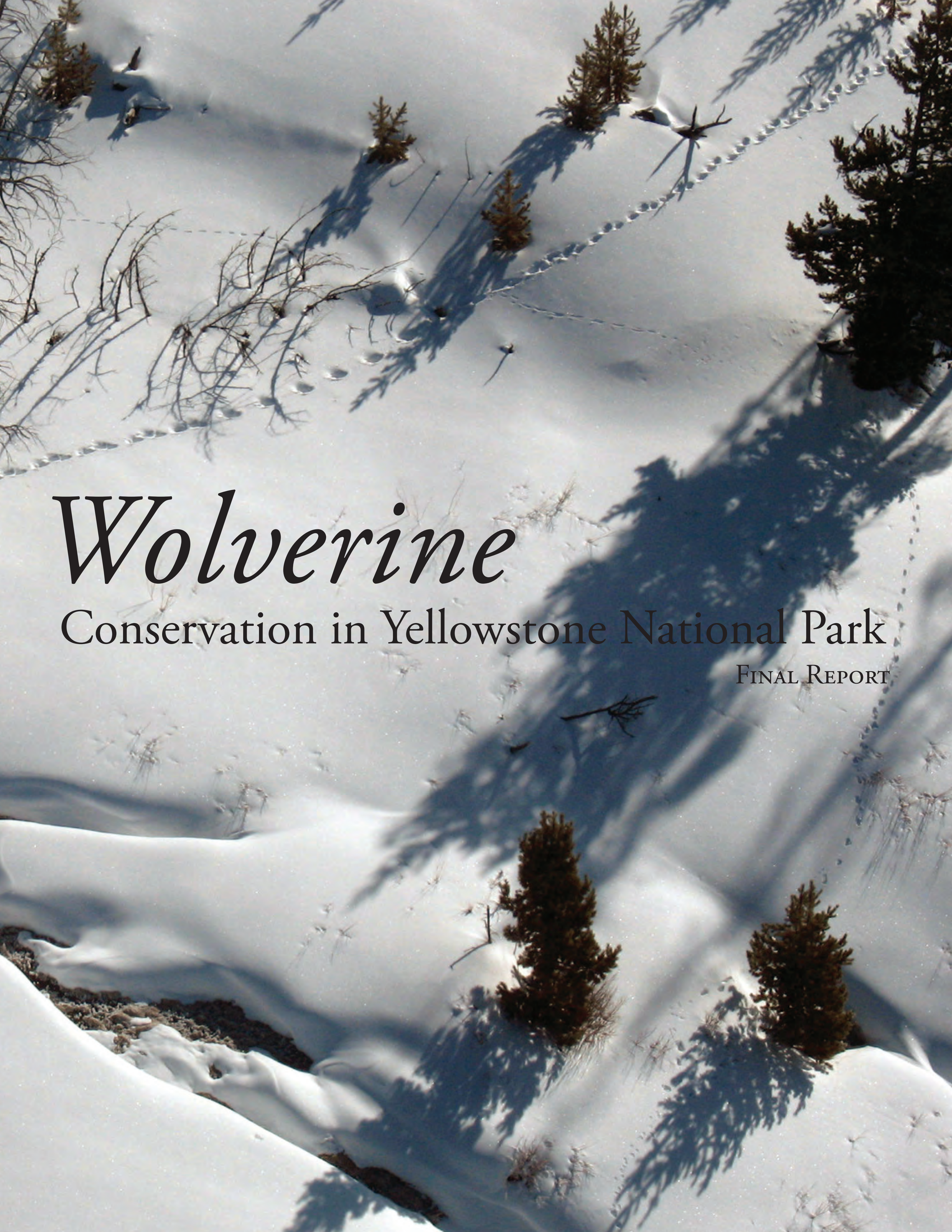


Wolverine

Conservation in Yellowstone National Park

FINAL REPORT

ON THE COVER
Wolverine tracks in the Greater Yellowstone Ecosystem. Photo by Jason Wilmot.

Wolverine Conservation in Yellowstone National Park

Final Report

Authors

Kerry Murphy
US Forest Service
Jackson Ranger District
PO Box 25
Jackson, Wyoming 83001
kmmurphy02@fs.fed.us
(formerly Yellowstone Center for Resources, Yellowstone National Park, Wyoming)

Jason Wilmot
Northern Rockies Conservation Cooperative
PO Box 2705
Jackson, Wyoming 83001
jason@nrccooperative.org

Jeff Copeland
US Forest Service
Rocky Mountain Research Station
800 East Beckwith Avenue
Missoula, Montana 59801
jpcopeland@fs.fed.us

Dan Tyers
US Forest Service
Gardiner Ranger District
PO Box 5
Gardiner, Montana 59030
dtyers@fs.fed.us

John Squires
US Forest Service
Rocky Mountain Research Station
800 East Beckwith Avenue
Missoula, Montana 59801
jsquires@fs.fed.us

With contributions from

Robert M. Inman
Wildlife Conservation Society
Wolverine Program Field Office
222 East Main Street
Lone Elk 3B
Ennis, Montana 59729
binman@wcs.org

Mark L. Packila
Wildlife Conservation Society
Wolverine Program Field Office
222 East Main Street
Lone Elk 3B
Ennis, Montana 59729
packila@yahoo.com

Doug McWhirter
Wyoming Game and Fish Regional Office
2820 State Highway 120
Cody, Wyoming 82414

National Park Service
Yellowstone National Park
Yellowstone Center for Resources
Yellowstone National Park, Wyoming

YCR-2011-02

March 2011

Suggested citation:
Murphy, K., J. Wilmot, J. Copeland, D. Tyers, J. Squires, R. M. Inman, M. L. Packila, D. McWhirter. 2011. Wolverine conservation in Yellowstone National Park: Final report. YCR-2011-02. National Park Service, Yellowstone National Park, Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

This report is available electronically: Greater Yellowstone Science Learning Center, www.greateryellowstonescience.org.

Printed on recycled paper.

Contents

Figures

Tables

JASON WILMOT

Wolverine distribution and population characteristics were documented from 2005 to 2009 in Yellowstone National Park and its neighboring wilderness areas by capturing and monitoring radio-marked individuals and conducting surveys for their tracks during winter.

Abstract

We documented wolverine distribution and population characteristics from 2005 to 2009 in Yellowstone National Park and its neighboring wilderness areas along the park's east, northeast, and south boundaries by capturing and monitoring radio-marked individuals, and conducting surveys for their tracks during winter. We captured four individuals and collaboratively monitored three others, including two immigrants, that were previously marked by Wildlife Conservation Society biologists in the western portion of the Yellowstone ecosystem. Wolverines in our study area selected habitats above 2,450 meters (8,000 ft), that is, in the Hudsonian (boreal) life zone, but did not use alpine habitats extensively. Live-trapping, telemetry data, and surveys for tracks indicated that wolverine numbers and distribution were more limited than expected, despite the fact that two contemporary models estimated an extensive coverage of wolverine habitat in the area. Wolverines occurred in the Absaroka-Beartooth Wilderness along the north boundary of the park, and at the southeast corner (Thorofare region) and the adjoining Washakie and Teton Wilderness areas. When conducting helicopter-based surveys for tracks during winter, we did not detect any wolverines in the park interior, including the portion of the Gallatin Range inside the park; the Washburn and Snake River Ranges; the Central and Madison Plateaus; and the Bechler region. We also did not detect resident wolverines in the North Absaroka Wilderness and the adjoining areas along the east boundary, including the upper Lamar River. Surveys for ungulates in this area during the winter did not indicate that the availability of carrion significantly limited wolverine numbers and distribution, although our anecdotal observations suggested that winter food might be limited in the heavily forested portions of interior Yellowstone. Wolverine home ranges did not overlap, and radio-marked individuals did not make extra-home range movements to forage in the major ungulate winter ranges in and near our study area, including the Pelican and Hayden Valleys, and the northern winter range. Our limited demographic data suggested that reproductive rates of wolverines were low, that home ranges were large, and that rates of survival were similar to estimates for other populations in the conterminous United States. The dynamics and distribution of our population appeared to be strongly linked to ingress from well-established populations in other parts of the ecosystem, rather than to recruitment of offspring born to our resident females. We developed and tested a reliable method to rapidly assess wolverine distribution over large areas using helicopter-based searches for tracks during the winter. We were highly successful in finding tracks of resident, radio-marked wolverines during both preliminary tests (searches in 10 x 10 km survey [grid] cells) on a Wildlife Conservation Society study site, and when applying our refined technique to wolverines on our study area. This survey method can be broadly applied to the incised terrain typical of the Rocky Mountains as a first step in assessing wolverine populations, provided that surveys are adequately replicated. We recommend that biologists continue to investigate the factors that limit the growth of wolverine populations, particularly in areas such as ours where models suggest that suitable habitat is abundant.

JASON WILMOT

This project would not have been successful without the extraordinary support of the Yellowstone Park Foundation, the principal funder of the project, and other partners. Here, Molly Pickall of the Yellowstone Park Foundation investigates a GPS cluster site in the Absaroka Range in 2009.

Acknowledgements

This project would not have been successful without the extraordinary support of the Yellowstone Park Foundation, the principal funder of the project, and dedicated staff such as Lisa Diekmann, Caroline Miceli, Kristi Mills, Molly Pickall, and Chessie Thacher. The park and national forests are indebted to these individuals for their tireless support of the project.

Other funding or indirect support was provided by the Gallatin National Forest, Greater Yellowstone Coordinating Committee, Rocky Mountain Cooperative Ecosystems Studies Unit, Rocky Mountain Research Station, Shoshone National Forest, Northern Rockies Conservation Cooperative, Wildlife Conservation Society, The Wolverine Foundation, Wolverine World Wide, Inc., Wyoming Game and Fish Department, and Yellowstone National Park.

We are very grateful to the technicians that served the project, including D. Brown, R. Eisfeldt, C. Foster, S. Framness, K. Gabrian, H. Goranson, B. Jimenez, M. Kurzen, M. Latini, T. Makkonen, T. May, C. McCarthy, S. McColley, R. Notin, H. Ristow, M. Runyon, H. Schwingel, M. Scrafford, K. Stewart, N. Stone, K. VanEtten, and M. Tyers. Special thanks to Andy Johnson and Jeremy Zimmer whose tireless work and tremendous expertise kept the project moving forward. We also thank volunteers J. Akins, K. Andrus, E. Bindseil, C. Byron, A. Miller, B. Rassi, T. Reese, W. Sicard, K. Shick, B. Summerer, D. Taylor, R. Watters, and J. Wood who kindly donated their time. The help of Youth Conservation Corps personnel, including ranger Steve Sarles and Linnea Renz, were key to timely removal of live-traps from the park and the national forests.

Pilots Doug Chapman, John Martin, Mark Packila, Tim Schell, and Dave Stinson provided excellent VHF telemetry support. Special thanks to Neil Cadwell and Elke Giem for providing safe helicopter flights and flight following during numerous surveys. Drs. J. Felton, D. Hunter, D. McCauley, and D. Pendray provided excellent veterinary services on short notice and worked at peril under adverse conditions.

We thank Rocky Mountain Research Station staff C. Engkjer, K. McKelvey, K. Pilgrim, L. Ruggerio, and M. Schwartz for their assistance with genetic analysis, project design, and other support. Contractor C. Copeland provided excellent GIS coverages and other assistance.

T. Patton and B. Fuhrmann of the Yellowstone National Park Interpretation Division led the ParKids outreach and allied educational efforts, an important and successful aspect of the project.

Many National Park Service and US Forest Service staff assisted and/or supported the project, including N. Alexander, R. Baerwald, R. Bock, K. Britton, M. Cherry, S. Christman, R. Connell, R. Dylchouse, C. Glenn, E. Hale, C. Hendrix, R. Feigley, J. Frederick, K. Gunther, W. Hafer, M. Keator, C. Koehler, J. Krish, M. Lindstrom, M. Longden, M. Maj, D. Morton, D. Myers, A. Pils, J. Ogle, L. Otto, P. Pederson, C. Phipps, D. Reinhart, B. Ross, B. Sefton, K. Speers, A. Truman, P. J. White, C. Whitman, M. K. Woodin, and T. Wyman. Special thanks to G. Plumb for his vision and long-term support of the project.

We thank Montana, Fish, Wildlife and Parks staff K. Alt, N. Anderson, B. Giddings, L. Hanauska-Brown, and T. Lemke. Wyoming Game and Fish Department personnel M. Bruscino, A. Johnson, D. McWhirter, B. Oakleaf, S. Patla, and C. Queen also provided guidance and support. R. Watters of the Northern Rockies Conservation Cooperative, J. and C. Long of the The Wolverine Foundation, and R. Spence of the Wildlife Conservation Society also assisted the project.

JASON WILMOT

The wolverine is one of the least studied carnivores in North America, particularly in the contiguous United States where it occurs at the southern extent of its range. Records suggest that wolverines historically occurred throughout the Greater Yellowstone Ecosystem. However, prior to this project little information was available concerning its distribution and ecology in Yellowstone National Park and the adjoining national forests. Here, Dan Tyers of the US Forest Service displays the attributes of wolverine F3.

Introduction

Wolverines in the contiguous United States are a strong concern for federal land managers and the public. The species was designated a candidate species (warranted for listing under the Endangered Species Act, but precluded by work on species of higher priority) by the US Fish and Wildlife Service in 2010. Wolverines are particularly vulnerable to extirpation due to their low numbers and large spatial requirements (Banci 1994; Copeland and Whitman 2003). Wolverine populations in the conterminous United States are small and isolated as compared to those in Canada due to naturally fragmented habitat (Aubry et al. 2007; Ruggerio et al. 2007) and infrequent exchange of individuals between mountain ranges (Cegelski et al. 2003; Kyle and Strobeck 2001, 2002). These attributes contribute to low genetic effective population sizes and low population viability (US Fish and Wildlife Service 2008). Due to its importance for the security and thermoregulation of neonates, spring snow cover may limit the wolverine's distribution and abundance, yet this habitat component is declining across the species' geographic range due to global climate change (Aubry et al. 2007; Copeland et al. 2010).

The wolverine is one of the least studied carnivores in North America, particularly in the contiguous United States where it occurs at the southern extent of its range (Ruggiero et al. 2007). Previous reports, surveys, and sightings records suggest that wolverines historically occurred throughout the Greater Yellowstone Ecosystem (Skinner 1927; Smith 1955; Mobley 1962; Hoak et al. 1982; Groves 1988; Consolo-Murphy and Meagher 1995; Robinson and Gehman 1998; Murphy et al. 2004). The Wildlife Conservation Society is conducting a long-term study in the western and southern portion of the ecosystem (Inman et al. 2007a, 2008). However, little information is available concerning this species' distribution and ecology in Yellowstone National Park and the adjoining national forests along the park's northeast, east, and southeast boundary. Our study objectives were to document (1) the distribution of wolverines in Yellowstone and eastern portion of the ecosystem; (2) their population characteristics, including reproduction, survival, sources of mortality, and food habits; (3) their habitat requirements, particularly those related to natal and maternal denning; and (4) their movements, including any that provide connectivity with populations in other ecosystems. To improve support for its conservation, it was also our aim to increase public awareness of this unique and mysterious carnivore (Appendix 1).

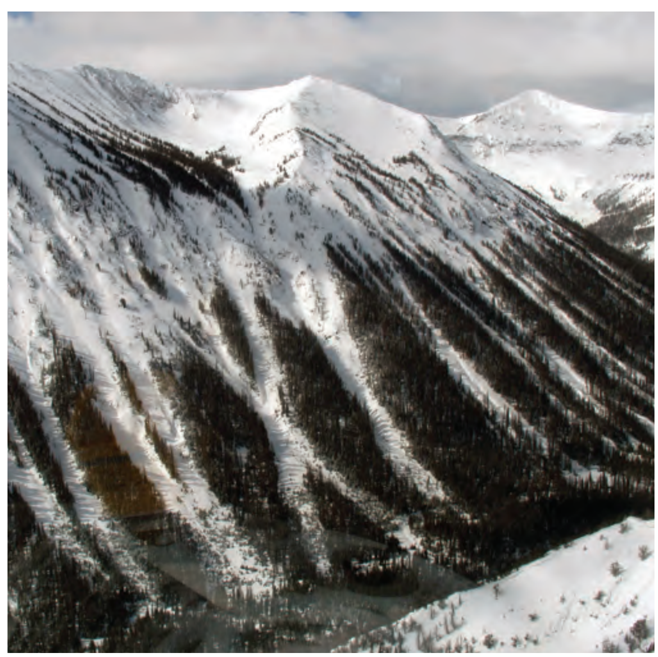
JASON WILMOT

The windswept Pitchstone Plateau (foreground), Yellowstone National Park, photographed during aerial surveys for wolverine tracks. The Teton Range (background) was not included in surveys. The project's core study area encompassed the eastern portion of Yellowstone National Park and the adjoining areas of the Bridger-Teton, Gallatin, and Shoshone National Forests.

Study Area

Our core study area was approximately 13,000 km^2 (8,000 mi^2) in size and encompassed the eastern portion of Yellowstone National Park and the adjoining areas of the Bridger-Teton, Gallatin, and Shoshone National Forests (fig. 1). The largely road-less area included portions of the Absaroka-Beartooth (north Yellowstone Park boundary), North Absaroka (northeast boundary), Washakie (southeast boundary), and the Teton (south boundary) Wilderness areas. Intensive snowmobile activity occurred at the park's northeast corner near Cooke City, Montana. A prominent geographic feature of the area is the Absaroka Mountain Range which extends from the southern margin of the Beartooth Plateau (near Cooke City) south along the park's east boundary to Dubois, Wyoming. The Absaroka Range reaches 3,720 meters (12,204 ft) in elevation (Trout Peak) and supports heavy snowpack from December through March. Here, the alpine zone supports krumholtz, talus, and exposed rocks. Beneath alpine habitats, lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanni*), and whitebark pine (*Pinus albicaulis*) provided the principal overstory cover in the Hudsonian zone. Conifers were interspersed with meadows, broad riparian habitats, and sagebrush (*Artemesia tridentata*) steppe. Fires occurring in 1988 burned large portions of the study area. Potential sources of carrion (or prey) included bighorn sheep (*Ovis canadensis*), bison (*Bison bison*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and mountain goats (*Oreamnos americanus*). Common small prey included blue grouse (*Dendragapus obscurus*), ruffed grouse (*Bonasa umbellus*), Uinta ground squirrels (*Spermophilus armatus*), snowshoe hares (*Lepus americanus*), and yellow-bellied marmots (*Marmota flaviventris*). Gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), and cougars (*Puma concolor*) were potential predators or competitors with wolverines for prey or carrion. American marten (*Martes americana*), coyotes (*Canis latrans*), red fox (*Vulpes vulpes*) common ravens (*Corvus corvax*), magpies (*Pica hudsonia*), and gray jays (*Perisoreus canadensis*) were also potential competitors for carrion.

When conducting aerial surveys for wolverine tracks we covered a broader (16,400 km^2; 10,200 mi^2) area than encompassed by our core study area. The survey area included all of Yellowstone National Park and habitats that extended 20 kilometers (12.4 mi) from the park boundary into the surrounding national forests. This irregularly shaped survey area encompassed home ranges of wolverines, as necessary, to evaluate our ability to detect radio-marked individuals during surveys.



JASON WILMOT

The Absaroka Mountain Range was a prominent feature of the core study area.

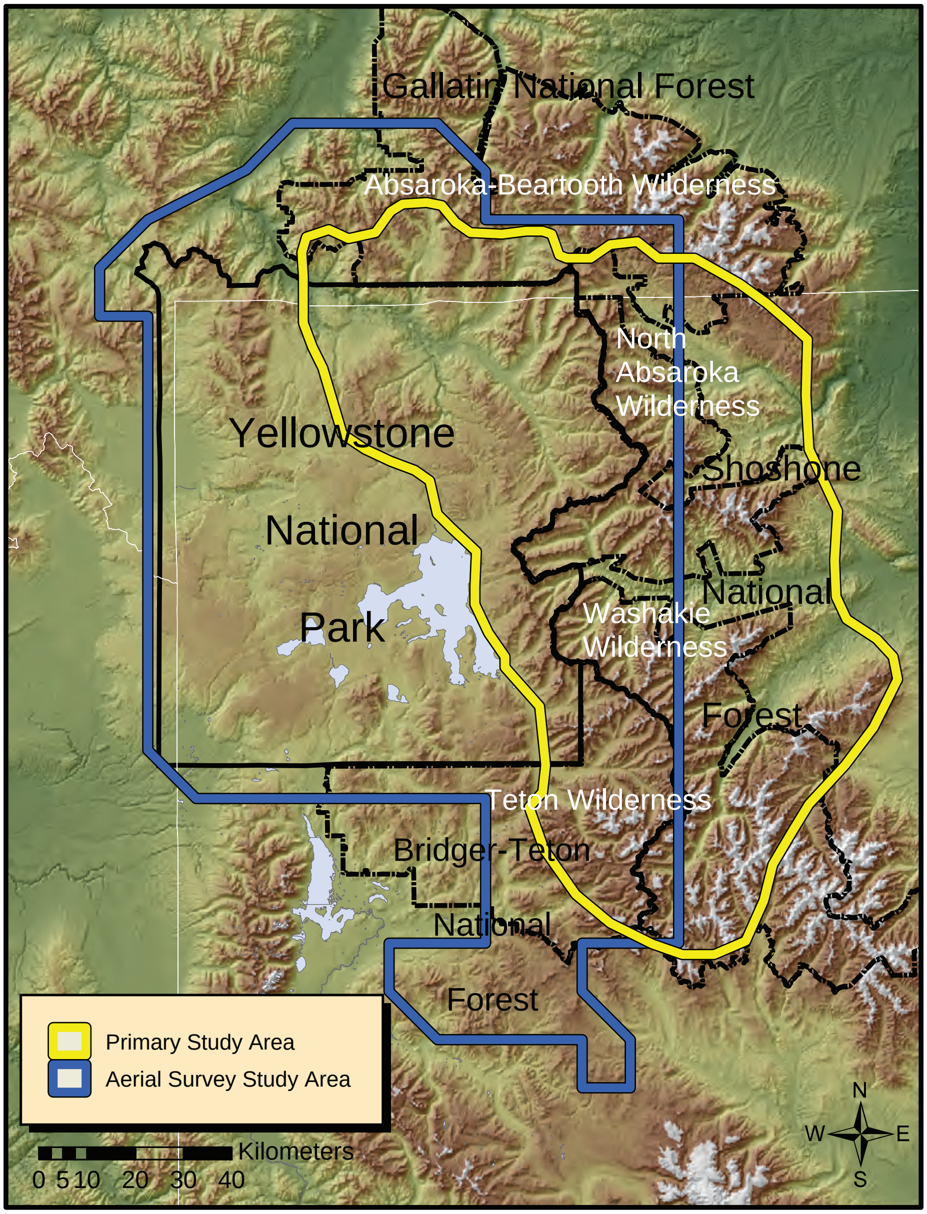


Figure 1. Primary Absaroka-Beartooth study area (2006–2009), and the area surveyed for wolverine tracks using a helicopter, 2008–2009.

