

SYNTHESIS OF SURVIVAL RATES AND CAUSES OF MORTALITY IN NORTH AMERICAN WOLVERINES

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Abstract: Understanding population vital rates is fundamental to the evaluation of conservation options for wolverines (*Gulo gulo*). We estimated survival rates and causes of wolverine mortality in trapped and untrapped populations within montane, boreal, and tundra environments using data from 12 North American radiotelemetry studies conducted between 1972 and 2001. Rates were based on data for 62 mortalities of 239 radiomarked wolverines. Mortalities included 22 wolverines that were trapped or hunted, 3 road or rail killed, 11 that were predated, 18 that starved, and 8 deaths of unknown cause. Annual survivorship rates were estimated for sex and age class using Kaplan-Meier staggered-entry techniques. Survival was substantially lower in trapped (<0.75 for all age-sex classes) than in untrapped (>0.84 for all age-sex classes) populations. Human-caused mortality was mostly additive to natural mortality for wolverines in a management context. Logistic growth rate estimates indicated that trapped populations would decline ($\lambda \approx 0.88$) in the absence of immigration from untrapped populations ($\lambda \approx 1.06$). We recommend a system of spatial harvest controls in northern, continuous populations of wolverines and reduction of harvest along with more spatially explicit conservation measures in southern metapopulations.

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The wolverine is a wide-ranging mustelid existing at low densities throughout much of northern and western North America, Scandinavia, and Eurasia (Wilson 1982, Hash 1987, Banci 1994). In North America, wolverines occur in the northern boreal forest, taiga, and tundra from Labrador to Alaska and in the western mountains from Yukon south to Wyoming. Wolverines are classed as endangered in Quebec and Labrador and have protected status in Washington, Oregon, California, Colorado, Idaho, and Wyoming (Dauphine 1989, Banci 1994). In the remainder of their range, wolverines are classed as furbearers and are managed primarily through the timing of open trapping or hunting seasons.

Overexploitation through hunting and trapping, as well as predator poisoning programs, likely caused wolverine populations to contract in the eastern and southwestern portions of their historical range in North America since the early 1900s (Banci 1994). Declines in Scandinavia have been

attributed to similar factors (Linden et al. 1994). Within the current range, extensive human activities including human settlement, highway and railway development, hunting and trapping, forest harvesting, mineral extraction, hydroelectric development, and backcountry recreation continue to pressure wolverine populations and habitat.

In exploited populations, age- and sex-specific mortality rates are key attributes used to determine sustainable harvests (Caughley 1977, Wolfe and Chapman 1987, Banci 1994). Coupled with reproductive rates and population sizes, quantitative estimates of population growth and sustainable harvest rates can be calculated. However, age- and sex-specific survival rates of wolverines are not available to parameterize population models. Wolverine population densities have been estimated as high as 15.4 animals/1,000 km² in Montana (Hornocker and Hash 1981), 4.7–5.2 animals/1,000 km² in south-central Alaska (Becker and Gardner 1992, Golden 1996), to as low as 1.3 animals/1,000 km² in southwestern Yukon (Banci 1987). At densities typically in the middle to low ranges and reproductive rates of <1 kit per

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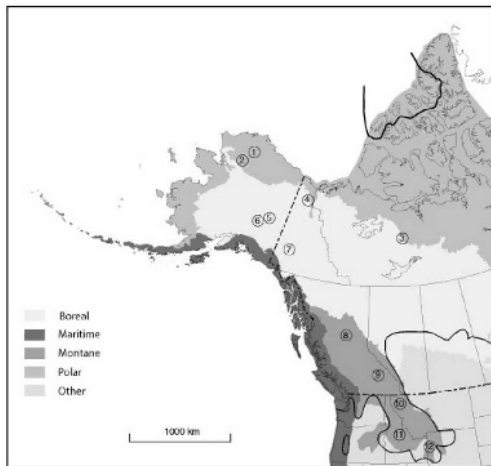


