Relative Importance of Episodic Versus Chronic Mortality in the Decline of Vancouver Island Marmots

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ABSTRACT

I used population count data collected from 1979 to 1998 to evaluate the relative importance of "chronic" versus "episodic" mortality patterns in Vancouver Island marmots (*Marmota vancouverensis*). I hypothesized that some factors (e.g., gradual vegetation change, forestry effects, or predation) should produce chronic patterns of mortality, and others (disease and weather) should produce episodic patterns. A few colonies had consistently low survival. These results are consistent with a hypothesis of poor quality "sink" habitats that are maintained by immigration from nearby "sources." However, most colonies had distinct episodes of high mortality, and these appear to be the primary cause of recent population declines. Spatial and temporal patterns of survival are consistent with a hypothesis of disease outbreak or increased hunting effort by predators within a small geographic area. The impact of both factors was probably exacerbated by forestry activities. Results underscore the precarious status of this endangered mammal and illustrate the value of carefully designed annual population surveys.

Key words: *Marmota vancouverensis*, mortality, population surveys, Vancouver Island marmot.

Caughley and Gunn (1996) offered a straightforward model for managing endangered species. First, determine whether populations are declining or whether other evidence suggests that a problem exists. Second, learn about the ecology of the organism and use the accumulated knowledge to construct hypotheses about possible causal factors. Third, subject the resulting hypotheses to rigorous scientific testing. Finally, use the results to reverse the factors that are causing the problem. In this paper I use long-term population count data from a critically endangered mammal to address a basic question: can annual population count data be used to test hypotheses about the causes of decline?

Vancouver Island marmots (*Marmota vancouverensis*) are endemic to Vancouver Island, B.C. (Nagorsen 1987). Apart from small colonies on Mount Washington, all known active sites are located within 5 adjacent watersheds on southern Vancouver Island (Bryant and Janz 1996). Recent population trends on southern Vancouver Island are intriguing. Many colonies expanded during the early 1980s and this was accompanied by colonization of some new habitats created by clearcut logging of forests above 700 m elevation. Unfortunately this expansion was limited both in geographic and temporal terms. Despite successful reproduction and survival in new habitats created by forest harvesting, marmot numbers subsequently declined from a peak of more than 300 animals during the mid-1980s to the present total of fewer than 100 animals (Bryant 1998).

Several hypotheses have been advanced to explain recent population dynamics, including natural habitat change (Milko 1984), source-sink and landscape connectivity dynamics caused by forestry (Bryant 1996), periods of inclement weather (Smith 1982), changing predator abundance (Merilees 1980), and disease outbreaks (Bryant et al. in press). These hypotheses are not mutually exclusive and there is no a priori reason to imagine that a single factor is responsible for observed population trends. However, the hypotheses are useful in generating testable predictions and exploring the fundamental question of whether declines are primarily due to what I describe as "chronic" or "episodic" processes.

CHRONIC PROCESSES

A variety of mechanisms could reduce habitat quality over time. In natural subalpine meadows, possible mechanisms of habitat change include invasion by trees or bracken ferns (*Pteridium* spp.), post-fire succession, and changing foodplant availability (Milko 1984, Martell and Milko 1986, Laroque 1998). Gradual processes such as these lead to the expectation of slow decline in survival or birth rates as individual habitats become increasingly unsuitable. There is no reason to expect that change would occur simultaneously at

L. M. Darling, editor. 2000. Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, B.C., 15 - 19 Feb.,1999. Volume One.
B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. and University College of the Cariboo, Kamloops, B.C. 490pp.

all sites or that there would be an abrupt temporal threshold between habitats being "suitable" or "unsuitable." Given the short duration of this study compared to rates of change in subalpine meadows (e.g., Schreiner and Burger 1994), one would expect to observe chronic low birth or survival rates at a subset of natural colonies.

In clearcuts, forest regeneration is the principal mechanism of change, and this process is exceptional because it can act over a temporal scale measured within the lifetime of individual marmots. The successional state of regenerating clearcuts could influence birth or survival in a linear fashion (i.e., a gradual reduction as a function of increasing forest age). Alternatively, it could be manifested by a threshold effect, in which conditions become unsuitable for birth or survival over a period of a few years. In either case the prediction is that when averaged across years, survival should be relatively low in clearcut habitats.