Methods

Wolverines were captured from winters 2005–2006 to 2008–2009 in live traps (Copeland et al. 1995) operated variously from December to late March. Skinned beaver carcasses obtained from Montana fur trappers were used as bait. Traps were fitted with remote trap transmitters (Telonics, Inc., TBT-600HC, Mesa, Arizona) that remotely signaled personnel up to 29 kilometers (18 mi) distant when traps were triggered and contained wolverines or non-target animals. Signals were checked remotely 1–4 times per day, the traps themselves a minimum of every 3–4 days. We used trap nights to measure capture effort, with one trap night equal to one trap set for one night.

Each year, we operated 1–6 trap lines with 1–8 traps per line. Traps were typically located within 200 meters of roads that were open to wheeled vehicles (Northeast Entrance Road, Yellowstone National Park), snowmobiles (East Entrance and Dunraven Pass Roads, Yellowstone National Park; Gardiner and Cooke City region, Gallatin National Forest; Beartooth Plateau and Sunlight Basin, Gallatin and Shoshone National Forests), or hiking trails (Clear Creek, Yellowstone National Park; Eagle Creek, Shoshone National Forest).

Wolverine capture and handling

We anesthetized wolverines in live traps with initial doses of Medetomidine hydrochloride (average 0.3 mg per kg body weight) and Ketamine hydrochloride (8.7 mg per kg) using a syringe mounted on a flexible fiberglass pole. Wolverines were given a physical (health) exam and their vital signs (heart rate, respiration, and body temperature) monitored. They were weighed and measured, fitted with an ear tag (left ear for females, right ear for males), provided an intraperitoneal implant (VHF) transmitter (Telonics, Inc., IMP400L) by a veterinarian, and/or equipped with a GPS/VHF radio collar (Sirtrack Ltd., Havelock North, New Zealand). Wolverine ages were estimated based on tooth development and wear (Copeland and Whitman 2003). Blood (2–3 cc) for serological analysis was provided to the Montana Department of Fish, Wildlife and Parks, and skin (ear punch; *Genetic analysis*, see below) and ectoparasite samples were collected. Atipamezole hydrochloride was administered (0.2 mg per kg body weight) as an antagonist to Medetomidine to speed recovery. Wolverines were returned to live traps and released 1.5–11 hours after processing. Our immobilization and handling procedures were annually approved by the University of Montana Institutional Animal Use and Care Committee.

Telemetry-based monitoring

We located wolverines with radiocollars from airplanes at approximately 10-day intervals to document home range sizes, movements, spatial organization, survival, and habitat use. We attempted to document reproductive events and den sites of radio-marked female wolverines by locating them 1–2 times per day over periods of three days, weather permitting, during the February–May maternal denning period. Fidelity to a hole in the snow suggested the presence of a birthing den (Magoun and Copeland 1998). Maternal females on foraging bouts were expected to return to birthing dens at interval of ≤ 12 hours (J. Copeland, unpublished data). Locations were also obtained from GPS store-on-board collars at three-hour intervals for females and two hours for males. Data were retrieved from collars after they fell from the animal and were recovered from the field.

We calculated 100% minimum convex polygon (Burt 1943; Mohr 1947) and fixed kernel (100%, 75%, and 50% isopleths; Worton 1987, 1989) home ranges for wolverines using VHF and GPS radio location data. To help insure their spatial

BOTTOM RIGHT: ERIC BINDSEIL; REST OF PAGE: KERRY MURPHY

and temporal independence, GPS locations were randomly chosen and limited to one per 24 hours and sub-sampled from all hourly GPS and weekly VHF data. Only high-precision GPS locations (≤ 10 HDOP; Sirtrack, Ltd.) were retained. Analysis of hourly and daily wolverine movements were based on the GPS data only. Movements across or between ecosystems were based only on VHF data. Daily and annual wolverine survival was calculated using program Micromort (Heisey and Fuller 1985). We tallied survival days beginning the day after the wolverine's release and censured them the day after their last location.

Habitat use and selection

We evaluated the use and selection of elevation, topographic position (Jenness 2006), and aspect (compass direction of mountain slopes) by our radio-marked wolverines using the same radio location data used to estimate their 24-hour, minimum convex polygon home ranges. We hypothesized that wolverine use of elevation and aspect was related to the availability of snow cover that supports reproductive denning during the winter and spring, and, at the southerly extent of wolverine range, helps maintain thermal neutrality during summer months (Aubry et al. 2007; Copeland et al. 2010). We also hypothesized that lower mountain slopes and valley bottoms would be selected. Here, carrion is more likely (O'Gara and Harris 1988), and travel on frozen waterways and in open riparian zones is presumably less energetically costly (J. Copeland, unpublished data). Radio locations were plotted on a rasterized, 30-meter digital elevation model (National Cartography & Geospatial Center,

Clockwise from top left: Jeff Copeland and Jason Wilmot prepare to immobilize wolverine M1 at its capture site in 2006 (*top left*) and perform a physical exam (*top right*); Project technicians Kelsey Gabrian and Keith VanEtten, and Wyoming Game and Fish Department biologist Andy Johnson process wolverine M4, 2007 (*bottom*).

DYLAN BROWN

Project technician Ben Jimenez checks a live trap in Yellowstone National Park, 2006. Traps were checked at least every three to four days and contained skinned beaver carcasses from Montana fur trappers as bait.

Natural Resources Conservation Service, http://datagateway.nrcs.usda.gov) and then categorized (as described below) for each of the three variables using Spatial Analyst (ArcMap 8.3; ESRI, Redlands, California) and a point intersection tool (Hawth's Analysis Tools; Beyer 2004). To generate points for comparison with wolverine radio locations, we estimated the percent coverage of the three variables using 5,000 points that were randomly chosen from the respective home ranges.

Topographic positions were classified ridge, upper slope, middle slope, lower slope, and valley using Weiss (2001) and a Topographic Position Index extension (Jenness Enterprises) available in ArcView 3.2 (ESRI, Redlands, California). Elevations were binned as 0–2,450 meters (0–8,000 ft), 2,450–2,740 meters (8,000–9,000 ft), 2,740–3,050 meters (9,000–10,000 ft), and >3,050 meters (10,000 ft). Aspects were categorized as North (315–44°), East (45–134°), South (135–224°), West (225–314°), and flat terrain.

Habitat selection was evaluated following Marcum and Loftsgaarden (1980), with summer (June 1 to November 30) and winter telemetry locations analyzed separately if Likelihood Ratio Goodness of Fit (G^2; $\alpha = 0.10$) tests indicated seasonal differences. For each variable, we determined if annual or seasonal habitat use differed statistically (G^2; $\alpha = 0.10$) from availability. If differences were detected, then we constructed 95% or 98% confidence intervals (as appropriate based on the number of categories) around the estimated proportion of locations to determine if use for the category was significantly different from random expectation. Constructed in this way, all the confidence intervals for the variable were simultaneously correct with 90% confidence (Marcum and Loftsgaarden 1980). We did not evaluate habitat selection of two wolverines (Wildlife Conservation Society M557 and M556) that used our study area because few (< 35 annually) radio locations were obtained for these individuals. Similarly, we lacked a sufficient number (> 5) of radio-marked individuals to use a multi-model approach to evaluate habitat selection, such as that applied by Copeland et al. (2007).

Evaluating wolverine habitat models

We evaluated the ability of the habitat model developed by Brock et al. (2007) and the niche model developed by Copeland et al. (2010) to predict wolverine occurrence at a large spatial (major watershed) scale on our study area, and to identify areas that were unsuitable habitat. Brock et al. (2007) determined that elevation, ruggedness, conifer cover, snow depth, forest edge, and road density were important variables that identified habitat selected by radio-marked wolverines on two Wildlife Conservation Society study areas located in western portion of the Yellowstone ecosystem (south-central Montana, western Wyoming, and southeast Idaho). Brock et al. (2007) extended model predictions to the entire northern and southern US Rocky Mountains, including our core Absaroka-Beartooth study area and Yellowstone

National Park. For our evaluation, we included their entire range ("high" to "low") of habitat qualities. Copeland et al. (2010) found that the wolverines' fundamental niche was defined by the coverage of spring (April 24–May 15) snowpack and ambient temperature. They found high concordance between these variables and the distribution of wolverine radio locations and natal den sites documented for the Northern Hemisphere, including those from the Wildlife Conservation Society and our project areas. In this model, any mapping unit that contained May snowpack for ≥ 1 year from 2000–2006, as determined through satellite technology, was mapped as wolverine habitat.

For the Brock et al. (2007) and the Copeland et al. (2010) habitat coverage, we plotted the sub-sampled wolverine telemetry data for our entire study area (described above in *Telemetry-based monitoring*) and calculated the percent of points that fell within (versus outside) predicted habitat. We also constructed a single 100% minimum convex polygon using the aggregate radio locations and calculated the enclosed habitat for each model coverage. Model performance was evaluated by comparing the ratio of the number of telemetry points that fell within predicted habitat to its acreage within the polygon. At a large spatial scale, an efficient model would maximize the number of telemetry points but minimize the acreage of predicted habitat.

Food habits

We documented ungulates that were scavenged by wolverines. Food items were found at clusters of radio locations that we visited on the ground and at sites where we recovered radio collars discarded by wolverines. Carrion was documented opportunistically from aircraft when monitoring radio-marked individuals.

Genetic analysis

The US Forest Service Rocky Mountain Research Station, Missoula, Montana, extracted DNA from hairs and scats collected along snow trails or at radio location clusters, and analyzed wolverine ear punches extracted during capture and handling. Species identification was based on analysis of mitochondrial DNA (mtDNA) amplified using universal mammalian primers (Shields and Kocher 1991). Individual wolverines were identified from analysis of their microsatellite DNA at 16 loci (Schwartz et al. 2007, 2009, and references therein).

Aerial survey development

Aircraft-based surveys for wolverine tracks have previously not been tested and widely applied in the mountainous terrain characteristic of the Rocky Mountains. To develop new survey techniques, we initiated a collaborative project with Wildlife Conservation Society biologists on their Madison and Gravelly Mountain Ranges study area (Inman et al. 2007a). During winter 2008, this area supported six female and two male radio-marked wolverines, each with a well-documented home range. These individuals, in addition to two Absaroka-Beartooth project wolverines (F3, M2), were used as a basis

JIM WOOD

Project technicians maintain a live trap near Cooke City, Montana, in 2006. Traps were typically located within 200 meters of roads open to wheeled vehicles or snowmobiles, or hiking trails.

for testing our ability to detect wolverine tracks from a helicopter. We used the results of this experimental work to survey Yellowstone National Park in late winter 2008 and winter 2009 (see *Applied* a*erial survey methods, Yellowstone National Park and Vicinity*).

Using a Bell L3 helicopter, we searched for wolverine tracks on the Wildlife Conservation Society and Absaroka-Beartooth study areas in numbered 10 km x 10 km grid cells (sampling units), each approximately one third of a female wolverine home range in the Yellowstone ecosystem (Inman et al. 2007a). Only cells with ≥ 25% coverage of wolverine habitat (Brock et al. 2007) and overlap with one or more 100% minimum convex polygon home ranges of radio-marked wolverines were selected for survey. These overlap requirements ensured that all survey cells occurred fully or partially within wolverine home ranges—a necessity to evaluate our ability to detect tracks—and that cells occurred within habitats where wolverine presence was plausible.

Prior to surveys, we monitored snow deposition and temperature using weather reporting services and remote Natural Resources Conservation Service SNOTEL (SNOwpack TELemetry) data sites. Flights were conducted ≥ 2.5 days after snowfall to allow ample time for tracks to accumulate. Surveys for different wolverines occurred within the same day, if possible. The survey crew consisted of two observers and the pilot. When searching for tracks, the helicopter was flown at about 60 miles (96 km) per hour and at approximately 1,000 feet in altitude. If a putative wolverine track was observed, the crew deviated from the general flight path if necessary to more closely inspect the track.

We attempted to locate tracks of wolverines using two different flight (search) patterns and two types of survey cells (fig. 2). For each wolverine, we searched for tracks in the cell it occupied, determined during an independent telemetry (airplane) flight the morning of the survey, and two randomly chosen cells in the individual's home range. "Occupied" cells were revealed to survey personnel before the survey, but the exact locations of animals were untold. Upon reaching an occupied cell, the observers typically searched for 6–10 minutes along a subjectively chosen "optimal" straight line (tree-less terrain identified using aerial photos) that extended across the entire grid cell. This transect was largely confined to wolverine habitat. All wolverine tracks, including those possibly associated with unmarked individuals, were treated as detections.

If a wolverine track was observed in the occupied cell, the crew then immediately left the cell to search the two randomly selected cells (as below) for tracks. If the observers failed to detect a track in the occupied cell using the straight-line transect, then all remaining treeless terrain in the cell was searched intensively for up to one hour using a subjectively chosen, tortuous (meandering) route.

Project staff (here, Kerry Murphy) tested the effectiveness and efficiency of helicopter-based surveys for wolverine tracks.

We also searched a randomly selected cell in the wolverines' home range using a straight-line pattern and a second, different random cell using an intensive search, as above. This provided information concerning the possible differences in detection rates between occupied and non-occupied cells. In each case, observers stopped searching if a track was detected. Intensive searches of random cells were limited to 30 minutes. Throughout the survey, we limited track searches to cells that had not been searched previously during the course of the entire survey. Search times for each cell were calculated as the sum of the time spent searching for tracks and the time spent inspecting them, if necessary, from the helicopter. The helicopter was never landed to inspect tracks on the ground or collect biological samples. We predicted that wolverine track detection success for occupied cells would be greater than for randomly chosen ones because tracks in the occupied cell were the freshest and therefore the least likely to be covered by snowfall. We also predicted that detection success would be greater for the intensive search method because more time was spent searching along tortuous routes and because treeless terrain could be better targeted for search than when traveling along a straight line that was selected a priori.

The purpose of this experiment was to gauge our ability to detect wolverine tracks in mountainous terrain from a helicopter, and to identify an efficient search method. We did not expect to detect wolverine tracks in every cell we searched, but a 100% detection rate for each cell was not essential for detecting resident wolverines. Over the course of three days, radio-marked wolverines in Glacier National Park typically left tracks in three 100 km^2 (62 mi^2) cells (J. Copeland, unpublished data). Thus, the collective chances of a detecting a wolverine were improved on our study area because a detection could occur in any of the multiple cells (≥ 3) that comprised a typical wolverine home range. Replicate surveys conducted over the course of a winter should also improve the collective chances of detection.

Applied aerial survey methods, Yellowstone National Park and vicinity

We used the results of preliminary work on the Wildlife Conservation Society study area to design new survey methods for documenting wolverine distribution in Yellowstone National Park and the surrounding national forests. Similar to the preliminary work on the Wildlife Conservation Society study area, we evaluated our ability to detect radio-marked wolverines on our area during blind tests. In this case, however, we tested our ability to detect tracks of radio-marked individuals at the home range scale, rather than in grid cells alone. In other words, we tested our ability to detect a resident wolverine throughout its home range if, in fact, an individual was present. The survey encompassed a larger area (16,400 km^2) than previously covered (about 13,000 km^2) by live trapping.

We conducted three replicated surveys for wolverine tracks from February to April during 2008 and 2009 using the same helicopter and survey conditions to those used on the Wildlife Conservation Study area. Complete replicates each required three days of flying, but poor weather conditions typically precluded work on consecutive days. The survey area was partitioned into 10 km x 10 km cells that extended 20 km beyond the park boundary. We surveyed every other cell—69 to 74 total—in a checkerboard fashion by flying a straight path along the diagonals of the cells (see fig. 17 in *Results*). This pattern allowed us to survey continuously without skipping over costly, non-survey cells. In addition

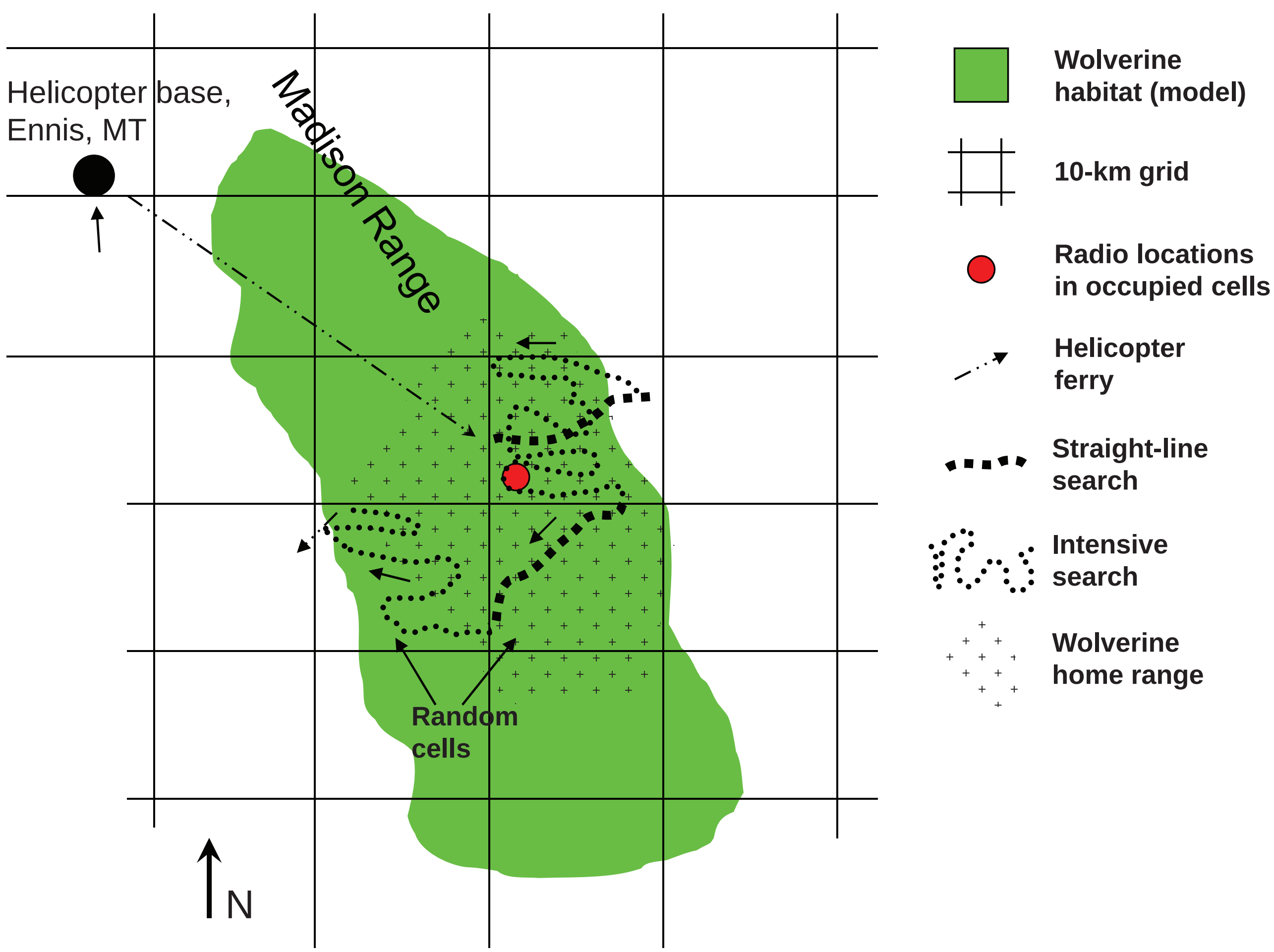


Figure 2. Two search patterns and grid cell types were used to test the ability of two helicopter-based observers to detect wolverine tracks on the Wildlife Conservation Society study area (2008) in the Madison and Gravelly Mountains, Montana, and the Absaroka-Beartooth study area (2009).

to the 20 kilometer buffer around the park boundary, we opportunistically extended the survey area 65 kilometer south to encompass the home range of a radio-marked wolverine (M556) to enable a test of our ability to detect his tracks.

Only cells with > 25% overlap with wolverine habitat mapped as the coverage of spring snow cover by Copeland et al. (2010) were included in the Yellowstone survey. This coverage included areas > 2,450 meters (8,000 ft) in elevation such as the Absaroka and Washburn Ranges, the Red Mountains, and much of the park interior. Copeland et al. (2010) found that the coverage of spring snow, measured from a satellite, encompassed 100% of documented wolverine natal dens, 95% of summer telemetry locations, and 86% of winter telemetry locations across the species' range in the northern hemisphere.

Aerial surveys for potential wolverine prey and sources of carrion

We hypothesized that food limitation might explain why we were unable to capture wolverines or locate their tracks in many areas. We documented the relative numbers and the distribution of ungulates during winter and early spring, 2008 and 2009, ad hoc in the North Absaroka Wilderness and along the east boundary of Yellowstone National Park. We shared survey costs and observer expertise with the Wyoming Game and Fish Department. The surveys focused on high elevation topography (typically > 2,450 m) where wind-swept ridges and plateaus provided forage for bighorn sheep and mountain goats. We also opportunistically searched creek bottoms and slopes for moose and elk.

A Google Earth image of a grid cell used to survey wolverine tracks. Project staff surveyed every other cell (69 to 74 total) in a checkerboard fashion by flying a straight path along the diagonals of the cells.

ERIC BINDSEIL

Project staff captured four individual wolverines a total of seven different times (M4 shown here after his release from the capture site in 2007). Three individuals, including two adult males and one subadult female, were first captured near the Absaroka-Beartooth Wilderness, Gallatin National Forest. A subadult male was also captured near Sylvan Pass in Yellowstone National Park.

Results

Trapping effort

We operated 33 live traps along eight trap lines, each with 1–6 live traps, during the four winter seasons from 2006 to 2009 (fig. 3, table 1, Appendix 2). Three trap lines occurred in Yellowstone National Park (Wyoming-Montana), three occurred in the Gallatin National Forest (Montana), and two occurred in the Shoshone National Forest (Wyoming). The average elevation for all traps was 2,418 meters (range = 2,097–2,870 m). Capture effort totaled 5,248 trap nights for the duration of the project and ranged annually from 26 nights (one trap) at Eagle Creek, Wyoming, to 596 nights (six traps) at Cooke City, Montana.

