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Sources and Patterns of Wolverine Mortality in Western Montana

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ABSTRACT We instrumented 36 wolverines (*Gulo gulo*) on 2 study areas in western Montana and one study area on the Idaho–Montana (USA) border: 14 (9 M, 5 F) on the Pioneer study area, 19 (11 M, 8 F) on the Glacier study area, and 3 (2 M, 1 F) on the Clearwater study area. During 2002–2005, harvest from licensed trapping accounted for 9 (6 M, 3 F) of 14 mortalities, including individuals from all 3 study areas. Based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c) rankings of 8 a priori models, a trapping model and a trapping-by-sex interaction model were equally supported ($\Delta\text{AIC}_c < 2$) in explaining wolverine survival. Estimated annual survival was 0.80 when we did not consider harvest, whereas additive mortality from harvest reduced annual survival to 0.57. Glacier National Park in the Glacier study area provided some refuge as evidenced by an annual survival rate of 0.77 compared to 0.51 for the Pioneer Mountain study area. We incorporated these survival rates into a simple Lefkovich stage-based model to examine rates of population change. The finite rate of population change (λ) for the Glacier study area was 1.1, indicating a stable to slightly increasing population, whereas λ for the Pioneer study area was 0.7, indicating a 30% annual population decrease during our study. Changes in λ for both study areas were most sensitive to adult survival. In 2004, we used a Lincoln Index to estimate that 12.8 ± 2.9 (95% CI) wolverines resided in the 4 mountain ranges comprising the Pioneer study area, suggesting that small, island ranges in western Montana supported few individuals. Our results suggest that if wolverines are harvested, they should be managed within individual mountain ranges or small groupings of mountain ranges to limit mortality to within biologically defined limits in recognition of the increased vulnerabilities owing to low fecundity and low population numbers in small mountain ranges. We found that refugia, such as Glacier National Park, were important by reducing trap mortality and providing immigrants to the surrounding population, but even large parks were inadequate to provide complete protection to wolverines from trapping as they ranged outside park borders. (JOURNAL OF WILDLIFE MANAGEMENT 71(7):2213–2220; 2007)

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KEY WORDS *Gulo gulo*, harvest management, known-fate modeling, Montana, mortality, Program MARK, survival rates, trapping, wolverine.

Understanding the status of wolverines (*Gulo gulo*) in Montana, USA, is particularly important given the central role these animals may play toward the persistence of populations throughout the southern extent of the species' range (Banci 1994). Populations persist as a balance between increases due to births and immigration versus decreases from deaths and emigration (Caughley 1977). Although simple conceptually, quantifying these basic vital rates is often exceedingly difficult. Across their North American range, wolverines live at low densities varying from as low as 5.6 per 1,000 km² in the Yukon (Banci 1987) to 15 per 1,000 km² in northwestern Montana (Hornocker and Hash 1981). Low wolverine densities are likely due to large spatial-use areas of 422–917 km² for adult males and 73–388 km² for adult females (Banci 1994), as well as to exclusive territories within sex classes (Magoun 1985, Banci 1994, Copeland 1996). Low densities, coupled with the proclivity of wolverines to live in remote and rugged landscapes, have hindered efforts to estimate population vital rates.

Male-mediated dispersal and female philopatry appear to

contribute to the genetic structuring of wolverine populations across North America (Chappel et al. 2004, Tomasik and Cook 2005, Cegelski et al. 2006). Wolverines in western Montana persist in presumably disjunctive populations compared to those in Canada and Alaska (Kyle and Strobeck 2002), which may limit dispersal and genetic interchange due to population insularity. Cegelski et al. (2006) separated Montana wolverines into 3 distinct genetic subunits defined largely by geographic separation. Isolated populations may be less able to compensate for population reductions related to chance events or harvest.

Throughout their geographic range, wolverines have been harvested for their fur, which is valued for its durability and capacity to resist frost accumulation. Harvest, however, may be a driving force behind local extirpations of wolverine populations because harvest is a principal and additive mortality factor for wolverines (Hornocker and Hash 1981, Krebs et al. 2004). Montana is the only state within the contiguous United States that allows harvest of wolverines. Although harvest rates in Montana have remained fairly constant over the past 10 years, the impact of trapping on population dynamics is not well-understood. This lack of

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Figure 1. Wolverine study areas located in western Montana, USA, 2002–2005.

understanding, along with ongoing litigation directed at listing wolverine under the Endangered Species Act (U.S. Fish and Wildlife Service 1995, 2003), leaves wildlife managers in the difficult position of regulating harvest based on limited information.