It is likely that mortality due to predation would be reasonably consistent across years and colonies. Known marmot predators such as wolves (*Canis lupus*), cougars (*Puma concolor*), and golden eagles (*Aquila chrysaetos*) are relatively long-lived compared to marmots, and their populations should not fluctuate greatly from year to year. In addition, individual predators are likely to benefit from learned hunting behaviour, and individuals would be expected to continue hunting at locations where they were successful in the past. For these reasons the predation hypothesis would be expected to produce chronic mortality patterns.

EPISODIC PROCESSES

Several factors could cause episodes of high mortality and therefore produce abrupt shocks to the marmot population. For example, marmots might suffer from "bad weather" years resulting from extremes in snowpack or rainfall (e.g., Armitage 1994). Disease events (epizootics) could also occur. In this case the fundamental prediction is that marmots would display "episodes" of high mortality. Weather effects would be expected to occur randomly over time, but disease events might occur over a period of a few consecutive years as the infection spreads.

SPATIAL CORRELATION OF SURVIVAL

Given the small size of the geographic area occupied by marmots, one would expect weather to influence the entire metapopulation. There should, therefore, be no spatial correlation of survival as a function of between-colony distance (i.e., there should be uniform correlation throughout the study area). Patterns of vegetative change in natural meadows or in clearcuts should also be independent of spatial location within the landscape.

In contrast, the disease hypothesis suggests that survival would be more highly correlated at nearby colonies due to increased risk of infection (May and Anderson 1979). Similarly, because predators may focus hunting efforts at locations that offer the highest probability of success, one would also expect mortality to be spatially correlated.

STUDY OBJECTIVES

My primary objective was to test whether spatial or temporal patterns of survival were congruent with any or all of the above hypotheses. My secondary objective was to illustrate the utility of some basic analytical tools in evaluating hypotheses about the causes of decline.

STUDY AREAS

The present study encompassed the known marmot metapopulation on southern Vancouver Island. Data from Mount Washington were excluded for reasons of small sample sizes, because colonies were infrequently sampled, and because it is unlikely that dispersal occurs between that mountain and the southern metapopulation (Bryant and Janz 1996). Within this area of approximately 150 km2 all colonies were mapped (1:50,000 National Topographic Series) and entered into a Geographic Information System (Arc/Info) to facilitate spatial measurements.

METHODS

POPULATION COUNTS

Marmot counts were made by many people (see Acknowledgements). Most counts were conducted before 1100 to coincide with known marmot activity rhythms. Counts were usually repeated 2–4 times annually, although some sites were visited only once, and not every site was visited in each year (Bryant and Janz 1996).

COMPILATION AND SURVIVAL ESTIMATION

I used a simple measure of marmot survival for all analyses. This measure was calculated from consecutive annual counts in which apparent survival, ϕ, was the count of adults at time $t+1$ divided by the count of adults and pups at time t. Using Pulliam's (1988) terminology, this actually represents "*i-d-e*" or net immigration–death–emigration, and will therefore accurately reflect survival only if immigration equals emigration. Mark–recapture work (Bryant 1998) shows many cases in which this assumption is violated, but because I was interested in the relative importance of episodes of high mortality I reasoned that slight changes in annual immigration:emigration rates would not mask overall trends. For the same reason, I assumed the upper boundary of survival to be 1.0 despite numerous instances in which colonies increased because of immigration. For example, the number of non-reproductive adults at Butler Peak "west roads" colony increased from 2 in 1982 to 9 in 1983. In this case I assumed survival to be 1.0 and not 4.5.

Finally, the shape of the population count data dictated that I focus analyses on changes between the "early period" (1981–87) and "late period" (1991–97). This was necessary because in the intervening years there was no inventory apart from the few sites that academic researchers or naturalists visited. Even in the high sampling years, marmot counts suffered from inconsistent sampling effort.

Statistical Analysis

I used locally weighted regression (LOWESS; Cleveland 1979) to elucidate trends in adult abundance within colonies and across time. This method has the effect of minimizing variance caused by "pulses" of reproduction (female marmots don't breed every year and few colonies contain more than a single reproductive-age female) or differences in sampling effort across years (see above). It therefore provides a useful overview of whether all colonies declined, and I used Pearson correlations to test for this (Zar 1974). However, by definition, employing "smoothers" such as LOWESS remove the peaks and lows of survival rates, therefore removing the very episodes of high mortality that are the subject of this paper.