Fig. 1. Ecological zones and locations of wolverine radiotelemetry studies in western North America between 1972 and 2001. 1 = Magoun 1985; 2 = B. Shults, U.S. National Park Service, unpublished data; 3 = Mulders 2001; 4 = D. Cooley, Renewable Resources–Fish and Wildlife Branch, unpublished data; 5 = Gardner 1985; 6 = Golden 1993; 7 = Banci 1987; 8 = Lofroth 2001; 9 = Krebs and Lewis 2000; 10 = Hornocker and Hash 1981; 11 = Copeland 1996; 12 = Copeland 2000. Broad habitat categories were derived from Wiken (1986), Demarchi (1994), and Nowacki et al. (2001). Heavy black line indicates approximate wolverine distribution (based on Hash 1987). Numbers correspond to descriptions in Table 1.

adult female per year (post weaning; Magoun 1985, Copeland 1996), wolverine populations are vulnerable to human-caused mortality. The ability of wolverine populations to compensate (Wolfe and Chapman 1987) for human-caused mortality through reduced natural mortality and/or increased reproduction has not been examined.

In most of the current North American wolverine range, wolverine harvests are controlled through regulated seasons and bag limits. Management strategies in some areas have emphasized maintenance of untrapped “refugia” (Hatler 1989) within trapline areas. In other areas, authorities have enacted trapping season closures (e.g., Idaho, Washington, Wyoming, USA, and southwestern British Columbia, Canada). Little guidance is available regarding the importance of refugia size, habitat characteristics, and proximity of harvested areas to wolverine populations. An effective management strategy must consider population vital rates, home-range size, and dispersal characteristics. In addition to the effects of harvest, productivity of wolverine populations may vary depending on food distribution and abundance, competition with other species, and

human-caused impacts such as roads, settlement, and land use (Banci 1994, Lyon et al. 1994, Weaver et al. 1996, Magoun and Copeland 1998). Because wolverines are logistically difficult and expensive to study, individual projects have been unable to collect sufficient information to estimate survival rates. Additionally, because management regimes and ecozones differed among studies, comparisons in population attributes were impractical. We synthesized available survival and mortality source data from 12 radiotelemetry studies carried out in western North America to compare survival rates among ecozones and management regimes. We also compared natural and human-caused mortalities in trapped and untrapped populations to assess potential compensation in survival rates. We considered lower natural mortality in trapped populations as support for survival-rate compensation.

STUDY AREA

We compiled data from 12 radiotelemetry studies of wolverines conducted in North America between 1972 and 2001 (Fig. 1). Study locations included polar and southern Arctic habitat in Alaska, USA, and Northwest Territories, Canada; taiga in northern Yukon, Canada; boreal forest in Alaska and Yukon; montane habitats in British Columbia, Canada, and Montana, USA; and Northern Rocky Mountain Forest in Idaho and Wyoming, USA (Table 1; Wiken 1986, Demarchi 1994, Nowacki et al. 2001). We classified study sites as tundra, boreal, or montane ecotypes.

Tundra study areas were dominated by treeless tussock tundra with shrubs in riparian areas. Northern Yukon taiga was included in this category. Climate in these areas was characterized by short, cool summers and long, cold winters. Average February snow depths were 35–49 cm (Brown et al. 2002). Elevations ranged from 360 to 1,800 m in the Alaska, Yukon, and Northwest Territories study areas. Migratory caribou (*Rangifer tarandus*) was the dominant ungulate food source for wolverines (Magoun 1985, Mulders 2001). Small mammals such as Arctic ground squirrel (*Spermophilus parryi*) also were important seasonal prey (Magoun 1987).

Boreal study areas were characterized by spruce (*Picea* spp.) forests intermixed with birch (*Betula* spp.), aspen (*Populus* spp.), and shrubs in low-elevation habitats. High-elevation habitats were dominated by alpine tundra vegetation. Elevations ranged from 275 to 2,360 m. Climate in these study areas was characterized by cool, dry

Table 1. Locations, ecological zones, and management characteristics of 12 wolverine studies conducted in North America between 1972 and 2001.