Wolverine captures and characteristics

We captured four individual wolverines a total of seven different times (table 2). Three individuals, including two adult males and one subadult female, were first captured near the Absaroka-Beartooth Wilderness, Gallatin National Forest. A subadult male was also captured near Sylvan Pass in Yellowstone. All except one individual were captured in March. The two adult males weighed 14.2–14.6 kilograms (31.2–32.1 lbs); the subadult female weighed 8.2 kilograms (18.0 lbs). All wolverines exhibited typical wolverine pelage coloration: dark in color, prominent or faint side stripes and cream to yellow chest and throat patches. They were instrumented with intraperitoneal implants. The four individuals were also equipped with GPS collars during six captures.

Wolverine monitoring

We monitored wolverines captured on the core Absaroka-Beartooth study area, as well as two individuals (F133, M557) that immigrated into our area and were originally radio-marked by Wildlife Conservation Society biologists in the western portion of the Yellowstone ecosystem. We also radio-located a third (M556; VHF) individual captured by the Wildlife Society at Togwotee Pass, Shoshone National Forest. In total, we monitored seven different wolverines (four Absaroka-Beartooth and three Wildlife Society subjects), obtaining 259 VHF locations from airplanes and collecting four GPS data sets that totaled 703 locations (table 3).

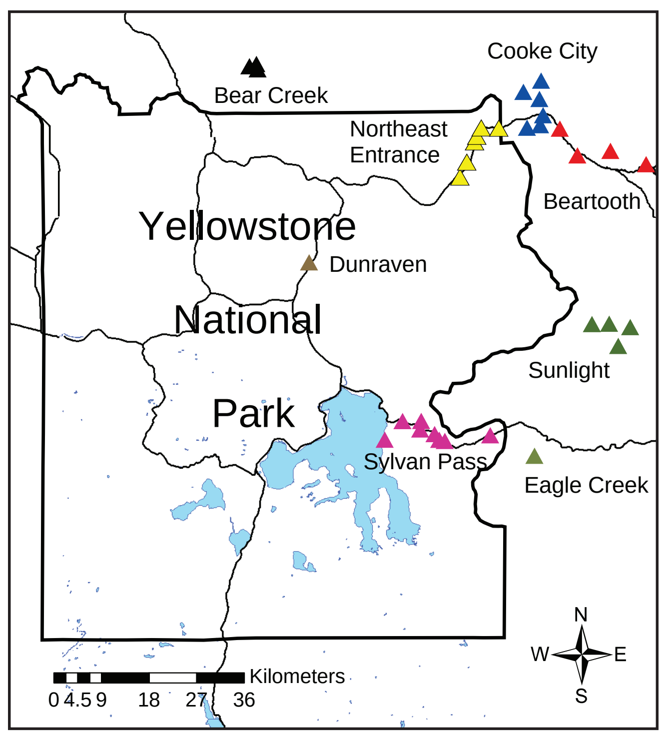


Figure 3. Locations of eight wolverine live traps maintained during winters 2005–2006 to 2008–2009 on the Absaroka-Beartooth study area.

Table 1. Locations and numbers of live traps set for wolverines on the Absaroka-Beartooth study area, 2005–2009

Trap line	Jurisdiction	# traps	Range in elevation (m)	Winter	Dates of operation	Traps nights
Bear Creek	Gallatin NF	3	2,203–2,510	2005–06	1/18/2006–3/31/2006	142
				2006–07	12/6/2006–3/20/2007	229
				2007–08	1/30/2008–4/15/2008	292
				2008–09	12/2/2008–3/31/2009	252
Cooke City	Gallatin NF	6	2,676	2005–06	1/16/2006–4/1/2006	297
				2006–07	12/6/2006–3/30/2007	596
Beartooth	Gallatin NF	4	2,097–2,240	2005–06	1/16/2006–4/1/2006	285
				2006–07	12/6/2006–3/3/2007	399
Eagle Creek	Shoshone NF	1	2,097	2007–08	2/25/2008–3/22/2008	26
Sunlight	Shoshone NF	4	2,198–2,509	2005–06	1/22/2006–3/22/2006	176
				2006–07	12/5/2006–3/18/2007	349
East Entrance	Yellowstone NP	8	2,191–2611	2005–06	1/21/2006–4/2/2006	492
				2006–07	12/11/2006–3/25/2007	593
				2008–09	2/11/2009–3/31/2009	132
Northeast Entrance	Yellowstone NP	6	2,097–2,240	2005–06	1/17/2006–4/2/2006	439
				2006–07	12/6/2006–3/21/2007	460
Total	—	33	—	—	—	5,248

Note: NP = National Park; NF = National Forest.

Table 2. Characteristics of wolverines captured on the Absaroka-Beartooth study area, 2006–2009

Wolverine	Capture date	Trap line	Age	Weight (kg)	Neck Circum-ference (cm)	Chest girth (cm)	Total length (cm)	Tail length (cm)	Pelage color	Chest color	Throat color
M1	3/3/2006	Bear Creek	Adult	14.2	34.0	43.0	—	89.0	Dark brown	Creamy yellow	Creamy yellow
M1	3/22/2006	Bear Creek	Adult	—	—	—	—	—	Dark brown	—	—
M2	3/10/2006	Sylvan Pass	Sub-adult	—	35.0	—	—	—	Dark brown	Creamy white	Dark Brown
F3	3/11/2007	Bear Creek	Sub-adult	8.2	28.5	40.5	91.0	17.5	Dark brown	Cream	Cream
	2/4/2008	Bear Creek	Adult (2 years)	8.4	—	—	—	20.0	Dark brown	Cream	Cream
	3/27/2008[a]	Bear Creek	Adult (2 years)	—	—	—	—	—	Dark brown	—	—
M4	3/18/2007	Bear Creek	Adult (3 years)	14.6	36.0	50.0	106.0	7.2	Dark brown	Cream	Faint cream

[a] Released without processing due to adverse weather.

Table 3. Telemetry-based monitoring periods for wolverines captured on the Absaroka-Beartooth Wolverine Project, 2006–2009

Wolverine	Monitoring year	Transmitter	Deploy date	Monitoring dates[a]	Number of relocations	Comments
F3	2007	VHF	3/11/2007	3/17/2007–7/21/2007	8	—
	2008	VHF	2/4/2008	2/14/2008–12/9/2008	19	Re-implanted 2/4/2008
	2009	VHF	—	1/14/2009–12/7/2009	17	Still on the air; project continuing
	2007	GPS	3/11/2007	3/12/2007–6/29/2007	359	—
	2008	GPS	2/4/2008	2/5/2008–4/11/2008	148	—
F133[b]	2007	VHF	WCS[b] 2006	4/30/2007–12/21/2007	9	—
	2008	VHF	—	1/1/2008–12/18/2008	34	—
	2009	VHF	—	1/4/2009–12/19/2009	33	—
M1	2006	VHF	3/3/2006	3/21/2006–12/9/2006	18	—
	2007	VHF	—	1/16/2007	1	Mortality date was 2/11/2007
	2006	GPS #1	—	3/21/2006	0	Collar not recovered; VHF signal failed
	2006	GPS #2	3/22/2006	3/22/2006–4/18/2006	181	—
M2	2006	VHF	3/10/2006	3/25/2006–12/2/2006	16	—
	2007	VHF	—	1/1/2007–12/21/2007	24	—
	2008	VHF	—	1/1/2008–12/18/2008	27	—
	2009	VHF	—	1/4/2009–10/23/2009	27	Transmitter expired
	2006	GPS #1	3/10/2006	3/11/2006–3/13/2006	15	—
M4	2007	VHF	3/18/2007	3/22/2007	1	Unable to locate
M556[c]	2009	VHF	WCS capture	1/15/2009–3/13/2009	6	Dispersed to Colorado; still transmitting
M557[d]	2009	VHF	WCS capture	5/2/2009–12/7/2009	19	Still transmitting
	2009	GPS #1	WCS capture	5/2/09–?	Unknown	Collar not recovered
Total	—	—	—	—	962	—

[a] Range for telemetry locations obtained from aircraft. Excludes captures.

[b] Wolverine captured on Wildlife Conservation Society (WCS) study area, Gallatin Mountain Range, Montana.

[c] Wolverine captured at Lava Butte (Togwotee Pass), western Wyoming, by the Wildlife Conservation Society. Currently being actively monitored by the Wildlife Conservation Society in Colorado.

[d] Wolverine captured at Menan Buttes (Rexburg), southeast Idaho, by the Wildlife Conservation Society. Cooperative monitoring north of the Yellowstone National Park boundary.

Spatial relationships and home range sizes

Four wolverines resided north of the Yellowstone National Park boundary, principally in the Absaroka-Beartooth Wilderness, and three wolverines resided in the Thorofare Region (southeast Yellowstone National Park, and the Teton and Washakie Wilderness areas; figs. 4 and 5). Two individuals were monitored in 2006, five in 2007, three in 2008, and five in 2009. Ranges of males overlapped those of females. We were not able to assess the extent of overlap within the sexes.

Annual home ranges of female wolverines were smaller than those of males (table 4). All three estimates for F3, a resident in the Absaroka-Beartooth Wilderness, were lower than those for F133 (Wildlife Conservation Society), an individual at the same age and located in the Thorofare region. Minimum convex polygon home ranges of both females increased as they progressed from the subadult (2007) to the adult class (2008, 2009). The range of M2, also first captured as a subadult, increased progressively. Six estimates of annual minimum convex polygon home ranges for the two females averaged 447 km^2 (278 mi^2) and ranged from 261–782 km^2 (162–486 mi^2). Their annual 95% fixed-kernel home ranges averaged 893 km^2 (555 mi^2) and ranged from 348–1,673 km^2 (268–1,040 mi^2). Six estimates of annual minimum convex polygon home ranges for the three males (too few locations for M556) averaged 908 km^2 (564 mi^2) and ranged from 446–1,268 km^2 (277–788 mi^2). Their annual 95% fixed kernel ranges averaged 1,815 km^2 (1,128 mi^2) and ranged from 1,355–2,501 km^2 (842–1,554 mi^2).

Survival and sources of mortality

We documented the fates of seven radio-marked wolverines in two female and three male sex-age classes over 3,920 monitoring days, including two males originally captured by the Wildlife Conservation Society (table 5). We censured one adult male (M4) that could not be located shortly after capture.

There were no deaths among subadult females, adult females, juvenile males, and subadult males over 2,413 days of monitoring (annual survival = 1.0). Annual survival for four adult males was 0.78 over 1,507 days. Adult M1 was legally taken by a Montana trapper in the Absaroka-Beartooth Wilderness.

Habitat use and selection

We documented the extent two female and two male radio collared wolverines used and selected elevations, aspects of mountain slopes, and topographic types within their home ranges. Sample sizes were insufficient to statistically evaluate habitat selection for two (M556, M557) individuals.

Use of elevation differed by winter and summer seasons (G^2=42.1, exact P < 0.001). During summer, all four wolverines used elevations differently than in proportion to their availability. Each wolverine avoided sites in the lowest (< 2,450 m; < 8,000 ft) elevation band (fig. 6). F3, M1, and F133 selected either of the two moderate (2,450–3,050 m; 8,000–9,000 ft) bands.

During winter, all four wolverines increased their use of the lowest elevation band, although they still predominantly used moderate elevations (fig. 7). All wolverines except F3 used elevations differently than in proportion to their availability. M1, F133, and M2 avoided the highest elevation band.

Use of topographic type did not differ seasonally (G^2 = 5.92, exact P = 0.21). Annually, all wolverines used the middle and lower portions of mountain slopes and valley bottoms extensively, and upper slopes and ridges relatively little (fig. 8). All except F3 used topography differently than available within home their ranges. Valley bottoms were selected by both males and females, and both ridges and upper slopes were avoided by the males.

Use of aspect did not differ seasonally (G^2 = 4.93, exact P = 0.18). Annually, wolverines used slopes facing in all the cardinal directions. They did not use flat areas, although sites in this category were uncommon (3% of random points) within wolverine home ranges (fig. 9). Two wolverines that resided in the Absaroka-Beartooth Wilderness used aspects differently than in proportion to their availability. F3 avoided south-facing, and M1 selected west-facing slopes. F133 and M2 resided in the Thorofare region and used aspects in proportion to availability.

KERRY MURPHY

Project technicians build a log box live trap in Yellowstone National Park, 2005. The average elevation for all traps was 2,418 meters (7,933 ft).

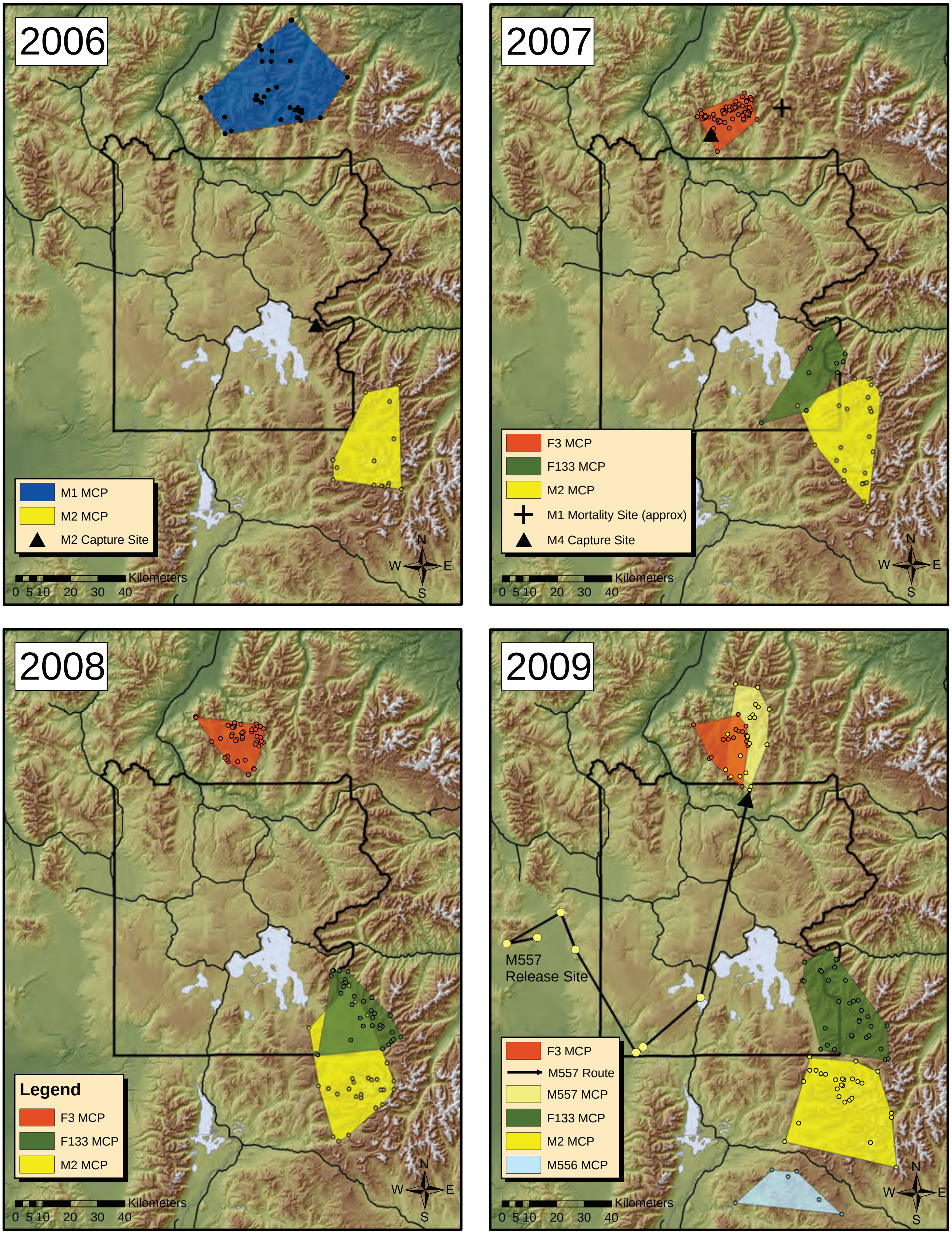


Figure 4. Annual 100% minimum convex polygon home ranges for wolverines, Absaroka-Beartooth study area, 2006–2009. Wolverines F133, M557, and M556 were originally captured and radio-marked by the Wildlife Conservation Society's Greater Yellowstone Wolverine Program.

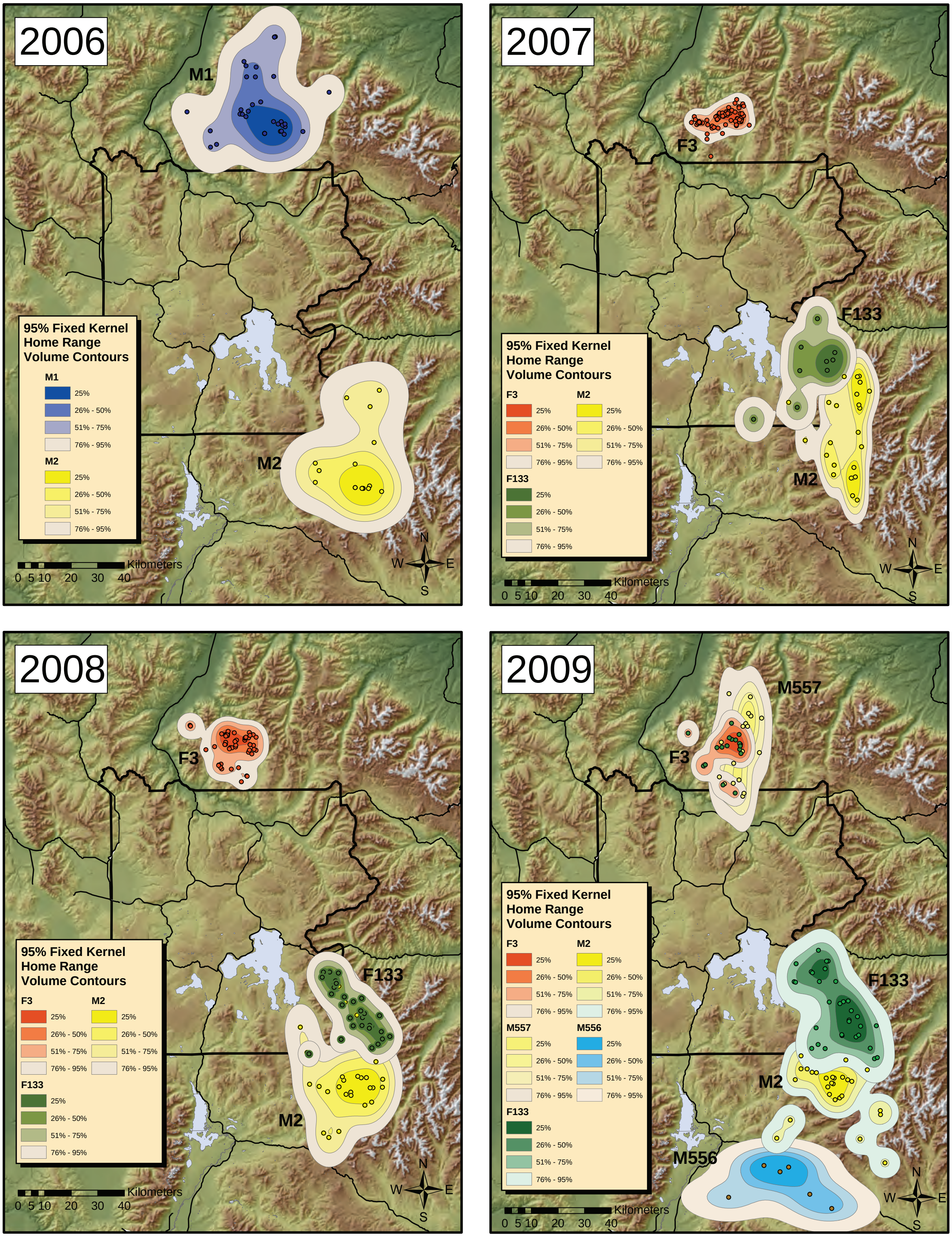


Figure 5. Annual 95% fixed kernel home ranges for wolverines, Absaroka-Beartooth Project study area, 2006–2009. Wolverines F133, M557, and M556 were originally captured and radio-marked by the Wildlife Conservation Society's Greater Yellowstone Wolverine Program.

Table 4. Sizes of minimum (100%) convex polygon and fixed kernel home ranges for wolverines, Absaroka-Beartooth project, 2006–2009

Wolverine	Year	# locations[a]	Minimum convex polygon (km^2)	Fixed kernel (km^2)		
				95%	75%	50%
F3	2007	81 GPS; 1 VHF	261	348	172	87
	2008	43 GPS; 16 VHF	297	626	303	132
	2009	17 VHF	316	578	259	109
F133[b]	2007	9 VHF	436	1,185	615	297
	2008	32 VHF	593	950	466	243
	2009	32 VHF	782	1,673	925	496
M1	2006	24 GPS; 13 VHF	1,268	2,501	1,176	546
M2	2006	16 VHF	700	2,368	1,189	546
	2007	24 VHF	816	1,355	801	351
	2008	27 VHF	1,066	2,121	1,064	486
	2009	27 VHF	1,153	1,397	599	251
M556[c]	2009	6 VHF	328	1,878	985	509
M557[d]	2009	19 VHF	446	1,148	599	311

[a] All GPS and VHF locations were sampled at 24-hour intervals, using a random start time in the first 24-hour period. VHF locations that were concurrent with GPS locations in same 24-hour period were excluded.

[b] Wolverine captured on Wildlife Conservation Society study area, Gallatin Mountain Range, Montana.

[c] Wolverine captured at Lava Butte (Togwotee Pass), western Wyoming, by the Wildlife Conservation Society. Currently being actively monitored by the Wildlife Conservation Society in Colorado.

[d] Wolverine captured at Menan Buttes (Rexburg), southeast Idaho, by the Wildlife Conservation Society. Cooperative monitoring north of the Yellowstone National Park boundary.

