Timing and causes of mortality in the endangered Vancouver Island marmot (*Marmota vancouverensis*)

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Abstract: We used radiotelemetry to evaluate seasonal survival rates and mortality factors for a critically endangered island endemic, the Vancouver Island marmot (*Marmota vancouverensis* Swarth, 1911). Recovery of radio transmitters and marmot remains suggested that predation was the major cause of mortality, accounting for at least 24 of 29 (83%) known-fate deaths recorded since radiotelemetry efforts began in 1992. Wolves (*Canis lupus* L., 1758) and cougars (*Puma concolor* (L., 1771)) apparently accounted for 17 deaths (59%). Three marmots (10%) were killed by golden eagles (*Aquila chrysaetos* (L., 1758)), four (14%) were killed by unknown predators that probably included all of the above species, two (7%) died from unknown causes, and three (10%) died during hibernation in a single burrow. Mortality rates varied seasonally. The daily probability of death during hibernation was very low ($P_{\mathrm{death}} = 0.016$). The probability of death was also low from spring emergence through 31 July ($P_{\mathrm{death}} = 0.051$), but was eight times higher in August ($P_{\mathrm{death}} = 0.395$) and four times higher in September ($P_{\mathrm{death}} = 0.175$). We concluded that predation was the proximate cause of recent declines in wild Vancouver Island marmot populations, that losses were highly concentrated in late summer, and that previous studies exaggerated the importance of winter mortality. We suggest that high predation rates were associated with forestry and altered predator abundance and hunting patterns.

Résumé : La radio-télémétrie nous a servi à évaluer le taux saisonnier de survie et les facteurs de mortalité chez la marmotte de l'île de Vancouver (*Marmota vancouverensis* Swarth, 1911), une espèce endémique insulaire fortement menacée. La récupération des émetteurs et des carcasses de marmottes laisse croire que la prédation est la cause principale de mortalité, représentant au moins 24 (83 %) des 29 cas étudiés depuis le début de l'utilisation de la radio- télémétrie en 1992. Les loups (*Canis lupus* L., 1758) et les couguars (*Puma concolor* (L., 1771)) sont apparemment responsables de 17 (59 %) des morts. Trois (10 %) des marmottes ont été tuées par des aigles royaux (*Aquila chrysaetos* (L., 1758)) et quatre (14 %) par des prédateurs inconnus qui incluent peut-être toutes les espèces mentionnées précédemment; deux (7 %) sont mortes de causes inconnues et trois (10 %) sont mortes dans un même terrier durant l'hibernation. Les taux de mortalité varient en fonction de la saison. La probabilité quotidienne de mortalité durant l'hibernation est très faible ($P_{\mathrm{mort}} = 0{,}016$). La probabilité de mortalité est aussi faible de l'émergence printanière jusqu'au 31 juillet ($P_{\mathrm{mort}} = 0{,}051$), mais elle est huit fois plus élevée en août ($P_{\mathrm{mort}} = 0{,}395$) et quatre fois plus élevée en septembre ($P_{\mathrm{mort}} = 0{,}175$). En conclusion, la prédation est la cause immédiate des déclins récents des populations sauvages de marmottes de l'île de Vancouver, les pertes sont fortement concentrées en fin d'été et les études antérieures ont exagéré l'importance de la mortalité hivernale. Nous croyons que les forts taux de prédation s'expliquent par les pratiques forestières, ainsi que par les changements dans l'abondance des prédateurs et les patterns de chasse.

[Traduit par la Rédaction]

Introduction

Estimating reproductive and survival rates is a critical first step towards solving many problems in wildlife management (e.g., Caughley 1977). The need for accurate demographic information is acutely felt by those faced with the task of managing endangered species (e.g., Heppel et al. 2000), precisely because differing hypotheses about causes of decline can lead to recovery strategies that are diametrically opposed (e.g., Caughley and Gunn 1996). It is sometimes unclear whether the more effective strategy might be enhance reproduction to offset mortality (e.g., through captive-breeding programs) or reduce mortality to enhance reproduction (e.g., through predator control). While the need to base wildlife management decisions on a sound understanding of demographics has long been advocated, in practice this is often easier said than done. Estimating demographic rates for endangered species can be especially problematic because such species tend to be, by definition, rare. Recovery efforts on behalf of endangered species can also generate substantial public and political controversy, particularly when they involve consideration of socioeconomic or ethical issues in addition to biological ones (Cam et al. 2003). The northern spotted owl (*Strix occidentalis caurina* (Xantus de Vesey, 1860)) and island gray fox (*Urocyon littoralis* (Baird, 1857)) are two well-known examples of endangered species that

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have generated controversy, in these cases, either through perceived economic costs to local resource-based communities (Franklin et al. 2000) or by proposed control of naturally occurring predators (Courchamp et al. 2003).

The Vancouver Island marmot (*Marmota vancouverensis* Swarth, 1911) may provide another example of a species-specific conservation program that has broader dimensions. This housecat-sized ground squirrel is endemic to Vancouver Island, Canada (Nagorsen 1987). Although first listed as endangered in 1978 (Shank 1999), the basic ecology of this mammal remained poorly understood until the 1990s (Bryant 1996). Population counts suggested expansion during the 1980s, including colonization of several man-made habitats created by clearcut logging (Bryant and Janz 1996). Later surveys revealed precipitous declines (Janz et al. 2000). The status of the Vancouver Island marmot remains precarious. Fewer than 35 marmots are thought to exist in the wild, with another 93 marmots housed in captivity (unpublished minutes, Vancouver Island Marmot Recovery Team, November 2004). A recovery program predicated on captive breeding and reintroduction is underway and has achieved some tangible successes to date, yet the specific causes of decline have remained elusive (Bryant 2000; Janz et al. 2000).

In this paper, we apply a modern modeling approach (White and Burnham 1999) to the problem of estimating survival rates and mortality factors. Our objective was to identify when and how marmots died, to provide robust annual survival estimates, and to further elucidate problems that need to be addressed if recovery efforts for this species are to succeed.