Prior to 1975, wolverines were classified as a predator in Montana with no limits on harvest. During 1975–2004, Montana Department of Fish, Wildlife and Parks issued a general trapping license that allowed the general public to harvest one wolverine per year per trapper during a trapping season that lasted from 1 December through 15 February. By August 2004, Montana Department of Fish, Wildlife and Parks established 3 wolverine management units in western Montana, with a total harvest quota of 12 wolverines: 5 wolverines from each of the Northern and Southern Units and 2 from the Central Unit (Montana Fish, Wildlife, and Parks 2005). The intent of the new quota was to distribute trapping pressure spatially.

To understand better the sources and patterns of wolverine mortality, our first objective was to estimate wolverine survival in our study areas and to evaluate how survival was influenced by study area, sex, age, and harvest. Our second objective was to develop a population estimate and to estimate lambda for wolverines for one study area in southwestern Montana.

STUDY AREA

The boundaries of our 3 study areas, the Pioneer, Clearwater, and Glacier study areas, were defined by 100% minimum convex polygons around telemetry locations for wolverines on each area (Hayne 1949; Fig. 1). The Pioneer study area was 7,460 km² with an elevation range of 1,570–3,400 m that included the Pioneer, Beaverhead, Anaconda-Pintler, and Flint Creek Mountain Ranges on the Beaverhead-Deerlodge

National Forest. Lodgepole pine (*Pinus contorta*) forests were the dominant forest cover throughout the 4 ranges. Engelmann spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*) forests were common in mesic areas, as was whitebark pine (*Pinus albicaulis*) near timberline. Riparian areas were dominated by willow (*Salix* spp.) that often transitioned into sagebrush (*Artemisia* spp.)-dominated meadows. At low elevations, Douglas-fir (*Pseudotsuga menziesii*) and sagebrush steppe occurred on south-facing slopes.

The Clearwater study area was 2,150 km², straddled the Idaho–Montana border (38% in ID, USA, 62% in MT), and included portions of the Clearwater National Forest in Idaho and the Bitterroot National Forest in Montana. Elevations in the study area were between 1,566 m and 3,383 m. The climate and vegetation on the Clearwater National Forest was unusual in the Rockies in that the warm, moist maritime air from the Pacific penetrated into this sub-basin during the winter. Mean annual precipitation was approximately 200 cm per year (measured at Lolo Pass), but in rare years exceeded 250 cm. The abnormally high moisture (considering distance from the coast) supported an ecosystem characterized by grand fir (*Abies grandis*), western red cedar (*Thuja plicata*), and hemlock (*Tsuga heterophylla*) stands at high and middle elevations. Intermixed with these typically coastal stands were xeric and mesic stands consisting of Douglas-fir, subalpine fir, lodgepole pine and ponderosa pine. East of the Clearwater River is the Bitterroot Mountain Range (Bitterroot National Forest) with a north–south axis and vegetation patterns similar to those in the Pioneer study area.

The Glacier study area was adjacent to the United States–Canadian border with Glacier National Park accounting for >5,700 km² of the 9,430-km² study area. Elevations ranged from 747 m to 3,190 m. Upper elevations were characterized by steep sedimentary rock, glacial cirque valleys, and alpine tundra habitats. High-elevation forests consisted of subalpine fir, limber pine (*Pinus flexilis*), and whitebark pine, whereas moderate temperatures associated with maritime environments at low elevations supported larch (*Larix occidentalis*), spruce, fir, and lodgepole pine forests, including red cedar and hemlock in the Lake McDonald valley.

The entire Pioneer study area was open to licensed trapping during the general trapping season of 1 December through 15 February each year, and the Clearwater study area was closed to trapping in Idaho but open to trapping in Montana. The portion of the Glacier study area within Glacier National Park provided a refuge from trapping for animals that remained within the park boundaries; animals that left the park boundaries could be harvested during Montana's general trapping season.