Table 5. Wolverine survival rates[a] and mortality on the Absaroka-Beartooth study area, 2006–2009

Wolverine class	Daily survival rate (s_i)	Annual survival rate[b]	Survival days	Number and type of mortalities	Wolverines
Subadult females	1.0	1.0	461	0	F3, F133
Adult females	1.0	1.0	1,307	0	F3, F133
Juvenile males	1.0	1.0	44	0	M556
Subadult males	1.0	1.0	601	0	M2, M556[c]
Adult males	0.9993[d]	0.785[e]	1,507	1 (trap)	M1, M2, M4, M557[f]
All classes	0.9997	0.896	3,920	1	all

Note: Independent Juveniles: ≤ 11 months of age; subadults: 12–23 months; adults 24+.

[a] Calculated using VHF-based monitoring and program Micromort (Heisey and Fuller 1985).

[b] s_i^{365} (Heisey and Fuller 1985).

[c] Captured by Wildlife Conservation Society near Togwotee Pass and jointly monitored.

[d] CI=(.998,1.0); Variance=4.39E-07

[e] CI=(0.49,1.0); Variance=3.61E-02

[f] M557 captured by the Wildlife Conservation Society near Rexburg, Idaho; dispersed into in the Absaroka-Beartooth study area.

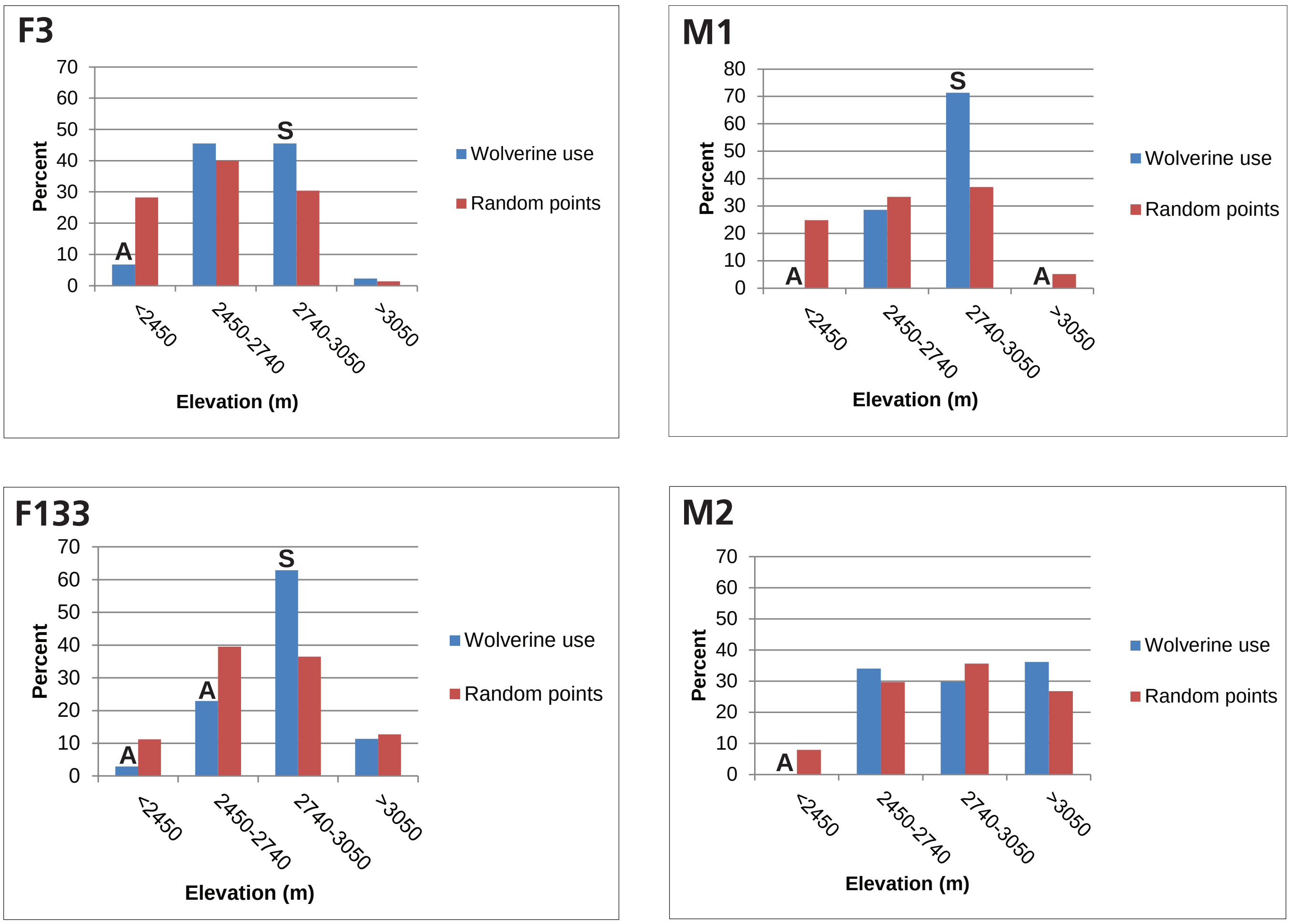


Figure 6. Elevations of summer (June 1 to November 30) wolverine radio locations and 5,000 randomly chosen points within individual home ranges on the Absaroka-Beartooth study area, 2006–2009. Individual (Bonferroni) intervals for the differences between the proportions of use and availability were individually correct with 95% confidence. The probability that all intervals were simultaneously correct was 90%. S: positive selection for the category. A: avoidance. No letter: use was not significantly different from availability. Elevation classes: < 2,450 meters (< 8,000 ft), 2,450–2,740 meters (8,000 ft band); 2,740–3,050 meters (9,000 ft band); > 2,450 meters (> 10,000 ft). F133 originally captured and radio-instrumented by the Wildlife Conservation Society's Greater Yellowstone Wolverine Program.

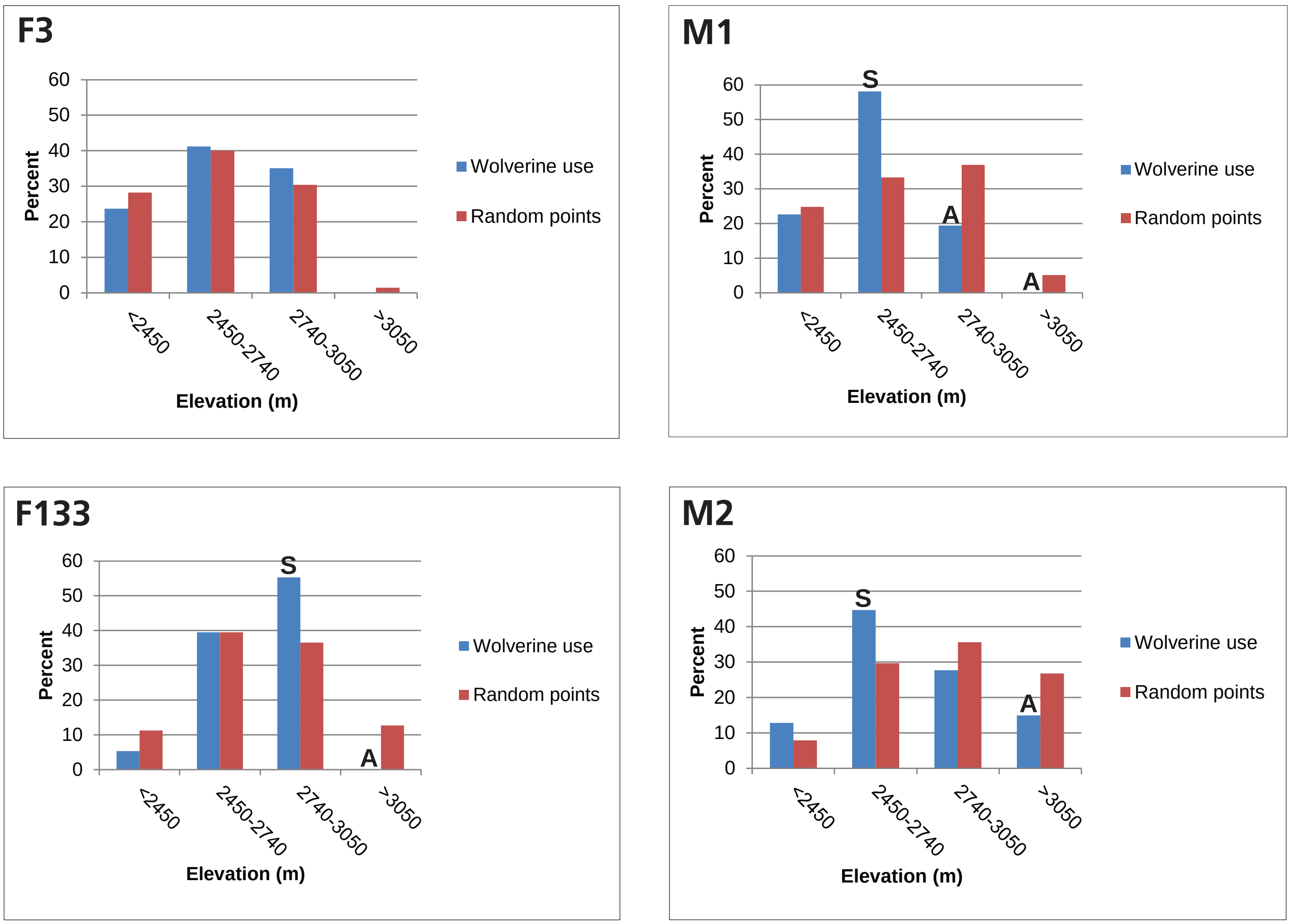


Figure 7. Elevations of winter (December 1 to May 31) wolverine radio locations and 5,000 randomly chosen points within individual home ranges on the Absaroka-Beartooth study area, 2006–2009. Individual (Bonferroni) intervals for the differences between the proportions of use and availability were individually correct with 95% confidence. The probability that all intervals were simultaneously correct was 90%. S: positive selection for the category. A: avoidance. No letter: use was not significantly different from availability. Elevation classes: < 2,450 meters (< 8,000 ft), 2,450–2,740 meters (8,000 ft band); 2,740–3,050 meters (9,000 ft band); > 2,450 meters (> 10,000 ft). F133 was originally captured and radio-instrumented by the Wildlife Conservation Society's Greater Yellowstone Wolverine Program.

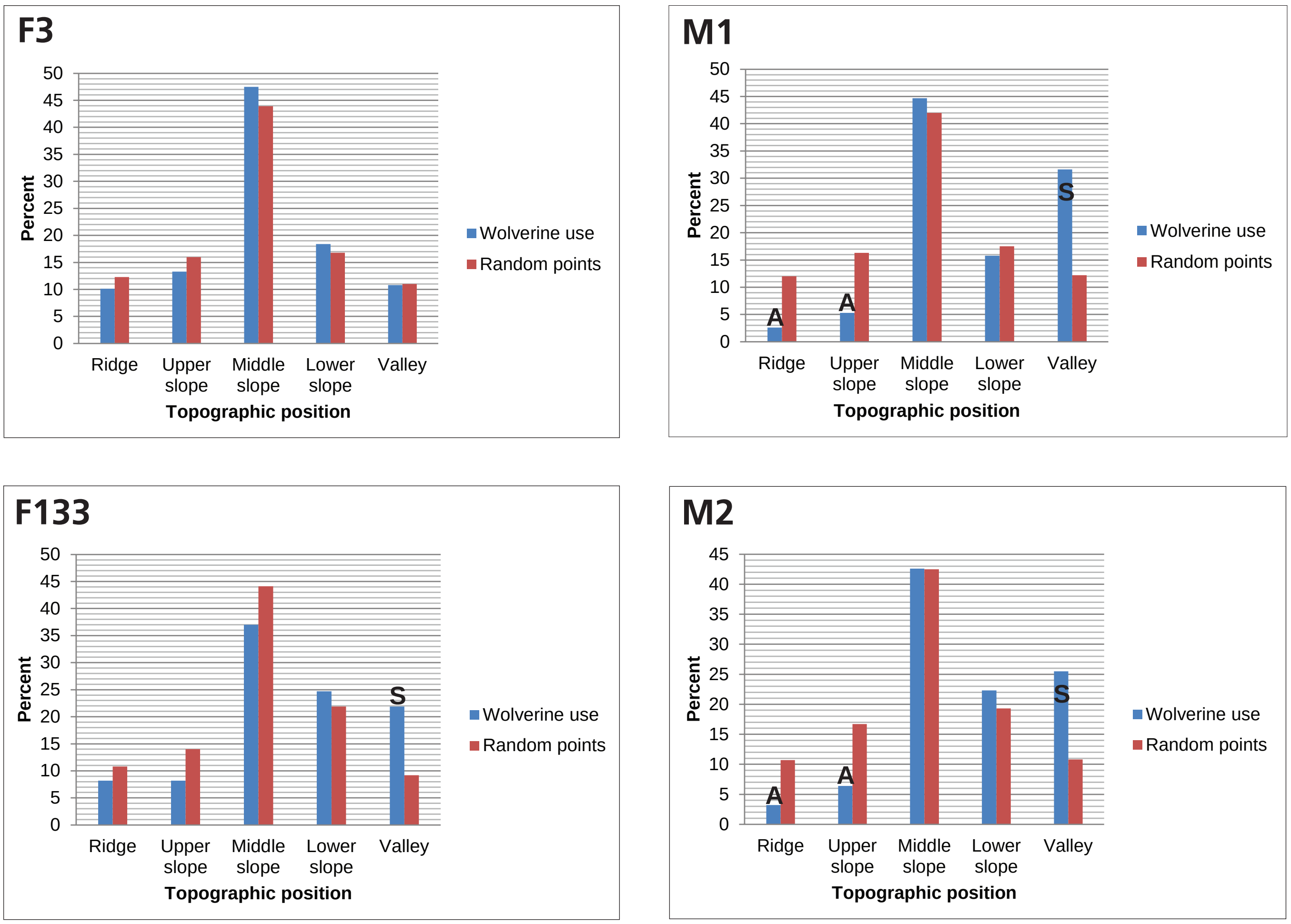


Figure 8. Topographic positions of wolverine radio locations and 5,000 randomly chosen points within individual home ranges on the Absaroka-Beartooth study area, 2006–2009. Individual (Bonferroni) intervals for the differences between the proportions of use and availability were individually correct with 98% confidence. The probability that all intervals were simultaneously correct was 90%. S: positive selection for the category. A: avoidance. No letter: use was not significantly different from availability. F133 was originally captured and radio-instrumented by the Wildlife Conservation Society's Greater Yellowstone Wolverine Program.

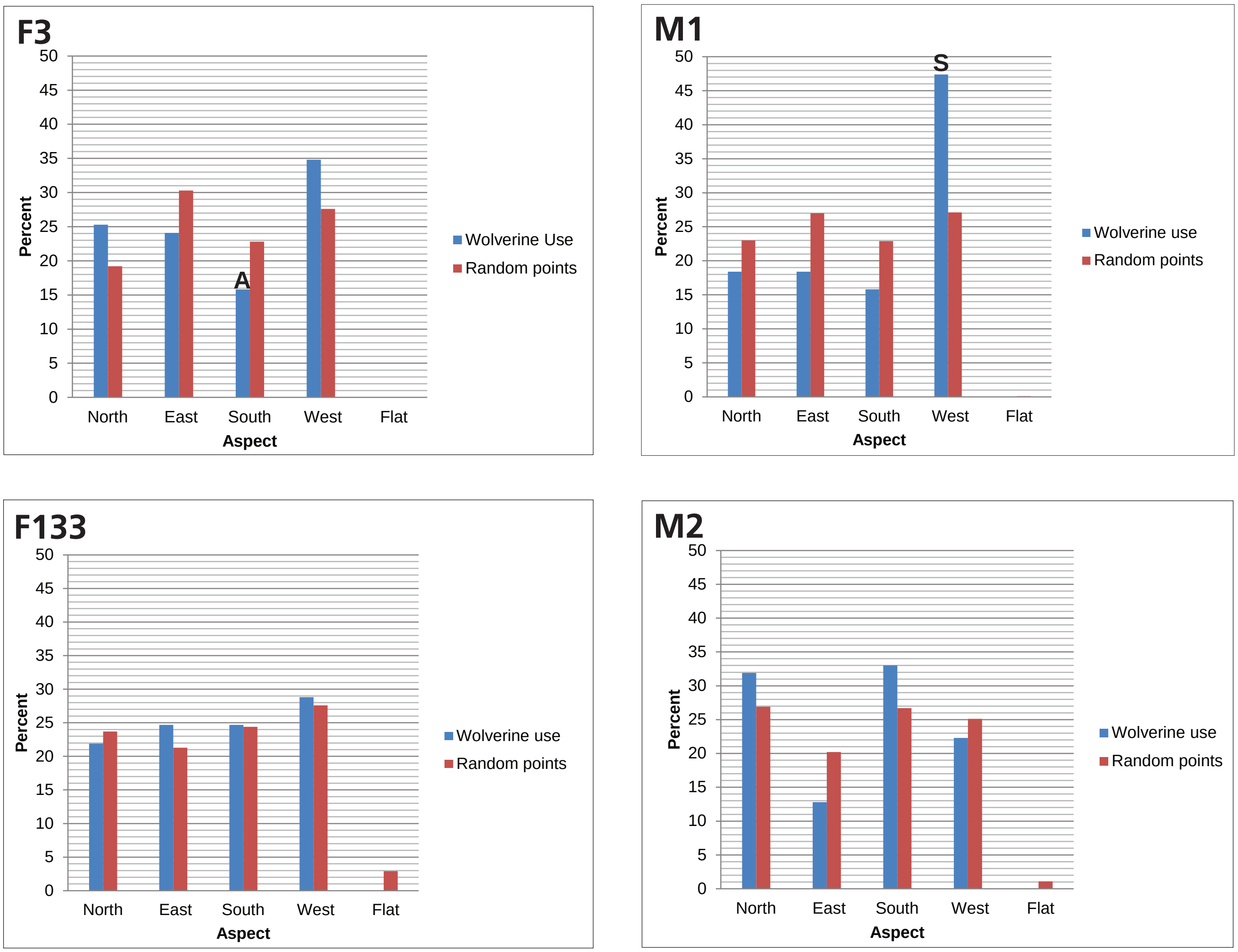


Figure 9. Aspect category of mountain slopes for wolverine radio locations and 5,000 randomly chosen points within individual home ranges on the Absaroka-Beartooth study area, 2006–2009. Individual (Bonferroni) intervals for the differences between the proportions of use and availability were individually correct with 98% confidence. The probability that all intervals were simultaneously correct was 90%. S: positive selection for the category. A: avoidance. No letter: use was not significantly different from availability. F133 was originally captured and radio-instrumented by the Wildlife Conservation Society's Greater Yellowstone Wolverine Program.

A photo of wolverine F3 taken by a remote camera revisiting a live trap (not captured at this visit), 2008. Remote cameras were used to record wolverine activity at the live traps.

Efficiency of wolverine habitat models, Yellowstone ecosystem

Wolverine habitat mapped for the Yellowstone ecosystem using the Copeland et al. (2010) niche model was distributed similarly to that of the Brock et al. (2007) habitat model, except that the former included much of the Yellowstone caldera (including Yellowstone Lake), the Pitchstone Plateau, and the Beartooth Plateau where late-season snowpack was persistent (fig. 10). The Brock et al. (2007) model encompassed more area at low (< 2,450 m; 8,000 ft) elevation. Both models excluded low-elevation terrain in the Gardiner basin, the northern winter range, and the upper Madison River watershed. Wolverine habitat modeled by Brock et al. (2007) accounted for 378 (97%) of wolverine radio locations and encompassed 77% of the minimum convex polygon constructed from the aggregate wolverine radio locations (table 6). The Copeland et al. (2010) niche model accounted for 368 (95%) of points and 84% of the minimum convex polygon.

Short-term wolverine movements

We obtained three GPS data sets from two wolverines (table 7, fig. 11). M1's 2006 GPS collar produced 181 accurate locations (58% fix rate) over 26 days from March 23 to April 18, 2006. M1 traveled a minimum of 443.3 kilometers (275.4 mi; sum of straight-line distances between relocations) during this period, averaging 685 meters (2,247 ft) per hour. His speed was highly variable, ranging from almost no movement (1 m between consecutive locations; 3.2 ft) to over 4.5 kilometers (2.8 mi) per hour. His movements indicated fidelity to the core of his home range, with occasional forays to its perimeter. During a two-hour foray on March 31, he moved 9.1 kilometers (5.6 mi).

F3's 2007 GPS collar produced 359 accurate locations (41% fix rate) over a period of 109 days (March 12–June 29, 2007). She traveled a minimum of 681 kilometers (423 mi) during this period, averaging 331 meters (1,086 ft) per hour. Her movement rate was also variable, ranging from almost no movement (1 m; 3.2 ft) to over 3 kilometers (1. mi) per hour.

F3's 2008 GPS collar produced 148 accurate locations (19% fix rate) over a period of 94 days (February 5–April 11, 2008). She moved a minimum of 363.9 kilometers (226.1 mi) during this period averaging 348 meters (1,141 ft) per hour. Her travel varied from almost no movement (1 m; 3.2 ft) to nearly 2 kilometers (1.2 mi) per hour.