Methods

Study areas

Vancouver Island marmots are restricted to the Coastal Western Hemlock and Mountain Hemlock biogeoclimatic zones on the leeward side of Vancouver Island (Demarchi et al. 1990). The climate is submaritime, with winter precipitation falling as rain or snow depending on elevation, and with air temperatures that are moderated by proximity to the sea (Klinka et al. 1989). The landscape occupied by marmots has been heavily modified by forestry (McNay and Voller 1995). Clearcut logging of primary forests in the region began in the late 1940s. Harvest rates accelerated during the 1960s and 1970s, remained high during the 1980s, and declined subsequently. The historical pattern was to develop road access along valley bottoms first, and then extend roads upwards as harvesting proceeded. The result was a rapidly changing landscape characterized by systematic replacement of mature forests by younger ones, combined with a growing profusion of logging roads, from valley floors at elevations of 300–500 m to more recent harvesting at elevations of 800–1000 m (Bryant 1998).

Vancouver Island marmots occupied only a small fraction (<1%) of this landscape in modern times (Bryant and Janz 1996). We tracked the fate of radio-equipped marmots at nine colonies in natural subalpine meadows and six colonies in clearcuts mapped by Bryant (1996). The "natural colonies" included Green Mountain summit, Haley bowl, "P" Mountain (2 sites), the unnamed mountain locally known as "Big Ugly", Heather Mountain, Mount Moriarty, and Mount Washington (2 sites). Sites were typically at elevations of 1000–1400 m on moderately steep (30°–50°) south- or west-facing slopes that were kept free of trees by avalanches or snowcreep. Vegetation conditions and food habits of marmots at three natural colonies were described by Milko and Bell (1986) and Martell and Milko (1986). The clearcut colonies included Sherk Lake, Vaughan road, Green road "K44, Butler Peak west roads, Pat Lake, and road D13e. Clearcut colonies were typically at lower elevation (700–1000 m). Vegetation conditions in clearcuts were dominated by the alder *Alnus viridis sinuata* (Regel) Löve and regenerating conifers.

Radiotelemetry

Trapping, handling, ear-tagging, and age-classification methods were as described by Bryant (1996, 1998) and Karels et al. (2004). Marmots were surgically implanted with radio transmitters initially supplied by Custom Telemetry® (Watkinsville, Georgia) and later by Telonics® (Mesa, Arizona; model IMP-300). Both types of transmitters were approximately 90 mm × 25 mm in size and weighed 35–40 g. Implant procedures followed Van Vuren (1989) with several refinements. Specifically, veterinarians used isofluorine gas anaesthesia, incisions through the linea alba, and transmitters programmed to either transmit body temperature data or become active or inactive using an 8–12 h per day "duty cycle" designed to maximize battery life. In practice the early temperature-calibrated transmitters (1992–1996) typically lasted 4–12 months, while later (1997–2004) duty-cycle models lasted 24–36 months.

Radiotelemetry data were obtained using ground-based personnel and helicopter overflights. We used receivers from Telonics® (Meza, Arizona; model TR-2), Lotek® (Newmarket, Ontario; model SRX-400), and Habit Research® (Victoria, British Columbia; model HR-2000). Detectability was imperfect; marmots in burrows, behind ridges, or obstructed by boulders were sometimes missed on particular ground visits or overflights. However, nondispersing marmots were relatively sedentary, with daily or weekly movements commonly restricted to within 100–1000 m of burrows predictably used for sleeping (hereinafter, home burrows). Thus, repeated field visits over several days ensured that detectability approached 100%. Individuals were observed visually on approximately 30%–40% of visits by ground-based personnel. Dispersing marmots occasionally made longer (10–30 km) movements and could only be tracked by helicopter.

Timing and intensity of monitoring efforts

Field efforts varied depending on budgets, hypotheses under examination, helicopter availability, weather and road access. For example, some marmots were monitored daily in late 1995 because the research objective that year was to elucidate the onset of hibernation. Conversely, marmots at one relatively inaccessible site in 2002 were monitored only 10 times, and two of those occasions involved searches for dead marmots after helicopter overflights indicated changes in radio transmitter pulse rates. This variability in sampling effort required us to make a trade-off between a desire for temporal precision (when did marmots actually die?) and a desire to use all available records. To do this we constructed a daily resighting file that recorded whether or not (*i*) the site was visited or overflown, (*ii*) the transmitter was detected, (*iii*) the marmot was torpid, (*iv*) the marmot was seen, and (*v*) the transmitter was recovered.

After inspecting resulting plots of sampling effort, marmot detections, and marmot deaths, we divided the annual marmot cycle into 13 periods: emergence to 8 May, 10 consecutive 2-week periods encompassing 9 May to 25 September, 26 September to immergence, and winter. The winter hibernation period was approximately 28 weeks long, but varied depending on when a given individual emerged or immerged. It was not possible to accurately ascertain emergence or immergence dates for most marmot-year combinations. However, Bryant and McAdie (2003), using a subset of the same data, reported that emergence (mean date = 3 May, SD = 7.1 days, $n = 66$) and immergence (mean date = 3 Oct., SD = 6.0 days, $n = 66$) dates varied similarly. We consequently ignored this individual variation in hibernation duration, because any resulting bias in survival rate estimation would be slight compared with the advantage gained by simplifying the modeling process.

Timing of mortality

We assumed death only if the radio transmitter was recovered or the radio-implanted marmot never emerged above ground. Cases in which the radio transmitter failed or could not be tracked were censored. In some cases, we believe transmitters failed at time of death, but obviously in these cases we could not assign causes or location. We recognize that this will result in overestimated annual survival, but inclusion of such records might bias estimates of the timing of death.

Some radio transmitters were programmed to report internal body temperatures. In such cases, observers could quickly detect hibernation or mortality based on changes in transmitter pulse rate. Other transmitters, although not specifically programmed to reflect body temperature, were found to do so in practice. Specifically, colder transmitters had slower pulse rates, allowing experienced observers to readily distinguish active marmots from dead or torpid ones. In some cases, marmot remains were recovered within hours or days of the last visual sighting. In other cases, remains were not recovered until several weeks after last observation or detection of “warm” transmitter pulse rate.

Causes of mortality

Remains from predation often provided clues about the identity of the species involved. Wolves (*Canis lupus* L., 1758) typically left fresh scat and radio transmitters with deep tooth marks visible in the external wax covering. Cougars (*Puma concolor* (L., 1771)) tended to be more surgical and secretive in their feeding habits, often skinning marmots of fur, removing digestive tracts, and “hiding” remains in a nearby copse of trees. Cougars sometimes left tooth marks in transmitters, but these were rarely as extensive as those left by wolves. Golden eagles (*Aquila chrysaetos* (L., 1758)) typically left feathers and plucked patches of marmot fur behind. We cannot preclude the possibility of scavenging behavior by wolves, cougars, and eagles after marmots died from other causes, but consider this to be unlikely given direct observations of these three species actively hunting marmots (Bryant 1998). Other potential predators do occur in the area, including black bears (*Ursus americanus* Pallas, 1780), bald eagles (*Haliaeetus leucocephalus* (L., 1766)), northern harriers (*Circus cyaneus* (L., 1766)), northern goshawks (*Accipiter gentilis* (L., 1758)), and red-tailed hawks (*Buteo jamaicensis* (J.F. Gmelin, 1788)), but we have no evidence to suggest that these species hunt marmots.