METHODS

Locating Study Animals

We initially chose the study areas based on funding opportunities and not through random searches throughout the region. From 2000 to 2005, we located wolverines on the Pioneer study area using snow-track-based surveys and in

2001 to 2003 on the Clearwater (Squires et al. 2004, Ulizio et al. 2006). We conducted track searches across 8×8 -km sample units in a grid across study areas. This size sample unit was smaller than a wolverine home range (Magoun 1985, Banci 1994, Copeland 1996), to provide a conservative survey in terms of reducing the risk of missing individuals, yet large enough to allow efficient coverage of broad landscapes. Technicians selected a sample unit randomly each day, without replacement, until they completed a census of all units. They searched ≥ 10 km on roads and trails for tracks within each sample unit. We considered all forested areas (excluding Ponderosa pine forests) and areas above tree line as potential wolverine habitat (Hornocker and Hash 1981, Copeland et al. 2007); we did not search low-elevation sagebrush and agricultural lands. We also did not survey steep mountain tops and central portions of the Anaconda Pintler Range due to safety and logistical constraints. Excluded areas were generally smaller than a wolverine's home range, so we assumed any individuals that occupied these sites also used areas that we surveyed. During 2003 and 2004 on the Pioneer study area only, we followed the snow trails of wolverines for approximately 2 km on snowshoes and skis to collect genetic samples (hair, scats) from footprints, daybeds, foraging areas, tree boles, and coarse woody debris. We collected and analyzed all hair and scat samples according to Ulizio et al. (2006).

On the Glacier study area, we did not conduct systematic surveys because snowmobile access was not permitted in the Park. Rather, using park historical records (R. Yates and S. Buhler, National Park Service, unpublished data) and winter surveys conducted on skis in valley bottoms, we documented that the Many Glacier and Two Medicine valleys on the east side of Glacier National Park supported wolverines. These areas became the focus of the Glacier study area.

Study Animals

We live-captured wolverines from winter 2001–2002 through winter 2004–2005 on the Pioneer study area and from winters 2002–2003 through 2004–2005 on the Glacier Park and Clearwater study areas. In high-use areas based on track surveys and topography (e.g., converging valleys), we trapped wolverines from December through 15 April, which coincided generally with Montana's trapping season. We captured wolverines using log cabin-style traps (Copeland et al. 1995) baited with beaver (*Castor canadensis*) and road-killed deer (*Odocoileus* spp.). We used remote monitors (TBT-600HC; Telonics, Mesa, AZ) on trap doors to provide an electronic signal when a trap door shut, allowing remote monitoring on a daily basis. In addition, we inspected all traps visually every 2 days to ensure that traps and remote transmitters functioned properly. We immobilized captured wolverines using a jab stick with a 0.8-ml dose of Capture All (Wildlife Pharmaceuticals, Fort Collins, CO), a Medetomidine–Ketamine solution with 4 mg/ml and 160 mg/ml, respectively. We weighed, measured, and collected genetic samples (blood, hair, and tissue) from all study animals. A licensed veterinarian surgically implanted an intraperitoneal radio transmitter (IMP400; 100 g,