Broad-scale wolverine movements, dispersal, immigration, and emigration

We captured adult M4 south of the Absaroka-Beartooth Wilderness boundary in March, 2007, and instrumented him with a VHF implant and a GPS collar. M4's DNA

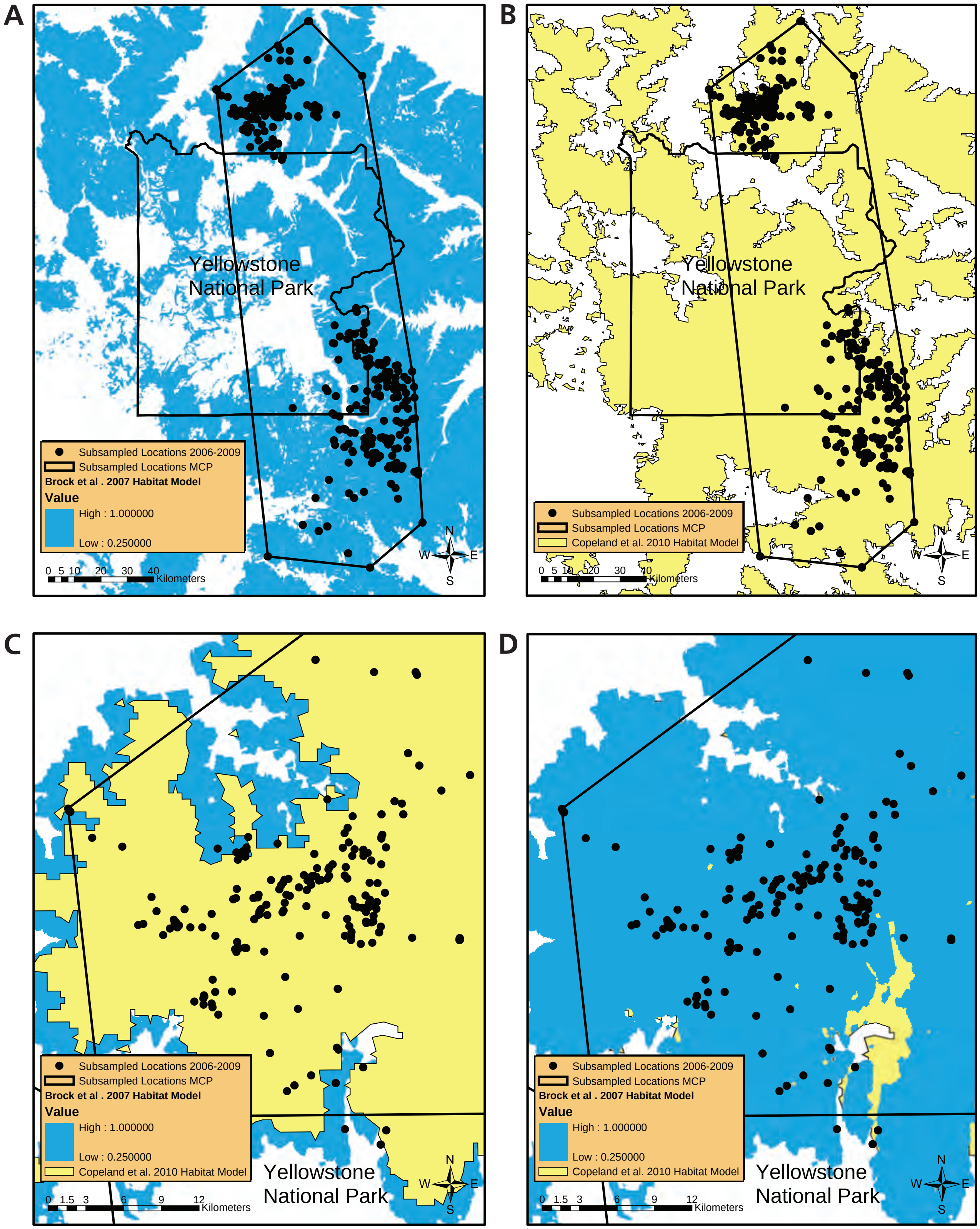


Figure 10. Coverage of wolverine habitat predicted by the (A) Brock et al. (2007) and (B) Copeland et al. (2010) models, as compared to a minimum convex polygon formed from 388 radio-locations for Absaroka-Beartooth wolverines, 2006–2009. (C): Copeland et al. (2010) model superimposed on the Brock et al. (2007) model for a portion of the Absaroka-Beartooth Wilderness. (D): Brock et al (2007) superimposed on the Copeland et al. (2010) model for the same area as in (C). For other model comparisons, see *Efficiency of wolverine habitat models, Yellowstone ecosystem* in *Results*.

Table 6. Concordance between 388 sub-sampled[a] radio locations of Absaroka-Beartooth wolverines and their habitat predicted by Brock et al. (2007) and Copeland et al. (2010)

Model	# locations in habitat coverage (%)	Coverage of predicted wolverine habitat (km²) [% of MCP[b]]
Brock et al. (2007)	378 (97%)	8,858 [77%]
Copeland et al. (2010)	368 (95%)	9,684 [84%]

[a] Sub-sampled (independent) wolverine radio locations, as described in *Methods*, *Telemetry-based monitoring* and in Table 4.

[b] Predicted habitat within a 100% minimum convex polygon (11,480 km²) formed from sub-sampled radio locations.

Table 7. Rates of movement for Absaroka-Beartooth wolverines instrumented with GPS radio collars, 2006–2009

Wolverine	Sampling interval (# days)	Fix schedule	Fix rate[a]	# fixes[a]	Total travel (km)[b]	Speed (meters/hour)		
						Mean	SD	Range
M1	3/23-4/18/2006 (26)	2 hour	57.6%	181	443.3	685	1,006	1–4,517
F3	3/12-6/29/2007 (109)	3 hour	41.3%	359	680.6	331	421	1–3,118
F3	2/5-4/11/2008 (94)	3 hour	19.5%	148	363.9	348	431	1–959

[a] Horizontal Dilution of Precision values of < 10, i.e., only accurate locations.

[b] Sum of the straight-line distances travelled for the range of dates; variable time intervals between locations.

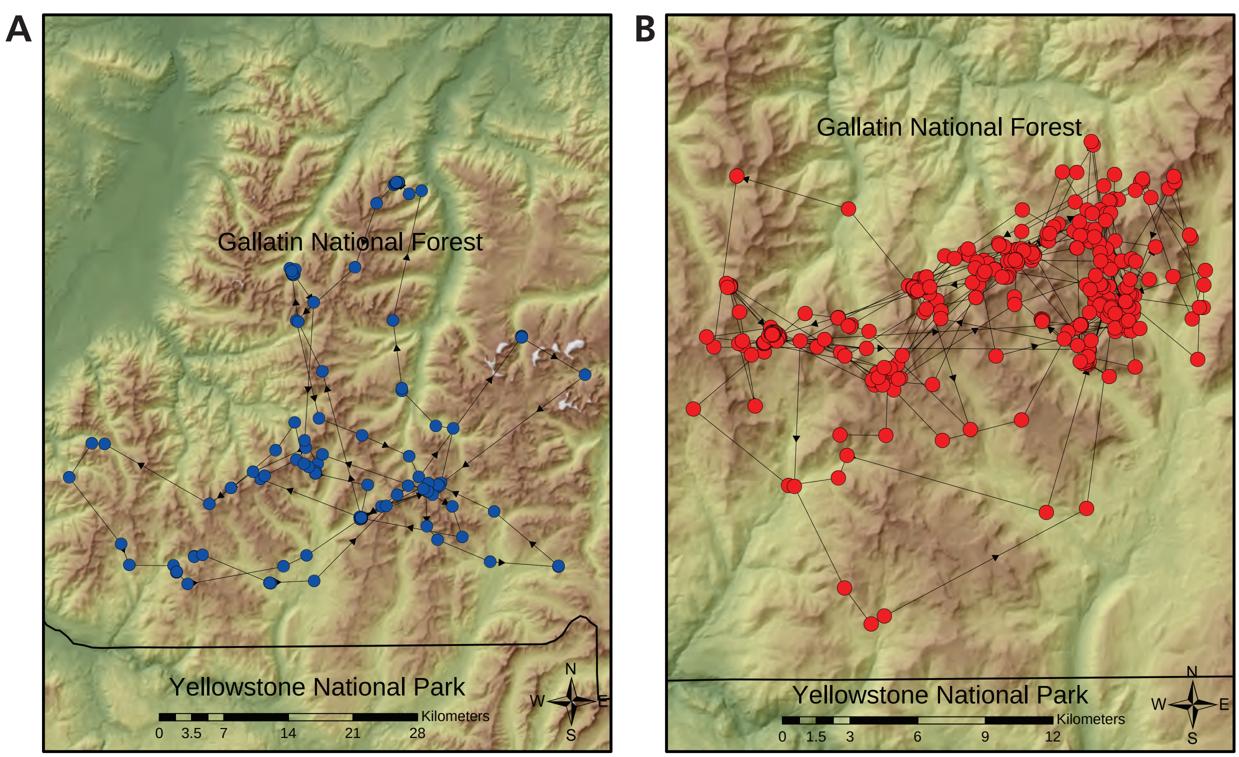


Figure 11. GPS collar locations and travel routes for (A) M1 over 26 days from March 23 to April 18, 2006, and (B) F3 over 109 days from March 12 to June 29, 2007, Absaroka-Beartooth study area.

matched that of a hair sample opportunistically obtained from a wolverine we observed eight months prior in the Thorofare region, approximately 145 kilometers (90 mi) away, suggesting that M4 moved extensively before his capture. We relocated M4 only once, nearby in the Absaroka-Beartooth Wilderness, despite numerous searches across much of the Yellowstone ecosystem.

F133 was captured and instrumented by the Wildlife Conservation Society with an intraperitoneal transmitter as a young kit in 2006 in the northern portion of the Gallatin Range. She subsequently dispersed into the Thorofare Region (fig. 12) where we monitored her cooperatively with the Society from April 2007, to December 2009.

M556 was captured by the Wildlife Conservation Society in December 2008, near Togwotee Pass. We monitored M556 with the Society for two-and-a-half months in upper Blackrock Creek, upper Spread Creek, and the Gros Ventre River watershed (southwest of Togwotee Pass); areas that supported high snowmobile activity and elk, deer, and moose winter ranges. During April 2009, the Wildlife Conservation Society documented M556's movement into the Wind River Range, south-east of Togwotee Pass, and on to high sagebrush steppe in central Wyoming. M556 eventually crossed Interstate 80, the Medicine Bow Mountains (south-central Wyoming), and eventually entered northern Colorado. This was the first confirmed wolverine in Colorado in 90 years. As of January 2011, he was being jointly monitored by the Wildlife Conservation Society and the Colorado Division of Wildlife.

M557 was accidently captured in January 2009 by a bobcat trapper on Menan Buttes on the Snake River Plain west of Rexburg, Idaho. Wildlife Conservation Society biologists instrumented him with a GPS collar and telemetry implant, and released him in the Centennial Mountain Range approximately 95 kilometers north of the capture site. After moving to and within Yellowstone National Park for a three-week period in February 2009, M557 established a home range that overlapped that of F3 in the Absaroka-Beartooth Wilderness (fig. 13).

Reproductive events

Reproductive-age females F3 and F133 did not reproduce during the five total birthing seasons we monitored them.

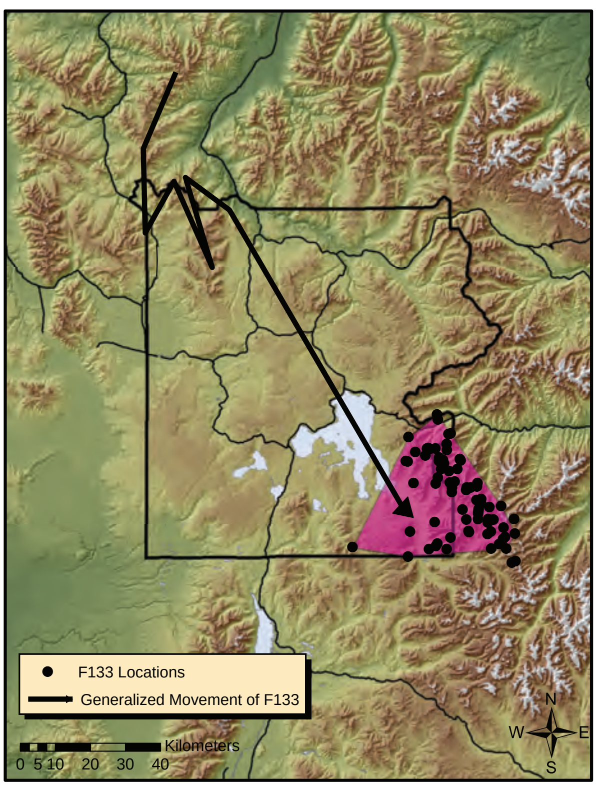


Figure 12. Travel of subadult F133 in 2007 documented collaboratively with the Wildlife Conservation Society from the Gallatin Range through Yellowstone National Park, and subsequent locations 2007–2009 in her resident area in the Thorofare region.

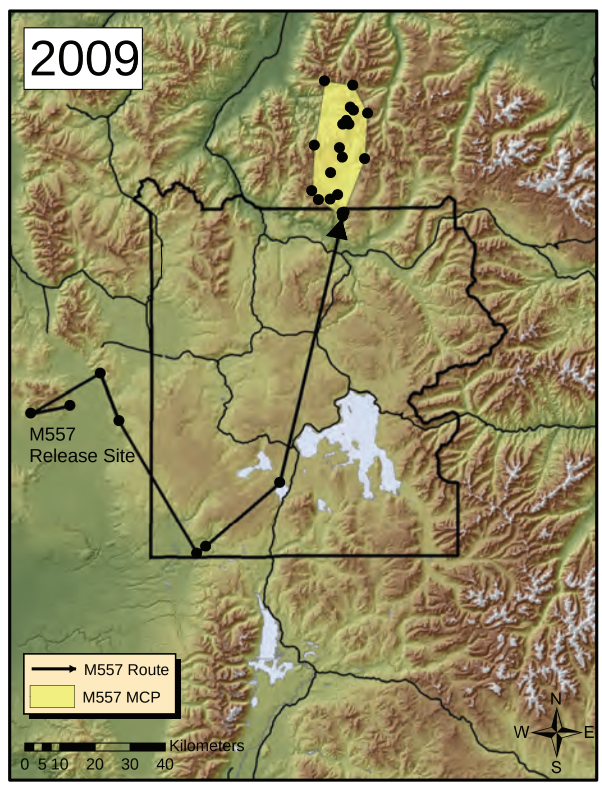


Figure 13. Travel of adult M557 in 2009 documented collaboratively with the Wildlife Conservation Society from the Centennial Range through Yellowstone National Park and into the Absaroka-Beartooth Wilderness where he established residency.

They were born in February or March, 2006, and reached their age of first possible birthing (their second birthday; Anderson and June 2008) in 2008. Relocation data collected for F3 indicated no site fidelity during the 2008, 2009, or 2010 natal denning period (February through May). We located F3 using telemetry (airplanes) six times from February 14 to May 31, 2008; six times from February 3 to May 8, 2009; and eight times from February 14 to April 2, 2010, including five flights in six days during mid-March, 2010. A physical examination of F3 during a March 2010, capture revealed that she was not lactating and apparently had not suckled offspring during any of the three monitoring years. F3's home range apparently did not overlap the home range of a male during the spring-summer breeding seasons preceding the birthing periods of 2008 and 2009. However, beginning spring 2009 her range was overlapped by M557, a new resident that apparently filled vacant male habitat. Telemetry data collected during the spring-summer breeding season of 2009 suggested that F3 and M557 periodically travelled together.

F133 was located 13 times from February 15 to May 15 (including five locations within a 48-hour period in mid-April), 2008, and 14 times from February 4 to May 1 (including five locations within a 72-hour period in late March), 2009. Her home range overlapped that of M2 during 2008 and 2009. She was not monitored after December 2008 when her transmitter likely failed.

Family relationships based on DNA analysis

F3, captured as a yearling in March 2007, was genotypically similar to M1. Prior to his death in early 2007, M1 was a reproductive-age resident that occupied a home range that presumably overlapped that of F3, his possible offspring. F3 was also genotypcially similar to M557, an apparent immigrant to our study area that was first captured in southeast Idaho, but her relationship to him was unknown. M2's relationship to other project wolverines was also unknown.

Food habits

Wolverines fed from carrion on five occasions: three times from mountain goats, once from an elk, and once from an unidentified ungulate (table 8, fig. 14). The elk was killed by wolves and scavenged by M2, but we were unable to determine the cause of death for the other ungulates. There was no identifiable scat or carrion at twelve cluster sites we searched.

Aerial survey development

We conducted detection trials on eight different wolverines, including four (three females and one male) located in the Madison Range (Montana), two (one female and one male) in the Gravelly Range (Montana), and two (female, Absaroka-Beartooth Wilderness; male, Thorofare region) in our study area. The work occurred over three nonconsecutive days and required about 15 hours of helicopter flight time. Survey work occurred 2–4 days after 3–5 inches of snowfall. We typically surveyed under optimal lighting and flying conditions, that is, clear or nearly clear skies and winds <10 miles (16 km) per hour.

In total, we made 25 attempts in 22 different grid cells to find wolverine tracks, spending 1–33 minutes per search (table 9). Approximately 120 tracks were inspected from the helicopter, 13 that were left by wolverines (fig. 15). Overall, detection success (cell type and search method categories combined) was 52% (13 detections for 25 searches). Detection success did not differ by cell type and search method (G^2 = 4.6; exact P = 0.35). We detected wolverine tracks in all (n = 3) the occupied cells that we searched intensively, but search success was lowest (37%; n = 8) for occupied cells searched with a straight-line transect. Overall, success was greater for occupied (54%, n = 11) than randomly chosen (50%, n = 14) cells, and greater for cells that were searched intensively (67% overall, n = 9) versus those searched following a straight survey line (44%; n = 16).

Search time per wolverine track detection (successful

Table 8. Food items documented for wolverines on the Absaroka-Beartooth study area, 2006–2009

Wolverine	Species	Documentation	Date	Location
M1	Mountain goat	Collar search site[a]	4/9/2006	East Fork Mill Creek, Montana
F3	Mountain goat	Carcass at radio location cluster	8/4/2007	Mt. Wallace, Montana
F133	Ungulate	Visual from aircraft[b]	4/6/2008	Falcon Creek, Wyoming
F3	Mountain goat	Scat at radio location cluster	8/16/2008	Emigrant Peak, Montana
M2	Elk	Visual from aircraft[c]	3/18/2009	Hawk's Rest, Wyoming

[a] Wolverine tracks on carcass.

[b] Wolverine tracks, hole in snow, ungulate long bone.

[c] M2 seen with ungulate leg bone from wolf-killed elk.

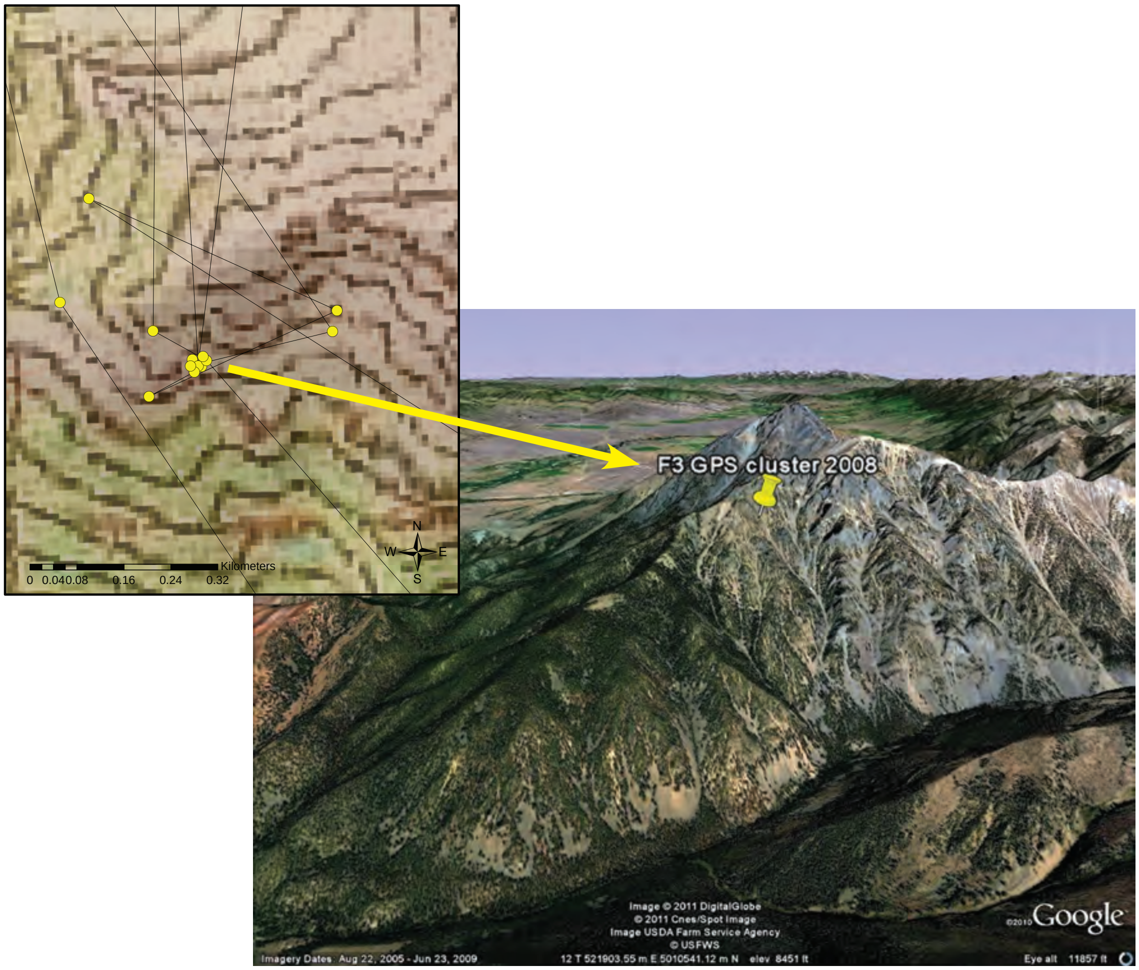
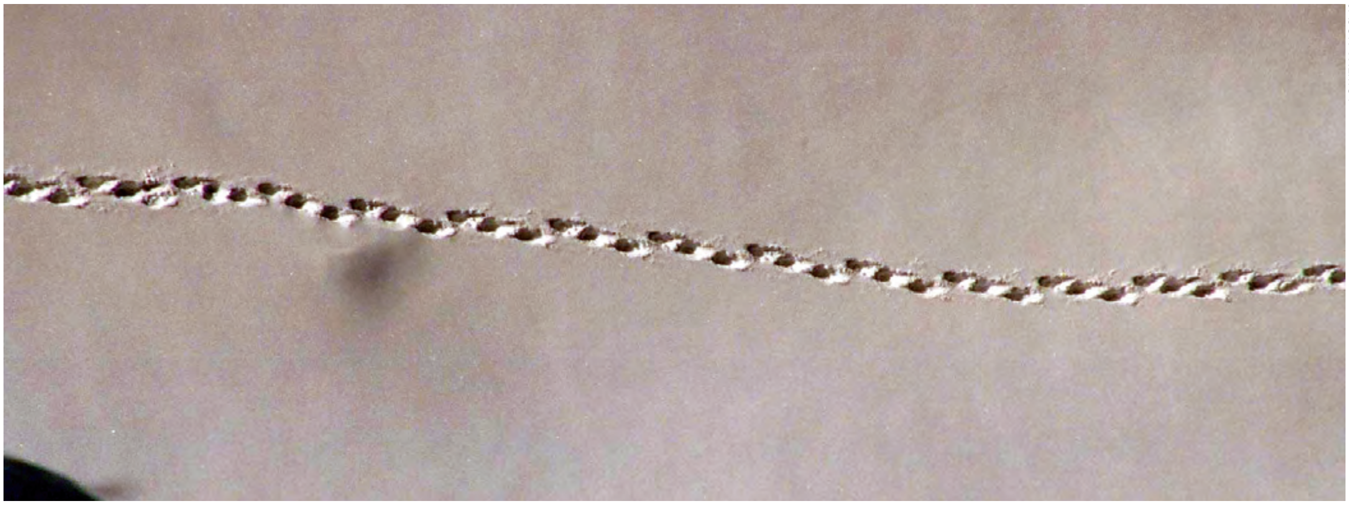


Figure 14. Sites used repeatedly by F3 in 2008, indicated by clusters of GPS-based radio locations, Absaroka-Beartooth study area. We visited clusters to document carrion and collect scats for food habits analysis.