No. ^a	Location	Study area size (km ²)	Source	Ecological zone	Population management	Habitat management ^b
1	Northwest Alaska	2,400	Magoun 1985	Polar	Untrapped	HU
2	Northwest Alaska	22,000	Shults ^c	Polar	Trapped	HU
3	Central Northwest Territories	2,000	Mulders 2001	Southern Arctic	Untrapped	HU
4	Northern Yukon	6,000	Cooley ^d	Taiga Cordillera	Trapped	HU
5	South-central Alaska	7,700	Gardner 1985	Boreal Cordillera	Trapped	HS
6	South-central Alaska	4,000	Golden et al. 1993	Boreal Cordillera	Trapped	HU, RC
7	Southwest Yukon	1,590	Banci 1987	Boreal Cordillera	Trapped	PA
8	North-central British Columbia	8,900	Lofroth 2001	Montane Cordillera	Trapped	FL,TC,HS,MN
9	Southeast British Columbia	7,000	Krebs and Lewis 2000	Montane Cordillera	Trapped	FL,TC,RC,HS
10	Montana	1,300	Hornocker and Hash 1981	Montane Cordillera	Trapped	FL,TC,HS
11	Central Idaho	8,000	Copeland 1996	Northern Rocky Mountain Forest	Untrapped	PA,RC,HS
12	Wyoming	1,500	Copeland 2000	Northern Rocky Mountain Forest	Untrapped	PA,RC,HS

^a Study numbers correspond to Fig. 1.^b Habitat management: FL = Forest harvesting; MN = Mineral extraction; RC = Backcountry recreation; TC = Major transportation corridor; HU = unpopulated; HS = sparsely populated; PA = protected area.^c B. Shults, U.S. National Park Service, unpublished data.^d D. Cooley, Renewable Resources–Fish and Wildlife Branch, unpublished data.

summers and cold, dry winters. Average February snow depths were 30–47 cm (Brown et al. 2002). Primary ungulate food sources for wolverines were moose (*Alces alces*), caribou, and Dall's sheep (*Ovis dalli*; Gardner 1985, Banci 1987). Arctic ground squirrels, snowshoe hare (*Lepus americanus*), and porcupine (*Erethizon dorsatum*) were identified as important diet items.

Montane study areas were characterized by relatively steep mountainous terrain, diverse forest habitats, alpine tundra at high elevations, cool winters, warm summers, and moderate to high precipitation. Average February snow depths were 100–140 cm (Brown et al. 2002). Elevations ranged from 460 to 3,280 m. Primary ungulate food sources for wolverines were moose and caribou in north-central British Columbia; moose, caribou, and mountain goats (*Oreamnos americanus*) in southeast British Columbia; and elk (*Cervus elaphus*), deer (*Odocoileus hemionus*, *O. virginianus*), and moose in Idaho, Montana, and Wyoming. Small-mammal prey, such as ground squirrels (*Spermophilus* spp.), porcupine, and hoary marmots (*Marmota caligata*), have been identified as seasonally important in some of these study areas (J. Krebs, unpublished data; E. Lofroth, unpublished data). As in tundra and boreal environments, the relative importance of other mammal and bird prey to wolverines in montane environments is not well described, especially for summer.

Wolverines were classed as a furbearer or game animal in 8 study areas and were trapped or hunt-

ed for their fur (Table 1). The southwest Yukon study was conducted in an area where trapping was not permitted. However, due to the small study-area size (1,590 km²), trapping activity on the perimeter of the study area, and the relative level of harvest of the study population, this was effectively a "trapped" sample population (Banci 1987). The same was true for the Montana study (Hornocker and Hash 1981; M. Hornocker, Wildlife Conservation Society, unpublished data), where trapping was permitted during the first 2 years of the study and on the perimeter of this small area (1,300 km²) for the duration of the study. Although the central Northwest Territories (Mulders 2001) and northwest Alaska (Magoun 1985) study areas had open trapping seasons, these areas were so remote that effectively no trapping occurred. Consequently, we classified these populations as "untrapped." The Idaho (Copeland 1996) and Wyoming (Copeland 2000) studies were conducted in untrapped wilderness areas.