Autocorrelation describes the pattern in which nearby things are more or less alike. In this case the word "nearby" can be interpreted in both a geographic (spatial) context and a temporal (year-to-year) context. To address the question of temporal autocorrelation I calculated coefficients of variation (CV) to evaluate the magnitude of year-to-year fluctuation in survival rates (Zar 1974). Colonies with chronic mortality patterns should show relatively low coefficients of variation.

To evaluate spatial autocorrelation I used Moran's I coefficient. The general form of the statistic is analogous to Pearson's R in that it is a general cross-product statistic (Sokal and Oden 1978). Values close to 1.0 indicate that similar values tend to cluster together in a spatial context, and values approaching -1.0 indicate that dissimilar values tend to cluster together. The essential formula is:

$$I = \Sigma\Sigma W_{ij} \Delta_{ij}$$

in which $\Delta_{ij}$is a measure of the proximity of the variate (in this case apparent survival) between the $_i$th and $_j$ th spatial positions, and W_{ij} is a spatial weighting function. A fundamental requirement of spatial correlation analysis is some measure of contiguity or "connectivity" of the locations. On a regular grid (e.g., quadrat data), contiguity (W_{ij}) is typically set to equal 1 for nearest neighbours and 0 if otherwise (Haining 1990). For

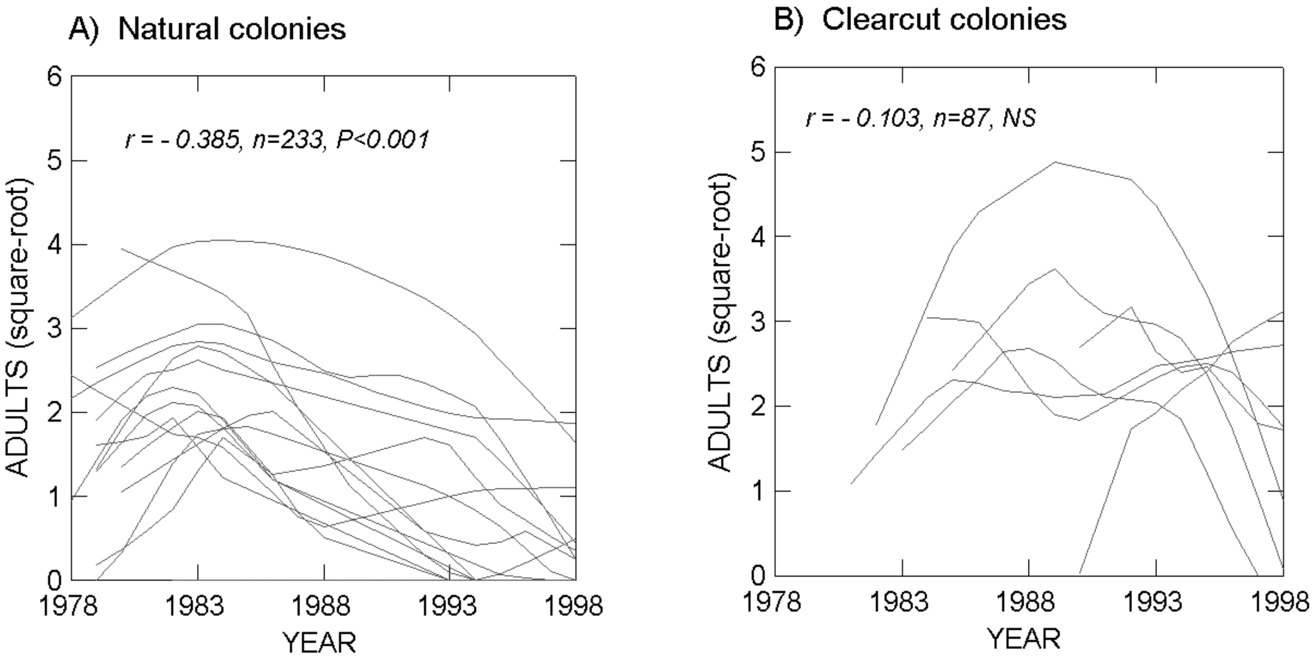

Figure 1. Population trends within and among colonies. Data are LOWESS regressions of maximum annual numbers of adults at natural meadows (A) and clearcuts (B). Abundance data were square-root transformed to facilitate comparison of trends among colonies of different sizes. Marmots in natural colonies declined significantly over time (Pearson correlations) but increased during the early 1980s. Marmots in clearcuts increased later, but most colonies subsequently declined.