Excavation of hibernacula facilitated unequivocal classification of deaths from “winter mortality”, although precise mechanisms of death could not be identified (Bryant et al. 2002). One radio transmitter that continued to function underground in summer was classified as death from “unknown causes”. Another death was similarly coded because the transmitter could not be retrieved for several weeks. Locations of marmot remains were pinpointed using either a handheld GPS unit or notes made by field observers. These locations were entered into a geographical information system (ArcView version 3.2; Environmental Systems Research Institute 2000).

Mark–recapture modeling

We used the known-fate model implemented in program MARK to estimate survival (White and Burnham 1999). Our input data reflected sampling of animals over a marmot-year, beginning and ending with emergence from hibernation in spring. Records of the same marmot in multiple years were treated as independent live–dead format (LDLD) records over the 12 two-week active season intervals and the single winter interval. This approach allowed use of records in which marmots were moved by wildlife managers, or moved of their own volition among habitats, or in which tagged marmots were equipped with radio transmitters during varying periods of their known lives. We speculated that survival rates might be influenced by sex, a pattern observed in other marmots (e.g., Barash 1973; Schwartz et al. 1998). Sample sizes were insufficient to test for age- specific, colony-specific, year-specific, or habitat-specific effects (Bryant 1996). Our input data therefore reflected two groups (females versus males). We evaluated model fit using Akaike’s Information Criterion (AIC) or its 2nd-order derivative (AIC_c), and tested for significance using likelihood-ratio χ^2 tests. We used standard statistical methods for all other tests.

Results

Sampling efforts relative to population size

Veterinarians performed 106 surgeries involving 78 individual marmots from 1992 through 2004 (42 females and 36 males). A few marmots ($n = 7$) were first implanted as pups, others as yearlings ($n = 22$), and the remainder were age 2 ($n = 11$) or older (minimum age = 3–6 years, $n = 38$). Age at first implantation was independent of sex ($\chi^2 = 3.92$, df = 3, $P = 0.271$). One adult male died from hyperthermia shortly after surgery in 1992 and was consequently omitted from the data. Hot weather and lengthy handling were believed to be important contributing factors in this instance, which remains the single known case of trapping or surgery-related mortality (Bryant 1998).

Several marmots ($n = 18$) experienced multiple surgeries (range = 2–3) to replace radio transmitters that failed. Thus, some marmots were successfully monitored for up to 6 years (median = 2 years, SD = 1.3, $n = 77$) and complete or partial annual survival data were available for n = 166 marmot–site–year combinations. Ages of males and females were similar across these site–year combinations (males: mean age = 3.22 years, SD = 1.71, n = 87; females: mean = 3.18 years, SD = 1.92, n = 79). The cumulative sample, although small, represents a substantial proportion (10%–80%) of wild marmots known to have been alive in any given year.

Timing and causes of mortality

Some marmots (n = 22) outlived their radio transmitters and were observed weeks or years later; their eventual fate remains unknown. Others (n = 18) were still alive at the onset of hibernation in October 2004. The remainder were either recovered (n = 29) or disappeared (n = 8).

The 29 radio transmitters that were recovered suggested particular times and causes of death (Appendix A). Probable causes of death included predation by wolves (38%, n = 11), cougars (21%, n = 6), eagles (10%, n = 3), unknown terrestrial predators that left tooth marks on transmitters (3%, n = 1), unknown predators that did not (10%, n = 3), unknown causes (7%, n = 2), and winter mortality (10%, n = 3). The winter-mortality records reflect three females that died in a single burrow at 1120 m after being experimentally transplanted to Mount McQuillan in 1996 (Bryant et al. 2002). Together with the recovery of a non-radio-implanted male from the same burrow, these records constitute the only confirmed evidence of death during hibernation in wild marmots. One unknown-cause record reflects a 4-year-old male that apparently emerged at 1280 m on Mount Washington in May 2002 but was not later seen above ground. The second unknown-cause record reflects recovery of a 5-year-old male 4 weeks after it was last confirmed alive in 2004, by which time little forensic evidence remained except the radio transmitter.

One radio transmitter was recovered 5.3 km away from the site of the unsuccessful 1996 reintroduction. The marmot might have been carried there by an avian predator, or perhaps it was killed by a terrestrial predator after it dispersed from the release site. In other cases, remains were typically found close to predictably used home burrows (median distance = 26 m, SD = 36, range = 3–160, n = 23).

Nine of 24 predation deaths involved multiple losses from particular colonies over short periods of time (range = 2–3 deaths per colony, range of recovery dates = 2–7 days, n = 4 cases). In one case, three marmots were killed over 2 days and an adult cougar was observed on the 3rd day (Green Mountain in 2003). In another case, both parents of a litter were recovered within 100 m of the birth burrow; recoveries occurred over 4 days and fresh wolf tracks and scat were observed nearby (Mount Washington in 2001).

Predation losses involved 11 females and 13 males. Data were insufficient to formally test for age–sex effects, but the records may suggest preferential targeting of adults rather than younger marmots. None of the 7 radio-implanted pups died, but predators killed 3 of 27 yearlings (11%), 2 of 28 two-year-olds (7%), and 19 of 104 adults (18%). Excluding two marmots that died of unknown causes in early spring, the mean age of marmots killed by predators was 3.9 years (SD = 1.8, n = 24), while the age of radio-implanted marmots available to be killed was 3.1 years (SD = 1.8, n = 140 marmot-years; Kruskal–Wallis test, P = 0.048). In three cases, deaths involved reproductive marmots (both parents at Mount Washington in 2001, both parents at "P" Mountain in 2002, and the female parent at Green Mountain in 2002). Possibly the presence of dependent pups increases the risk of predation upon parents. Predator kills were not equally distributed thoughout the active season. Most deaths (75%) occurred between 1 August and the onset of marmot hibernation in late September or early October, with an obvious concentration of deaths in August (Fig. 1).