METHODS

Capture

We captured wolverines using box traps (e.g., Copeland 1996, Krebs and Lewis 2000), barrel traps (Hornocker and Hash 1981, Banci 1987), or darting from a helicopter (e.g., Gardner 1985, Magoun 1985, Golden et al. 2002). We trapped or darted wolverines in areas where we believed captures were most likely to occur and areas that

Table 2. Wolverine mortalities from 12 radiotelemetry studies conducted in North America between 1972 and 2001. The number of wolverines includes all animals monitored for >10 days. Mortalities include natural and human-caused deaths of monitored wolverines. Excluded mortalities list wolverines that died after regular monitoring ceased.

Study area location	Ecotype	Management regime	No. of wolverines	Wolverine-years	Mortalities	Excluded mortalities
Northwest Alaska	Tundra	Untrapped	20	12.94	0	1
Central Northwest Territories	Tundra	Untrapped	28	24.66	1	3
Northwest Alaska	Tundra	Trapped	15	6.36	5	2
Northern Yukon	Tundra	Trapped	13	7.04	2	0
South-central Alaska	Boreal	Trapped	10	4.61	3	1
South-central Alaska	Boreal	Trapped	21	21.41	8	4
Southwest Yukon	Boreal	Trapped	9	5.45	6	1
North-central British Columbia	Montane	Trapped	40	30.96	11	2
Southeast British Columbia	Montane	Trapped	49	56.82	15	4
Montana	Montane	Trapped	15	5.92	4	0
Central Idaho	Montane	Untrapped	16	26.00	7	0
Wyoming	Montane	Untrapped	3	5.26	0	0
Total			239	207.43	62	18

were logistically accessible within the confines of project study areas. We immobilized wolverines using ketamine hydrochloride (HCl; e.g., Hash and Hornocker 1980, Copeland 1996) or with mixtures of tiletamine HCl and zolazepam HCl (e.g., Golden et al. 2002), phenylcyclidine and xylazine (e.g., Magoun 1985), or etorphine and xylazine (e.g., Gardner 1985) delivered via a pole syringe or tranquilizer dart. Wolverines were radiomarked with Telonics MOD315 or MOD335 radiocollars (Telonics, Inc., Mesa, Arizona, USA) or surgically implanted with Telonics IMP300 or IMP400 radiotransmitters by a veterinarian. Radiotransmitters were equipped with mortality sensors.

We classified wolverines as subadults (≤ 2 yr old) and adults (> 2 yr old). Wolverines are reported as reproductively mature between age 2 and 3 (Banci 1994). Poole et al. (1994) reported difficulty in discriminating age of wolverines based on cementum annuli alone and found the proportion of pulp in tooth sections could accurately separate animals < 16 months from those > 16 months-of-age. Because wolverine parturition spanned the period of captures in our study (i.e., Jan–Apr; Magoun and Copeland 1998), we assigned age 1 (subadult) to wolverines on the basis of premolar or canine (postmortem) tooth-section characteristics and age 2+ (adult) based on tooth section and on tooth wear, the presence of cataracts, pelage appearance, or nipple and testes size (Magoun 1985). We chose 1 March as the birth date for all wolverines based on reported denning times for female wolverines (Magoun and Copeland 1998; J. Krebs, unpublished data; E. Lofroth, unpublished data). Juveniles (age ≤ 4 months) that were captured and radiomarked

with their mother were considered as subadults in the analysis.

Monitoring

Radiomarked wolverines were relocated at least monthly via aircraft. Mortalities were investigated on the ground immediately following detection. Postmortem necropsies were conducted whenever possible. We broadly classified causes of death as natural (starvation, predation, unknown) or human caused (trapped–hunted, road–rail kill). We did not include in our analyses 18 deaths of radiomarked wolverines that occurred after they were no longer being regularly monitored (Table 2). Wolverine deaths ($n = 7$) attributed to research activities also were not included in analyses.

