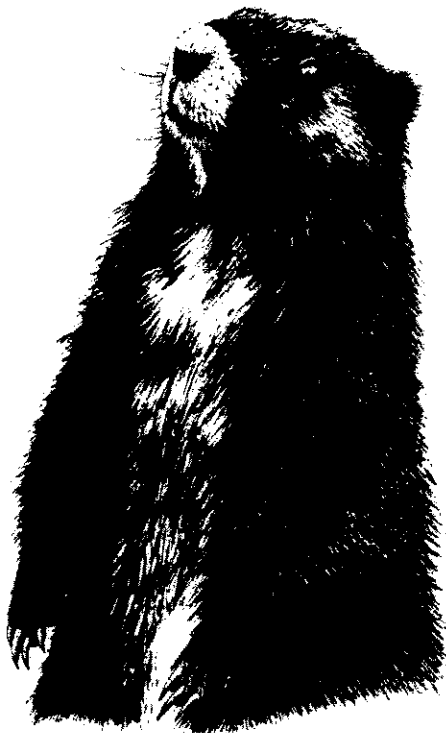


Demography of Vancouver Island Marmots
(Marmota vancouverensis):

year-end report for 1991



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ABSTRACT

Research on Vancouver Island marmots (*Marmota vancouverensis*) continued in 1991. This report includes a summary of all results to date. As of 1991, 61 individual marmots have been captured from two "natural" and two cutover "logging-slash" habitats. Including animals captured more than once, 73 treatments (capture-releases) have been made without apparent mortality. Cumulatively, results since 1987 indicate that:

- Marmot populations at study colonies remained stable since work began in 1987. Pat Lake and Haley "slash" colonies have declined since 1988, possibly because forest regeneration at those sites is reducing habitat quality.
- Electrophoresis of 55 blood samples from four colonies show levels of genetic variability comparable to other marmot species (Bryant 1990a). These results, together with solitary marmots found near Coombs, Comox, Cedar and Cassidy, suggest that *M. vancouverensis* is a capable disperser.
- Mark-recapture data revealed or corroborated several facets of marmot ecology. Significant findings include confirmation of equal sex-ratio at birth, typical litter size of three infants, physiological capability of reproduction at age three, probable average first reproductive age of four, physiological capability of reproduction in consecutive years, absence of any trend toward "alternate-year" reproduction, monogamous sexual relationships, no persistence of pair-bonds from year-to-year, re-use of burrows in consecutive years, average annual fecundity of 1.3 young/female, and highly variable colony reproductive success from year-to-year.
- Mark-recapture data indicate significant demographic differences between "natural" and "slash" colonies. Family group persistence data show that "slash" families re-use burrows significantly less often than those inhabiting higher elevation "natural" habitats. Survivorship of adults is also significantly lower in "slash", although data are still too sparse to convincingly demonstrate that this is a "real" population trend and not an artifact produced by small samples, or even a trend exhibited by only the two studied "slash" colonies. There are demonstrable differences between the two colony types.
- Existing data continue to support the logging-slash "sink" hypothesis. Several methods are proposed to test components of this hypothesis empirically.

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As in past years, B. Kurtz of MacMillan Bloedel Limited and F. Berto of Fletcher Challenge Canada ensured that I had keys to the various gates. K. Langelier of Island Veterinary Hospital again provided necessary supplies. C. Bryant accompanied me in the field and drew the pen-and-ink marmot which appears on the cover. Finally, thanks to R. McLaughlin of MacMillan Bloedel Limited, who allowed me to inspect marmot colonies by helicopter in mid-April, while engaged in an unrelated project.

INTRODUCTION

This report describes results of continued research on Vancouver Island marmots (*Marmota vancouverensis*). The data contained herein supplement those presented in Bryant (1990a, 1990b). Study objectives in 1991 were to:

- 1) monitor reproductive success and survivorship at the Haley Lake, Haley "slash", Green Mountain and Pat Lake "slash" study colonies.
- 2) monitor burrow-use by individuals and family groups.
- 3) capture and ear-tag marmots to facilitate continued monitoring.
- 4) gather preliminary information regarding microclimatic conditions at marmot hibernacula.

METHODS

Field efforts were limited this summer, both by funding constraints and by poor weather conditions in late summer. Summer visits began on July 28th. Two days were spent in July, including one "trap-day" (one trap used for one day) at Haley Lake. Comparable figures for August are 11 field-days (36 trap-days), and 7 field-days (26 trap-days) in September. Due to deteriorating road conditions, Green Mountain was visited only once this year, and was not trapped. As in previous years, I attempted to spread trapping efforts evenly among the other sites in order to facilitate inter-group comparisons. My last field-day was on November 3rd. Some data were also gathered on early spring trips to check hibernacula conditions (see below). Trapping methods were as used in previous years (Bryant 1990a).

Minimum-maximum recording thermometers were placed in 2 marmot burrows at Haley "slash" and 2 others at Pat Lake. Snow stakes were also installed to measure snowpack conditions in early spring. Unfortunately, by the time I initiated work in November of 1990, it was not possible to install similar equipment in the higher-elevation "natural" colonies. The two burrows at Pat Lake were definite hibernacula (vegetation plugs were present); the two burrows at Haley "slash" had no plugs but were used by marmots well into late September of that year.

Limited samples continue to dictate a cautious approach to analysis and interpretation. Chi-square tests were used to test for differences in family group persistence and survivorship rates; 2x2 tests employ Yate's correction for continuity (Zar 1974). Life-table methods and nomenclature follow Krebs (1989). Because litter size is a discrete variable, I used a non-parametric Mann-Whitney *U*-test to assess observed differences. Statistical analyses were performed using programs written in QUATTRO (Borland 1987) for this project. Statistical procedures follow Krebs (1989) and Sokol and Rohlf (1980). In all cases, significance of results was evaluated at the 95% confidence level.

RESULTS

Blood samples and measurements from 6 new marmots were taken, and 5 animals from previous years were re-captured, in 1991. Since I began the project in 1987, a total of 61 individual marmots have been marked and released on at least one occasion. Including animals captured more than once, 73 "treatments" have been made, and >20 captured animals have been released without being anesthetized, handled or measured. Apart from one case of apparent heat exhaustion (see Bryant 1990b), I have no evidence that trapping caused injury. All released marmots were observed behaving normally hours, days or weeks after release.

The size record for *M. vancoverensis* is still held by adult male #941942 ("Einstein") from Haley Lake (6.8 kg on August 23rd, 1990); the age record is now held by adult female #1312 ("Rocky Raccoon") from Green Mountain (presumed to be three-years-old in 1987, and therefore at least seven years-old in 1991).