The timing of mortality records is suggestive, but alone they constitute data without context. Specifically, the high number of recoveries in August might simply reflect numbers of radio-implanted marmots that were available to die. Most marmots were implanted with radio transmitters in August (mean implant date = 7 August, SD = 18.3 days, range = 10 June – 16 September, n = 106). Given battery life of transmitters, it is conceivable that recoveries alone might therefore produce a biased estimate of the timing of death, or that the implant process might itself influence mortality. We addressed this possibility by comparing likely death dates with implant dates.

Twelve of the 24 predation deaths (50%) occurred in the same year a marmot was implanted, 8 deaths (33%) occurred in the following year, 3 (13%) occurred 2 years later, and 1 (4%) occurred 3 years later. Despite the large variation in number of days elapsed between surgery and death (median = 169 days, SD = 325, range = 12–118 days), the ANOVA showed no difference in the mean Julian date of death ($F_{[3,20]}$ = 1.93, P = 0.900). Death dates varied from 26 August (SD = 16.9 days, n = 12) in the same year to 12 August (SD = 41.8 days, n = 12) for cases in which 1 or more years had elapsed since surgery. These results, combined with observations of marmots behaving normally, later weaning pups, and showing no abnormalities upon recapture, led us to believe that implantation of radio transmitters did not significantly alter marmot vulnerability to predation. Even more suggestive is the observation that non-implanted marmots disappeared at similar times (Bryant 1998).

Annual survival

Excluding seasonal or sex effects, the annual survival estimate $S_{(.)}$ was = 0.74 (95% confidence intervals (CI) = 0.65–0.81). This value is higher than that reported from resightings of ear-tagged marmots ($S_{(.)}$ = 0.63; Bryant 1998). However, we note that 8 radio-implanted marmots vanished at the same time that radio signals disappeared, so strictly speaking our data violate the assumptions of known-fate analysis (White and Burnham 1999). The disappearing animals included two yearling females, two 2-year-old males, a 3-year-old male, two 4-year-old reproductive females, and a 5-year-old male.

Possibly some of these marmots dispersed but survived, although we consider it likely that some did not (dispersal apparently occurs at age 2 in marmots; Bryant 1998). By censoring these cases, we essentially used their interval-specific survival records but ignored their disappearance. We explored this difficulty by adjusting our input data to reflect the assumption that two records from 4-year-olds actually represented deaths. The result was a reduction in $S_{(.)}$ to 72%. The corollary is that radiotelemetry allowed successful tracking of

Fig. 1. Timing interval and probable causes of death of 29 radio-implanted Vancouver Island marmots (*Marmota vancouverensis*). One radio transmitter from a single underground death during summer (unknown causes, 9–22 May) was not recovered. Three deaths during hibernation (winter) occurred in a single burrow.

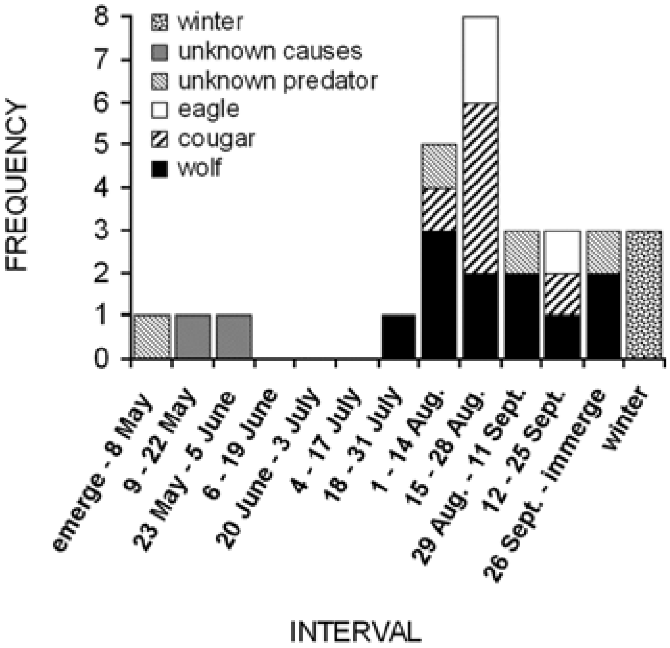
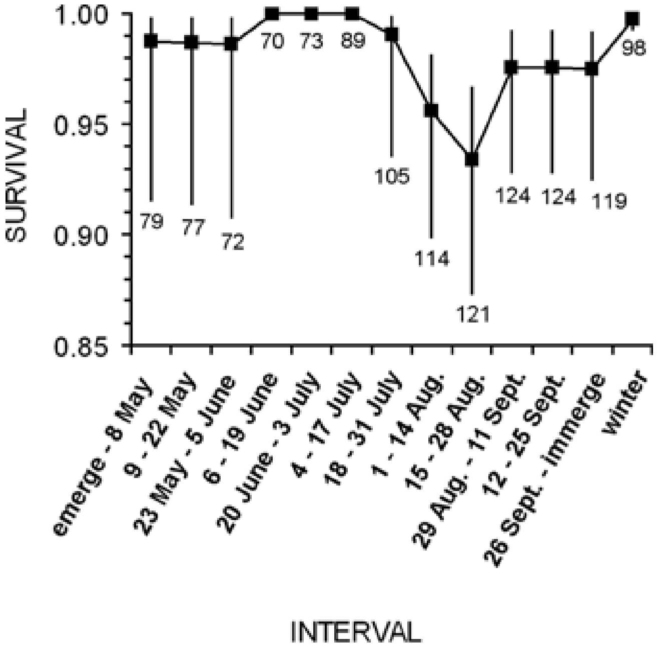


Fig. 2. Seasonal survival of radio-implanted Vancouver Island marmots. Data are means and 95% confidence intervals using data pooled across sexes. Interval-specific sample sizes are shown.



several 2-year-old marmots that dispersed; these would have been reported as "apparent deaths" using mark–resighting methodology alone. We conclude that while survival estimates from the two methods were similar, our known-fate approach slightly overestimates survival and the mark–resighting approach slightly underestimates it.