Table 9. Wolverine track detection success and search times for 10 km x 10 km survey (grid) cells on the Wildlife Conservation Society study area (2008) in the Gravelly and Madison Mountain Ranges, Montana, and the Absaroka-Beartooth study area (2009)

Cell type and search method	# of detections (minutes each)	# unsuccessful searches (minutes each)	Detection success (%)	Minutes per detection
Occupied, Straight	3 (12, 2, 1)	5 (14, 19, 21, 22, 9)	37	33.3
Occupied, Intensive	3 (10, 30, 7)	0	100	15.7
Random, Straight	4 (18, 4, 2, 7)	4 (16, 13, 17, 20)	50	24.8
Random, Intensive	3 (17, 33, 1)	3 (30, 30, 30)	50	47.0
Total	13	12	52	29.8



JASON WILMOT

Figure 15. The distinctive gate of a wolverine evident from its tracks seen from the air during helicopter-based surveys conducted in 2009 in Yellowstone National Park.

and unsuccessful searches combined) averaged 30 minutes. Time per detection was least for intensive searches of occupied cells (16 minutes per detection), and most for intensive searches of randomly chosen (47 minutes) cells. Overall, search time per detection differed appreciably for occupied (24 minutes) and randomly chosen (34 minutes) cells, but not for intensive (31 minutes) and straight-line (28 minutes) searches. The cumulative percentage of detections plotted against the time required to detect a wolverine track (unsuccessful search times omitted) suggested that continuing to search cells longer than 20 minutes would yield few (15% of total) additional detections (fig. 16).

Applied aerial survey methods, Yellowstone National Park and vicinity

During winters 2008 and 2009, we completed three survey replicates that required an average of 13.2 hours of flight each, excluding ferry time (table 10, fig. 17). Survey time per cell for all three replicates averaged 12 minutes, including the time to inspect tracks.

We detected thirteen sets of wolverine tracks, nearly all in areas that supported radio-marked individuals (fig. 18). One track detected outside the northwest corner of the park in the Madison Range may have been a resident that was radio-marked by the Wildlife Conservation Society. We identified three tracks outside and east of the home range of F3. These could have been left by an unmarked individual or by F3 during a travelling foray. This individual was in route to F3's home range. Similarly, we found one track 8 kilometers (5 mi) north of Sylvan Pass that was left by an unmarked individual, or by F133 on a travelling foray north of her home range. We found no tracks in the park interior, including the Washburn and Snake River Ranges, the portion of the Gallatin Range inside the park, the Red Mountains, the Central and Madison Plateaus, and the Bechler Region.

In blind tests, we detected wolverine tracks each day (six trials on three individuals) we attempted to locate radio-marked wolverines using our applied survey methodology. We also detected tracks of river otter (*Lutra canadensis*), cougars, gray wolves, grizzly bears, snowshoe hares, American marten, and a possible Canada lynx (*Lynx canadensis*).

Surveys for winter food sources

We completed helicopter-based surveys for ungulates and ungulate carrion on May 13, 2008, and over six days from January through April 2009. Elevations of survey areas ranged from approximately 2,450 to 3,500 meters (8,000 to 11,490 ft). The 2008 survey occurred southerly from Cooke City, Montana, following the crest of the Absaroka Mountain

JASON WILMOT

Foraging site of F133 as seen from a helicopter in the Thorofare region, Yellowstone National Park, in 2008.

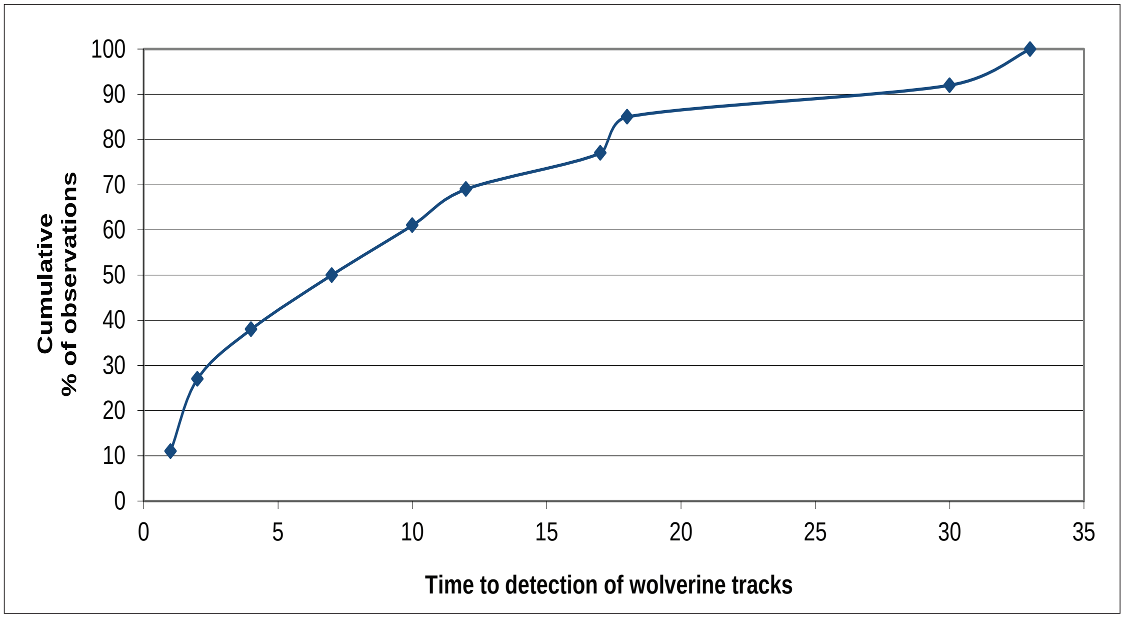


Figure 16. Accumulation (%) of wolverine track detections as a function of the time required to detect them in 10 x 10 km survey (grid) cells on the Wildlife Conservation study area (2008) in the Madison and Gravelly Mountain Ranges, Montana, and the Absaroka-Beartooth study area (2009).

Range along the east boundary of Yellowstone National Park to the head of the Yellowstone River, and easterly along the divides of several major watersheds (fig. 19). Two observers counted 157 bighorn sheep in 37 groups. No ungulate carcasses were observed. The area between Sylvan and Togwotee Passes (Wyoming Game and Fish bighorn sheep hunting units #3 and #4) accounted for 129 (81%) of bighorn sheep, and one visual observation of a radio-marked wolverine (M2). Twenty-eight bighorn sheep (19%) were counted north of Sylvan Pass (units #1 and #2). No other ungulates (e.g., mountain goats and moose) were seen in wolverine habitats. Scattered groups of elk were encountered at low (about 2,450 m) elevations.

Compared to 2008, the 2009 surveys were more representative of the high-elevation areas consistently used by wintering ungulates because surveys occurred over the course of the entire winter, and before spring snows accumulated on wind-swept plateaus and forced animals to use sites at low elevations. The 2009 survey included portions of the Soda Butte Creek watershed in Yellowstone National Park and the South Fork Shoshone River, areas not visited in 2008. However, surveys did not include the portion of the Absaroka Divide between Sylvan Pass and upper Sunlight Creek. For the entire survey (Togwotee Pass to Beartooth Plateau), two observers counted 2,165 ungulates, including bighorn sheep, mountain goats, elk, and mule deer. Three coyotes and one family of three cougars were seen, as well as one wolverine track. Bighorn sheep (the most abundant ungulate) numbered 1,396 individuals, counted in 185 groups. The area south of Sylvan Pass accounted for 930 (67%) bighorn sheep, and the area north accounted for 466 (33%) individuals. Bighorn sheep in both regions appeared to increase their activity at lower elevations as winter progressed. Mountain goats were observed in Yellowstone National Park and at the south margin of the Beartooth Plateau.

Table 10. Characteristics of helicopter-based wolverine track surveys, Yellowstone National Park and vicinity, 2008–2009

Replication number	Survey dates	Total survey time[a] (min)	# survey cells[1]	Survey area (km²)[b]
1	4/3/2008 4/4/2008 4/6/2008	764	59	11,800
2	2/4/2009 2/5/2009 3/1/2009	843	70	14,000
3	3/13/2009 3/14/2009 4/6/2009	771	75	15,000

[1] 10 x 10 km^2 per survey cell.

[a] Excludes ferry time.

[b] Estimated as the number of survey cells x 2 x 100 km^2/cell.

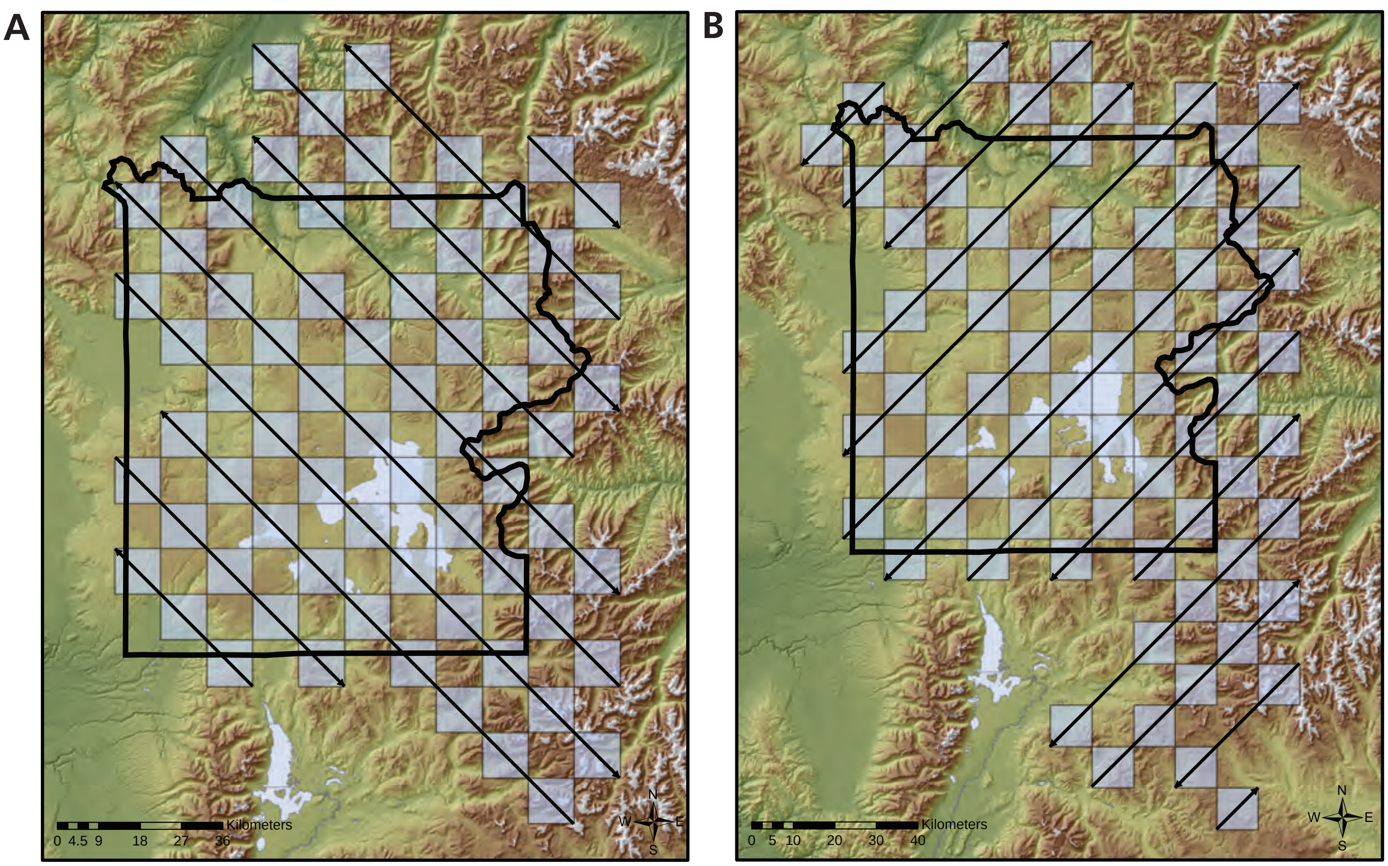


Figure 17. Survey cells (10 km x 10 km) and transect line for two of three helicopter-based surveys for wolverine tracks completed during February–March (A) and March–April (B) 2009, Yellowstone National Park and vicinity. The first survey (April 2008; not shown) was similar to (B), but was not as spatially extensive. Surveys were extended in 2009 to include a large area southeast of the park boundary to enable tests of the observer's ability to detect radio-marked wolverines within their home ranges.

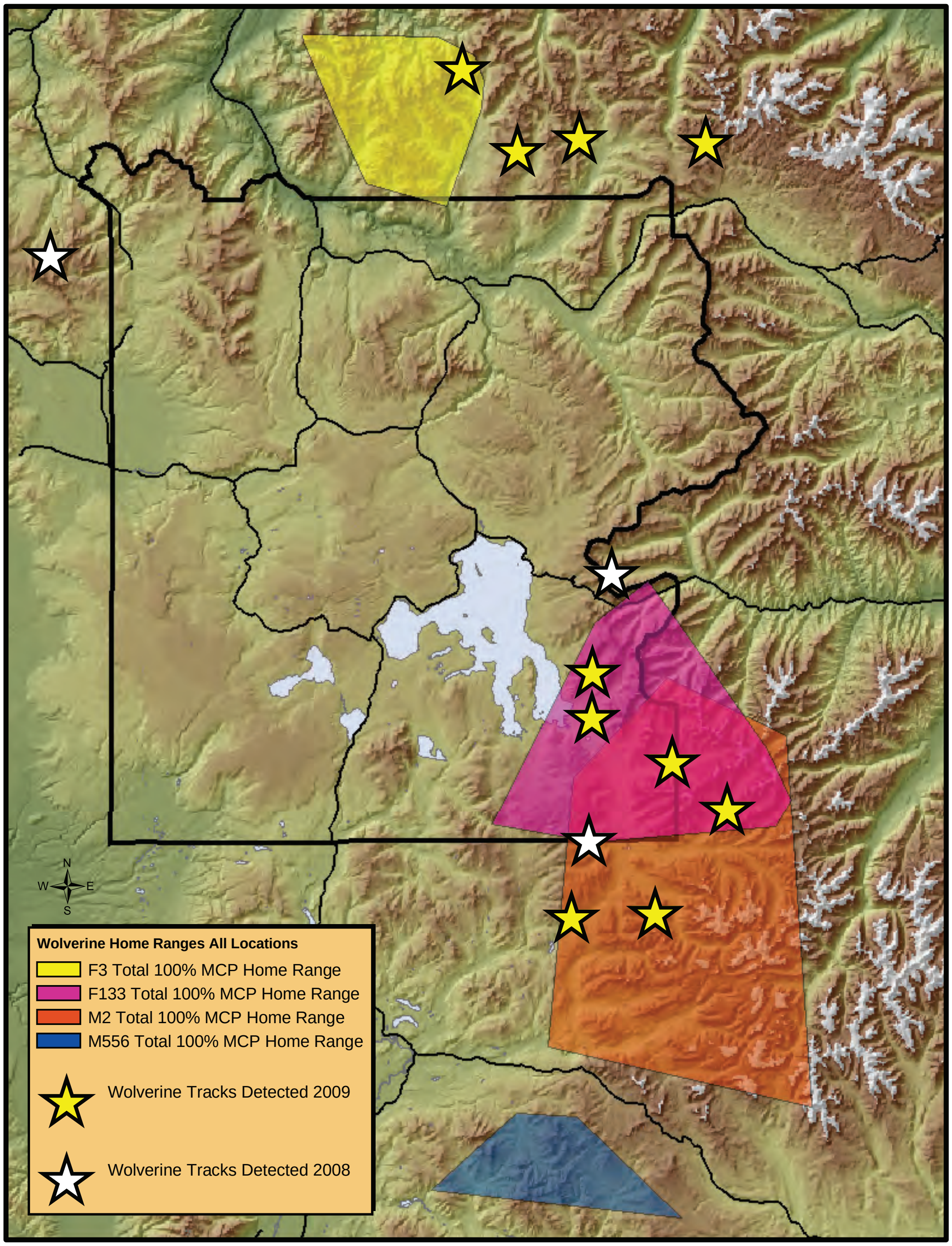


Figure 18. Distribution of wolverine tracks detected in Yellowstone National Park and vicinity, 2008–2009, during helicopter-based surveys. F133 and M556 originally captured and radio-instrumented by the Wildlife Conservation Society's Greater Yellowstone Wolverine Program.

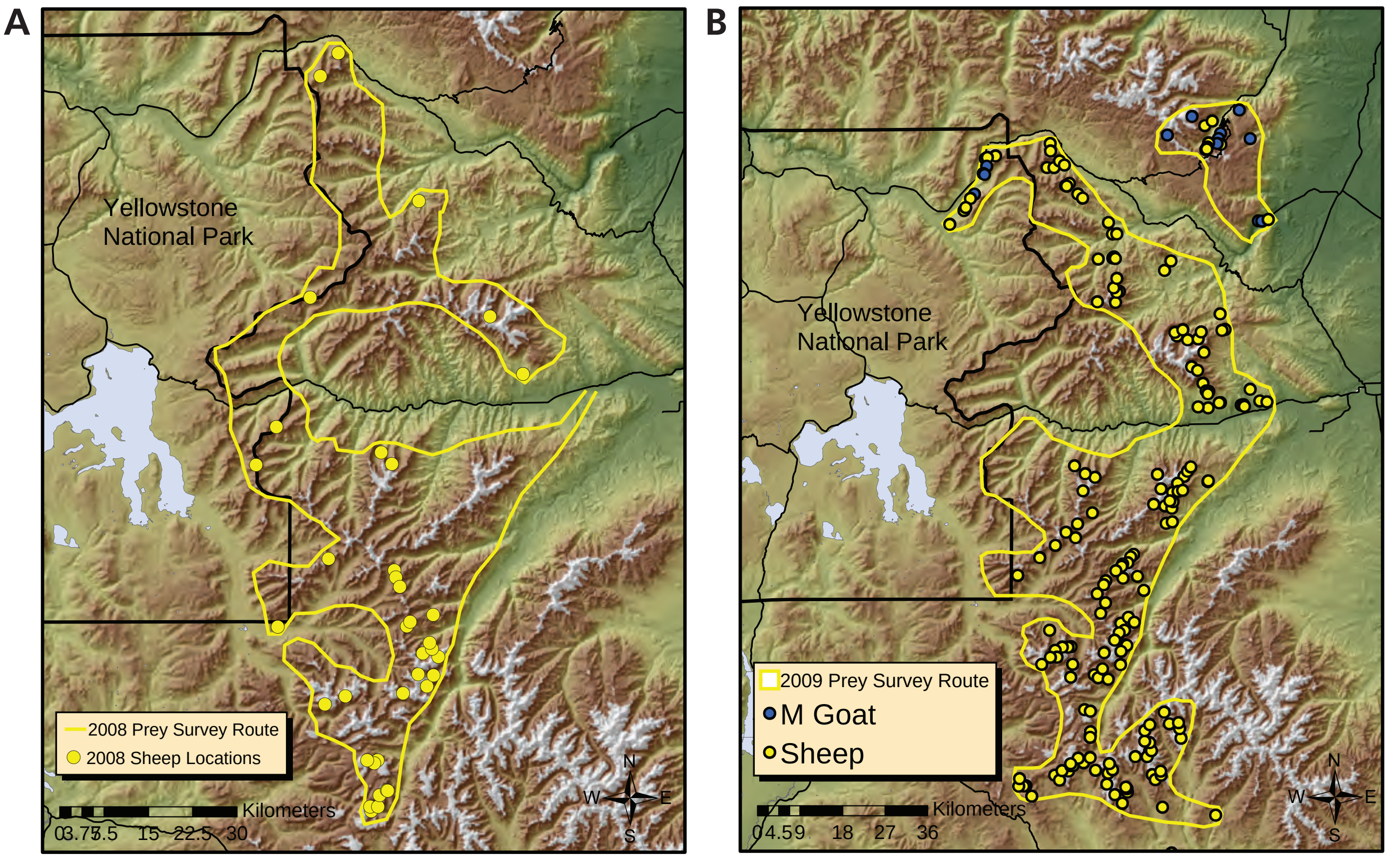


Figure 19. Survey areas and occurrence of ungulates documented as potential wolverine prey or carrion on the Absaroka-Beartooth study area, (A) 2008 and (B) 2009.