Statistical Analysis

We estimated annual survivorship rates for each age–sex class (adult female, subadult female, adult male, subadult male) by ecological zone (montane, boreal, tundra) and management regime (trapped, untrapped). We used a bootstrapped Kaplan-Meier technique (Pollock et al. 1989) following McLellan et al. (1999) to accommodate staggered entry of individuals into and out of the data set. We used retrospective 2-way analysis of variance (ANOVA) to compare bootstrapped survival rates among management regimes, habitats, and age–sex classes. A 3-way ANOVA was not possible because 1 cell (“boreal untrapped”) of the design was empty. Two retrospective 2-way ANOVAs also were used to compare rates of mortality associated with natural and human-caused factors by age–sex, management regime, and ecological zone.

Table 3. Sources of wolverine mortality by age–sex class in trapped and untrapped study groups. Data were compiled from 12 radiotelemetry studies completed in western North America between 1972 and 2001. Wolverines were considered adults at 2 years-of-age.

Management regime	Age–sex class	Mortality source				
		Natural		Unknown	Human caused	
		Predation	Starvation		Trapped/Hunted	Road/Rail
Trapped	Adult female	0	4	1	5/0	0/0
	Adult male	2	5	0	6/0	0/0
	Subadult female	3	4	1	2/0	0/1
	Subadult male	4	3	2	8/1	2/0
Subtotal		9	16	4	21/1	2/1
Untrapped	Adult female	1	1	1	0	0
	Adult male	1	1	0	0	0
	Subadult female	0	0	3	0	0
	Subadult male	0	0	0	0	0
Subtotal		2	2	4	0	0
Total		11	18	8	22	3

Population Growth Simulations

To explore the effect of human-caused mortalities on population growth, we estimated lambda using our adult and subadult female survival rates bounded by their respective standard errors as well as 3 reproductive rates (0.25, 0.375, 0.5 females/adult female/yr) that bracket reported rates of 0.3 (Persson 2003), 0.345 (Magoun 1985), and 0.445 (Copeland 1996) from untrapped populations. We set age at first parturition at 3 years (Banci 1994, Copeland 1996, Magoun 1985, Persson 2003). Maximum age was set at 13 years for all simulations because this was the maximum age of carcass samples reported in Banci (1987) and Liskop et al. (1981). We did not vary reproductive rates by age or density because the relationship between these variables was unclear. Density-dependent compensation in reproduction is unlikely because unpredictable environmental conditions are likely far more influential in low-density populations (Taylor et al. 1987). Although we lack detailed demographic data from wolverine populations across a range of densities, recent work by Persson (2003) highlights the importance of winter food availability and reproductive status the previous year as determinants of reproductive success in wolverines. Because winter food availability (i.e., ungulate carrion) for wolverines is suggested to vary with environmental conditions (van zyl de Jong 1975), variation in reproductive rates is most likely driven by stochastic rather than density effects.

RESULTS

In the 12 studies, 239 wolverines (110 F, 129 M) were radiomarked and monitored for 207.4 radiotracking years (Table 2). Sixty-seven wolver-

ines from 4 studies in Idaho, Wyoming, Alaska, and Northwest Territories were monitored in untrapped populations. The remaining 172 animals were from trapped populations in Montana, British Columbia, Yukon, and Alaska. Sixty-two (25.9%; 35 M, 27 F) wolverines died while being monitored (Table 3).

Human-caused mortality (22 trapping–hunting and 3 road–rail kills) accounted for 25 of 54 (46%) deaths in trapped populations and was not detected in untrapped populations (Table 3). Eleven of 25 human-caused mortalities were of subadult male wolverines. Starvation was the most common natural mortality source within trapped populations followed by predation and unknown (Table 3). Predation deaths included attacks from wolves (*Canis lupus*), mountain lions (*Felis concolor*), and conspecifics. In untrapped populations, numbers of wolverines dying from starvation, predation, and unknown natural mortalities were similar (Table 3).

Survival rates differed markedly between management regimes ($F_{1,281} = 12.86$, $P < 0.001$) but were similar among age–sex class ($F_{3,281} = 2.50$, $P = 0.06$; Table 4). The interaction between age–sex class and management regime was not significant ($F_{3,281} = 1.82$, $P = 0.143$). Survival rates in untrapped populations were substantially higher than trapped populations (Table 4). Within age–sex classes, subadult males had the lowest survival.