Seasonal and sex-specific effects on survival

Models based on seasonal differences in survival produced better fit and corroborated suspicion that mortality was concentrated in late summer (Fig. 2). The most parsimonious seasonal model included four survival periods, including emergence through 31 July (S_{summer} = 0.993), 1–28 August (S_{August} = 0.945), 1 September through immergence (S_{autumn} = 0.975), and hibernation (S_{winter} = 0.998). The seasonal effect becomes even more pronounced when one considers the length of the winter-sampling interval compared with other intervals. Expressed in daily terms, the probability of death was eight times higher in August (P_{death} = 0.395%) than it was in May, June, or July (P_{death} = 0.051%). The August rate was also double the rate for September (P_{death} = 0.175%), and 25 times higher than it was during hibernation (P_{death} = 0.016%).

The derived annual survival estimate from this model was slightly higher than that estimated from the no-seasonal-effect model (S_{annual} = 0.76; 95% CI = 0.68–0.83). Inclusion of sex did not significantly improve model performance (Table 1), although observed survival was slightly lower for males (S_{male} = 0.74, 95% CI = 0.62–0.84) than females (S_{female} = 0.79, 95% CI = 0.67–0.87). We conclude that there was a significant seasonal component to mortality, but no strong effect of sex.

Discussion

Researchers need to make thoughtful choices when choosing temporal intervals over which to estimate survival rates (Caswell 2001). Our results illustrate the problem well. Had we estimated survival of Vancouver Island marmots over calendar years or other arbitrarily defined intervals, the pronounced late-summer mortality might have remained undetected. Indeed previous studies based on ear-tagging concluded that consistent resightings of marmots in summer combined with lack of subsequent observations suggested death during hibernation (Bryant 1996, 1998). Although this is the same conclusion made by researchers working on other alpine-dwelling marmots (e.g., Barash 1973; Armitage and Downhower 1974; Schwartz et al. 1998; Stephens et al. 2002; Farand et al. 2002), it was apparently wrong in the case of the Vancouver Island marmot.

We suggest that several factors conspired to mask the high late-summer mortality. Visibility in marmot habitats deteriorates after plant growth peaks in mid-August (Meidinger and Pojar 1991). Weather conditions worsen at high elevations, field crews tire (our experience), and marmots become less active above ground (Heard 1977). Observers with academic obligations typically left the field in early September, some 2–5 weeks prior to the onset of hibernation (Bryant and McAdie 2003). None of these factors are unique to studies of Vancouver Island marmots. What is unusual is the temporal concentration of mortality during the very period in which marmots were less likely to be resighted. Thus, mortality patterns observed in other, more common, marmots produced misleading expectations about when deaths would occur. Ultimately, these expectations, combined with the limitations of mark–resighting techniques and the conflu-

Table 1. Relative performance of seasonal survival models for radio-implanted Vancouver Island marmots (*Marmota vancouverensis*).

Model	AIC_c	$\triangle\text{AIC}_c$	Parameter	Deviance	P
Spring + summer, August, fall, winter (sex)	266.5	0.0	8	5.9	0.060
Spring + summer, August, fall, winter	267.5	1.0	4	15.0	0.158
Spring, summer, August, fall, winter	267.5	1.0	5	13.0	0.111
Spring, summer, August, fall, winter (sex)	268.7	2.2	10	4.0	0.028
Spring + summer + fall, August, winter	270.3	3.8	3	19.8	0.136
Spring + summer + fall, August, winter (sex)	270.8	4.3	6	14.2	0.762
$S_{(t)}$ (13 intervals)	280.6	14.3	13	10.1	0.688
$S_{(g\times t)}$ (13 intervals, sex)	297.6	34.1	26	0	0.003
$S_{(.)}$ (constant survival)	302.8	36.3	1	56.3	0.603
$S_{(g)}$ (sex)	304.5	38.0	2	56.0	—

Note: Pooled time intervals include emergence through 22 May (spring), 23 May through 31 July (summer), 1–28 August (August), 29 August through immergence (fall), and winter (hibernation). P values reflect likelihood-ratio χ^2 tests. Numbers of parameters estimated are also shown. The first four models were not significantly different.

ence of marmot and researcher behavior, led to an exaggerated view of the importance of winter mortality.

In fact, only three radio-implanted Vancouver Island marmots died in winter, and these occupied a single burrow. Overwinter survival elsewhere was 100% despite variable weather, group sizes, and habitats (n = 68 hibernacula). Two lines of evidence suggest that the Vancouver Island marmot is a relatively efficient hibernator. The first comes from interspecific comparisons of daily mass loss (DML) in torpid marmots. Mass loss in Vancouver Island marmot (DML = 0.95) was very similar to that reported in the yellow-bellied marmot (*Marmota flaviventris* (Audubon and Bachman, 1841; DML = 0.92), but half that reported for the alpine marmot (*Marmota marmota* (L., 1758; DML = 1.96) and woodchuck (*Marmota monax* (L., 1758; DML = 1.93) (Armitage et al. 2000; Armitage and Blumstein 2002; Bryant and McAdie 2003).

We also noted several records of successful hibernation under unusal circumstances. A solitary male overwintered at an elevation of 60 m near the village of Coombs (Bryant and Janz 1996). A female moved to a clearcut after being released in a natural meadow; here she dug a new burrow at 650 m over 2 weeks in late September, just prior to immergence. Two yearlings dug a new burrow and hibernated successfully after their mother was killed by a predator. There is much interspecific variation in the genus *Marmota*, a condition that presumably reflects differing evolutionary pressures produced by different habitat conditions (Armitage 2000). A trend towards more efficient hibernation might be the predictable evolutionary response of a rare species that has apparently lived, at least in modern times, in small colonies containing fewer than five adults (Bryant and Janz 1996).

Our results indicated that most marmots were killed by predators. Although identification of predator species from remains is subjective, the forensic evidence suggests that terrestrial predators are more important than avian ones, and wolves are more important than cougars. The high predation rates are consistent with other findings. On the strength of consecutive annual population counts, Bryant (2000) reported that mortality rates were spatially autocorrelated and that colony-specific losses often occurred in “episodes”. The inference was that declines might reflect localized hunting behavior by predators. Our data were too sparse to allow formal testing of spatial pattern, but we noted that almost half of the observed deaths represented cases in which multiple marmots were killed over periods spanning a few days and distances involving a few tens or hundreds of metres. We were surprised by the concentration of deaths in August and, to a lesser extent, during the autumn period. These results pose several intriguing questions.