Table 1. Variation in colony-specific survival. Data are median survival rates for 16 Vancouver Island marmot colonies with at least 5 years of data. Several additional sites (e.g., Mount Whymper, "P" Mountain, and Mount Buttle) showed similar trends, but sporadic sampling effort precluded analysis. (N = population size, CV = coefficient of variation.)

		1981–87			1991–97		
Colony	Type	N	Median	CV	N	Median	CV
Butler Peak	clearcut	4	0.93	13	6	0.43	57
Bell Creek	natural	7	0.90	21	7	0.50	72
Vaughan Road	clearcut	5	0.90	34	5	0.50	83
Gemini	natural	6	0.75	50	*extinct*		
South Green	natural	5	0.75	42	*extinct*		
Haley Lake	natural	7	0.70	29	7	0.50	37
Westerholm	natural	6	0.68	60	*extinct*		
K44E	clearcut	7	0.67	33	7	0.75	46
D13E	clearcut	4	0.66	35	5	0.75	30
Green Mountain	natural	7	0.65	29	7	0.80	39
G2C	clearcut	5	0.60	44	*extinct*		
West Green	natural	6	0.58	62	*extinct*		
Green NW	natural	6	0.51	74	*extinct*		
Pat Lake	clearcut	1			6	0.63	29
Sherk Lake	clearcut		*not yet colonized*		6	0.89	24
Mount Franklin	clearcut		*not yet colonized*		6	0.61	14

more spatially complex data (such as locations of marmot colonies), contiguity can be calculated using the principle of an "effects radius" (Smith and Gilpin 1997).

For marmots, I reasoned that mortality due to weather would occur over the entirety of the Nanaimo Lakes metapopulation, but that mortality due to predators or disease would occur over progressively smaller areas. I therefore tested for spatial autocorrelation using a cumulative effects radius in which only those neighbours within the radius were tallied as being contiguous (i.e., $W_{ij} = 1$). Significance of Moran's I was evaluated using Z scores (Sokal and Oden 1978). The null hypothesis in this case is that the observed distribution of events is no different from a distribution in which values are randomly assigned to the same set of spatial locations.

RESULTS

Population Trends among Colonies

Sequential population estimates could not be made for many colonies because of gaps in sampling coverage, but LOWESS regressions were useful in exploring trends over time. Apparently no colony remained stable over the study period (Fig. 1). Marmot numbers in natural habitats declined systematically with year. The data suggest a definite upward bulge that occurred in 1983, which probably reflects high reproduction in 1982 or earlier. Numbers of marmots in clearcuts increased greatly during the late 1980s (the Butler Peak "west roads" colony was the largest), but from about 1992 on most colonies declined rapidly.

Chronic and Episodic Patterns of Mortality

Some colonies were apparently more successful than others, and there were distinct differences between the early and late sampling periods (Table 1). Survival was generally higher during the early (1981–87) sampling period. Some colonies (e.g., Bell Creek and Butler Peak) had relatively high survival (>90%) and low annual coefficients of variation (<30%). However, the reverse was not true. Colonies with relatively low survival (i.e., West Green and Green NW) generally had high coefficients of variation (62–74%). High CVs suggest that mortality was exceptionally high in some years (episodic) rather than chronic.

A similar pattern was evident during the late (1991–97) sampling period. A few colonies (e.g., Mount Franklin and Sherk Lake) had relatively consistent survival rates (CV <25%) with no suggestion of high-mortality events. However, most colonies suffered dramatic changes in survival from year to year (CV >50%). For example, the Bell Creek natural colony exhibited moderate survival (50–100%) in most years, but lost most of its marmots in a single year (1995). Data from the well-known Haley Lake colony are also illustrative. At this colony, 3 of the 4 survival years since 1994 represented high-mortality events (<50% survival). Given the natural history of *M. vancouverensis*, no colony could be expected to withstand such losses within a 4-year period, and this was the fundamental cause of near-extinction at this site by 1998.

Temporal Incidence of High-Mortality Events

High-mortality events were apparently not uniformly distributed across time (Fig. 2). Annual survival data coded as high-mortality "events" or low-mortality "non-events" using a variety of criteria suggest that the frequency of events increased over time. Using the median survival rate (65%), results suggest a gradual increase in the event:non-event ratio. Other event criteria produce different results. Using the high survival event criterion (<80%), results suggest that marmots have generally not experienced high survival since the mid-1980s.