We detected significant variation in survival among ecological zones ($F_{2,281} = 6.12$, $P = 0.003$) and a nonsignificant age–sex effect ($F_{3,281} = 2.13$, $P = 0.097$). The interaction between habitat and age–sex was not significant ($F_{6,281} = 0.78$, $P = 0.583$). Survival estimates derived from tundra populations were higher than those in boreal and montane groups (Table 4). However, because survival

Table 4. Wolverine annual survival rates by ecological zone and management regime. Rates were estimated from 12 North American radiotelemetry studies conducted between 1972 and 2001. Wolverines were considered adults at 2 years-of-age. Standard errors were generated by bootstrap samples of survivorship data for each group. Groups represent pooled data among studies within the same ecological zone and/or management regime.

Ecological zone	Management regime	Deaths	Wolverine-years	Annual survival rate ($\pm$ SE)			
				Adult female	Adult male	Subadult female	Subadult male
Tundra	Untrapped	1	37.60	1.0 (0)	1.0 (0)	0.92 (0.082)	1.0 (0)
Boreal	Untrapped	no data	no data	no data	no data	no data	no data
Montane	Untrapped	7	31.26	0.69 (0.149)	0.80 (0.129)	0.73 (0.167)	1.0 (0)
Tundra	Trapped	7	13.40	1.0 (0)	1.0 (0)	0.50 (0.382)	0.35 (0.195)
Boreal	Trapped	17	31.47	0.60 (0.167)	0.62 (0.155)	0.64 (0.141)	0.36 (0.181)
Montane	Trapped	30	93.70	0.78 (0.083)	0.73 (0.081)	0.72 (0.101)	0.55 (0.119)
Pooled	Trapped	54	138.57	0.73 (0.076)	0.74 (0.062)	0.69 (0.080)	0.45 (0.088)
Pooled	Untrapped	8	68.86	0.88 (0.065)	0.87 (0.095)	0.85 (0.082)	1.0 (0)
Tundra	Pooled	8	51.10	1.0 (0)	1.0 (0)	0.87 (0.089)	0.64 (0.121)
Boreal	Pooled	17	31.47	0.60 (0.161)	0.62 (0.155)	0.64 (0.141)	0.36 (0.181)
Montane	Pooled	37	124.96	0.76 (0.071)	0.74 (0.069)	0.72 (0.085)	0.70 (0.088)

rates of 1.0 are unachievable, tundra rates require larger sample sizes in several age–sex classes to detect mortalities. Survival data from untrapped boreal wolverine populations were not available.

Natural survivorship rates did not differ significantly among the combined management–ecological zone groups ($F_{4,273} = 2.22$, $P = 0.067$; Table 5) or by age–sex ($F_{3,273} = 1.07$, $P = 0.364$). We found no significant interaction between management–ecological zone and age–sex ($F_{12,273} = 1.26$, $P = 0.245$).

Within trapped populations, survival rates associated with human-caused mortalities did not differ significantly by ecological zone ($F_{2,201} = 1.46$, $P = 0.235$) or by age–sex class ($F_{3,201} = 2.31$, $P = 0.078$). The interaction between habitat and age–sex class was not significant ($F_{6,201} = 0.62$, $P = 0.715$; Table 6). Although subadult males experienced lower survival than other age–sex groups, human-caused mortalities were present in all age–sex groups.

DISCUSSION

Banci (1994) reported mortality percentages of radiomarked wolverines from trapped and un-

trapped populations to suggest annual mortality rates of 0.025 to 0.20 (mean = 0.106). However, Banci (1994) did not apply staggered-entry procedures (Pollock et al 1989) in estimating mortality rates, likely resulting in a significant negative bias. Further, Banci (1994) did not provide separate estimates for sex and age classes. Our data suggest that annual mortality rates (i.e., 1 – annual survival rate) in trapped populations are much higher (0.27 to 0.55 depending on age–sex class; pooled ecological zones Table 4), while mortality rates in untrapped areas were similar (0.0 to 0.15; pooled ecological zones Table 4) to those reported by Banci (1994).