Two marmots were observed in unusual locations this year. K. Brunt and G.W. Smith of the Wildlife Branch investigated a report near the Cassidy airport in early July. In addition, another animal is apparently now hibernating beneath a horse stable on Mr. T. Oster's property in eastern Cedar.

Pat Lake

Numbers of marmots at the Pat Lake "slash" colony remain lower than they were in 1988 and 1989. The two "established" burrow complexes which were used last year were also occupied this summer (i.e., "Apex" and "Midrock"), and another was apparently re-occupied ("Bluff" was not used in 1990; see Bryant 1990a for burrow locations). The new

(in 1990) burrows on the east-facing sidehill above road "J3" showed minimal evidence of use this year.

One litter of 3 young was observed at Pat Lake in 1991 (at the "Apex" burrow). Recaptured marmots this year included the reproductive "Apex" female #963964 (presumed two year-old in 1989, not observed in 1990). Note that her first reproductive event was at age four, and that she was recaptured at the identical location as in 1989. Other tagged marmots seen at Pat Lake were females #907908 (yearling or 2 year-old in 1988, lactating in 1989, captured in 1990, not captured this year) and males #901902 (YOY in 1988), and #903904 (from the same litter). Two "new" untagged adult males were captured this year at the "Midrock" location.

The "sun-avoidance" behavioral pattern which was observed at this colony last year (Bryant 1990b) was less in evidence this year, presumably because weather conditions were much wetter and overcast. The golden eagles (*Aquila chrysaetos*) which apparently nested near the site in 1990 were still present in 1991. However, in contrast to last year, I did not observe juvenile eagles this summer. Finally, the access road has deteriorated, and Pat Lake is now "walk-only" access.

Haley "slash"

It was a poor year for marmots at Haley "slash". Only the "Menza" and "Patches" burrows showed much sign of use, and only two marmots were observed habitually using these burrows. Although neither was tagged, note that very few animals have been marked at this site over the years. No evidence of reproduction was observed here in 1991.

On August 14th, I counted four marmots using the rock scree adjacent to the waterfall (just uphill from the "Red-tail" burrow). I also heard at least two marmots above the road on August 17th and again on August 22nd. As I have suggested elsewhere (1990a), this timing suggests a "wave" of colonizing marmots which will probably not remain at the site.

Haley Lake

It was a good year for marmots at Haley Lake. As in 1990, the "Mom #1", "Mom #2", "Tonto" and "Newfie" burrows were all used daily. Some use of the "Mom #3" burrows (not used in 1990) was also observed.

This colony produced at least three litters, of 3 young each, at the "Mom #2, "Tonto" and "Newfie" burrows. An additional litter of 3 was also observed on the Bell Creek side, outside of my usual study area. Unfortunately, I was able to confirm only one of the lactating females (at the "Newfie" burrow). "Live-wire" (#7172) was a presumed two-year-old in 1988, and was therefore at least 4 years old, and probably 5 years old, at the time of her first reproduction (she was recaptured in full nursing condition). Although I could not confirm this, I strongly suspect that "Oprah" (#3536) was the mother of the litter at the "Tonto" burrow. If so, this would be the second case in which a female produced litters in consecutive years. Finally, either "Luna" (#909910) or "Tweedledum" (#976977) was probably responsible for the litter at the "Mom #2" location.

The latter marmot is especially interesting. "Tweedledum" was not observed in 1990, but was observed this year at the same burrow where she was originally captured in 1989. Together with #963964 and #903904 from Pat Lake, this is the third record of 3 year-old animals "reappearing", after one year's absence, at or very near the same burrow where originally captured.

Finally, one tagged adult male was observed at the "Newfie" burrow at Haley Lake this summer, but could not be positively identified. For survivorship analyses, I assumed that this was "Newfie" (#6364) because that animal has been observed in association with "Live-wire" in three previous summers. In addition, the style of ear-tags (i.e., the "rabbit-ear" tags originally used) meant that it must of been one of six animals, four of which would be the same age (5 years old).

Green Mountain

Deteriorating road conditions precluded all but one visit to Green Mountain this year. I did not attempt to trap marmots. Neither of the two established burrow systems were abandoned at Green Mountain; however, I saw only three marmots. On September 4th, I observed adult female #1312 ("Rocky Raccoon") on the west-facing sidehill. This is the fifth consecutive year that she has been observed at this location and, in fact, is the first marmot I ever captured (presumed 3 year-old on July 30th, 1987). I also saw adult male #926927 ("Samson") and his sibling (#923924 "Delilah") at the same location (both YOY in 1988, known 3 year-olds). I was saddened by the apparent absence of "Betsy" (#1820), who is known to G.W. Smith as "old faithful", and who also would have been at least seven years old this year.

However, I was encouraged by the quantity of scat observed on the west sidehill and elsewhere, and not unduly concerned by the dearth of marmots. It was cold and fairly wet on the day I visited Green Mountain. I remain hopeful that the alleged shooting incident here in 1990 did not actually happen (see Bryant 1990b).

Sex-ratio, family group persistence, and survivorship

New data do not substantially alter most previous findings (Bryant 1990a, 1990b).

However, because sample sizes are improving, I re-tested several hypotheses, with results as follows:

- Equal sex-ratio at birth: Including 13 captured young-of-the-year, observed sex-ratio does not differ from 1:1 ($X^2=1.14$ with 1 df, $p>0.05$).
- Equal sex-ratio of all marmots: Including 61 captured marmots, observed sex-ratio does not differ from 1:1 ($X^2=0.02$ with 1 df, $p>0.05$).
- Equal sex-ratio in "natural" and "slash" colonies: Including 61 captured marmots, sex-ratios do not differ among colony types ($X^2=0.96$ with 1 df, $p>0.05$).
- Equal sex-age structure in "natural" and "slash" colonies: Data are insufficient to statistically test for differences (limited samples lead to expected cell frequencies <5). However, a plot of observed age-sex structure suggests a preponderance of males, and a dearth of older females, in "slash" colonies (Figure 1).
- Equal persistence of family groups in "natural" versus "slash" habitats: Use of the same burrow in consecutive years by *at least* one member of a family group is defined as a case of "persistence". In contrast, "abandonment" is defined as a previously-used burrow with no recent signs of use, or at which only definitely untagged "new" marmots are observed. Failure to observe marmots at a burrow with signs of recent use is not considered "abandonment"; rather, those burrows are excluded from analysis. Pooled data from Haley/Green and Pat Lake/Haley "slash" colonies indicate that family groups in "natural" colonies are significantly more likely to persist from year-to-year ($X^2=8.23$ with 1 df, $p<0.01$; Figure 2).
- Equal survivorship of marmots in "natural" versus "slash" habitats: Mark-recapture data show differences in year-to-year survivorship of "natural" versus "slash"