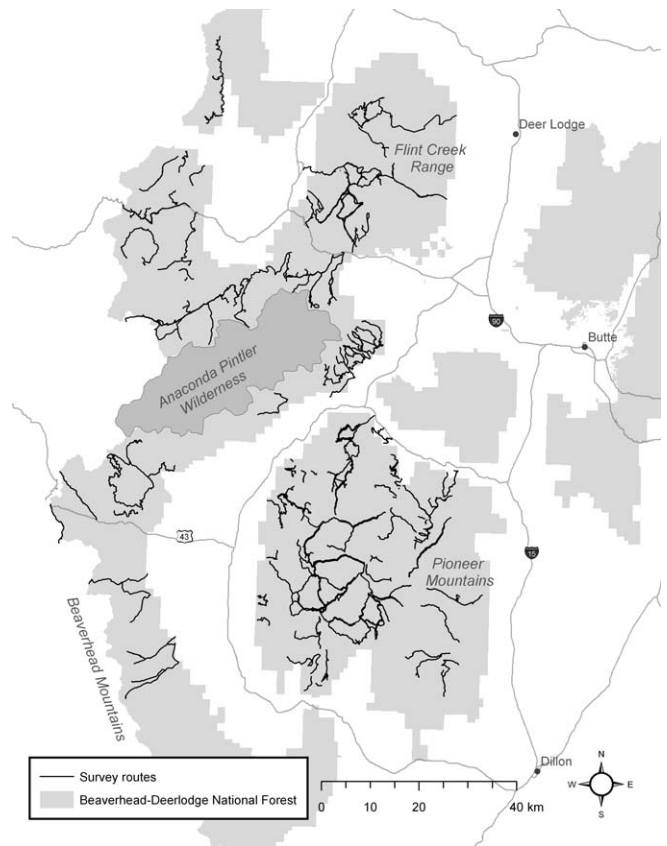


Figure 2. Locations of snow-track surveys for wolverines on the Pioneer study area in southwestern Montana, USA, 2002–2005 (after Squires et al. 2004, Ulizio et al. 2006).

Telonics) in each animal and monitored respiration and body temperature during processing. Transmitters had an expected battery life of 24 months. We also collared wolverines with ARGOS satellite collars (200 g; Sirtrack Limited, Havelock, New Zealand) to monitor broad-scale movements. We returned study animals to the trap after processing to be released after recovering from drug effects. We conducted all trapping and handling procedures under Institutional Animal Care and Use Committee oversight.

Estimating Population Numbers

We obtained a Lincoln–Petersen estimate of the number of wolverines on the Pioneer study area (White and Garrott 1990). Only this study area had rigorous, systematic surveys suitable for estimating population numbers (Squires et al. 2004, Ulizio et al. 2006; Fig. 2). Instrumented individuals constituted the initial marked population with recaptures occurring with individuals identified through nuclear DNA from hair and scat collected during track surveys (Ulizio et al. 2006). In the laboratory, we created a 7-locus genotype using highly variable microsatellites (Ulizio et al. 2006). We detected errors associated with noninvasive genetic sampling using a multi-tube approach (Taberlet et al. 1996) and the procedures of McKelvey and Schwartz (2005). We compared genotypes from backtracks to our reference genotypes from captured animals using absolute exclusion tests (Marshall et al. 1998) to determine whether individuals detected on backtracks were new or recaptured. We estimated a

Table 1. Mortality factors of instrumented wolverines ($n = 14$) in western Montana, USA, 2002–2005.

Study area	Predation		Trapping		Other	
	M	F	M	F	M	F
Pioneer Mountains and adjacent ranges	1 ^a	0	4	2	1 ^b	0
Glacier study area	0	0	2	0	1 ^c	1 ^d
Clearwater study area	0	0	0	1	1 ^c	0
Total	1	0	6	3	3	1

^a Predator unknown—massive hemorrhaging on crushed head and neck (Sep 2002).

^b Blunt trauma to head and neck (Jul 2004).

^c Unknown mortality factor (Oct 2004).

^d Located in avalanche debris with body trauma (Mar 2005).

^e Emaciated condition with large patches of missing hair—disease tests inconclusive.

combined population size for the Pioneer, Flint Creek, and Anaconda-Pintler Ranges in 2003 and estimated a combined population size for the same ranges plus the Beaverhead Mountains in 2004. In 2005, the population estimate excluded the Anaconda-Pintler Mountains because inconsistent snow cover limited our survey effort.

Estimating Survival

Securing an adequate sample to estimate survival of wolverines is challenging owing to the species' large home ranges and low densities (Quick 1953, Magoun 1985, Banci 1987, Copeland 1996). Nonetheless, known-fate models can provide valid survival estimates even when based on small sample sizes (White and Burnham 1999). We monitored wolverine survival on a monthly basis using aerial and ground-based telemetry. We classified individuals as alive, dead, or censored each month in a staggered-entry design (Pollock et al. 1989). We classified individuals by age as juvenile, subadult, or adult. We considered wolverines juvenile from birth to year 1, subadult from year 1 to year 2, and adults thereafter. We determined age classes subjectively based on tooth wear, body conformation, and reproductive maturity derived from test and testes development (Iverson 1972, Magoun 1985, Copeland 1996).

