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Anti-Predator Behavior of Vancouver Island Marmots: Using Congeners to Evaluate Abilities of a Critically Endangered Mammal

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Abstract

Behavioral comparisons between endangered species and their congeners may provide valuable data with which to test ideas about declining populations or the future direction of recovery efforts. We considered the case of the highly endangered Vancouver Island marmot (*Marmota vancouverensis*). Predation is a current source of mortality, and inadequate anti-predator behavior could have profound ramifications for the future success of re-introductions. We tested whether *M. vancouverensis* anti-predator behavior was unusual or 'deficient' by quantifying it and comparing it to 13 other marmot species. We found no evidence that Vancouver Island marmots were unwary. If anything, the converse was true. Vancouver Island marmots were responsive and vigilant towards real and simulated predatory threats. They dug numerous escape burrows that reduced the likelihood of predation. Our results have several implications for future recovery efforts, one of which was to establish 'baseline' flight-response targets that captive-bred Vancouver Island marmots will have to meet or exceed prior to release into predator-rich environments.

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Introduction

The importance of behavioral studies to conservation biology has recently been recognized (Caro 1999). Bessinger (1997) proposed that behavioral ecologists could make a substantial contribution by studying individual endangered species.

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In this paper we illustrate a more comparative approach: we evaluated anti-predator skills of one of the world's most endangered species and compared it to the behavior of its more common congeners.

The comparative method has long been an important tool in studying the evolution of behavior and other traits (Harvey & Pagel 1991), but its application for conservation has been limited mostly to defining evolutionary significant units and studying historical population processes (e.g. Moritz 1996). We suggest that comparisons between an endangered species and its non-endangered close relatives may reveal important information about causes of endangerment and may suggest novel re-mediation (see also Bunin & Jamieson 1996). Comparative studies may be particularly useful if behavioral 'deficiencies' are a cause of endangerment or if deficiencies make a species particularly vulnerable to extinction.

The Vancouver Island marmot (*Marmota vancouverensis*) is a critically endangered ground squirrel endemic to Vancouver Island, Canada (Nagorsen 1987). The species normally inhabits small subalpine meadows maintained by avalanches (Milko 1984). Colonies typically contain fewer than five adults and display obvious metapopulation structure. Total numbers in recent geological times were probably always small, given habitat availability. However, in the past few decades the species has almost completely disappeared from northern Vancouver Island (Bryant & Janz 1996).

The southern Vancouver Island metapopulation has declined precipitously from an estimated 300–350 animals in the mid 1980s to approximately 100 in 1998 (Bryant 1999). This metapopulation is extremely localized, with all colonies found within five adjacent watersheds in a small (150 km^2) geographic area (Bryant 1999). In addition to declining numbers, this metapopulation has experienced structural changes associated with forestry and marmot colonization of recently clear-cut habitats above 700 m elevation. More than half of the world's *M. vancouverensis* were living in recently harvested clear-cuts in 1997, compared to $\approx 25\%$ in the mid 1980s and none prior to high elevation logging that began during the 1960s.

Cumulative effects of predation on marmot population dynamics remain unknown, but predators undeniably cause losses at particular colonies (radio-transmitters are found in predator scats) and such losses are important given small colony sizes (Bryant 1996, 1999). Predators such as cougars (*Felis concolor*), wolves (*Canis lupus*) and golden eagles (*Aquila chrysaetos*) remain relatively abundant on Vancouver Island. Recovery plans for this species call for re-introductions of captive-reared marmots (Janz et al. 1994). Ontogenetic isolation from predators may make it imperative that marmots are trained to properly express anti-predator behavior (Griffin et al., in press; McLean 1997; McLean et al. 1999).

Thus, it is crucial to document anti-predator abilities. If Vancouver Island marmots have markedly 'deficient' anti-predator behavior, it might be possible to 'train' marmots to recognize predators and to be more cautious in their environment (McLean 1997; McLean et al. 1999). If successful, training might also improve the survival of released animals. Obtaining baseline behavioral data is critical. Comparing anti-predator behavior in wild individuals with captive-reared individuals will be required to determine whether captive-reared animals are ready for release.

In this paper we measured four types of anti-predator behavior to evaluate the efficacy of Vancouver Island marmot anti-predator behavior. We focus on vigilance while foraging, refuge density in marmots' home ranges, the distance at which marmots orient toward, run from, and disappear when approached by humans, and the frequency of predator-elicited alarm communication. Data from other marmot species combined with an understanding of marmot phylogenetic relationships provide a framework with which to evaluate Vancouver Island marmot anti-predator behavior.