Observed age/sex structure

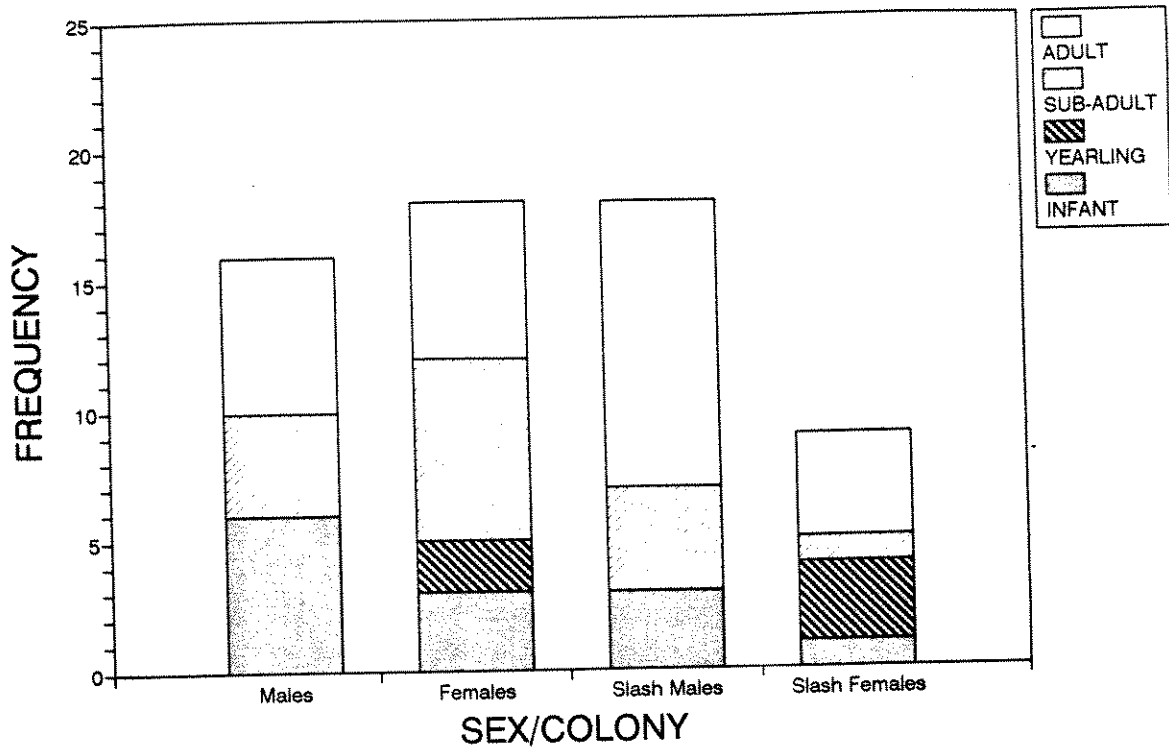


Figure 1: Cumulative age-structure of *M. vancouverensis* at time of first capture, 1987-1991. Although data are too sparse to test for statistical differences, there is an apparent preponderance of adult males, and dearth of adult females, in "slash" colonies.

Family group persistence

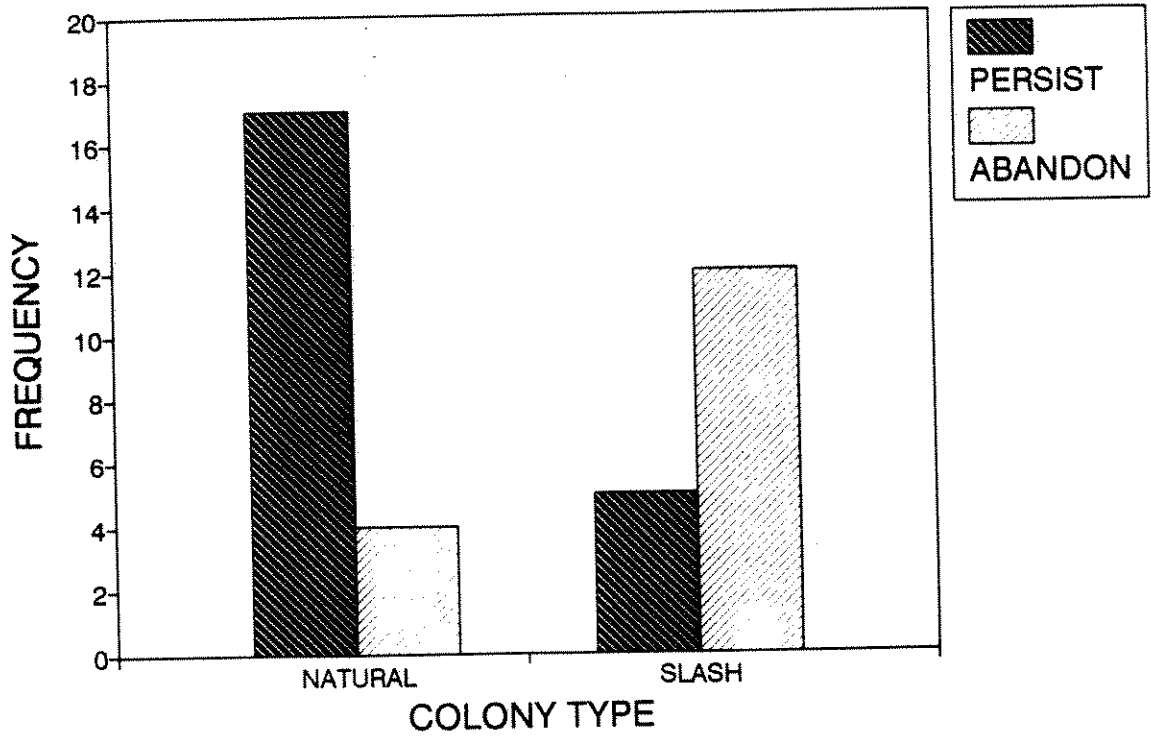


Figure 2: Persistence of family groups using "natural" and "slash" burrows. "Persistence" is defined by use of a given burrow in consecutive years by *at least one* member of a family group. "Abandonment" is defined as a previously-occupied burrow with no recent signs of use, or observed occupancy by untagged "new" marmots. The ratio of "persistence" to "abandonment" is significantly higher in "natural" colonies.

marmots (Figure 3). Mark-recapture survivorship data are summarized in Table 1, and raw data are included as Appendix I. Unfortunately, these data are still insufficient to test for sex/age-specific differences (limited samples lead to expected cell frequencies <5, and therefore invalid chi-square results). However, increasing samples allowed me to make approximate tests by pooling data for "juveniles" of both sexes (i.e., all animals <3 years-old) and for "adults" (all animals >3 years-old) of both sexes. The biological rationale for doing this is to explore possible survivorship differences in "non-reproductive-age" versus "reproductive-age" marmots. Results show no difference in survivorship of juveniles in "natural" versus "slash" environments ($X^2=0.46$ with 1 df, $p>0.05$). However, results for "adults" show a significantly higher probability of survival in "natural" habitats ($X^2=6.20$ with 1 df, $p<0.05$).