Discussion

Wolverine distribution in Yellowstone National Park and vicinity

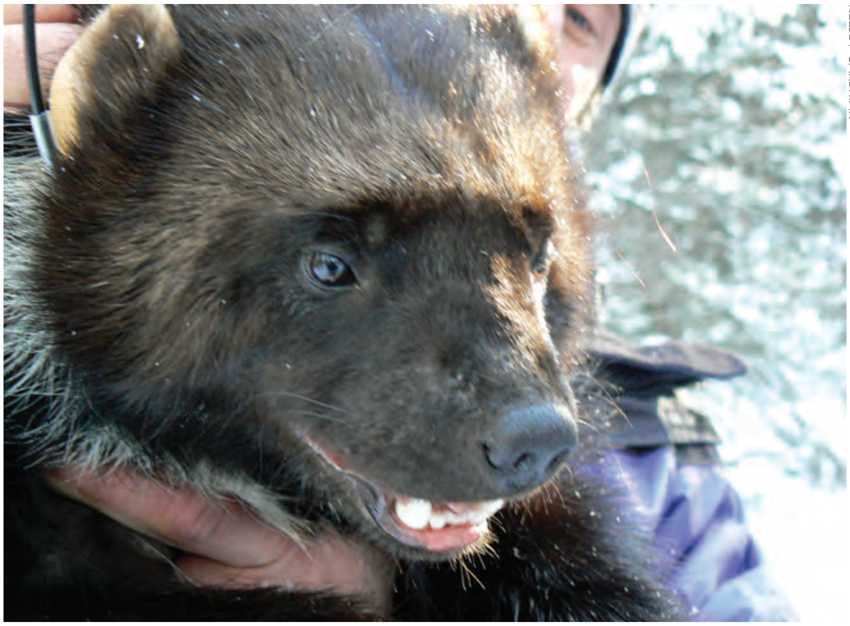
Resident wolverines in our study area were largely limited to high-elevation (> 2,450 m; 8,000 ft) mountainous areas of the Hudsonian (boreal) life zone, a finding similar to other studies in the conterminous United States (Hornocker and Hash 1981; Copeland et al. 2007; Brock et al. 2007). In addition to basic requirements such as food (e.g., carrion in winter), these environments provided persistent snow cover, a physical habitat component needed to maintain the warmth and security of offspring in reproductive dens during late winter and spring, and for compensating warm temperatures during summer months (Magoun and Copeland 1998; Aubry et al. 2007; Copeland et al. 2010). Our wolverines were not associated with major ungulate winter ranges located in and surrounding Yellowstone, such the northern range, Pelican Valley, and the upper Clark's Fork River, a finding similar to those of Copeland et al. (2007) and Brock et al. (2007). Although most areas within wolverine home ranges were in wilderness or backcountry that supported little human activity except during fall hunting seasons, wolverines may select these jurisdictions because of their physical characteristics, rather than avoidance of anthropogenic activity (Copeland et al. 2007; Brock et al. 2007; but see Hornocker and Hash 1981; Rowland et al. 2003; May et al. 2006; Krebs et al. 2007).

Despite sporadic sightings (Consolo-Murphy and Meagher 1995; Robinson and Gehman 1998; Murphy et al. 2006; Yellowstone National Park files), and recent models that suggest an abundance of suitable habitat (Brock et al. 2007; Copeland et al. 2010), wolverines are currently rare and limited in distribution throughout the park and in the national forests along its north-east, east, and southern boundaries (figs. 4, 5, and 18). This conclusion was supported by our meager capture results. Intensive trapping (5,248 nights) over four winters produced captures of only four individual wolverines along eight well-distributed trap lines (fig. 3), and track surveys conducted on foot and from aircraft throughout the entire region also suggested a limited distribution.

We documented resident wolverines only in the Absaroka-Beartooth Wilderness (north of the Yellowstone National Park boundary) and the Thorofare region (Washakie and Teton Wildernesses, and south-east portion of the park). We failed to document residents in the North Absaroka Wilderness and vicinity, an area of apparent prime habitat that extends south of Cooke City to Sylvan Pass and that includes the Upper Lamar River and Sunlight Basin. We did not detect wolverines in the Red Mountains or the Washburn, Snake River, and southern portion of the Gallatin Ranges. However, the Wildlife Conservation Society


JASON WILMOT

This mountain goat, documented during the project, was scavenged by a wolverine. Carrion was documented opportunistically from aircraft.



Our data provided no indication that particular aspects of mountain slopes were used disproportionately more often by wolverines. F3, shown here, avoided south aspects in the northern portion of the study area, consistent with the hypothesis that wolverines avoid warm environments at southern latitudes to avoid hyperthermia.

documented resident wolverines with home ranges that extended into the park along the northwest and southwest boundaries (Inman et al. 2007a), individuals associated with well-established populations in the northern portion of the Gallatin Range, the Madison Range, and the Teton Range. Although many areas of our study area did not support residents, wolverines commonly used it during dispersal and for periodic forays (Inman et al. 2004, 2007a; figs. 12 and 13), behaviors that may explain the occasional historical sightings and anecdotal information on wolverine occurrence in areas such the southern Gallatin Range.

We hypothesized that several historical and contemporary factors accounted for the dearth of wolverines in our study area. The species experienced significant population declines throughout its range in the conterminous United States during late 1800s and early 1900s, primarily due to trapping, shooting, and poisoning of predators, activities that were widespread in the region, including in Yellowstone, through the 1930s (references in Schullery and Whittlesey 1999; Aubry et al. 2007). Following improved regulation of furbearer trapping and predator control, wolverine populations partially recovered in northwest Montana by 1955, apparently due to immigration from Canada and adjacent Glacier National Park (United States; Newby and Wright 1955). By 1963, wolverine breeding range extended into west-central and southwest Montana, including the Yellowstone region (Newby and McDougal 1963). Thus, wolverines in the ecosystem, particularly our study area, may still be recovering in numbers and improving in distribution. A protracted recovery period, that is, from the 1930s to the present, is expected for wolverine populations in our area owing to the fragmented distribution of their habitat in the northern US Rockies (Inman et al. 2007a; Brock et al. 2007), some trapping losses (Montana), and the low reproductive rates characteristic of the species in both Montana and the ecosystem (Inman et al. 2007c; Anderson and Aune 2008; our data). Ingress from source populations, likely in the western, southern, and northern portions of the ecosystem (e.g., F133 an immigrant from the northern portion of the Gallatin Range) is apparently sustaining wolverine numbers in our area. We did not detect offspring of the two resident females we monitored over four total reproductive seasons.

Wolverine numbers and distribution on our study area were apparently not strongly limited by the availability of carrion during winter. By travelling long distances and relying on its extraordinary sense of smell, wolverines are capable of detecting carrion that is widely distributed in their large home ranges (Hornocker and Hash 1981). Our two aerial surveys for ungulates conducted during winter, and our observations made incidental to wolverine surveys, suggested that adequate numbers of ungulates, primarily bighorn sheep, were available as a supply of carrion in most parts of our study area that also lacked resident wolverines. For example, we counted 466 ungulates in 64 groups during a 2009 ungulate survey of high elevation areas in the North Absaroka Wilderness, an ample food source for one or two individuals, and an area where we made no captures and only one wolverine detection. However, the near absence of moose, elk, and bison in the extensive lodgepole pine and spruce-fir forests in interior Yellowstone National Park led us to believe that winter food limitation may currently preclude wolverine residency in this area. Wolverines did not use interior winter ranges such as the Firehole River corridor, Hayden Valley, and Pelican Valley—areas that support wintering elk and bison.

Home ranges and spatial relationships

Overlap between our resident male and female wolverines was substantial, similar to other studies (Magoun 1985; Inman et al. 2007a; Copeland 1996). Although estimated using different methods across the species' range, home range sizes of two female and three male wolverines on our study area appeared larger than in other studies (Whitman et al. 1986; Banci and Harstead 1990; Landa et al. 1998; Magoun 1985). Female and male home ranges (100% minimum convex polygon) averaged 388 km^2 and 422 km^2 (241 mi^2 and 262 mi^2), respectively, in northwest Montana (Hornocker and Hash 1981), compared (same methods) to 477 km^2 and 809 km^2 (296 mi^2 and 502 mi^2) for females and males on our study area. Adult female and male home ranges (95% kernel) averaged 453 km^2 and 1,160 km^2 (281 mi^2 and 721 mi^2), respectively, in the western and southern portion of the ecosystem (Inman et al. 2007a), compared to our 893 km^2 and 1,815 km^2 (555 mi^2 and 1,128 mi^2) for females and males, respectively.

Wolverines have large area requirements (Hash 1987; Copeland and Whitman 2003), but the reasons why our wolverines used larger areas than elsewhere are unclear. Habitat, food availability, topography, the availability den sites may influence home range sizes and spacing (Gardner 1985; Hornocker and Hash 1981; Krott 1959). Because both females and males show little intra-sex overlap (Magoun 1985; Inman et al. 2007a, but see Hornocker and Hash 1981), our resident wolverines may also have used larger ranges because they were unconfined by same-sex individuals with immediately adjacent ranges.

Movements

Wolverine movement patterns are characterized by alternating bouts of travel punctuated by periods of localized activity at feeding sites, reproductive dens, or other locations of their interest (Copeland and Yates 2008). Our limited data were consistent with this characterization—periods of rest, or other stationary activities, were followed by bouts wherein wolverines travelled at great speeds for long distances (fig. 11). These two extremes in activity were indicated by high coefficients of variation (standard deviations divided by the respective means) for rates of travel (table 7).

Maximum speeds for adult M1 and F3 were 4.5 and 3.1 kilometers (2.8 and 1.9 mi) per hour. Similarly, Copeland and Yates (2008) estimated that wolverines in Glacier National Park travelled 4.0 kilometers (2.5 mi) per hour between periods of significantly reduced movements. M1 travelled an average of 17 kilometers (10 mi) daily, a value similar to males (15 km; 9 mi) in the western and southern portion of the ecosystem (Inman et al 2007b). In contrast, F3 moved an average of only 6.2 and 4.5 km (3.8 and 2.8 mi) per day (two different data sets), hinting that daily movements might vary by sex. The mean speed of M1 (685 m per hour; 2,247 ft per hour) was almost twice that of F3 (331 and 348 m per hour; 1,086 and 1,142 ft per hour).

The extended wolverine movements we documented in collaboration with the Wildlife Conservation Society were consistent with other studies in North America, that is, that wolverines are capable of dispersing long distances from their natal home ranges or travelling similarly as adults (Gardner et al. 1986; Copeland 1996; Inman et al. 2004, 2007a; Copeland and Yates 2008). These movements, such as that made by F133, are likely to occur through areas characterized by persistent snow cover (Schwartz et al. 2010), and help maintain the genetic and demographic integrity of wolverine populations in the US Rocky Mountains where wolverine habitat and populations are naturally fragmented (Brock et al. 2007).

Habitat use and selection by residents

During winter, our wolverines increased their use of low elevations, consistent with other studies in the Rocky Mountains (Hornocker and Hash 1981; Copeland et al. 2007). Our anecdotal observations suggested that these areas supported small numbers of elk, moose, and bison at the upper margins of ungulate winter range, ready sources of carrion. Three wolverines actively avoided the alpine zone during winter, habitats that supported few ungulates due to the accumulation of deep snow and harsh weather, save for the occasional use of wind-swept plateaus and mountain peaks by scattered bands of bighorn sheep and mountain goats. Use and selection of the two highest elevation bands during the summer may have been due to a preference for sites with low ambient temperature coupled with an increase in rodent availability (Hornocker and Hash 1981).

Our radio-marked wolverines selected valley bottoms and lower mountain slopes, and avoided use of ridges and upper mountain slopes. During aerial surveys, we observed most wolverine tracks along creeks and rivers in open valleys, and few on upper mountain slopes and ridges. Extensive use of the flat gradients that characterize many valley bottoms

KERRY MURPHY

KELSEY GABRIAN

Left: Jason Wilmot and project technician Ben Jimenez with collared wolverine M1 in 2006. *Right*: Jason Wilmot returns wolverine F3 to the log box live trap for release in 2008. Wolverine F3 was captured as a yearling in March 2007 and was genotypically similar to M1. Prior to his death in early 2007, M1 was a reproductive-age resident that occupied a home range that presumably overlapped that of F3, his possible offspring.

may provide the most energetically efficient way to access and cross ridges of major mountains during long treks (J. Copeland, unpublished data). Where valley bottoms also support mature and old-growth subalpine forests, valley bottoms may support less snow pack than other topographic types (Wright and Ernst 2004) and disproportionately large amount of moose and elk carrion (Hornocker and Hash 1981; Whitman et al. 1986; O'Gara and Harris 1988).

Our data provided no indication that particular aspects of mountain slopes were used disproportionately more often by wolverines. The male and females in the southern portion of our study area used aspects in proportion to availability. F3 avoided south aspects in the northern portion of the study area, consistent with the hypothesis that wolverines avoid warm environments in southern latitudes to avoid hyperthermia (Copeland et al. 2010). However, M1 selected west aspects in the same area, which also have direct exposure to the sun during much of the day. No wolverines in our study selected north or east aspects, those that are coolest. However, our limited samples included the winter months when wolverines would presumably not seek out cool environments to avoid overheating. Hornocker and Hash (1981) reported that wolverines in northwest Montana travelled less frequently during daylight hours, predominantly used easterly and westerly aspects, and sought high-elevation subalpine fir forests in the summer, apparently because they were cooler temperature. Banci and Harestad (1990) reported that wolverines used aspects in proportion to their availability, but their study occurred in the Yukon where mean summer temperatures are cooler than our study area and where thermoregulation may be less important.

Reproduction and survival

We are uncertain why the two reproductive-age females (F3, F133) we monitored failed to reproduce. Because females spend considerable time foraging long distances from natal dens (J. Copeland, unpublished data), our determinations were less reliable in two cases where we relied solely on clusters of telemetry locations to detect births. However, because we neither captured juvenile wolverines in the adult female territories nor observed their tracks, our estimates of birth rates for these adult females should be reliable.

Low reproductive rates are characteristic of wolverines, particularly in the conterminous United States where habitat is fragmented (Brock et al. 2007). Anderson and Aune (2008) found that wolverine reproductive rates in southwest Montana were the lowest reported for North American wolverines. In their study, 12% of females that were due for their second birthday, and 68% of older females, were pregnant, percentages that were far lower than for wolverines from northwest Montana. Their findings for southwest Montana were consistent with low reproductive rates documented by Inman et al. (2007c) in the western portion of the Yellowstone ecosystem, and our results. The absence of males apparently did not completely explain the low reproductive rate we observed because males resided near females in at least three of the five monitoring years.

The annual survival of our radio-marked wolverines (90%) was similar to that of wolverines in other studies, although we lacked an adequate sample size for a close comparison. Our population was subject to trapping in one portion of the ecosystem (Montana) and was un-trapped in the remainder (Wyoming and Idaho). One adult male was legally taken by a trapper in our study, the only documented mortality. Annual survival in un-trapped North American populations (all age-sex classes) typically exceeds 84%, but is < 75% where wolverines are harvested (Krebs et al. 2004; Inman et al. 2007a; Squires et al. 2007). Trapping appears to be a major, additive mortality factor for North American wolverines and creates mortality sinks (Krebs et al. 2004). Persson et al. (2008) documented 86–91% annual survival among adult wolverines in northern Sweden.

Helicopter-based track survey

Because our aerial surveys were conducted independently of live trapping and track searches, they provided an independent assessment of the relative number of wolverines and their distribution that improved the robustness of our conclusions. Our aerial surveys were very effective in detecting wolverine tracks—we had 100% success in detecting radio marked wolverines, and with only a single replicate. As expected, the detection rate at the home range scale was higher than for 100 km^2 (62 mi^2) survey cells (52%; Wildlife Conservation study area), probably because the wolverine home ranges encompassed several cells.

Becker and Gardner (1990) and Magoun et al. (2007) concluded that aerial surveys for wolverine tracks should cover large areas and be replicated. Broad coverage and replication were important features of our survey method that improved inferences to wolverine distribution and the technique's potential application to other, unsurveyed areas. Because wolverines naturally use diverse habitats in the course of their extensive travels (Aubry et al. 2007; Inman et al. 2004), we designed our surveys not to restrict search efforts to environments they selected, such as the 2,450–3,050 meters elevation band, or to where tracks were most visible from the air, such as areas that lacked dense conifers. Rather, our survey lines were distributed systematically and covered all mapped habitat identified by Copeland et al. (2010). Thus, our approach permitted inferences to wolverines throughout the entire survey area, not just particular habitats. However, the terrain we surveyed varied from relatively flat and covered with dense lodgepole pine in the unburned portion of the Yellowstone caldera to incised, open terrain at or near timberline in the Thorofare region and the Absaroka-Beartooth Wilderness. These differences likely contributed to disparity in track detection probabilities, that is, our chances of detecting wolverine tracks, if present, were probably lower in areas extensively covered with conifers than in tree-less landscapes


JASON WILMOT


JASON WILMOT

Left: Project technician Heather Ristow en route to retrieve a GPS collar in the Absaroka Mountain Range, Montana, 2006. *Right*: A GPS collar as found after its release mechanism fired and the collar dropped.

(see Koen et al. 2008 for factors that influence aerial survey results). Although this problem was partly remedied by replicated surveys that improved the overall odds that tracks would be detected (see below), we still may have not detected some tracks left by wolverines in heavy cover.

We also used survey replication to improve our conclusions regarding wolverine distribution. First, each additional replication improved our collective changes of detecting a travelling wolverine, if present, at least once over the course of several surveys (Mackenzie and Royle 2005). Second, because the replicates were typically separated by several weeks, at least one survey was likely to occur when the wolverine was travelling widely, rather than when localized by feeding or natal denning activities that resulted in few long and detectable snow trails. Finally, repeated detections in the same area over different replications suggested that wolverines were resident, as opposed to dispersing individuals that are less likely to be detected multiple times in the same area.

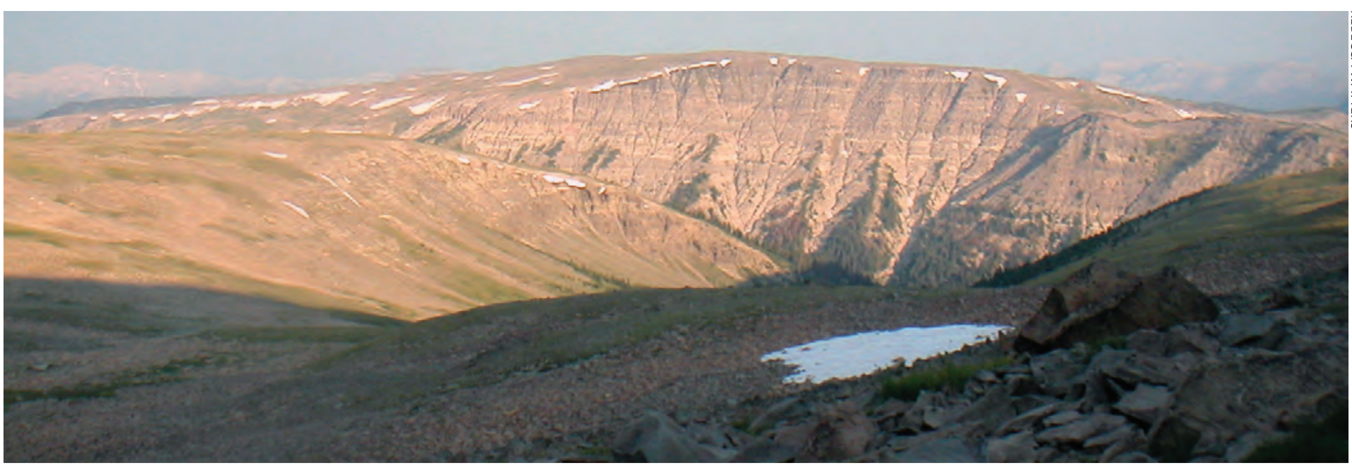
The efficiency of our surveys was probably improved by increasing the number of survey cells at the expense of mean survey time per unit (see Mackenzie and Royle [2005] regarding surveys for rare species). Rates of detection for individual survey cells declined on the Wildlife Conservation Society study area when we searched them more than 20 minutes. We typically traversed and inspected tracks along the diagonal of our Yellowstone surveys in 12 minutes. Decisions to search a grid cell for less than this threshold, say six minutes, may be cost-effective, but funding, topography, and replication should be considered.

Our use of a helicopter, as opposed to an airplane, permitted us to hover and closely inspect tracks. Choice of aircraft was an important consideration in our study area where windy conditions were common, and terrain was often highly incised and extensively covered with conifers. Airplanes are a less expensive platform that is feasible for surveying gentle terrain with numerous breaks in conifer cover. Becker and Gardner (1990) and Magoun et al. (2007) used an airplane to estimate wolverine occupancy, distribution, or density in Alaska, United States, and Ontario, Canada.

Time constraints and the wilderness status of our survey area precluded us from landing the helicopter to confirm our wolverine track detections, an important drawback of our survey. Many factors affect the appearance of tracks as seen from an aircraft, including snow conditions (time since snowfall), animal behavior associated with the track, the height of the aircraft above the ground, and the intensity and directionality of sunlight (see Koen et al. 2008). The prints of wolverine tracks left in slanted groups of three (diagonal lopes; Halfpenny et al. 1995) are readily identifiable from a helicopter (fig. 15), although other gaits of wolverines may be difficult to distinguish from other carnivores. We used highly experienced observers to differentiate between the gaits of wolverines and mammals such as gray wolves that leave similar snow-trails, and are confident we consistently identified wolverine tracks correctly if they were reasonably fresh, details of the track were apparent (e.g., not windblown), and weather conditions allowed us to inspect the track closely. However, when tracks could not be closely inspected or details were unclear, we may have incorrectly recorded some wolverine tracks as left by other species, an error that was falsely negative, but none-the-less conservative in documenting wolverine presence. The other error, the false positive—recording a track left by another species as from a wolverine—was far less likely because we were reluctant to record a wolverine track unless confident in the identification.

Conclusion and Recommendations

Our research suggested that wolverines are rare and their distribution limited in both Yellowstone National Park and the eastern portion of the Yellowstone ecosystem, although well-established populations occur in nearby south-central Montana and the Teton Range, Wyoming. Thus we caution managers not to assume that modeled wolverine habitat (Brock et al. 2007; Copeland et al. 2010) is indeed occupied and/or saturated. Resident wolverines were apparently absent from large portions of our study area, despite that the models predicted an abundance of suitable habitat. However, with the possible exception of many portions of the park interior (e.g., the upper Central and Madison Plateaus) where few ungulates (carrion) occur during the winter, biophysical aspects habitat such as snow cover, vegetation, and terrain appeared adequate to support resident wolverines. Such areas include the upper Lamar River; the Washburn, Gallatin, and Snake River Ranges; and the Red Mountains. Wolverine numbers in our study area may increase due to a slow but gradual improvement in the northern US Rockies population that dates from the 1950s, and a likely source population in Glacier National Park and Canada (Newby and Wright 1955; Newby and McDougal 1964). Populations in south-central Montana and the Teton Range may also contribute immigrants. However, if and when it occurs, a protracted recovery in wolverine numbers is expected due to this species' naturally low fecundity.


REBECCA WATTERS

This study suggests that wolverines are rare and limited in distribution in Yellowstone National Park and the eastern portion of the Yellowstone ecosystem (Buffalo Plateau of the Upper Snake River Watershed in Teton Wilderness, south of the Thorofare, shown here during a cluster visit), although well-established populations occur in nearby south-central Montana and the Teton Range, Wyoming. Wolverine numbers in our study area may increase due to a slow but gradual improvement in the northern US Rockies population that dates from the 1950s, and a likely source population in Glacier National Park and Canada. If and when this occurs, a protracted recovery in wolverine numbers is expected due to this species' naturally low fecundity.