Methods

Study Population and Data Collected

We observed marmots for a total of 328 h between 30 May and 27 July 1997 at four colonies in the mountains west of Nanaimo, British Columbia, Canada: Haley Lake (four adults), Green Mt Summit (two adults and 3 yearlings), K44A (four adults), and F19 (four adults and 5 yearlings). The first two habitats are natural habitats and the latter two are high elevation clear-cuts. These 22 marmots represented about 15% of the known population and about 28% of the entire population of known non-pups. Of these, 11 were marked with numbered ear-tags (methods in Bryant 1996; marked marmots did not suffer higher mortality than unmarked marmots; Bryant 1996, 1999) and four more were easily identifiable based on unique color patterns and molt marks.

Most observations (78%) were made between 05:00 and 12:00 h, the morning period of peak activity (Heard 1977). Observers sat in the open at distances that did not obviously affect marmot behavior. In addition to *ad libitum* observations of marmot behavior and event recording of all predator interactions and anti-predator alarm calls, we conducted 2-min focal animal samples to quantify vigilance behavior whilst foraging (Blumstein 1996). Marmots spend much of their time either 'foraging' (feeding with head held down) or 'looking' (watching their environment with head held high). We focused on identified foraging subjects and noted transitions between foraging and looking by speaking into a tape recorder. Tapes were transcribed using event-recording software. From the focal record, we then calculated the frequency of looking events, the total time spent looking, and the average duration of looking bouts. For subjects with multiple focal observations, a single observation was selected at random for subsequent analysis.

Group size and a number of other factors may influence time allocated to foraging and anti-predatory vigilance (Bednekoff & Lima 1998; Blumstein et al. 1999). Previous studies of marmots found no consistent effect of group size on anti-predator vigilance (reviewed in Blumstein 1996). For this study we did not quantify the number of conspecifics within 10 m, the number of 'social-group-mates', or other potential factors that may influence dominance when conducting focal observations. By not including group size (or any other factor) as a covariate, we may have inflated our variance and reduced the power of the comparative tests.

However, because there was no bias in observing subjects with respect to group size, dominance status, etc., we assume our results adequately sampled the variation in each species and thus provide an adequate estimate of a species' anti-predator behavior.

In addition to studying vigilance behavior, we also counted burrow entrances along six 4 × 40 m transects in the core area of each of four social groups and walked toward marmots to measure flush distances. Marmots retreat to burrows when alarmed and burrows provide safe refuge from most of their predators (Blumstein 1998).

Marmots respond to humans as predatory threats, perhaps because of the long history of human predation on marmots, including *M. vancouverensis* (Bibikow 1996; Nagorsen et al. 1996). We recorded the distance at which an identified focal marmot first oriented to a human directly approaching at a constant pace of 0.5–1.0 m/s, the distance at which it retreated to their burrow entrances, and the distance at which it disappeared underground. Marmots retreat to their burrows when alarmed (Blumstein 1998). Whilst different predators may represent different levels of risk, the response to humans generates an index suitable for comparative study. For subjects approached more than once, we selected, at random, a single approach for subsequent analysis.

We also recorded, analyzed, and replayed alarm calls in controlled experiments to marmots, in order to study the complexity of their anti-predator communication (Blumstein 1999). Here we discuss how Vancouver Island marmot alarm call repertoire size compares with their congeners.

We compared vigilance and flush distance results to data collected similarly on other species in areas where marmots were not hunted by humans but were exposed to varying degrees of human contact. Consistent methods of studying flush distance were ensured because identical observers (Blumstein and Daniel) and identical methods were used to study the other species. Golden marmots (*M. caudata*) were studied in Khunjerab National Park, Pakistan, in an area where marmots were exposed to limited human contact (detailed description in Blumstein 1996). Steppe marmots (*M. bobac*) were studied from 11 to 20 Aug. 1997 in Russia's Chuvash Republic, in areas where marmots were exposed to moderate human contact (site descriptions in Ajdak et al. 1997; Soldatov 1997). Woodchucks (*M. monax*) were studied outside Lawrence, Kansas and Athens, Ohio, in areas where marmots were exposed to moderate human contact. Focal analyses were conducted from 26 to 28 Apr. 1996, outside Athens. Yellow-bellied marmots (*M. flaviventris*) were studied in Capitol Reef National Park, Utah, Rocky Mountain Biological Laboratory, Colorado, and around Boulder, Colorado – in areas where marmots were exposed to a range of human contact. Details of the study sites are described elsewhere (Blumstein & Armitage 1997); data were collected from 3 May to 29 June 1995. Olympic marmots (*M. olympus*) were studied in Olympic National Park, Washington, and hoary marmots (*M. caligata*) in Mt Rainier National Park, Washington. Individuals of both species lived in areas where marmots were exposed to considerable human contact. Details of the study sites can be found in Blumstein (1999). Observations were conducted on Olympic marmots from 19 June to 2 July 1996, and on hoary marmots from 31 July to 10 Aug. 1996.