We used Program MARK to evaluate relationships among 8 *a priori* models (White and Burnham 1999) that considered sex, study area, harvest season, and interactions between these variables (e.g., sex $\times$ study area $\times$ time, sex $\times$ study area, sex $\times$ trap) based on 450 wolverine-months of monitoring. We considered sex because of high vulnerability of subadult males to trapping (Krebs et al. 2004) and study area because each area has unique physical characteristics and harvest regulations. Given that harvest from trapping was the dominant factor affecting wolverine demography in North America (Banci 1994, Krebs et al. 2004), we estimated survival during the harvest (3 months) and nonharvest seasons (9 months), to provide a combined survival estimate for the year that accounted for harvest effects.

In addition to biologically based models, we also evaluated whether time-effects or the base model explained observed mortality patterns. Candidate Models were evaluated based on Akaike's Information Criterion adjusted for small sample size (AIC_c) consistent with information-theoretic methods (Burnham and Anderson 1998, Anderson and Burnham

2002), while recognizing potential pitfalls associated with this framework (Guthery et al. 2005, Stephens et al. 2005). We considered ranked models different if AIC_c > 2 (Burnham and Anderson 1998).

Population Modeling and Survival

We used a Lefkovich stage-based model to project survival rates from the Glacier study area (an area with some refuge effect) compared to the Pioneer study area (little refuge effect) based on published fecundity rates (Persson 2003). We assumed females to be 3.4 years of age at first reproduction, and we considered only 54% of these females successfully reproductive in a given year (Persson 2003). We assumed wolverine litter sizes to average 1.9 kits (Persson 2003). Thus, we estimated a potential female birth rate of 0.51 female offspring per year (50% F offspring $\times$ 1.9 kits/litter $\times$ 0.54 reproductive F that den/yr) as an estimate of fecundity. This rate is slightly higher than the reproductive rate reported by Copeland (1996; 0.445) in Idaho and Magoun (1985; 0.345) in Alaska. In the stage model, we assumed an equal death rate for the subadult and adult age classes given our limited information concerning population vital rates (Lefkovich 1965, Noon et al. 1992). We made this assumption knowing that subadults may have a lower survival rate compared to adults (Krebs et al. 2004), thus yielding a more liberal estimate of λ ; our sample size was inadequate to estimate age-specific survival rates. This simplified modeling approach required few assumptions; more complex methodologies may be inappropriate given our limited state of knowledge. We calculated proportional sensitivities (elasticity analysis) of demographic rates to determine the age class with largest effect on λ (Caswell 1989; Mills et al. 1999, 2001; Ehrlén et al. 2001).

RESULTS

Mortality Factors

We investigated the survival of 36 wolverines in western Montana, with 14 (9 M, 5 F) from the Pioneer study area, 19 (11 M, 8 F) from the Glacier study area, and 3 (2 M, 1 F) from the Clearwater study area. During 2002–2005, we documented 14 mortalities (10 M, 4 F) and lost contact with 5 males. We were unable to determine if lost individuals were the result of dispersal, radio failure, or undocumented mortality. Trapping harvest accounted for 9 (6 M, 3 F) of 14

Table 2. Akaike's Information Criterion adjusted for small sample size (AIC_c) ranking of 8 a priori models used to estimate monthly survival rates of wolverine ($n = 36$) in western Montana, USA, 2002–2005.

Model	AIC_c	ΔAIC_c	AIC_c wt	Model likelihood	No. of parameters
{S(trap)}	108.345	0.000	0.614	1.000	2
{S(sex $\times$ trap)}	109.324	0.979	0.376	0.613	4
{S(study area)}	118.331	9.987	0.004	0.007	3
{S(sex)}	119.324	10.980	0.003	0.004	2
{S(.)}	119.491	11.146	0.002	0.004	1
{S(sex $\times$ study area)}	122.025	13.680	0.001	0.001	6
{S(time)}	160.769	52.425	0.000	0.000	40
{S(sex $\times$ study area $\times$ time)}	469.635	361.290	0.000	0.000	134

mortalities and included individuals from all 3 study areas (Table 1). The harvest rate of instrumented individuals in the Pioneer study area was 27% (3 harvested/11 instrumented wolverine) in 2003, 11% (1 harvested/9 instrumented) in 2004, and 25% (2 harvested/8 instrumented) in 2005. In Glacier study area, one male was harvested near the Glacier Park border and a second male approximately 175 km straight-line distance from the animal's original capture site in the park as he dispersed west into the Kootenai National Forest in northwestern Montana. One female harvested on the Clearwater study area occupied a trans-boundary home range between Idaho and Montana. The 5 nonharvest mortalities all died outside the harvest season due to diverse factors, including one individual from predation and one from an avalanche (Table 1).