Survivorship data warrant additional comment. Estimated survivorship of juveniles is biased by the small number of marked animals which *could have been alive in later years* (for infants, $n=11$, for yearlings, $n=13$, and for 2 year-olds, $n=23$). When these data are partitioned by sex, or colony class, it is not surprising that analysis does not produce statistically significant results. For young marmots, even a small number of recaptures or disappearances in the future will alter my results, in some cases profoundly. For example, recapture of a single male (#903904) at Pat Lake adjusted yearling survivorship at that site from 50% to 66%. Although life-table curves are beginning to show signs of "smoothing", I must reiterate my (1990b) conclusion. Overall, current estimates of survivorship in young (infant and yearling) marmots are of little value. Having said this, cumulative records suggest a 1st year survivorship rate of 64% (7/11) and yearling survivorship of 54% (7/13).

In contrast, data for adult marmots are beginning to show trends independent of increasing sample sizes. Specifically, samples of 3 year-old ($n=38$), 4 year-old ($n=24$) and 5 year-old ($n=7$) marmots continue to suggest that "natural" animals are more likely to "survive" (or, more specifically, to be present in the same area) in subsequent years. Pooled data for adult marmots yield average year-to-year survival rates of 78% and 14% in "natural" and "slash" habitats respectively. (Elimination of "juveniles" from my 1990b report yield equivalent values of 72% adult survivorship in "natural" colonies, and 18% in "slash" colonies).

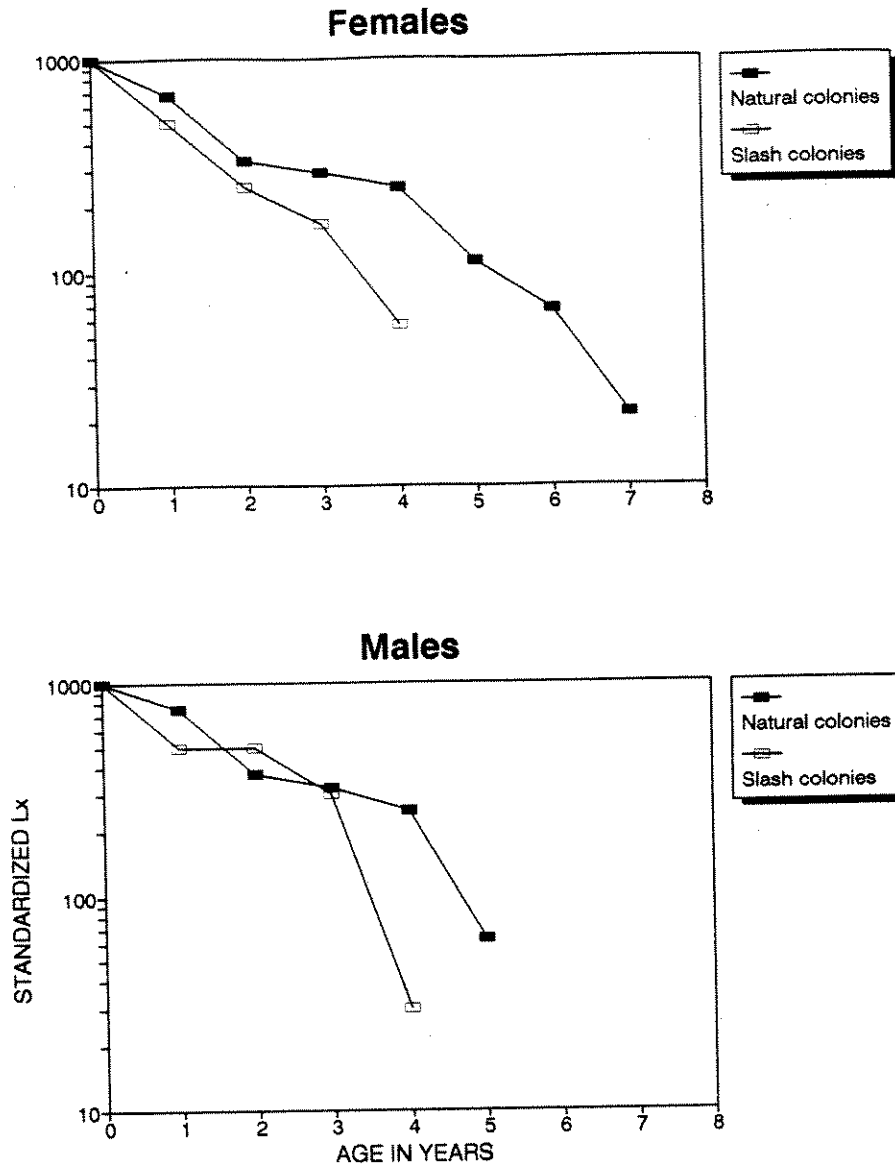


Figure 3: Age-specific survivorship of *M. vancouverensis* in "natural" and "slash" colonies. Data are standardized logarithmic L_x survivorship values (eg., Krebs 1989). Cumulatively, adult marmots have a significantly higher probability of survival in "natural" habitats. Data for infants and yearlings remain sparse. A few additional recaptures could dramatically alter young-age data points, but would not influence overall curve shape for older animals.

Table 1: Survivorship of marked *M. vancouverensis*, 1987-1991.

Sex and assigned age at 1st capture	<i>n</i> ^a	estimated age at recapture ^b						
		1-2	2-3	3-4	4-5	5-6	6-7	7-8
"natural" colonies^c								
infants	3(4) ^d	2(3)	1(1)	1(1)	0(0)			
yearlings	2(1) ^e		1(1)	1(1)	1(1)	1(1)		
2-year-olds	6(5)			5(4)	5(3)	1(0)	1(0)	
3-year-olds+	6(4)				5(3)	3(1)	2(0)	1(0)
"slash" colonies^f								
infants	2(2)	1(1)	1(1)	0(1)				
yearlings	3(0)		1(0)	1(0)	1(0)			
2-year-olds	1(4)			1(2)	1(1)	0(0)		
3-year-olds+	4(9)				0(0)	0(0)	0(0)	
Total <i>n</i>	27(29)							

NOTES:

- ^a See Bryant (1990a) for aging criteria. Animals which were "first-time" captures in 1991 are not included in these data.
- ^b Animals were often "recaptured" with spotting scope only. Given ear-tag loss and dispersal, these data represent minimum survivorship rates.
- ^c Pooled data from Haley Lake and Green Mountain.
- ^d Numbers in parentheses are males.
- ^e This includes one male (#6364) which was observed one year prior to capture (as a two-year-old, in 1988).
- ^f Pooled data from Haley "slash" and Pat Lake. Note that the latter site has only been studied since 1988.