The data set describing each species includes no more than one observation per individual. We conducted a single focal observation and a single predation probe experiment on most individuals. In those cases where there was more than one observation per individual, we selected, at random, a single observation and used the set of single observations to calculate the species mean.

Recent phylogenetic work (Kruckenhauser et al. 1999) permits us to order species with respect to their relationship to Vancouver Island marmots. Vancouver Islands marmots are a member of the 'caligata' group, a clade which contains hoary and Olympic marmots. Yellow-bellied marmots fall outside the 'caligata' group. Woodchucks and Eurasian species are more distantly related to these marmots.

Statistical Analyses

Descriptive and non-parametric statistics were calculated using StatView (Abacus Concepts Inc. 1993). Most dependent variables were heteroscedastic and were not fully normalized after transformation. Thus, we analyzed the comparative vigilance data set and the flush distance data set with one-way non-parametric Kruskal–Wallis ANOVAs. We then compared each species' response to Vancouver Island marmots with Mann–Whitney U-tests. For these post hoc analyses, we identify significant comparisons after calculating a sequential Bonferroni test (Rice 1989). The proportion of human approaches that elicited alarm calls were analyzed by a χ^2-test. Each species' proportion was subsequently compared to Vancouver Island marmot responses with a Fisher exact test.

Results

Vancouver Island marmots responded to natural and artificial predatory stimuli by returning to their burrows, orienting toward the stimulus, and occasionally by emitting alarm calls. Like other marmots, Vancouver Island marmots typically retreated to locations near their burrows before emitting alarm calls.

Vigilance

Vancouver Island marmots were as vigilant or more vigilant whilst foraging than six other species (Fig. 1). During 2-min foraging periods, Vancouver Island marmots spent 40% of their time looking (48 s looking/120 s foraging bout), raised their head 12.5 times and spent 4.8 s on each bout of looking behavior. Vancouver Island marmots spent significantly more time looking than golden marmots. Frequency of looking was significantly higher than golden marmots and significantly less than yellow-bellied and Olympic marmots. There were no significant differences in the average duration of a look among the species.

There was no obvious relationship between the relative amount of exposure to humans or relative phylogenetic relationship on marmot vigilance. Golden marmots, another species with limited human contact, were much less vigilant than