The strength of the difference in survival between trapped and untrapped populations of wolverines in our study suggests that trapping had a significant effect on population demography. Nearly half of all wolverine mortalities recorded in trapped populations were human caused. These mortalities occurred across all age–sex classes but were most prevalent within subadult males. Greater encounter rates with human-caused mortality sources (traps, roads) for young, inexperi-

Table 5. Wolverine annual survivorship rates by management regime, ecological zone, and age–sex class based on natural mortalities only. Rates were estimated from 12 radiotelemetry studies completed in western North America between 1972 and 2001. Groups represent pooled data among studies within the same ecological zone and management regime. Wolverines were considered adults at 2 years-of-age. Standard errors (in parentheses) were generated by bootstrap samples of survivorship data for each group.

Management regime	Habitat	Adult female	Adult male	Subadult female	Subadult male
Trapped	Tundra	1.0 (0)	1.0 (0)	0.50 (0.377)	0.44 (0.232)
	Boreal	0.89 (0.107)	0.92 (0.075)	0.64 (0.144)	0.80 (0.196)
	Montane	0.87 (0.061)	0.83 (0.065)	0.86 (0.077)	0.82 (0.083)
Untrapped	Tundra	1.0 (0)	1.0 (0)	0.92 (0.082)	1.0 (0)
	Boreal	no data	no data	no data	no data
	Montane	0.69 (0.149)	0.80 (0.129)	0.73 (0.167)	1.0 (0)

Table 6. Wolverine annual survivorship rates based on human-caused mortalities only, by ecological zone and age–sex class in trapped populations. Rates were estimated from 8 radiotelemetry studies completed in western North America between 1972 and 2001. Groups represent pooled data among studies within the same ecological zone. Wolverines were considered adults at 2 years-of-age. Standard errors (in parentheses) were generated by bootstrap samples of survivorship data for each group.

Habitat	Adult female	Adult male	Subadult female	Subadult male
Tundra	1.0 (0)	1.0 (0)	1.0 (0)	0.80 (0.133)
Boreal	0.70 (0.152)	0.67 (0.162)	1.0 (0)	0.48 (0.194)
Montane	0.89 (0.073)	0.88 (0.071)	0.84 (0.089)	0.67 (0.128)

enced males during dispersal may explain this observation. We speculate that because natural mortalities occurred independent of management regime, harvest was additive mortality. Additional data, particularly from untrapped populations, would improve our ability to interpret this result. In simulations, McLellan et al. (1999) suggested that for grizzly bears (*Ursus arctos*), at least 42 animals in each age–sex class would be required to detect 5% differences in survival.

For trapped populations, estimates of λ clearly suggest potential population declines in all but the most favorable survival and reproductive rate scenarios (Table 7). The best estimate (using mean adult and subadult survival, reproductive rate = 0.375) suggests a 12.2% annual decline ($\lambda = 0.878$) in the absence of immigration from untrapped areas. In contrast, λ is increased in most of the scenarios modeled for untrapped populations (Table 7). Based on these simulations, untrapped populations are capable of increasing at 6.4% per year ($\lambda = 1.064$).

Table 7. Population growth rates for trapped and untrapped wolverine populations based on survivorship rates estimated from 12 North American radiotelemetry studies conducted between 1972 and 2001. Growth rates are modeled for the mean ($\pm$ SE) of adult and subadult survivorship rates. Growth rates are modeled for 3 different reproductive rates (R ; female kits/adult female/year). Maximum age in the model is estimated at 13; first age of parturition is estimated at 3.

Survivorship rates	Logistic rate of population growth (λ)		
	$R = 0.25$	$R = 0.375$	$R = 0.5$
Trapped populations			
Adult (+SE); Subadult (+SE)	0.914	0.972	1.020
Adult (mean); Subadult (mean)	0.825	0.878	0.920
Adult (–SE); Subadult (–SE)	0.736	0.783	0.821
Untrapped populations			
Adult (+SE); Subadult (+SE)	1.081	1.151	1.207
Adult (mean); Subadult (mean)	1.000	1.064	1.116
Adult (–SE); Subadult (–SE)	0.920	0.979	1.026