Reproduction

As with other data, increasing sample sizes permit retesting of several reproduction-related hypotheses, with results as follows:

- Equal litter sizes in "natural" versus "slash" habitats: Incorporation of data from 1991 had the effect of reducing variability, and altered one conclusion reported previously. Specifically, "natural" litters average 2.9 young ($n=12$, range of two to three) and "slash" litters average 3.3 young ($n=6$, range of three to four; Table 2). Mann-Whitney U -test shows this difference to be non-significant ($U_{(6,12)}=50$, $p>0.05$), which is in contrast to previous results (Bryant 1990a, 1990b). This is plainly the result of increasing sample sizes; litters of four appear to be more exceptional than I previously believed. Cumulatively, there is little deviation from the "norm" of three infants/litter (of 18 litters observed during the project, 15 included three young, 1 was comprised of two young, and 2 litters included four young).
- Equal fecundity in "natural" versus "slash" habitats: Estimated female fecundity rates for both "natural" and "slash" females have been recalculated (Table 2). Fecundity is expressed as average-number-of-young-produced/adult-female-year, in which an "adult-female-year" is simply an ear-tagged, age-three-or-older female known to be alive in one year. Using these criteria, the average per-female yearly productivity of "slash" animals is significantly higher than that of "natural" animals (Mann-Whitney $U_{(7,28)}=129.5$, $p<0.05$). On the surface, it appears that "slash" females have a higher probability of producing young. However, estimated fecundity for "slash" females is biased by small total number of adult-female-years ($n=7$). In addition, due to high disappearance rate of adult females, only $n=3$ adult-female-years represent non-reproductive females. The resulting "slash" fecundity rate is therefore almost certainly overestimated.
- Equal age-of-first-reproduction in "natural" versus "slash" habitats: Data for known-age reproductive animals remain too sparse to accurately determine average age-of-first-reproduction, or to correlate this with colony type.

However, as reproductive age is critical to understanding marmot ecology, some discussion of the data is warranted. One female, originally tagged as an infant, is three years old (#923924), and has not yet reproduced. In addition, I have two records of

Table 2: Fecundity of *M. vancouverensis* at "slash" and "natural" colonies.

	<i>n</i> of litters	mean litter size	range	fecundity ^a	s.e.
"Natural" colonies	12	2.92	2-3	1.17 ^b	0.28
"Slash" colonies	6	3.33	3-4	1.91	0.72
All colonies	18	3.06	2-4	1.34	0.27

NOTES

^a fecundity is expressed as total number of young (of both sexes) produced/adult-female-year. An "adult-female-year" is one reproductive-age female alive in one year.

^b fecundity is significantly greater in "slash" colonies (Mann-Whitney $U_{(6,12)}=129.5$, $p<0.05$).

surviving yearling females (i.e., *presumed yearlings at time of first capture*) which have since reproduced. Marmot #7172 produced a litter at Haley Lake as a 5 year-old in 1991. More interesting is #907908, which was captured, in full lactating condition, as a 2 year-old at Pat Lake in 1989. In fact, I suspect that #907908 was older. My field notes for 1988 describe her as a "probable yearling...2 year-old?", and while her physical measurements are comparable to other known-age yearlings, it is possible that she was a small 2 year-old when I first captured her (meaning that she would have been age three when she produced young in 1989). Finally, I have three records for surviving *presumed* 2 year-olds which have since reproduced. Both #963964 and #909910 first bred as 4 year-olds (or, more accurately, two years after they were presumed to be age two), and #3536 produced young three and four years after her original capture (i.e., at *presumed* ages five and six).

Based on these limited data, it appears that although *M. vancouverensis* may be physiologically capable of reproduction at age three (or even two?), the average age-of-first-reproduction is close to four. Lifelong reproductive potential remains unknown. Litters produced in consecutive years by female #1820 ("Betsy") from Green Mountain and #3536 ("Oprah") from Haley Lake, while exceptional, may suggest that average reproductive females produce more than two litters (see Bryant 1990a).

Hibernacula conditions

Attempts to measure microclimatic conditions at hibernacula were fraught with several difficulties. First, timing and weather constraints precluded placement of recording thermometers at higher-elevation "natural" colonies. Second, no vegetation plugs were observed at the Haley "slash" colonies, suggesting that my sampled burrows there were not in fact used as hibernacula this year (although I am convinced that the "Patches" and "Red-tail" burrows were so used in 1988; see Bryant 1990a). Third, maximum recorded temperatures were biased at Haley "slash" both because the snowpack had disappeared by mid-March, and because marmots had, in the course of using burrows, ejected thermometers from the burrows. Because thermometers were therefore exposed to direct sunlight, they undoubtedly overestimate actual temperatures within the burrows. Fourth and finally, although I inserted thermometers at arm's length into burrows, I do not know how deep the burrows are, and it is therefore possible that thermal conditions deeper in the burrow are quite different.

Table 3: Microclimatic conditions at four hibernacula.^a

Burrow	minimum (° C)	maximum ^b (° C)	range (° C)	March snow depth (m)	April snow depth (m)
"Patches"	-6.2	+9.2	15.4	0.2	0.0
"Menza"	-2.7	+14.6	17.3	0.0	0.0
"Midrock"	-0.2	+3.4	3.6	1.4	0.3
"Apex"	-1.8	+2.6	4.4	2.3	1.5

NOTES

^a The "Patches" and "Menza" burrows at Haley "slash" were not plugged by vegetation in November of 1990, and may not have been used as hibernacula.

^b Note that maximum recorded temperatures are biased by lack of snow cover at the Haley "slash" colony. Thermometers were retrieved in mid-March.

However, despite these problems, some valuable information was collected (Table 3). The primary but unsurprising conclusion is that snow cover disappears more quickly from the "slash" colonies than from the higher-elevation "natural" sites. On a helicopter overflight on April 17th, fresh marmot tracks were observed in the snowpack on Green Mountain (this hibernacula exit is pictured in Bryant 1990a). Photographs made on that date show a nearby tree still buried to a depth of approximately 2 metres. At Haley Lake, no signs of activity were observed, but substantial patches of snow remained near the "Tonto" burrows, which I believe were used as hibernacula in 1988 (Bryant 1990a). In contrast, virtually no snow remained at the Haley "slash" colony by April 17th; indeed, I was able to retrieve my thermometers from that site on March 20th, at which time snow cover at the actual burrow entrances was gone. The situation was only slightly different at Pat Lake. By March 21st, snowpack depths at the two sampled burrows was considerably less than 1 metre, (although actual burrow entrances were still buried). By April 14th, snow was completely gone from both "slash" colonies and, as I have said, by the 17th at least some marmots were active (on Green Mountain).