Of particular interest are the results based on a more stringent (<50%) event criterion. Episodes of high mortality occurred often (60 events and 141 non-events; rate = 30%). In 9 years the event:non-event ratio was higher than this, and in 10 years it was lower. The data suggest a "normal" event:non-event ratio of 20–25%. The ratio has been higher than 35% since 1994, and it was also higher than this during the 1984–86 period. The early sampling period is interesting because it does not suggest high spatial correlation. Inspection of the data suggests that events occurred at widely separated colonies (e.g., Mount Whymper, "P" Mountain, Mount Buttle, Green Mountain) during the mid-1980s. It is also interesting that these events went largely unnoticed by wildlife managers, perhaps because attention was focused on the expanding clearcut colonies at that time.

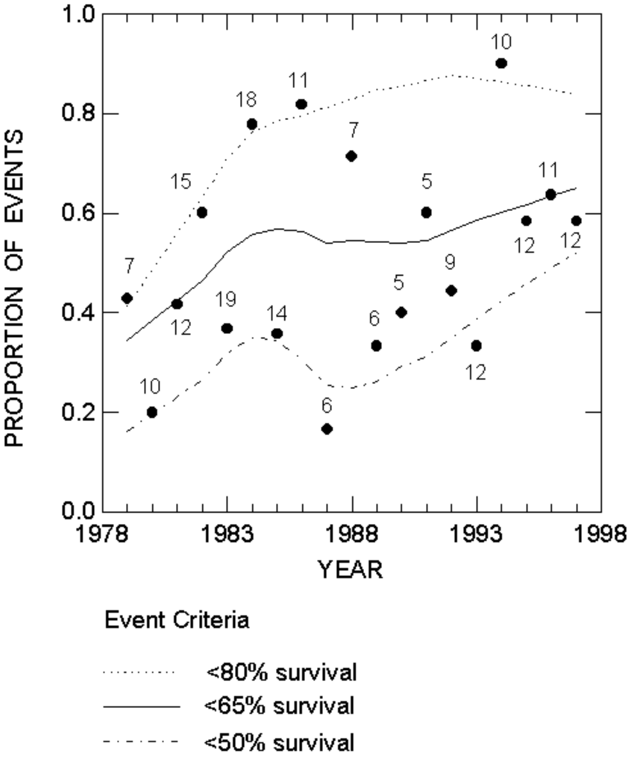

Figure 2. Increasing incidence of high-mortality events. Data points are event:non-event ratios using median annual survival (65%) as the event criterion. Lines are LOWESS regressions using 3 event criteria (50%, 65%, and 80%, as described in the text). Numbers of colonies in the sample are shown. Vancouver Island marmots have suffered from increased frequency of high-mortality events in recent years.

SPATIAL CORRELATION OF SURVIVAL

Marmot survival was spatially autocorrelated during both sampling periods (Fig. 3). Moran's *I* varied from 0.09 to 0.52, indicating weak to moderate positive correlation at all effects radii. The strength of the correlation declined with increasing distance. Significant positive correlation was obtained at the largest radii that encompassed the entire study area (15 km), but strengths of the associations were low (*I* = 0.09 and 0.25). At shorter distances (<5 km) stronger correlations were obtained (*I* = 0.15 to 0.36).

Spatial autocorrelation differed between the early and late periods although the shapes of the curves were similar. Survival rates were more highly correlated during the late sampling period. This is an interesting result because recent extinctions ensured that the metapopulation was more dispersed in the late period than in the early period.

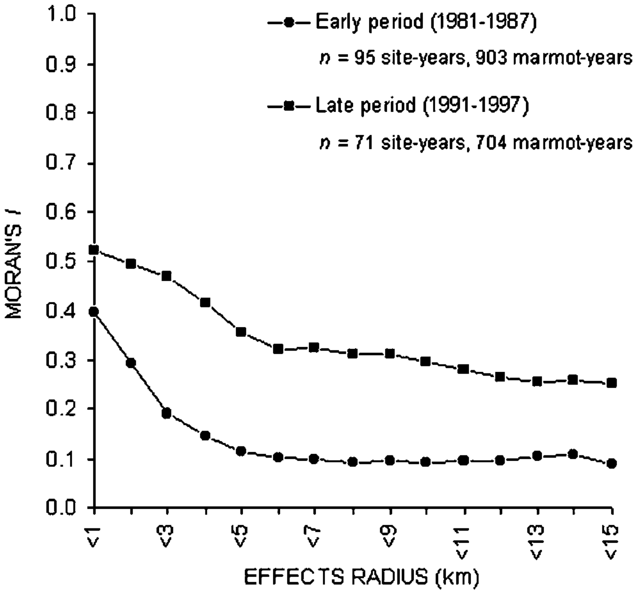

Figure 3. Spatial autocorrelation of marmot survival. Data are Moran's I coefficient using annual survival rates weighted by the numbers of adults and pups present. All correlations were significant and positive (Z > 1.65, P < 0.05). The degree of spatial autocorrelation increased between the early and late sampling periods, despite a more dispersed population structure.