First, the small population sizes and dispersed nature of colonies suggest that marmots cannot have constituted the principal prey item for any predator species, at least in modern times. How could predation have suddenly become so important? Unlike the situation facing many island endemics in which populations were threatened by newly introduced predators (e.g., Vitousek 1988), Vancouver Island marmots evolved in a landscape that included wolves and cougars (Banfield 1977). Had these predators been able to cause extinction under naturally occurring conditions, presumably this would have happened long ago. The novelty of the present situation is underscored by evidence that marmots survived for milennia despite large changes in climate and vegetation (Brown and Hebda 2002). We therefore need to ask “what else has changed?”

One possibility is that marmots themselves have changed, somehow becoming increasingly unable to avoid predators. We find little evidence to support such a hypothesis. Blumstein et al. (2001) reported that Vancouver Island marmots exhibit vigilance, alarm calling, and burrowing behavior at similar or higher rates than observed in other marmots. Neither is it likely that parasites (e.g., Hudson et al. 1992), environmental contamination, nor genetic changes have recently increased marmot vulnerability to predation. Examinations of wild marmots by veterinarians, together with health monitoring records of captive marmots, have revealed no unusual parasite loads or pathogens in this species (M. McAdie, DVM, personal communication). Lichota et al. (2004) detected PCBs and other persistent chemicals in marmot blood, but they concluded that levels were too low to have resulted in acute or chronic health problems. Data from allozyme and DNA studies (Bryant 1990; Kruckenhauser et al. 1999; A. Bryant, unpublished data) suggest that while Vancouver Island marmots exhibit lower levels of genetic variation than other marmots, remnant populations are not highly inbred. We suspect that high predation rates therefore reflect changes in external conditions rather than changes intrinsic to marmots.

A study of endangered island gray foxes in California may provide an important clue (Roemer et al. 2001). This study concluded that naturally occurring predators began to exert unsustainable pressure (hyperpredation; Holt 1977) when the availability of alternative prey changed. In this case the apparent cause was the introduction of feral pigs (*Sus scrofa* L., 1758), followed by increased golden eagle abundance, and predation upon foxes (Courchamp et al. 2003). While no new prey or predator species have been introduced to areas occupied by Vancouver Island marmots, the predator–prey system has experienced other significant changes.

Wolves and cougars on Vancouver Island prey mostly on black-tailed deer (*Odocoileus hemionus hemionus* (Rafinesque, 1817)) (Scott and Shackleton 1980; Gladders 2000), and deer abundance has fluctuated greatly over recent decades (Hatter and Janz 1994). Populations increased during the 1970s, perhaps due in part to newly available food resources in regenerating clearcuts (Bunnell 1990). Black-tailed deer have subsequently suffered dramatic declines, with nonhuman predation accounting for most mortality (McNay and Voller 1995). Predator populations have also changed. Cougar sightings have doubled since records began in 1979 (unpublished hunter-sighting data, B.C. Ministry of Water, Land and Air Protection). Wolves were rarely encountered during most of the 1900s, and by 1970 serious consideration was given to listing Vancouver Island wolves as endangered (Hebert et al. 1982). However, sightings increased during the 1970s to the extent that legal hunting was reinstituted in 1977 (Archibald et al. 1991). Declining black-tailed deer populations provided justification for a controversial 1983–1989 wolf-control program in areas also occupied by Vancouver Island marmots (Janz and Hatter 1986; Atkinson and Janz 1994). We note that it was during this period that marmot numbers increased and the colonization of clearcuts occurred (Bryant and Janz 1996).

The recent catastrophic decline of Vancouver Island marmots may therefore reflect a numerical response of cougars and wolves to changing black-tailed deer availability. We suspect that functional responses may also be important. Observers have noted the propensity of marmots and predators to use logging roads, the reduced visibility in clearcuts that occurs after a few years of forest succession, and the abnormally high local density of marmots produced by colonization of clearcuts adjacent to natural meadows. All of these factors might increase the likelihood that predators hunt marmots in particular areas, or hunt more successfully in them (Bryant 1998). Thus, while predation is proximately responsible for the recent precipitous decline of Vancouver Island marmots, we speculate that hyperpredation is ultimately the result of changes to the landscape created by modern industrial forestry. The extraordinary concentration of deaths in late summer is also curious. Further work is needed to identify what aspects of marmot behavior, or predator behavior, produce this unusual pattern.

Regardless of whether one chooses to use the 63% survival estimate from ear-tagging that omitted dispersers (Bryant 1998), or the 74% radiotelemetry estimate that included dispersers (this study), these survival rates are relatively low. For example, Stephens et al. (2002) reported 88%–93% summer survival rates for a population of alpine marmots in Germany, while Van Vuren and Armitage (1994) reported similar (93%) survival of yellow-bellied marmots in Colorado. Both of those populations are apparently thriving (K.B. Armitage and W. Arnold, personal communications). Given a life-span of 10 years or so and average reproductive performance (Bryant 1996), a life-table calculation suggests that survival rates approaching 80% would be necessary to sustain the population. Such survival rates are not unobtainable, and in fact have been observed before on numerous occasions at specific colonies (Bryant 1998, 2000).

Demographic projections suggest that we can keep Vancouver Island marmots in the wild indefinitely by continuing to breed them in captivity and releasing them to the wild. We have no doubt that this is possible, but unless survival rates are improved, at the end of the exercise the result will still be a small, highly vulnerable population. In the short-term, managers need to reduce predation. In the long-term, managers need to begin thinking about what kind of landscape might successfully provide habitat for marmots, black-tailed deer, cougars, wolves, and loggers, and what level of ongoing management will be required to pursue this ideal in the heavily modified landscape that already exists.

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References

Archibald, W.R., Janz, D., and Atkinson, K. 1991. Wolf control: a management dilemma. Trans. N. Am. Wildl. Nat. Resour. Conf. **56**: 497–511

Armitage, K.B. 2000. The evolution, ecology and systematics of marmots. Oecologia (Berl.), **9**: 1–18.

Armitage, K.B., and Blumstein, D.T. 2002. Body-mass diversity in marmots. *In* Holarctic marmots as a factor of biodiversity. *Edited by* K.B. Armitage and V.U. Rumianstev. ABF Publishing House, Moscow. pp. 22–40.

Armitage, K.B., and Downhower, J.F. 1974. Demography of yellow-bellied marmot populations. Ecology, **55**: 1233–1245.

Armitage, K.B., Woods, B.C., and Salsbury, C.M. 2000. Energetics of hibernation in woodchucks (*Marmota monax*). *In* Life in the cold. *Edited by* G. Heldmaier and M. Klingenspor. Springer-Verlag, New York. pp. 73–80.