Temperature data, although sparse, reflect differences in snowpack conditions. Where burrows remained buried by snow into March (i.e., at Pat Lake), minimum temperatures were higher, and variability between high and low temperatures was comparatively slight. It appears likely that *M. vancouverensis*, like most hibernating mammals, seeks out thermally stable environments with temperatures near freezing.

DISCUSSION

Submission of this report marks the end of five years of field-research on Vancouver Island marmots. The following discussion is designed to summarize important results to date, identify research problems and prospects for the future, and present several testable hypotheses for discussion and *action*.

Population trends

Marmot populations at four study colonies have remained relatively stable since I began work in 1987. Pat Lake and Haley "slash" colonies have declined in the past two years, possibly because forest regeneration at those sites is reducing habitat quality. Despite dramatic variability in reproductive success from year-to-year, Green Mountain and Haley Lake colonies continue to persist at relatively stable population levels. In addition, marmots have been reported in several new areas since 1987; however, the overall geographic range of the animal has apparently remained unchanged. Notably, despite increased publicity for the animal, new colonies have *not* been confirmed in areas outside of the central Vancouver Island "core" area.

Genetics and population structure

Electrophoresis of 55 blood samples from four colonies revealed levels of genetic variability comparable to other marmot species (Bryant 1990a). These results, together with the solitary marmots found near Coombs, Comox, Cedar and Cassidy, indicate that *M. vancouveris* is a capable disperser. Overall, marmots exhibit a "meta-population" structure, in which a patchwork of marmot "islands" (colonies) appear to be periodically extinguished and re-colonized, but between which successful dispersal apparently occurs reasonably frequently (or at least occurred recently). Genetic analyses were frustrated by my inability to find or sample marmots from outside of the central Vancouver Island "core" area. It is possible that marmots from Mount Washington, Forbidden Plateau or elsewhere may show evidence of inbreeding (if such colonies still exist).

In 1991, Helix Bio-tech Incorporated of Vancouver completed extraction of DNA from 55 marmot blood samples. Alas, funds have been unavailable with which to complete this analysis. At a cost of \$2500, this company has proposed to conduct a "pilot study", using 12 samples, in order to create a DNA probe specific to this animal. At a cost of \$6,000-\$10,000, the available 55 samples could be employed to refine estimates of overall

population variability. Although the technique is attractive, existing samples of infants and parents would be inadequate to confirm or refute suspicions of sexual monogamy in *M. vancouverensis*. However, DNA analysis would probably confirm my results showing abundant genetic variability in this species.

It might be worthwhile to establish baseline DNA standards so that future marmot colonies, if found outside the "core" area, could quickly be compared with animals from known colonies; this baseline data may become more expensive in future years. On the other hand, \$10,000 is a large sum given current project finances. As the Helix "iron" is hot, and irreplaceable blood samples will slowly deteriorate with age, a decision whether or not to proceed is quickly needed from the Recovery Team.

Mark-recapture and demographic results

Capture-mark-release technology works relatively well for Vancouver Island marmots. Apart from a single case of heat-exhaustion in 1990, no obvious injury occurred during the project (see Bryant 1990b). Including that case, subsequent observations suggest that trapping has not directly caused the death of any marmot.

The mark-recapture experiment has revealed several important facets of marmot ecology. Significant results include confirmation of equal sex-ratio at birth, typical litter size of three infants, physiological capability of reproduction at age three, probable average first reproductive age of four, physiological capability of reproduction in consecutive years, absence of any trend toward "alternate-year" reproduction, monogamous sexual relationships, no persistence of pair-bonds from year-to-year, re-use of burrows in consecutive years, average annual fecundity of 1.3 young/female, and highly variable colony reproductive success from year-to-year. Increasing sample sizes will undoubtedly serve to refine these conclusions.

However, mark-recapture data remain problematic. The major difficulty is that I cannot distinguish disappearances reflecting mortality from those caused by marmot dispersal. This is a limitation of the technique itself; note that increasing sample sizes will not resolve the problem. Another important limitation is that I cannot accurately age animals first captured as adults. There are few known-age animals with which to validate the *presumed* age of older animals, even if physical measurement data showed less "scatter" than they do (Bryant 1990a). In particular, samples of recaptured young-of-the-year and yearling marmots remain small. This is the result of poor marmot reproduction in 1988,

1989 and 1990, poor trapping success, and relatively short (in marmot terms) duration of the study. In addition, because of my non-random trapping and resighting methods (specifically, I place traps where I see marmots), my recapture data fail the "equal probability of recapture" assumption required for Jolly-Seber estimation of population size (Krebs 1989).

The mark-recapture experiment has also been hindered by logistic constraints. Since 1988, I have been limited to spending less than two weeks at each study colony. My field-season in 1989 lasted eight weeks, in 1990 it lasted seven, and in 1991 it lasted five weeks. I was therefore not surprised to recover four marmots which were missed in previous years. Ultimately, I believe that failing to observe animals is a more likely hypothesis than the alternative; i.e., that adults moved elsewhere for a year and then returned to the original site.

Despite such difficulties, there are some highly suggestive trends. Survivorship rates are lower and more variable in the youngest age-classes. In particular, infant litters experience either complete survivorship or mortality in their first winter, with few cases of partial survivorship. Although I cannot distinguish "mortality" from "dispersal", there are two factors which suggest that disappearances in this age-class reflect mortality. First, most disappearances occur after late autumn and second, observations of yearlings in early spring almost invariably include either the complete litter or none at all. For this reason I suspect that these data are consistent with a hypothesis of overwintering mortality (i.e., unsuccessful hibernation).

There is also a substantial disappearance "bulge" among yearling and two-year-old marmots, which probably represents dispersal as well as mortality. In particular, I am intrigued by the observed influx of "new", untagged marmots in July-early August in most years (Bryant 1990a, 1990b). When captured, most of these animals were classified as *presumed* 2 year-olds on the basis of physical measurements; they could have been older than this.

Persistence of adults is generally high, especially for females which have reproduced at least once. Overall, the most striking feature of the mark-recapture data are the apparent differences between colonies inhabiting "natural" sub-alpine meadows, versus those in "slash" habitats produced by clear-cut logging.