Modeling Survival

We monitored wolverines for 1–36 months ($\bar{x} = 13$, $SD = 10$). Based on AIC_c rankings of the a priori models, the trapping model {S(trap)} and the trapping-by-sex interaction model {S(trap $\times$ sex)} explained wolverine survival best ($\Delta AIC_c < 2$; Table 2). The trapping model assumed 9 months of nonharvest from March through November followed by a 3-month harvest season lasting December through February. In the absence of harvest (3-month harvest season excluded), we estimated annual survival to be 0.80 for all study areas combined. The annual survival rate declined to 0.57 when we considered a harvest season (Table 3). We estimated female survival at 0.75 {S(sex)}, compared to 0.51 for males (Table 3). The third-best model considered only study area effects {S(study area)} and produced an increased AIC_c of almost 10

compared to models that included trapping, indicating that the third-best model was inferior in explaining observed survival patterns.

Population Modeling

Applying our estimated survival rate of 0.5 for all age classes in the Pioneer study area (Table 3) yielded a λ of 0.7, indicating a 30% annual population decline during our study. When we applied the observed survival rate of 0.8 from the Glacier study area, λ was estimated to be 1.1, indicating a stable or possibly increasing population. We attributed the difference in λ values between the 2 study areas to the refuge from trapping provided by Glacier National Park. The elasticity analysis of model parameters for the Pioneer study area were birth rate (b) = 0.21, juvenile survival (s_0) = 0.21, subadult survival (s_1) = 0.21, and adult survival (s) = 0.56, as compared to $b = 0.21$, $s_0 = 0.21$, $s_1 = 0.21$, and $s = 0.57$ for Glacier. Changes in λ for both study areas were most sensitive to adult survival.

Estimated Wolverine Population—Pioneer Study Area

Our ability to make a Lincoln–Petersen estimate of the population on the Pioneer study area was helped by the high proportion of instrumented wolverines that we subsequently recaptured through DNA collected from backtracks. In 2003, we later detected 5 of 7 marked individuals in the Pioneer, Flint Creek, and Anaconda–Pintler Ranges through DNA, providing a population estimate of 8.3 ± 0.9 (95% CI) wolverines. In 2004, we recaptured 7 of 9 individuals for an estimated population of 12.8 ± 2.9 (95% CI) wolverines in the same ranges but including the Beaverhead Range. Based

Table 3. Survival estimates of wolverine from 2002 to 2005 in western Montana, USA, by primary known-fate models that consider sex, study area, and harvest season based on Program MARK.

Primary survival models	Monthly survival estimate	SE	95% CL		Monthly survival estimate annualized
			Lower	Upper	
Base model	0.960	0.011	0.933	0.976	0.613
M	0.945	0.017	0.901	0.970	0.509
F	0.976	0.012	0.938	0.991	0.746
Pioneer study area ^a	0.945	0.019	0.894	0.972	0.509
Glacier National Park	0.979	0.010	0.945	0.992	0.774
Survival assuming no trapping season ^b	0.982	0.008	0.957	0.992	0.804
Survival assuming a trapping season ^c	0.875	0.039	0.777	0.934	0.569

^a Lolo study area not reported due to small sample size.

^b Annualized rate assumes 12 months without trapping.

^c Annualized rate assumes 9 months without trapping followed by a 3-month trapping season (Dec–Feb).

Table 4. Wolverine snow-track survey and research trap effort on the Pioneer study area in southwestern Montana, USA, 2002–2005.