Atkinson, K.T., and Janz, D.W. 1994. Effect of wolf control on black-tailed deer in the Nimpkish valley on Vancouver Island. Wildl. Bull. No. B-73, B.C. Ministry of Environment, Lands and Parks, Victoria.

Banfield, A.W.F. 1977. The mammals of Canada. University of Toronto Press, Toronto.

Barash, D.P. 1973. The social biology of the Olympic marmot. Anim. Behav. Monogr. **6**: 171–245.

Blumstein, D.T., Daniels, J.C., and Bryant, A.A. 2001. Antipredator behavior of Vancouver Island marmots: using congeners to evaluate abilities of a critically endangered mammal. Ethology, **107**: 1–14.

Brown, K.J., and Hebda, R.J. 2002. Late Quaternary vegetation, climate and fire history from the Mountain Hemlock Zone on southern Vancouver Island, British Columbia, Canada. Rev. Palaeobot. Palynol. **2497**: 1–23.

Bryant, A.A. 1990. Genetic variability and minimum viable populations in the Vancouver Island marmot (*Marmota vancouverensis*). M.E.Des. thesis, University of Calgary, Calgary, Alta.

Bryant, A.A. 1996. Reproduction and persistence of Vancouver Island marmots (*Marmota vancouverensis*) in natural and logged habitats. Can. J. Zool. **74**: 678–687.

Bryant, A.A. 1998. Metapopulation dynamics of Vancouver Island marmots (*Marmota vancouverensis*). Ph.D. dissertation, University of Victoria, Victoria, B.C.

Bryant, A.A. 2000. Relative importance of episodic versus chronic mortality in the decline of Vancouver Island marmots (*Marmota vancouverensis*). *In* Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, British Columbia, 22–25 February 1999. Vol. I. *Edited by L* Darling. B.C. Ministry of Environment, Lands and Parks, Victoria, and University College of the Cariboo, Kamloops. pp. 189–195.

Bryant, A.A., and Janz, D.W. 1996. Distribution and abundance of Vancouver Island marmots (*Marmota vancouverensis*). Can. J. Zool. **74**: 667–677.

Bryant, A.A., and McAdie, M. 2003. Hibernation ecology of wild and captive Vancouver Island marmots (*Marmota vancouverensis*). *In* Adaptive strategies and diversity in marmots. *Edited by* R. Ramousse, D. Allaine, and M. Le Berre. International Marmot Network, Lyon, France. pp. 159–166.

Bryant, A.A., Schwantje, H.M., and deWith, N.I. 2002. Disease and unsuccessful reintroduction of Vancouver Island marmots (*Marmota vancouverensis*). *In* Holarctic marmots as a factor of biodiversity. *Edited by* K.B. Armitage and V.U. Rumianstev. ABF Publishing House, Moscow. pp. 101–107.

Bunnell, F.L. 1990. Ecology of black-tailed deer. *In* Deer and elk habitats in coastal forests of southern British Columbia. *Edited by* J.B. Nyberg and D.W. Janz. B.C. Ministry of Forests and B.C. Ministry of Environment, Victoria. pp. 31–65.

Cam, E., Lougheed, L., Bradley, R., and Cooke, F. 2003. Demographic assessment of a marbled murrelet population from capture–recapture data. Conserv. Biol. **17**: 1118–1126.

Caswell, H. 2001. Matrix population models: design, analysis and interpretation. Sinauer Associates, Inc., Sunderland, Mass.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York.

Caughley, G., and Gunn, A. 1996. Conservation biology in theory and practice. Blackwell, Cambridge, Mass.

Courchamp, F., Woodroffe, R., and Roemer, G. 2003. Removing protected populations to save endangered species. Science (Wash, D.C.), **302**: 1532.

Demarchi, D.A., Marsh, R.D., Harcombe, A.P., and Lea, E.C. 1990. The environment. *In* The Birds of British Columbia. Vol. 1. *Edited by* R.W. Campbell, N.K. Dawe, I. McTaggart-Cowan, J.M. Cooper, G.W. Kaiser, and M.C.E. McNall. Royal B.C. Museum, Victoria. pp. 55–151.

Environmental Systems Research Institute. 2000. ArcView®. Version 3.2 [computer program]. Environmental Systems Research Institute, Redlands, Calif.

Farand, E., Allaine, D., and Coulon, J. 2002. Variation in survival rates for the Alpine marmot (*Marmota marmota*): effects of sex, age, year and climatic factors. Can. J. Zool. **80**: 342–349.

Franklin, A.B., Anderson, D.R., Gutiérrez, R.J., and Burnham, K.P. 2000. Climate, habitat quality and fitness in the Northern Spotted Owl. Ecol. Monogr. **70**: 539–590.

Gladders, A.D. 2000. Predation behavior of Vancouver Island cougars (*Puma concolor vancouverensis*) and its relation to micro and macroscale habitat. M.Sc. thesis, University of British Columbia, Vancouver.

Hatter, I.W., and Janz, D.W. 1994. Apparent demographic changes in black-tailed deer associated with wolf control on northern Vancouver Island. Can. J. Zool. **72**: 878–884.

Heard, D.C. 1977. The behavior of Vancouver Island marmots (*Marmota vancouverensis*). M.Sc. thesis, University of British Columbia, Vancouver.

Hebert, D.M., Youds, J., Davies, R., Janz, D.W., and Smith, G.W. 1982. Preliminary investigations of the Vancouver Island wolf (*Canis lupus crassadon*) prey relationships. *In* Wolves of the world: perspectives of behavior, ecology and conservation. *Edited by* F.H. Harrington and P.C. Paquet. Noyes Publications, Park Ridge, BC. pp. 54–70.

Heppel, S.S., Caswell, S., and Crowder, L.B. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology, **81**: 654–665.

Holt, R.D. 1977. Predation, apparent competition and the structure of prey communities. Theor. Popul. Biol. **12**: 197–229.

Hudson, P.J., Dobson, A.P., and Newborn, D. 1992. Do parasites make prey more vulnerable to predation? Red grouse and parasites. J. Anim. Ecol. **61**: 681–692.

Janz, D.W., and Hatter, I.W. 1986. A rationale for wolf control in the management of the Vancouver Island predator–ungulate system. Wildl. Bull. No. B-65, B.C. Ministry of Environment, Lands and Parks, Victoria.