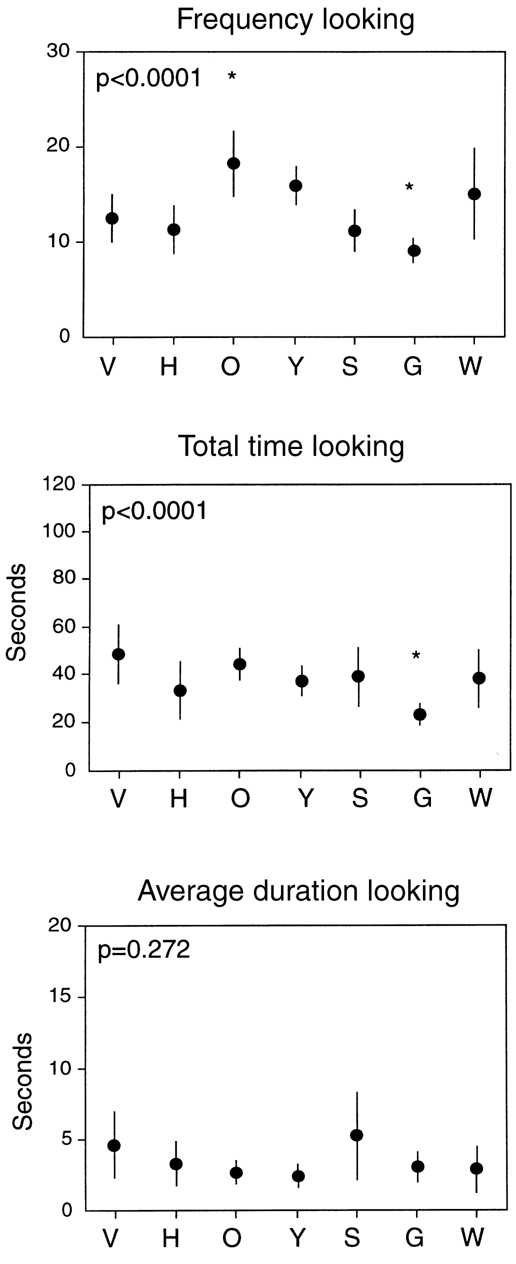

Fig. 1: $\bar{x}$ ± 95% CI of number of looks, total time looking, and average duration looking during 2-min focal animal samples whilst marmots foraged. Species codes (and sample sizes) are: V, Vancouver Island marmot ($n = 18$); H, hoary marmot ($n = 16$); O, Olympic marmot ($n = 20$); Y, yellow-bellied marmot ($n = 33$); S, steppe marmot ($n = 24$); G, golden marmot ($n = 73$); W, woodchuck ($n = 7$). Species are arranged according to their approximate phylogenetic distance from Vancouver Island marmots. p-values are from a Kruskal–Wallis one-way non-parametric ANOVA. Asterisks illustrate species significantly different from Vancouver Island marmots after a sequential Bonferroni test (see Methods)

Vancouver Island marmots. Vigilance of species exposed to moderate and considerable human contact both differed and did not differ from Vancouver Island marmot vigilance. If phylogeny was important, more distantly related species might have significantly different vigilance behavior than more closely related species. Given the available phylogenetic evidence, there is no obvious relationship between whether or not a species exhibits significantly different vigilance from Vancouver Island marmots and its relative phylogenetic distance from Vancouver Island marmots.

Burrow Density

We recorded an average of 148 burrow entrances/ha in the sampled habitat. These data on burrow densities in Vancouver Island marmot's core areas are not strictly comparable with burrow densities of other species which were averaged over their entire home range (Table 1); nevertheless they clearly reveal that Vancouver Island marmots had many potential burrows in which to seek refuge. A comparison with published data on other marmot species (Table 1) demonstrates that Vancouver Island marmots have typical-sized home ranges (one sample sign test for a hypothesized mean of 3.0, $p > 0.999$). Thus, they are not obviously exposing themselves to greater risk by ranging widely.

Flush Distance

Vancouver Island marmots first oriented to approaching humans at 49.4 m (Table 2), a distance significantly less than golden marmots, but greater than hoary marmots. Orientation distance was indistinguishable from Olympic and yellow-bellied marmots. Vancouver Island marmots returned to locations near their burrows at an average of 32.8 m. This distance was significantly smaller than in golden marmots but not in hoary, Olympic, or yellow-bellied marmots. Vancouver Island marmots allowed humans to approach to 23.3 m before they disappeared into their burrows, a distance significantly closer than golden marmots, but not as close as hoary, or Olympic marmots. They went underground at distances indistinguishable from yellow-bellied marmots.

Although sample sizes are small, there was no detectable difference between responses in clear-cuts to those observed in natural habitat (distance first oriented to approaching human, Mann–Whitney $p = 0.46$, $n = 9$ in natural meadows, $n = 13$ in clear-cuts; distance return-to-burrow, Mann–Whitney $p = 0.15$, $n = 1$ in natural meadows, $n = 4$ in clear-cuts; distance out-of-sight, Mann–Whitney $p = 0.87$, $n = 9$ in natural meadows, $n = 13$ in clear-cuts). Once marmots responded, Vancouver Island marmots went out of sight proportionally sooner (distance first oriented/distance out of sight) than Olympic or hoary marmots. Vancouver Island marmots have relatively limited human contact compared to the Olympic and hoary marmots studied in popular national parks, where they may have been somewhat habituated to humans. Nevertheless, Vancouver Island marmots appeared to be vigilant and responsive to potential predators.