Testing the logging-slash "sink" hypothesis

The "sink" idea is really a combination of three hypotheses, two of which could be tested directly, and one which may be tested indirectly. Essentially, the "sink" hypothesis suggests that landscape changes resulting from clear-cut forestry practices influence marmot populations in three ways, as follows:

- 1) That cutover habitats near "natural" colonies tend to foreshorten normal dispersal movements, by presenting dispersing animals with nearby habitats that closely resemble, at least during summer, the "avalanche-run" conditions of more typical (i.e., "natural") *M. vancouverensis* habitats.
- 2) That marmots selecting cutover habitats suffer reduced survivorship, thus making "slash" colonies less capable of population growth, persistence, and production of dispersers. One possible mechanism for reduced survivorship in "slash" relates to increased variability in snowpack and temperature conditions, therefore making hibernacula less thermally stable, and overwintering mortality more frequent. Another possibility is the hypothesis of Türk and Arnold (1988), who proposed that higher summer temperatures at lower elevations force marmots to curtail daily foraging patterns, resulting in decreased seasonal growth and overwintering survival.
- 3) That reduced numbers of long-distance dispersers, together with the increased quantity of potential habitat, lessens the probability that animals will re-colonize a more distant mountain, find a mate, and reproduce successfully (i.e., that they will disperse *successfully* to new habitats).

The evidence for hypothesis #1 is ambiguous. We know that marmots have colonized several "slash" areas near existing "natural" sub-alpine colonies. Although we do not know where these animals originated, existing genetic data, together with the fact that "slash" colonies *are* invariably near "natural" colonies, suggest that they did in fact come from nearby locations. We also know that marmots can make long-distance dispersal movements despite having to traverse large areas of "slash" in order to do so (we know this from the solitary animals observed at Coombs, Comox, Cedar and Cassidy). Clearly "slash" does not represent a physical barrier for dispersing animals. However, whether extensive "slash" areas influence the length of "normal" dispersal patterns remains unclear.

This first hypothesis can be tested empirically using radio-telemetry, although it will be difficult. Obtaining a sufficient sample of dispersing animals will be an expensive and lengthy process. Due to the burrowing habits of the study animal, radio-telemetry must involve surgically implanted transmitters, the technology for which, fortunately, is well-developed (eg., Van Vuren 1989). Developing appropriate field-surgery methods involves logistic problems, although the experience of others suggests that these problems can be overcome (C. Salsbury, Rocky Mountain Biological Laboratory, and K. Langelier, Island Veterinary Hospital, pers. com., 1990).

Finding a "control" area, in which to measure average dispersal distances in a "natural" landscape, is also problematic, since nowhere on Vancouver Island is there a known marmot colony inhabiting an unlogged watershed. Although imperfect, probably the best data would be obtained by comparing marmots from an extensive "slash" environment (eg., the "F19" colony) with others from the more pristine Haley Lake/Gemini Peak/Green Mountain ridge system. Although some of the latter animals would undoubtedly descend into lower-elevation "slash" habitats, others would probably utilize "natural" travel corridors along the ridge (some observational data exist to support this; see Bryant 1990a), and these could be used to approximate "normal" dispersal trends. In any event, radio relocations indicating substantial inter-mountain movement *through* "slash" environments would present strong grounds for rejecting the first hypothesis.

The evidence for hypothesis #2 is tantalizing but presently inadequate. Family group persistence data show that "slash" families re-use burrows significantly less often than those inhabiting higher elevation "natural" habitats. Survivorship of adults is also significantly lower in "slash", although data are still too sparse to convincingly demonstrate that this is a "real" population trend and not an artifact produced by small samples, or even a trend exhibited by only the two studied "slash" colonies. Despite this, there are demonstrable differences between the two colony types.

Why this might be the case remains unclear. Observations suggest that hibernacula located in lower-elevation "slash" areas exhibit reduced snowpack depths, and higher temperature variability within burrows. Marmot behavior at Pat Lake suggests that thermoregulation may limit overall habitat availability. Daily movements from sunlit to shaded areas support the ideas of Türk and Arnold (1988). Although observed behavior could explain why many "slash" habitats at lower elevations have *not* been colonized by

M. vancouverensis, measurements of Pat Lake marmots do not suggest slower growth rates at this site (quite the reverse is true; see Bryant 1990a).

Ultimately, the major difficulty with existing data arises when I attempt to equate "disappearance" with "mortality". For reasons already discussed, this may not be the case. Clearly, determining whether mark-recapture data reflect mortality or dispersal is more important than seeking possible mechanisms for increased mortality (if my data reflect movement, then obviously there *is* no such mechanism). Again, radio-telemetry would be the most logical way in which to distinguish death from movement. Inability to detect increased mortality in "slash" habitats, or observed movement in concert with mark-recapture "disappearances", would present strong grounds for rejecting the second hypothesis.

By definition, hypothesis #3 depends upon the first two hypotheses being true. If normal dispersal patterns are not being foreshortened by the presence of "slash" (rejection of hypothesis #1), then there will be no reduced number of potential recolonizing marmots at "more distant mountains". In addition, if there is no increased mortality in "slash" colonies (rejection of hypothesis #2), there will likely be *more* potential colonizers than there ever were historically, since "slash" colonies will themselves be producing dispersing marmots. Short of creating and monitoring a new experimental population in an unlogged region (Strathcona Provincial Park?), combined with a massive radio-telemetry experiment and comparison of results from the "core" central Vancouver Island area (this is probably beyond our financial capability), I believe that hypothesis #3 is untestable by direct means.

However, this does not preclude its utility. Hypothesis #3 generates two predictions, either of which, if disproved through use of "natural experiments" (i.e., good documented observations of the "real world"), would present strong inference for its rejection. Specifically, hypothesis #3 predicts that the likelihood of marmots successfully re-colonizing "distant mountains" (eg., Mount Arrowsmith, Mount Joan?) is presently low. Future marmot population expansion on any such mountains would represent contrary evidence, and would cause considerable difficulty for the "sink" hypothesis. This would be particularly true if genetic data showed similarity to animals from known source populations (this is perhaps the strongest argument for completing baseline DNA experiments).

Similarly, hypothesis #3 predicts that long-distance dispersers are unlikely to find a mate and form reproductive colonies. Observations of long-distance dispersers which reproduce in anomalous locations (eg., Cassidy Airport?) would represent grounds for dismissing this hypothesis. If Vancouver Island marmots typically disperse in pairs or in "bunches", then landscape issues would clearly be of reduced importance, because dispersing groups would comprise self-propagating "units". To date, observations of marmots in unusual habitats do not support this idea (data suggest single individuals).