As with other low-density species, such as polar bear (*Ursus maritimus*; Taylor et al. 1987) and grizzly bear (Hovey and McLellan 1996), maintaining high annual survival (≥ 0.85) of adult female wolverines is central to sustaining populations and harvest (Eberhardt 1990). Because wolverine trapping techniques are nonselective with respect to sex and age, conservative harvest strategies are required. At harvest rates experienced during the timespan of this dataset, trapped populations likely were declining or being maintained via immigration from untrapped refugia. Because trapping occurs in most jurisdictions within the western North American range of the wolverine, the presence and spatial distribution of source populations within protected refugia may be critical to the persistence of wolverines in harvested areas. Resiliency of wolverine populations to harvest and fluctuations in food abundance is considered to be lower than grizzly bears (Weaver et al. 1996).

During the past century, wolverine distribution in North America has contracted substantially along the species' southern boundary (van Zyll de Jong 1975). Factors proposed to explain reductions invariably include human exploitation and changes in prey distribution and abundance. Overexploitation of the wolverine in Scandinavia drove populations nearly to extirpation until protection was granted in Sweden and Norway (Landa et al. 1997). Our results confirm the strong potential effect of harvest on survival and therefore persistence of wolverines in North America.

We found significant differences in survival among habitats. However, because the boreal ecological-zone group did not include untrapped population data, we were unable to control for the effect of management regime on survival. Therefore, this result possibly is spurious. Additional survival data from untrapped tundra, and particularly untrapped boreal forest, would improve knowledge of baseline wolverine demography. However, statistical support for quantifying subtle differences in vital rates likely will continue to be weak since sample size requirements

are considerable (McLellan et al. 1999). Maritime habitats, which extend from Alaska to Oregon along the Pacific coast, also are completely lacking in wolverine demographic data. Very limited reproductive rate data also hampers our understanding and conservation of North American wolverine populations.

MANAGEMENT IMPLICATIONS

Our data show sustained harvest of wolverine populations likely is maintained by dispersal from untrapped refugia. The ability of refugia to continue to support harvest in neighboring areas may be threatened by human activities that displace or diminish source populations or fragment habitat, particularly in the southern (southern British Columbia, Idaho, Montana, Wyoming) portion of their range. Even in the northern Arctic regions of Northwest Territories and Nunavut, which historically provided expansive refugia for wolverines, snowmobile-assisted access has changed the spatial distribution of the harvest. Since untrapped populations are potentially capable of increasing at 6.4% per year and trapped areas are potentially decreasing at 12.2% per year, refugia need to cover twice as much similarly productive wolverine habitat as harvested areas to support harvests that reflect our observed survivorship values. Protected areas that are targeted to include no more than 12% of the landbase (World Commission on Environment and Development 1987, British Columbia Commission on Resources and Environment 1994) cannot fulfill the role of refugia alone. Additional modeling will be needed to refine the size and distribution of a functional refugia system. Work on grizzly bears clearly suggests that population density and surrounding management context strongly influence reserve sizes (Wielgus 2002).

In continuous populations such as those in the boreal forest and tundra ecosystems of northern British Columbia, Yukon, Alaska, Nunavut, and Northwest Territories, a system employing spatial controls (McCullough 1996) of trapped and large untrapped areas might ensure long-term persistence of the wolverine. These untrapped refugia would need to encompass sufficient reproductive habitat to generate dispersers (Magoun and Copeland 1998).

In southern British Columbia, registered trapline tenures are too small (50–1,000 km²) to contain viable refugia. Evidence from Banci (1987) and Hornocker and Hash (1981) demonstrate the futility of small (<1,600 km²) trapping

refuges. Within southern, fragmented populations—where dispersal ability among units may be impaired—conservative harvest strategies that include intensive management and monitoring may be necessary to conserve metapopulations (McCullough 1996). In some areas, harvest should be reduced to protect wolverine metapopulations and reduce subpopulation extirpation risk. Future harvest should be managed spatially, by defined metapopulation units. The continued functioning of dispersal linkages between and among southern British Columbia, Alberta, Montana, Idaho, and Washington is essential to long-term persistence of wolverines in the southern portion of their range.

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