Table 1: Burrow density and home range size in marmot habitat. Species are listed in order of increasing burrow density

Species	Burrow density[a]	Home range area (ha)[b]	x̄ area (ha)[c]	References
M. camtschatica	1.5–2.1	13.0	13.0	Mosolov & Tokarsky (1994)
M. monax	3.6–6.4	0.6–1.3	0.95	Henderson & Gilbert (1978); Ferron & Ouellet (1989); Swihart (1991); Meier (1992)
M. flaviventris	4.3	0.1–7.2	3.65	Svendsen (1974); Armitage (1975, 1988)
M. olympus	6.1–26.5	2.0–8.7	5.35	Barash (1973); Wood (1973); Blumstein 1999
M. baibacina	10–45	2.1–3.6	2.85	Pole & Bibikov (1991); Rogovin (1992)
M. sibirica	16–37	1.7	1.7	Seredneva (1991); Rogovin (1992)
M. caligata	32	13.8–20.5	17.15	Holmes (1979); Blumstein 1999
M. marmota	34.3–46.9	0.7–5.0	2.85	Arnold (1993); Perrin & Allainé (1993); Perrin et al. (1993); Allainé et al. 1994; Bel et al. (1995); Sala et al. (1996); Herrero et al. (1997)
M. caudata	35.4	0.6–7.0	3.8	Davydov (1991); Blumstein 1998; Blumstein & Arnold (1998) unpubl. data
M. bobac	94.1, core area	0.7–1.5	1.1	Savchenko & Ronkin (1997); Blumstein, unpubl. data
M. vancouverensis	148.4, core area	3.0	3.0	Heard 1977; this study

[a] Total number of main and escape burrows in marmot home ranges. [b] Average social group home range, when reported. In the case of multiple studies, we report the total range. [c] Average home range size, or midpoint of the range.

Table 2: Responses (median; Q1–Q3, [$\bar{x} \pm$ SD], n[a]) of marmots to approaching humans. p-values are from post-hoc Mann–Whitney U-tests, or Fisher exact tests comparing each species' response to Vancouver Island marmots. Species are listed according to their approximate phylogenetic distance with respect to Vancouver Island marmots

Species	Human contact[b]	Distance (m) first oriented to approaching human[c]	Distance (m) return-to-burrow[d]	Distance (m) out-of-sight in burrow[e]	n alarm calls/ n experiments[f]
M. vancouverensis	limited	37.0; 27.25–85.0 [49.4 ± 30.5] n = 22	21.0; 12.0–59.5 [32.8 ± 31.1] n = 5	15.5; 8.0–24.0 [23.3 ± 23.5] n = 22	2/22
M. caligata	high	23.0; 12.0–30.0 [26.3 ± 21.6] n = 15 p = 0.008*	8.0; 3.0–25.0 [13.0 ± 11.7] n = 7 p = 0.14	2.5; 2.0–5.0 [5.0 ± 6.4] n = 15 p < 0.001*	0/15 p = 0.50
M. olympus	high	25.0; 18.5–35.0 [28.3 ± 15.0] n = 16 p = 0.03	7.5; 6.25–9.5 [7.8 ± 1.7] n = 4 p = 0.14	4.0; 3.0–7.0 [5.7 ± 3.9] n = 16 p < 0.001*	1/16 p > 0.99
M. flaviventris	moderate	30.0; 12.75–63.75 [40.2 ± 35.0] n = 48 p = 0.16	40.0; 20.0–62.5 [42.4 ± 26.1] n = 14 p = 0.35	9.0; 3.75–26.25 [15.9 ± 15.5] n = 48 p = 0.08	12/48 p = 0.20
M. caudata	limited	97.5; 62.5–160.0 [122.4 ± 79.7] n = 30 p < 0.001*	120.0; 80.0–160.0 [124.5 ± 69.1] n = 11 p = 0.011*	77.5; 49.5–101.25 [85.8 ± 49.2] n = 30 p < 0.001*	16/30 p = 0.001*

*significant after a sequential Bonferroni correction. [a]Number of unique marmots contributing to this statistic. To avoid pseudo-replication, for individuals observed more than once, we report only a single, randomly selected observation. [b]A relative estimate of human visitors to marmot colonies (researchers excluded). [c]Kruskal–Wallis $p < 0.001$. [d]Kruskal–Wallis $p < 0.001$; many marmots were within 1 m of their burrow, thus sample sizes are not equal to the distance first oriented. [e]Kruskal–Wallis $p < 0.001$. [f]$\chi^2 = 24.589$, df = 4, $p < 0.001$.

There was no obvious relationship with how Vancouver Island marmots responded to approaching humans and the relative degree of human contact, but we cannot rule out a phylogenetic effect. Golden marmots, another species studied at a location with extremely limited contact and the most distantly related of these five species, responded at significantly greater distances than Vancouver Island marmots. Closer relatives exposed to more human contact either did not differ, or responded at closer distances than Vancouver Island marmots.