Yr	Survey distance (km)	Total detections	Distance (km/detection)	Trap-nights	New captures	Trap-nights/capture
2002	4,692	112	41.9	358	5	72
2003	6,160	103	59.8	855	4	213
2004 ^a	5,272	94	56.1 ^a	595	4	148 ^a
2005	3,728	40	93.2	448	1	448

^a We expanded study area to include an additional mountain range that was occupied by 3 wolverines resulting in decreases in both detection and trapping efforts.

on these estimates, the ecological density of wolverine on the Pioneer study area was estimated at 1.4 wolverines per 1,000 km² in 2003 and 1.8 wolverines per 1,000 km² in 2004. By 2004, 6 of 13 instrumented wolverines were harvested from the Pioneer study area. This harvest rate apparently resulted in a net decline of wolverines the following year based on only a single unmarked capture in 2005 (i.e., no evidence of replacement through immigration and birth) and a 78% increase in the distance surveyed per detection (93 km/detection) compared to the observed detection rate of 53 km per detection for 2002–2004 (3-yr $\bar{x}$; Table 4).

DISCUSSION

We found, based on survival patterns of 36 radio-instrumented wolverines from western Montana during 2001–2005, that harvest-effect models best explained observed mortality patterns. This result was consistent with 9 of 14 known mortalities (64%) being attributed to trapping. Thus, harvest from trapping was the primary factor that affected wolverine survival. The effect of trapping, however, was not consistent across study areas. Using a liberal estimate for reproduction, the population λ for the Pioneer study area was 0.7, indicating a steeply decreasing population, compared to a λ of 1.1 in Glacier, no different from a stable population given the vital rates we calculated.

Although Glacier National Park appeared large enough (5,700 km²) to support a stable population of wolverines that could provide immigrants to the surrounding region, its wolverines were still subject to trapping harvest when individuals traveled outside the park. Krebs et al. (2004) estimated that untrapped areas would need to be twice as large as trapped areas to compensate for differences in survival. Small mountain ranges, such as those in our Pioneer study area, are unlikely to contain refugia because high densities of forest roads and high-performance snowmobiles allow human access in all seasons. Thus, wolverines that reside in the small, insular mountain ranges of western Montana may depend on harvest management rather than on refugia to achieve a $\lambda > 1$.

The Pioneer study area illustrates the vulnerability of wolverines inhabiting small, isolated mountain ranges and the disruption that harvest can have on small populations. Krebs et al. (2004) concluded that subadult males were most vulnerable to harvest as they disperse. Yet, in the Pioneer study area, the harvest consisted of 4 adult males and 2 pregnant adult females; adult harvest has a disproportionately large effect on wolverine demography as indicated by our elasticity analysis. Although we captured 2 subadults

during the first year of live-trapping (2002), we failed to capture any subadults in the 3 subsequent years, suggesting that the harvesting of reproductive adults may have suppressed reproduction in the area. The wide-ranging nature of individual wolverines coupled with the limited extent of these small mountain ranges most likely increased the susceptibility of wolverines of all age classes to harvest.

We were not surprised that harvest was the dominant factor affecting wolverine survival across our study areas, given the consistency of this result with other wolverine studies (Hornocker and Hash 1981, Banci 1994, Krebs et al. 2004). Krebs et al. (2004) estimated wolverine survival rates in trapped versus nontrapped populations based on 12 radio-telemetry studies in North America. Krebs and his colleagues found that survival was lower in trapped (<0.75 for all age-sex classes) than in untrapped (>0.84 for all age-sex classes) populations and that human-caused mortality (trapping and vehicle–animal collisions) was additive to natural mortality. Nearly half of all mortalities in trapped populations were human-induced. Krebs et al. (2004) estimated that populations would decrease ($\lambda \cong 0.88$) in the absence of immigration from untrapped populations ($\lambda \cong 1.06$).

Wolverines exist at low population densities, which may be regulated through density-dependent factors (Magoun 1985, Banci 1987, Copeland 1996, Sæther et al. 2005). Our mark-recapture results showed that few individuals occupied the small ranges that comprised the Pioneer study area. Given the few individuals that occupy small ranges, localized trapping pressure can affect these small populations despite a moderate state-wide harvest limit. For example, the wolverine population on the Pioneer study was reduced by an estimated 50% from harvest during 2003–2005.