Janz, D.W., Bryant, A.A., Dawe, N.K., Schwantje, H., Harper, B., Nagorsen, D., Doyle, D., deLaronde, M., Fraser, D., Lindsay, D., Leigh-Spencer, S., McLaughlin, R., and Simmons, R. 2000. National recovery plan for the Vancouver Island marmot (2000 update). Rep. No. 19, Recovery of Nationally Endangered Wildlife, Ottawa, Ont.

Karels, T.J., Bryant, A.A., and Hik, D.S. 2004. Comparison of discriminant function and classification tree analyses for age classification of marmots. Oikos, **105**: 575–587.

Klinka, K., Krajina, V.J., Ceska, A., and Scagel, A.M. 1989. Indicator plants of coastal British Columbia. University of British Columbia Press, Vancouver.

Kruckenhauser, L., Pinsker, W., Haring, E., and Arnold, W. 1999. Marmot phylogeny revisited: molecular evidence for a diphyletic origin of sociality. J. Zool. Syst. Evol. Res. **37**: 49–56.

Lichota, G.B., McAdie, M., and Ross, P.R. 2004. Endangered Vancouver Island marmots (*Marmota vancouverensis*): sentinels of atmospherically delivered contaminents to British Columbia, Canada. Environ. Toxicol. Chem. **23**: 402–407.

Martell, A.M., and Milko, R.J. 1986. Seasonal diets of Vancouver Island marmots. Can. Field-Nat. **100**: 241–245.

McNay, R.S., and Voller, J.M. 1995. Mortality causes and survival estimates for adult female Columbian black-tailed deer. J. Wildl. Manag. **59**: 138–146.

Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. B.C. Ministry of Forests, Victoria.

Milko, R.J., and Bell, A.M. 1986. Subalpine meadow vegetation of south central Vancouver Island. Can. J. Bot. **64**: 815–821.

Nagorsen, D.W. 1987. *Marmota vancouverensis*. Mamm. Species, **270**: 1–5.

Roemer, G.W., Coonan, T.J., Garcelon, D.K., Bascompte, J., and Laughrin, L. 2001. Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. Anim. Conserv. **4**: 307–318.

Schwartz, O.A., Armitage, K.B., and Van Vuren, D. 1998. A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). J. Zool. (Lond.), **246**: 337–346.

Scott, B.M.V., and Shackleton, D.M. 1980. Food habits of two Vancouver Island wolf packs: a preliminary study. Can. J. Zool. **58**: 1203–1207.

Shank, C.C. 1999. The committee on the status of endangered wildlife in Canada (COSEWIC): a 21-year retrospective. Can. Field-Nat. **113**: 318–341.

Stephens, P.A., Frey-Roos, F., Arnold, W., and Sutherland, W.J. 2002. Model complexity and population predictions: the alpine marmot as a case study. J. Anim. Ecol. **71**: 343–362.

Swarth, H.S. 1911. Two new species of marmots from Northwestern America. Univ. Calif. Publ. Zool. **7**: 201–204.

Van Vuren, D. 1989. Effects of intraperitoneal transmitter implants on yellow-bellied marmots. J. Wildl. Manag. **53**: 320–323.

Van Vuren, D., and Armitage, K.B. 1994. Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? Oikos, **69**: 179–181.

Vitousek, P.M. 1988. Diversity and biological invasions of oceanic islands. *In* Biodiversity. *Edited by* E.O. Wilson. National Academy Press, Washington, D.C. pp. 181–189.

White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study, **46**: 120–138. Available from http://www.cnr.colostate.edu/~gwhite/mark/mark.htm [accessed 12 October 2003].

Appendix A

Table A1. Radio transmitters recovered from Vancouver Island marmots, 1992–2004.

Case	Location	Year	Last seen	Recovered	Age	Sex	Cause*	Tooth marks
1	Pat Lake	1994	11 Sept.	27 Sept.	5	Female	Cougar	No
2	Haley Lake	1994	7 Sept.	30 Sept.	5	Male	Wolf	Yes
3	Sherk Lake	1995	Emerged	26 Apr.	5	Male	Predation	Yes
4	McQuillan	1996	6 Aug.	1 Oct.	1	Male	Predation	No
5	McQuillan	1996	5 Sept.	19 June	4	Female	Winter	No
6	McQuillan	1996	5 Sept.	19 June	1	Female	Winter	No
7	McQuillan	1996	5 Sept.	19 June	1	Female	Winter	No
8	Washington	1998	27 July	17 Aug.	2	Male	Wolf	Yes
9	Green road K44a	1998	2 Aug.	18 Aug.	1	Female	Wolf	Yes
10	Green road K44a	1998	19 Aug.	15 Sept.	1	Male	Wolf	Yes
11	Washington	2001	8 Aug.	16 Aug.	7	Male	Wolf	Yes
12	Washington	2001	16 Aug.	20 Aug.	3	Female	Wolf	Yes
13	Washington	2002	Emerged	—	3	Male	Unknown	—
14	Green	2002	16 Aug.	20 Aug.	3	Female	Eagle	No
15	Big Ugly	2002	7 Aug.	8 Aug.	6	Female	Cougar	Yes
16	Heather	2002	28 Sept.	10 Oct.	3	Male	Wolf	Yes
17	"P" Mountain	2002	16 Sept.	16 Oct.	5	Male	Wolf	Yes
18	"P" Mountain	2002	10 Oct.	21 Oct.	5	Female	Wolf	Yes
19	"P" Mountain	2002	16 Sept.	16 Oct.	4	Male	Predation	No
20	Green	2003	15 Aug.	16 Aug.	3	Male	Cougar	No
21	Green	2003	15 Aug.	16 Aug.	3	Female	Cougar	No
22	Green	2003	16 Aug.	17 Aug.	3	Male	Cougar	No
23	Heather	2003	2 Aug.	18 Aug.	6	Male	Wolf	No
24	Big Ugly	2003	31 July	28 Aug.	4	Female	Wolf	Yes
25	"P" Mountain	2003	21 Aug.	11 Sept.	6	Female	Predation	No
26	Big Ugly	2004	23 Apr.	28 May	6	Male	Unknown	No
27	Washington	2004	13 Aug.	16 Aug.	8	Male	Cougar	Yes
28	Moriarty	2004	20 Aug.	30 Aug.	3	Female	Eagle	No
29	Buttle	2004	31 Aug.	17 Sept.	2	Male	Eagle	No

*See Methods for criteria used to assign timing and causes of death.