Alarm Vocalizations

Vancouver Island marmots called in response to a variety of potential aerial and terrestrial predators. When people walked towards marmots they called 9% of the time (Table 2). When compared with the four other species, this is about as frequently as expected for all but golden marmots, who called significantly more than expected. Because golden and Vancouver Island marmots had limited human contact, calling frequency appears not to be influenced by human contact. We cannot rule out a strong phylogenetic effect in the propensity to alarm call; Vancouver Island marmots call as much as expected as their relatively close relatives in the 'caligata' group.

Discussion

Whilst sample sizes were unavoidably small, three lines of evidence suggest that Vancouver Island marmots have a highly developed suite of anti-predator behaviors. First, they are as vigilant or more vigilant than other studied marmots. Secondly, they dig numerous burrows throughout their home ranges and are therefore often close to refugia. Thirdly, they have a highly developed anti-predator alarm communication system compared to other marmots (Blumstein 1999). In comparison to their close relatives in the 'caligata' group, *M. vancouverensis* has evolved at least one more type of loud alarm call (the 'keeaw'; Heard 1977).

Vancouver Island marmots permit potential predators (humans) to get relatively close before responding and disappearing into burrows. This may be due to environmental conditions; specifically to low visibility resulting from dense vegetation. Our observation that Vancouver Island marmots responded to humans at significantly closer distances than golden marmots may be an artifact of the distance that they first could respond to an approaching human. Golden marmots were studied in a high alpine open environment with relatively greater visibility. When compared with other marmots that inhabited relatively patchy habitats often with limited visibility (Olympic, hoary, yellow-bellied), Vancouver Island marmots responded at significantly greater distances to approaching humans. A single experimental encounter with a dog emphasizes the importance of limited visibility. Marmots did not respond in any obvious way to an approaching leash-controlled dog until it climbed onto an elevated stump and became visible 17 m from the marmots. In contrast, golden marmots often responded to dogs that were > 200 m away (Blumstein, pers. obs.).

Vancouver Island marmots are not unique in living in habitats with limited visibility. Woodchucks live in forest edge habitat where shrubs and herbaceous vegetation may obstruct their view. Olympic and hoary marmots may also live in alpine clearings with limited visibility. Some subalpine populations of yellow-bellied marmots live in areas with 1–2 m high vegetation at the height of the growing season. Additionally, high-alpine species living in areas with low vegetation (e.g. golden marmots) may inhabit areas where sight lines are limited by broken terrain.

Unlike natural meadows, as replanted clear-cuts re-grow, visibility decreases. It is possible that Vancouver Island marmots are 'adapted' to life in open meadows and are not able to modify their anti-predator behavior in clear-cuts. In support of this hypothesis, our data suggest that Vancouver Island marmots living in clear-cuts did not respond differently to marmots living in natural meadows. However, Vancouver Island marmots living in natural meadows often foraged in the adjoining forest, suggesting that the trees and limited visibility in re-growing clear-cuts was not a novel experience.

Comparative studies place the behavior of each species in perspective. In this case we used studies of congeners to test whether Vancouver Island marmots exhibited different or 'deficient' anti-predator behavior patterns. Results suggest that Vancouver Island marmot anti-predatory behavior does not obviously differ from most congeners and that they respond to potential predatory threats in a variety of ways. Marmots dig numerous burrows in their home ranges. These home ranges are not significantly larger than those of most other marmots, suggesting that Vancouver Island marmots are not necessarily exposing themselves to greater risks by ranging more widely than other species. Marmots trade-off foraging with looking and thus devote time to anti-predatory vigilance. Marmots vocally communicate the relative risk of predation to conspecifics in a sophisticated way (Blumstein 1999).

We conclude that Vancouver Island marmots fall prey to terrestrial and aerial predators, not because they are unprepared or unable to recognize them, but rather because they are unlucky. Before captive-reared animals are released into the wild, they must be able to perform natural anti-predator behavior. Our results may provide 'baseline' flight-response targets that marmots bred in captivity will have to meet or exceed prior to release into predator-rich environments. It is possible that these responses require early experience for their proper performance (McLean 1997). Training captive, and therefore somewhat naive, animals to recognize predators, and stimuli associated with predators, may be an effective way to increase vigilance, response distances, and rates of alarm calling. However, because marmots reared in the wild exhibit 'normal' anti-predator behavior, it is unlikely that sensitizing wild marmots to predators would be an effective way to reduce mortality.

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