Because wolverines typically occur at low density, and because of the island-like nature of their habitat, wolverine populations in the northern US Rocky Mountains are likely to be genetically and demographically interdependent.

Our small sample sizes suggested that subadults can readily establish home ranges and that residents have rates of survival that are similar to those in untrapped populations. However, the reproductive-age females we monitored apparently had low reproductive rates. The abundance, distribution, and persistence of wolverines on our study area were seemingly more tied to ingress from the other parts of the ecosystem than to recruitment of offspring produced by resident females. Thus, ingress from peripheral habitat such as the Gallatin and Madison Ranges, or even areas outside the Yellowstone ecosystem, may be critical for wolverine persistence in our area.

Because wolverines typically occur at low density, and because of the island-like nature of their habitat, wolverine populations in the northern US Rocky Mountains are likely to be genetically and demographically interdependent. At full capacity, wolverine habitat in the Yellowstone ecosystem supports too few female home ranges to maintain genetic viability, absent of genetic exchange with populations in peripheral mountain ranges (Cegelski et al. 2006; Brock et al. 2007). This conclusion, and ours concerning the role of ingress in influencing demographic stability on our study area, underscores the need to design and implement regional-scale conservation measures (Inman et al. 2007a).

Increasing global temperature may degrade wolverine habitat quality and quantity in the conterminous United States during the 21st century, triggering reductions in the size of wolverine habitat patches and their connectivity (Schwartz et al. 2009; Copeland 2010). Indeed, reductions in the coverage of spring snow due to a warming climate have already occurred (Mote et al. 2005). Because of its high average elevation and location in the continent's interior, the Yellowstone ecosystem has some of the largest and most contiguous patches of wolverine habitat in the conterminous United States (Brock et. al. 2007; Copeland et. al. 2010). Thus, the ecosystem is likely to play an increasingly important role in the population dynamics and persistence of wolverine populations as the regional-scale coverage of spring snow declines.

Wolverine habitat mapped at large spatial scales is of strong interest to land managers in the Yellowstone ecosystem and elsewhere across the species range. The habitat models we evaluated should be applied differently by managers based on the location and context of their use. For our study area, both the Brock et al. (2007) and the Copeland et al. (2010) models accounted for a high proportion, 97% and 95%, respectively, of wolverine radio locations. The areas of habitat predicted by the models varied by elevation, but the coverage maps were quite similar at a broad scale, partly because they both used the coverage of spring snowpack (or snow depth) as independent variables (fig. 10). The Brock et al. (2007) model was developed using data from the Yellowstone ecosystem, probably explaining why its coverage encompassed slightly more radio locations and mapped less area than the Copeland et al. (2010) coverage. A range (low to high) of wolverine habitat quality is also an attribute of the Brock et al. (2007) model that is useful. In contrast, the Copeland et al. (2010) model uses spring snowpack and ambient temperature to describe the wolverines' fundamental niche across its global range, and was not intended to quantitatively differentiate wolverine habitat, other than to suggest where (or where not) the environment may be suited for wolverines. Remarkably, the Copeland et al. (2010) coverage performs admirably in predicting wolverine radio locations and natal den sites across the species' global range. Because it was developed and evaluated using a global data set, the Copeland et al. (2010) coverage may thus better apply to habitats that differ from those characteristic of the Brock et al. (2007) study area. For example, despite that much of the occupied wolverine range across the northern hemisphere is flat, or nearly so (e.g., Ontario, Canada), terrain ruggedness is a significant predictor of wolverine habitat in the Brock et al. (2007) model.

Our survey design can be broadly applied in the conterminous United States to document the distribution and relative abundance of wolverines. Work can be completed rapidly over large areas and it provides reliable results. Although the costs of helicopter-based surveys is typically high—for us, $1,000 per hour for the aircraft alone—they are an ideal first step for undocumented populations, particularly for the large, incised, and remote areas common in the Yellowstone ecosystem. The technique also readily lends itself to periodic surveys to document changes in wolverine distribution. In our case, constraints on landing in designated (US Forest Service) or administrative (National Park Service) wilderness, and the time available to survey during fleeting periods of good weather limited our ability to land the helicopter to closely inspect and verify tracks. In such areas, the consistent detection of wolverine tracks from aircraft over the course of one or more winters may merit the verification of tracks from the ground, an endeavor that typically requires extensive pre-planning and personnel experienced with the winter conditions and hazards that characterize wolverine habitat.

We recommend that our survey of Yellowstone National Park and vicinity be repeated at five-year or ten-year intervals. The survey can readily detect changes in the distribution and relative numbers of wolverines in the park and vicinity and, coupled with similar work in other ecosystems, can help identify temporal changes in the relative numbers of wolverines at a regional scale. We also recommend additional studies to document aspects of wolverine populations such as survival, reproduction, and the movements of individuals that support genetic and numerical exchanges with distant populations. This information is critically important for understanding how all wildlife populations persist, including wolverines, a species for which this information is particularly lacking.

JASON WILMOT

Helicopter-based wolverine surveys can readily detect changes in the distribution and relative numbers of wolverines in the park and vicinity and, coupled with similar work in other ecosystems, can help identify temporal changes in the numbers of wolverines at a regional scale. The authors recommend surveys be repeated at five- or ten-year intervals.


JASON WILMOT

Because of its high average elevation and location in the continent's interior, the Yellowstone ecosystem has some of the largest and most contiguous patches of wolverine habitat in the conterminous United States. Thus, the ecosystem is likely to play an increasingly important role in the population dynamics and persistence of wolverine populations as the coverage of spring snow declines at the northern latitudes of North America. There is a need for regional-scale conservation measures and additional studies about the persistence of wolverines.

Literature Cited

Anderson, N. J., and K. E. Aune. 2008. Fecundity of female wolverine in Montana. Intermountain Journal of Sciences 14:17–30.

Aubry, K. B., K. S. McKelvey, and J. P. Copeland. 2007. Geographic distribution and broad-scale habitat relations of the wolverine in the contiguous United States. Journal of Wildlife Management 71:2147–2158.

Banci, V. 1994. Wolverine. Pages 99–127 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski, editors. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. USDA Forest Service Rocky Mountain Forest and Range Experiment Station, General Tech. Report RM-254, Fort Collins, Colorado, USA.

Banci, V., and A. S. Harestad. 1990. Home range and habitat use of wolverines *Gulo gulo* in Yukon, Canada. Holarctic Ecology 13:195–200.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools

Becker, E. F., and C. Gardner. 1990. Wolf and wolverine density estimation techniques. Alaska Department of Fish and Game Research Progress Report. Project W-23-3, Study 7.15.

Brock, B. L., and R. M. Inman, K. H. Inman, A. J. McCue, M. L. Packila, and B. Giddings. 2007. Broad-scale wolverine habitat in the conterminous Rocky Mountain States. Pages 21–53 *in* Greater Yellowstone Wolverine Program, Cumulative Report, May, 2007. Wildlife Conservation Society, Ennis, Montana, USA.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24:346–352.

Cegelski, C. C., L. P. Waits, and N. J. Anderson. 2003. Assessing population structure and gene flow in Montana wolverines (*Gulo gulo*) using assignment-bases approaches. Molecular Ecology 12:2907–2918.

Celgelski, C. C., N. J. Anderson, O. Flagstad, C. Strobeck, and C. J. Kyle. 2006. Genetic diversity and population structure of wolverine (*Gulo gulo*) populations at the southern edge of their current distribution in North America with implications for genetic viability. Conservation Genetics 7:197–211.

Consolo-Murphy, S., and M. M. Meagher. 1995. The status of wolverines, lynx, and fishers in Yellowstone National Park. Pages 57–62 *in* P. A. Curlee, A. Gillesberg, and D. Casey, editors. Proceedings of the Third Biennial Conference on the Greater Yellowstone Ecosystem. Northern Rockies Conservation Cooperative, Jackson, Wyoming, USA.

Copeland, J. P., E. Cesar, J. M. Peek, C. E. Harris, C. D. Long, and D. L. Hunter. 1995. A live trap for wolverine and other forest carnivores. Wildlife Society Bulletin 23:535–538.

Copeland, J. P, and J. S. Whitman. 2003. Wolverine (*Gulo gulo*). Pages 672–682 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild Mammals of North America: Biology, Management, and Conservation, 2nd Edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Copeland, J.P. 1996. Biology of the Wolverine in Central Idaho. Thesis, University of Idaho, Moscow, USA.

Copeland, J. P., J. M. Peek, C. R. Groves, W. E. Melquist, K. S. McKelvey, G. W. McDaniel, C. D. Long, and C. E. Harris. 2007. Seasonal habitat associations of the wolverine in Central Idaho. Journal of Wildlife Management 71:2201–2212.

Copeland, J. P., K. S. McKelvey, K. B. Aubry, A. Landa, J. Persson, R. M. Inman, J. Krebs, J., E. Lofroth, H.

Golden, J. R. Squires, A. Magoun, M. K. Schwartz, J. Wilmot, C. L. Copeland, R. E. Yates, I. Kojola, and R. May. 2010. The bioclimatic envelope of the wolverine (*Gulo gulo*): Do climatic constraints limit its geographic distribution? Canadian Journal of Zoology 88:1–14.

Copeland, J. P., and R. E. Yates. 2008. Wolverine population assessment in Glacier National Park, comprehensive summary update, January, 2008. USDA Forest Service, Rocky Mountain Research Station, Missoula, Montana, USA.

Gardner, C. L. 1985. The ecology of wolverine in south central Alaska. Thesis, University of Alaska, Fairbanks, USA.

Gardner, C. L., W. Ballard, and R. Jessup. 1986. Long distance movement by an adult wolverine. Journal of Mammalogy 67(3):603.

Groves, C. R. 1988. Distribution of the wolverine in Idaho as determined by mail questionnaire. Northwest Science 62:181–185.

Halfpenny, J. C., R. W. Thompson, S. C. Morse, T. Holden, and P. Rezendes. 1995. Snow tracking. Pages 91–163 *in* W. J. Zielinski and T. E. Kucera, editors. American marten, fisher, lynx, and wolverine: Survey methods for their detection. General Technical Report PSW GTR-157, Pacific Southwest Research Station, USDA Forest Service, Albany, California, USA.

Hash, H. S. 1987. Wolverine. Pages 575–585 *in* M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild Furbearer Management and Conservation in North America. Ontario Ministry of Natural Resources, Toronto, Canada.

Heisey, D. M., and T. K. Fuller. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. Journal of Wildlife Management 49:668–674.

Hoak, J. H., J. L. Weaver, and T. W. Clark. 1982. Wolverines in Wyoming. Northwest Science 56:159–161.

Hornocker, M. G. and H. S. Hash. 1981. Ecology of the wolverine in northwestern Montana. Canadian Journal of Zoology 59:1286–1301.

Inman, R. M., K. H. Inman, A. J. McCue, and M. L. Packila. 2007a. Wolverine harvest in Montana. Pages 85–97 *in* Greater Yellowstone Wolverine Program, Cumulative Report, May, 2007. Wildlife Conservation Society, Ennis, Montana, USA.

Inman, R. M., K. H. Inman, A. J. McCue, M. L. Packila, G. C. White, and B. C. Aber. 2007b. Wolverine space use in Greater Yellowstone. Pages 1–20 *in* Greater Yellowstone Wolverine Program, Cumulative Report, May 2007. Wildlife Conservation Society, Ennis, Montana, USA.

Inman, R. M., K. H. Inman, M. L. Packila, and A. J. McCue. 2007c. Wolverine reproductive rates and maternal habitat in Greater Yellowstone. Pages 65–84 *in* Greater Yellowstone Wolverine Program, Cumulative Report, May, 2007. Wildlife Conservation Society, Ennis, Montana, USA.

Inman, R. M., M. L. Packila, K. H. Inman, R. S. Spence, and D. McCauley. 2008. Fixed-wing den surveys yield promising results for distribution and monitoring technique, dispersal data. Greater Yellowstone Wolverine Program Progress Report. Wildlife Conservation Society, Ennis, Montana, USA.

Inman, R. M., R. R. Wigglesworth, K. H. Inman, M. K. Schwartz, B. L. Brock, and J. Dieck. 2004. Wolverine makes extensive movements in the Greater Yellowstone Ecosystem. Northwest Science 78:261–266.

Jenness, J. 2006. Topographic Position Index (tpi_jen.avx) extension for ArcView 3.x, v. 1.3a. Jenness Enterprises, Flagstaff, Arizona, USA. Available at: http://www.jennessent.com.

Koen, E. L., J. C. Ray, J. Bowman, F. N. Dawson, and A. J. Magoun. 2008. Surveying and monitoring wolverines in Ontario and other lowland, boreal forest habitats: Recommendation and protocols. NWSI Field Guide FG-06 94. Ontario Ministry of Natural Resources, Northwest Science and Information, Thunder Bay, Ontario, Canada.

Krebs, J., E. C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia, Canada. Journal of Wildlife Management 71:2180–2192.

Krebs, J., E. Lofroth, J. Copeland, V. Banci, D. Cooley, H. Golden, A. Magoun, R. Mulders, and B. Shults. 2004. Synthesis of survival rates and causes of mortality in North American wolverines. Journal of Wildlife Management 68:493–502.

Krott, P. 1959. Demon of the north. Alfred. A. Knopf. New York, New York, USA.

Kyle, C. J., and C. Strobeck. 2001. Genetic structure of North American wolverine (*Gulo gulo*) populations. Molecular Ecology 10:337–347.

Kyle, C. J., and C. Strobeck. 2002. Connectivity of peripheral and core populations of North American wolverines. Journal of Mammalogy 83:1141–1150.

Landa, A., O. Strand, J. D. C. Linnell, and T. Skogland. Home-range sizes and altitude selection for arctic foxes and wolverines in an alpine environment. Canadian Journal of Zoology 76:448–457.

Mackenzie, D. L., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology 42:1105–1114.

Magoun, A. J. 1985. Population characteristics, ecology, and management of wolverines in Northwestern Alaska. Dissertation, University of Alaska, Fairbanks, USA.

Magoun, A. J., and J. Copeland. 1998. Characteristics of wolverine reproductive den sites. Journal of Wildlife

Management 62:1313–1320.
Magoun, A. J., J. C. Ray, D. S. Johnson, P. Valkenburg, F. N. Dawson, and J. Bowman. 2007. Modeling wolverine occurrence using aerial surveys of tracks in snow. Journal of Wildlife Management 71:2221–2229.
Marcum, C. L., and D. O. Loftsgaarden. 1980. A nonmapping technique for studying habitat preferences. Journal of Wildlife Management 44:963–968.
May, R., A. Landa, J. van Dijk, J. D. C. Linnell, and R. Anderson. 2006. Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. Wildlife Biology 12:285–295.
Mobley, D. 1962. Ways of the wolverine. Wyoming Wildlife, January. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.
Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. American Midland Naturalist 37:223–249.
Mote, P. W., A. F. Hamlet, M. P. Clark, and D. P. Lettenmaier. 2005. Declining mountain snowpack in western North America. Bulletin American Meteorological Society 86:39–49.
Murphy, K. M., T. Potter, J. Halfpenny, K. Gunther, T. Jones, and P. Lundberg. 2004. The presence and distribution of Canada lynx (*Lynx canadensis*) in Yellowstone National Park, Wyoming. Unpublished final report, Yellowstone National Park, Wyoming, USA.
Newby, F. E., and J. J. McDougal. 1964. Range extension of the wolverine in Montana. Journal of Mammalogy 45:485–487.
Newby, F. E., and P. L. Wright. 1955. Distribution and status of the wolverine in Montana. Journal of Mammalogy 36:248–253.
O'Gara, B. W., and R. B. Harris. 1988. Age and condition of deer killed by predators and automobiles. Journal of Wildlife Management 52:316–320.
Persson, J., G. Ericsson, and P. Segerström. 2008. Human caused mortality in the endangered Scandinavian wolverine population. Biological Conservation 142:325–331.
Robinson, B., and S. Gehman. 1998. Search for "skunk bears": the elusive wolverine. Yellowstone Science 6:2–5.
Rowland, M. M., M. J. Wisdom, D. H. Johnson, B. C. Wales, J. P. Copeland, and F. B. Edelmann. 2003. Evaluation of landscape models for wolverines in the interior Northwest, United States of America. Journal of Mammalogy 84:92–105.
Ruggiero, L. F., K. S. McKelvey, K. B. Aubry, J. P. Copeland, D. H. Pletscher, and M. G. Hornocker. 2007. Wolverine conservation and management. Journal of Wildlife Management 71:2145–2146.
Schullery, P. and L. H. Whittlesey. 1999. Greater Yellowstone carnivores: a history of changing attitudes. Pages 11–49 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Karieva, editors. Carnivores in ecosystems: The Yellowstone Experience. Yale University Press, New Haven, Connecticut, USA.
Schwartz, M. K., K. B. Aubry, K. S. McKelvey, K. L. Pilgrim, J. P. Copeland, J. R. Squires, R. M. Inman, S. M. Wisely, and L. F. Ruggiero. 2007. Inferring geographic isolation of wolverines in California using historical DNA. Journal of Wildlife Management 71:2170–2179.
Schwartz, M. K., J. P. Copeland, N. J. Anderson, J. R. Squires, R. M. Inman, K. S. McKelvey, K. L. Pilgrim, L. P. Waits, and S. A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. Ecology 79:2170–2179.
Shields, G., and T. D. Kocher. 1991. Phylogenetic relationships of North American ursids based on analysis of mitochondrial DNA. Evolution 45:218–221.
Skinner, M. P. 1927. The predatory and fur bearing animals of the Yellowstone National Park. Roosevelt Wildlife Bulletin 4:163-281.
Smith, G. 1955. Will the devil beast return? Wyoming Wildlife 20:20–25
Squires, J. R., J. P. Copeland, T. J. Ulizio, M. K. Schwartz, and L. F. Ruggerio. 2007. Sources and patterns of wolverine mortality in western Montana. Journal of Wildlife Management 71:2213–2220.
U.S. Fish and Wildlife Service. 2008. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the North American wolverine as endangered or threatened. Federal Register 73:12929–12941.
Whitman, J. S., W. B. Ballard, and C. L. Gardner. 1986. Home range and habitat use by wolverines in south central Alaska. Journal of Wildlife Management 50:460–463.
Weiss, A. 2001. Topographic Position and Landforms Analysis. Poster presentation, ESRI User Conference, San Diego, California, USA *in* J. Jenness. 2006. Topographic Position Index (tpi_jen.avx) extension for ArcView 3.x, v. 1.3a. Jenness Enterprises, Flagstaff, Arizona, USA. Available at: http://www.jennessent.com.
Wright, J. D. and J. Ernst. 2004. Effects of mid-winter snow depth on stand selection by wolverines, *Gulo gulo luscus*, in the boreal forest. Canadian Field-Naturalist 118:56–60.
Worton, B. J. 1987. A review of models of home range for animal movement. Ecological Modeling 38:277–298.
Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168.

JASON WILMOT

The aerial survey design of this project can be broadly applied in the conterminous United States to document the distribution and abundance of wolverines. The authors also recommend additional studies to document wolverine survival, reproduction, and the movements of individuals that support genetic and numerical exchanges with distant populations. This information is critically important for understanding how wolverine populations persist.

Appendix 1

Summary of Public Education and Outreach Activities, Absaroka-Beartooth Wolverine Project

The objective of the our educational activities were to increase public awareness of this unique and mysterious carnivore in the Yellowstone ecosystem, the wolverine's social and ecological values, and current research and conservation efforts for the species. Depending on the target audience, we used several different approaches. First, we partnered with the Yellowstone National Park Division of Interpretation outreach program ParKids (Interpretive Ranger Trudy Patton) to educate middle school children and generate excitement about wolverines. From 2006 to 2008, the three-day course "Wolverines, Wilderness, and Wonder" was taught seven times in summer day-camp format in community schools surrounding Yellowstone National Park. ParKids used hands-on learning techniques for children such as building and operating a mock wolverine trap (see photo) during class and visiting real traps on site in the park. Other messages emphasized predator-prey relationships and wildlife stewardship. Rangers also presented similar information to the general public at booths located at environmental fairs, tribal powwows, museums, and zoos and in talks to national park visitors. Project biologists provided life history information and visual aids such as wolverine hides and skulls. The activities were also used in Expedition: Yellowstone!, the park's curriculum-based residential program for students.

NPS

Project staff partnered with the Yellowstone National Park outreach program ParKids to educate middle school children and generate excitement about wolverines.

Project biologists taught nine courses on the ecology and management of wolverines and other forest carnivores; made 15 presentations to professional audiences or the general public; provided two radio interviews, and produced and distributed four annual project (update) newsletters. The study was featured, or at least mentioned, in seven magazine or newspaper articles, including *National Wildlife* and *National Parks.* We contributed subject-matter content and guidance for a wolverine film and online video.

Counter clockwise from left: Interpretive Ranger Trudy Patton works with a ParKids class that assembled and operated a mock wolverine trap built by the Absaroka-Beartooth Wolverine Project, June 2008; ParKids learn about wolverines at their school; Field Coordinator Jason Wilmot delivers a presentation to the public in Jackson, Wyoming, 2010; Interpretive Ranger Trudy Patton explains to a ParKids class the operation of a wolverine live trap along the East Entrance Road, Yellowstone National Park, June 2008; A ParKids student, inspired by the class, demonstrates a wolverine live trap he built by himself.

BOTTOM LEFT: LYDIA DIXON; REST OF PAGE: NPS

Appendix 2

Locations of Live Traps, Absaroka-Beartooth Wolverine Project, 2006–2009

See table.

JASON WILMOT

The project employed live traps that were fitted with remote trap transmitters that remotely signaled personnel up to 29 kilometers (18 mi) when traps were triggered and contained wolverines or non-target animals. Signals were checked remotely 1–4 times per day; the traps themselves a minimum of every 3–4 days. Here, project volunteer Wendy Sicard embarks on the daily check of live traps in Sunlight Creek, 2006.

Table A2-1. Locations of live traps, Absaroka-Beartooth wolverine project, 2006–2009

To receive a copy of this table, contact report author Jason Wilmot (see title page).

This project would not have been successful without the extraordinary support of the Yellowstone Park Foundation, the principal funder of the project.

National Park Service
Yellowstone National Park
Yellowstone Center for Resources

YCR-2011-02

March 2011