CONCLUSIONS

Five years of field-work on *M. vancouverensis* result in several conclusions. These are:

- Marmot populations at four study colonies have remained relatively stable since work began in 1987. Pat Lake and Haley "slash" colonies have declined since 1988, possibly because forest regeneration at those sites is reducing habitat quality.
- Electrophoresis of 55 blood samples from four colonies revealed levels of genetic variability comparable to other marmot species (Bryant 1990a). These results, together with the solitary marmots found near Coombs, Comox, Cedar and Cassidy, indicate that *M. vancouverensis* is a capable disperser.
- Mark-recapture data revealed several important facets of marmot ecology. Significant results include confirmation of equal sex-ratio at birth, typical litter size of three infants, physiological capability of reproduction at age three, probable average first reproductive age of four, physiological capability of reproduction in consecutive years, absence of any trend toward "alternate-year" reproduction, monogamous sexual relationships, no persistence of pair-bonds from year-to-year, re-use of burrows in consecutive years, average annual fecundity of 1.3 young/female, and highly variable colony reproductive success from year-to-year.
- Mark-recapture data indicate significant differences between "natural" and "slash" colonies. Family group persistence data show that "slash" families re-use burrows significantly less often than those inhabiting higher elevation "natural" habitats.

Survivorship of adults is also significantly lower in "slash", although data are still too sparse to convincingly demonstrate that this is a "real" population trend and not an artifact produced by small samples, or even a trend exhibited by only the two studied "slash" colonies. There are demonstrable differences between the two colony types.

- The logging-slash "sink" hypothesis is alive and well, but remains untested. Several methods are proposed to confirm or refute this idea .

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Appendix I: Observed marmot survivorship at four colonies, 1987-1991.

KEY

- o = initial capture
- + = positive identification (recaptured or confirmed with spotting scope).
- x = young-of-the year not captured but where location of birth was established.
- ? = not positively identified.
- * = animals identified one year before initial capture from pelage characteristics, scars etc.
- Ⓢ = reproductive female (capture or observed lactating).
- = no observation of animal.

NOTES

- ^a burrow name is based on initial adult female present.
- ^b presumed or known age at time of initial capture.

Green Mountain

Burrow ^a	tags	sex	age ^b	1987	1988	1989	1990	1991	Name
Betsy	1820	f	3	Ⓢ	Ⓢ	+	+	-	Betsy
" "	2726	m	3	o	+	-	-	-	O. 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	+	-	+	Delilah
" "	926927	m	0		o	+	+	+	Samson
" "		-	0		x	-	-	-	
Total n of tagged adults				4	4	4	3	3	
Total n of young				3	6	0	0	0	
n of reproductive incidents				1	2	0	0	0	

Haley Lake

Burrow	tags	sex	age	1987	1988	1989	1990	1991	Name
Tonto	3334	f	3	o	®	-	-	-	Tonto
" "	-	?	0		x	+	-	-	
" "	-	?	0		x	-	-	-	
" "	-	?	0		x	-	-	-	
" "	6162	m	3	*	o	-	-	-	Oscar
" "	2829	m	2	o	+	+?	-	-	Haley's Comet
" "	3132	f	2	o	+	-	-	-	Blackie
" "	3738	m	2	o	-	+	-	-	Boss
" "	3536	f	2	o	+	+	®	®	Oprah Winfrey
" "	0708	m	0					o	
" "	0910	m	0					o	
" "	1718	f	0					o	
" "	0506	m	0				o	+	Meanie
" "	0304	m	0				o	+	Zen
" "	971972	f	0				x	+	Xavier
" "	1112	m	3				o	-	Dillenger
" "	941942	m	3				o	-	Einstein
Mom #1	5354	f	3		®	+	+	-	Mom #1
" "	4748	m	3	*	o	+	-	-	Cardinal
" "	-	?	0		x	+	-	-	
" "	-	?	0		x	-	-	-	
" "	-	?	0		x	-	-	-	
Mom #2	6970	f	3		®	+	-	-	Mom #2
" "	4950	m	2		o	-	-	-	No-name
" "	-	?	0	x	-	-	-	-	
" "	8586	f	1	x	o	-	-	-	yearling #1
" "	-	?	0		x	+	-	-	
" "	-	?	0		x	+	-	-	
" "	-	?	0		x	-	-	-	
" "	-	?	0					o	
" "	-	?	0					o	
" "	-	?	0					o	
Mom #3	7879	f	3		®	-	-	-	Mom #3
" "	-	?	0		x	-	-	-	
" "	-	?	0		x	-	-	-	
" "	-	?	0		x	-	-	-	
" "	909910	f	2			o	+	®	Luna
" "	976977	f	2			o	-	+	Tweedledum
" "	978979	f	2			o	+	-	Alice
" "	980981	f	2			o	-	-	Tweedledee

Appendix I continued.....

Newfie	7172	f	2	*	o	+	+	Ⓢ	Live-wire
" "	6364	m	2	*	o	+	+	+	Newfie
" "		?	0					o	
" "		?	0					o	
" "		?	0					o	

Total n of tagged adults	9	11	9	8	7
Total n of young	2	12	0	3	9
n of reproductive incidents	1	4	0	1	3

Pat Lake

Burrow	tags	sex	age	1987	1988	1989	1990	1991	Name
Endrock	919920	f	3		Ⓢ	-	-	-	
" "	901902	m	0		o	+	+	+	GIJoe
" "	903904	m	0		o	+	-	+	
" "	905906	m	0		o	-	-	-	
" "	913914	f	0		o	-	-	-	
" "	957958	m	4			o	-	-	
" "	959960	m	3			o	-	-	
" "	961962	m	3			o	-	-	
Midrock	955966	f	3			Ⓢ	-	-	Midrock
" "	911912	m	3		o	-	-	-	
" "	915916	m	2		o	+	-	-	
" "			0			x	-	-	
" "			0			x	-	-	
" "			0			x	-	-	
" "			0			x	-	-	
" "	943944	f	2				o	-	
" "	945946	f	3				o	-	Goldilocks
Triangle	907908	f	1		o	Ⓢ	+	+	Cher
" "	932933	f	1		o	-	-	-	
" "	934935	f	1		o	-	-	-	
" "	928929	f	2		o	+	+	-	Sundance Kid
" "	917918	m	3		o	-	-	-	
" "	921922	m	4		o	-	-	-	
" "	951952	m	2			o	-	-	

Appendix I continued.....

Apex	953954	m	3	o	-	-	
" "	930931	m	3	o	-	-	
" "	963964	f	2	o	-	@	Iris
" "		?	0			o	
" "		?	0			o	
" "		?	0			o	

Total <i>n</i> of tagged adults identified	>9	>10	5	2
Total <i>n</i> of young identified	>4	4	0	3
<i>n</i> of reproductive incidents	>2	1	0	1

Haley Slash

Burrow	tags	sex	age	1987	1988	1989	1990	1991	Name
Tophat	4243	m	2	o	-	-	-	-	Sylvester
" "			2	+	-	-	-	-	Eyebrows
Patches		m	3		*	+	-	-	Patches
" "	1516	m	2				o	-	Ernie
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	-	-	-	

Total <i>n</i> of tagged adults identified	2	4	4	5	0
Total young identified	0	6	4	0	0
<i>n</i> of reproductive incidents	0	2	1	0	0