Recent investigations of genetic structuring of wolverines in western Montana provide evidence for relative isolation and low gene flow. Cegelski et al. (2003) suggested that insular populations in west-central Idaho may provide <2.5 migrants per generation, whereas more contiguous populations of western Montana may provide up to 6.5 migrants per generation. Preventing local extirpations of wolverines from small mountain ranges is an important management concern, given our poor understanding of recolonization rates. Sæther et al. (2005) recommended that wolverine harvest remove only a fraction of excess individuals (40–60% of surplus individuals that exceed carrying capacity). Considering the recommendations by Sæther et al. (2005) and assuming $\leq 6\%$ harvest rate needed to maintain stable population without immigration (Krebs et al. 2004), we calculated that the 4 mountain ranges comprising the

Pioneer study area should provide together <1 wolverine to be trapped per year. The practical challenge of estimating wolverine abundance for setting harvest limits is substantial. At minimum, it requires a representative survey to delineate local distributions (Squires et al. 2004) combined with DNA from backtracks (Ulizio et al. 2006) to estimate minimum numbers of individuals (Schwartz et al. 2006). We do not think it is sufficient simply to extrapolate estimated densities from the literature. For example, Cegelski et al. (2006) estimated that the Crazy and Belt Mountain Ranges of west-central Montana provide sufficient habitat for approximately 300 wolverines given a density of one individual per 105 km² (Krebs and Lewis 1999). Based on our results, we seriously question whether these isolated ranges could support this estimated population, which has important ramifications for setting harvest levels.

Conservative harvest rates are especially important for species like the wolverine, whose population sizes are small, difficult to estimate, and probably have impaired connectivity (Lande et al. 1997). The combination of low dispersal rates, low fecundity, and annual harvest pressure, as witnessed in the Pioneer study area, affects the core population and not just surplus individuals. We do not know how rapidly populations in small mountain ranges recover following intense harvest pressure, but basic principles of conservation biology suggest that recolonization rates will vary as a function of isolation. Nevertheless, maintaining a low harvest rate for wolverines in isolated mountain ranges is necessary given the important role these animals may play in sustaining and recovering regional populations.

Our survival models are limited in that they assume that observed mortality patterns remain constant over time and space, and that they ignore potential immigration. We do not know how the survival estimates derived during this short-duration study may compare to a long-term average (Brongo et al. 2005). The observed harvest rate in the Pioneer study area may have increased due to our research confirming the presence of wolverines, which may have encouraged harvest from local trappers; we do not know the extent that this may have affected our results. Nevertheless, these results illustrate the potential impact of a harvest that occurred within the state's legal framework. We believe the pattern of concentrated pressure in small mountain ranges is not an artifact of our study; the pattern is supported by anecdotal observations of heavy harvest or local extirpations in other ranges (e.g., Little Belt Mountains, Swan Mountains) of western Montana. The long-term effect of concentrated harvest in isolated mountain ranges on meta-populations is unknown, as is the rate that localized extirpations are recolonized.

MANAGEMENT IMPLICATIONS

We found that trapping was the primary factor explaining decreased survival in western Montana. Harvest pressure was capable of reducing isolated populations beyond sustainable levels despite a regulated harvest within a state-wide quota system. If populations are exploited, we suggest that

wolverine harvest be managed by individual mountain ranges or small groupings of mountain ranges. The intent of managing at this fine scale is to reduce harvest to within biologically defined limits in recognition of the increased vulnerabilities of wolverines owing to their low fecundity and low population numbers in small mountain ranges. Our results indicate that few individuals occupy small mountain ranges, which argues that harvest rates need to be conservative (<1 wolverine/yr [possibly through rotating temporary closures] for the 4 mountain ranges comprising the Pioneer study area). Our results also support the importance of protected areas, like Glacier National Park, which afforded refuge from trapper harvest and provided immigrants to surrounding unoccupied habitats. Nevertheless, we also acknowledge that wolverines within such refugia are not immune from harvest along refuge borders. The need for refugia will become more important to wolverine persistence as wolverine habitat becomes increasingly patchy at the southern extent of the species range (Banci 1994). Nevertheless, depending on refugia to maintain harvested populations in small mountain ranges is questionable because few areas are large or remote enough to impede access.

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