DISCUSSION

There is little evidence in support of the hypothesis that marmots have recently responded to natural habitat change. Only 2 natural colonies (Westerholm basin and Green NW ridge) showed consistently poor survival, as would be predicted under a hypothesis of post-fire succession or tree invasion. In clearcut habitats, several sites (e.g., Pat Lake, G2C, Mount Franklin) showed relatively low and consistent survival. These results are congruent with a hypothesis of low-quality "sinks," particularly among habitats created by clearcut logging of high-elevation forests (Bryant 1996).

The apparent increase in frequency of high-mortality events is disturbing, and this trend appears to be at the root of recent population declines. Many apparently large and well-established colonies in natural subalpine meadows suffered abrupt and catastrophic mortality events over a short period ("P" Mountain, Mount Whymper, Gemini Peak, Bell Creek, Haley Lake). This pattern is inconsistent with a suggestion of gradual vegetation changes because habitats are not likely to change simultaneously. Moreover the temporal pattern of high-mortality events is inconsistent with the "bad weather" hypothesis because high-mortality events were not restricted to particular years.

Nearby colonies displayed similar survival rates. Significant positive spatial autocorrelation is consistent with a hypothesis of localized predator effort or disease events, but it is inconsistent with the suggestion of "bad weather" years or changing natural habitats. Most importantly, increased magnitude of spatial autocorrelation in the later sampling period suggests growing importance of mortality factors such as disease or predation. Neither predation nor disease can be divorced from forestry activities. It is likely that the importance of both factors has been increased by the changes in population density produced by marmot colonization of clearcuts.

Vancouver Island marmots illustrate many of the practical difficulties involved in applying Caughley and Gunn's (1996) approach to a real endangered species issue. Some difficulties were unavoidable. For example, funding limitations produced high variance in survey effort among years. Other difficulties were avoidable. Specifically, despite substantial count efforts in some years, results were often biased by uneven sampling. Interpretation remained difficult because results were not mapped, analyzed, or tested for consistency. The result was that as recently as the early 1990s there remained considerable uncertainty about whether marmots were increasing or declining (Janz et al. 1994).

Superficial analysis of population counts without benefit of demographic knowledge or spatial context led to the mistaken impression that marmots were thriving in clearcuts. Similarly, much speculation was made about issues such as dogs, ski-hill development, all-terrain vehicles, weather, natural habitat change, and changing predator abundance (e.g., Merilees 1980, Smith 1982, Dearden and Hall 1983, Milko 1984). There is nothing wrong with making such hypotheses, but unfortunately they were not accompanied by testable predictions. The result is that several ideas gained widespread acceptance without a shred of evidence to support them.

Population surveys can provide much valuable information with which to pursue what Caughley and Gunn (1996) called the "diagnostic" phase of endangered species management. However, simple measures of abundance will only be useful if the basic biology of the organism is understood, if proper sampling design is employed, and if results are tested for consistency. Conversely, poorly designed surveys in the absence of basic life-history knowledge may provide highly misleading results. Most importantly, hypotheses unaccompanied by testable predictions may provide excuses for inaction or encourage inappropriate management activities.

ACKNOWLEDGEMENTS

Many people participated in marmot counts, including K. Atkinson (deceased), D. Blumstein, C. Bryant, L. Campbell, J. Daniels, M. deLaronde, R. Davies (deceased), D. Doyle, L. Dyck, K. Fry, V. Hiensalu, D. Janz, F. Lockwood, J. Lewis, M. Loedel, B. Mason, G. MacDermott, K. McDonald, D. Milne, J. Morgan, D. Pemberton, J. Pendergaast, C. Ramsay, G. Smith, K. Sturmanis, W. Swain, J. Voller, L. Wilson, and M. Wong. K. Armitage provided helpful comments on the manuscript. I am greatly indebted to the Vancouver Island Marmot Recovery Team, who indulged my desire to spend a decade chasing obscure ground squirrels. The views in the paper are mine and may not necessarily reflect those of the Recovery Team.

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