O. Knox
08/05/87	Green	3	f	2522		15.2	8.6	29.1	35.8		16.5	6.4	Friar Tuck
06/23/88	Haley	3	f	4950		16.2	9.6	29	39	68	20	5.5	
06/22/88	Haley	3	f	4748		15.5	9.5	28	38	69	18.5	5.4	Cardinal
06/16/88	Haley	3	f	6162		16.2	9.4	27	35.9	71	20	5	Mad Max
08/26/87	Haley	3	f	3738		13.9	9.4	25.3	33.9	58.8	12.6	5.5	Boss
06/29/89	Pat Lake	3	f	961962	E6	14.6	10.1	24.5	31	69	19.6	4.6	
06/29/89	Pat Lake	3	f	959960	E3	15.2	10.4	23.5	31.9	70	20.4	4.5	
06/29/89	Pat Lake	3	f	928929		15.5	10	25.4	32.3	67	19.5	5.5	
06/28/89	Pat Lake	3	f	930931	C2	17.2	10.1	24.3	31	71	18.6	4.3	
06/27/89	Pat Lake	3	f	953954	C0	15.8	9.5	23.5	40	72	15.8	4.5	
08/26/88	Pat Lake	3	f	917918	D5	15.8	9.5	28	36	68	17.8	5.5	
08/04/88	Pat Lake	3	f	911912	E2	16.6	10.4	29.4	36	67	17	5.3	
08/05/87	Green	3	m	1820		13.3	8.8	24	32.9		14.9	4.6	Betsy
07/30/87	Green	3	m	1312		14.2	8.5	27.2	33		18.6	5.1	R. Raccoon
07/06/88	Haley	3	m	7879	E1	13.8	9	23.2	30.5	62.3	18.1	4	Mom #3
07/03/88	Haley	3	m	6970	F0	14.5	9.5	23	32	63	17.8	4.1	Mom #2
06/27/88	Haley	3	m	5354		15	9.5	24.5	37	62	17	4.5	Mom #1
06/27/88	Haley	3	m	5556		15	9	23.5	31.5	64	14	4.1	Oprah
06/24/88	Haley	3	m	5758		14.5	9	25	33	66	17	4	Blackie
08/25/87	Haley	3	m	3433		14.1	8.9	27.9	36.7		16.5	6.5	Tonto
06/27/89	Pat Lake	3	m	955966	A2	15.2	9.6	25.5	36.2	72	20.1	5.5	Midrock
08/26/88	Pat Lake	3	m	919920	A3	15.8	10.1	32	38	69	20	6	
06/29/89	Pat Lake	4	f	957958	D1	17.3	10.5	28	38	79	23.5	6.2	
08/26/88	Pat Lake	4	f	921922	C7	16.9	10	28	38.2	71	17.8	6.5	
07/07/88	Green	4	m	8789	F2	15.2	9.4	28	35.5	65	18	3.5	R. Raccoon
06/27/88	Haley	4	f	7475	A1	15	9	24	37	67	17	4.5	Tonto

Appendix III continued: Raw genetic data

#	tag#	Site	LDH	EST-1	PEP-pp	PEP-lgg
1.	1820	Green Mtn.	*AA*	*AA*	*Aa*	*Aa*
2.	1514	" " "	*Aa*	*Aa*	*Aa*	*Aa*
3.	1617	" " "	*Aa*	*AA*	*Aa*	*Aa*
4.	2522	" " "	*AA*	*AA*	*Aa*	*AA*
5.	926927	" " "	*AA*	*Aa*	*AA*	*aa*
6.	923924	" " "	*Aa*	*Aa*	*AA*	*Aa*
7.	2726	" " "	*AA*	*AA*	*AA*	*AA*
8.	1312	" " "	*aa*	*Aa*	*AA*	*Aa*
9.	6162	Haley Lake	*AA*	*Aa*	*aa*	*aa*
10.	5152	" " "	*AA*	*Aa*	*Aa*	*Aa*
11.	4748	" " "	*AA*	*Aa*	*AA*	*Aa*
12.	1928	" " "	*Aa*	*AA*	*Aa*	*Aa*
13.	5556	" " "	*AA*	*AA*	*Aa*	*AA*
14.	3738	" " "	*aa*	*aa*	*Aa*	*AA*
15.	5758	" " "	*AA*	*AA*	*AA*	*Aa*
16.	4342	" " "	*AA*	*Aa*	*AA*	*AA*
17.	7172	" " "	*AA*	*AA*	*AA*	*Aa*
18.	6364	" " "	*AA*	*Aa*	*AA*	*aa*
19.	4950	" " "	*AA*	*AA*	*Aa*	*Aa*
20.	5354	" " "	*AA*	*AA*	*Aa*	*Aa*
21.	6970	" " "	*AA*	*Aa*	*Aa*	*Aa*
22.	7879	" " "	*AA*	*Aa*	*AA*	*AA*
23.	8586	" " "	*AA*	*AA*	*Aa*	*Aa*
24.	911912	Pat Lake	*AA*	*AA*	*AA*	*Aa*
25.	919920	" "	*AA*	*aa*	*Aa*	*AA*
26.	903904	" "	*AA*	*Aa*	*AA*	*Aa*
27.	901902	" "	*AA*	*Aa*	*Aa*	*AA*
28.	905906	" "	*AA*	*Aa*	*AA*	*Aa*
29.	913914	" "	*AA*	*AA*	*aa*	*Aa*
30.	907908	" "	*AA*	*AA*	*aa*	*Aa*
31.	932933	" "	*AA*	*Aa*	*AA*	*Aa*
32.	915916	" "	*AA*	*Aa*	*aa*	*Aa*
33.	928929	" "	*AA*	*Aa*	*Aa*	*Aa*
34.	934935	" "	*AA*	*AA*	*aa*	*AA*
35.	917918	" "	*AA*	*Aa*	*AA*	*AA*
36.	921922	" "	*AA*	*aa*	*Aa*	*aa*
37.	953954	" "	*AA*	*Aa*	*AA*	*aa*
38.	955956	" "	*AA*	*Aa*	*Aa*	*aa*
39.	951952	" "	*AA*	*AA*	*Aa*	*aa*
40.	930931	" "	*AA*	*Aa*	*Aa*	*Aa*
41.	957958	" "	*AA*	*aa*	*AA*	*aa*
42.	959960	" "	*AA*	*AA*	*Aa*	*aa*
43.	961962	" "	*AA*	*AA*	*AA*	*Aa*
44.	963964	" "	*AA*	*AA*	*Aa*	*AA*