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Long-Distance Wolverine Dispersal from Wyoming to Historic Range in Colorado

Abstract

Wolverines (*Gulo gulo*) within the conterminous U.S. exist as a metapopulation dependent upon individuals dispersing between patches of habitat to persist. Dispersal events can be difficult to document for long-ranging carnivores, but have implications for understanding gene flow and connectivity between both currently occupied and historically occupied habitat. Here, we describe the long-distance dispersal of a subadult, male wolverine (M56) from a reproductive population in northwest Wyoming to northern Colorado where wolverines had been absent for 90 years. M56 was ultimately killed in North Dakota in 2016, the first verified wolverine in that state in over 200 years. Following capture and collaring, we collected aerial VHF telemetry locations as M56 navigated potential barriers, including interstate highways and subdivisions, and travelled extensively outside of primary wolverine habitat through the arid grasslands and shrublands of the Wyoming Basin Ecoregion. Straight-line distances for dispersals from Wyoming to Colorado (516 km) and from Colorado to North Dakota (826 km) are the longest straight-line dispersal distances reported for the species at this time. The Wyoming Basin Ecoregion M56 traversed is dominated by sagebrush and topography less rugged than that typical of the high elevation, mountainous habitat wolverines use in the conterminous U.S. This dispersal event offers evidence of connectivity between occupied habitat in Wyoming and unoccupied habitat within the species' historic range in Colorado and provides a detailed account of the path M56 took through atypical habitat.

Keywords: wolverine, dispersal, metapopulation, connectivity

Introduction

For wide-ranging carnivore species that occur at low densities, long-distance dispersals between areas of suitable habitat can be crucial for gene flow and metapopulation connectivity (Noss et al. 1996, Weaver et al. 1996). In many cases these dispersals occur across areas containing atypical habitat (Sweaner et al. 2000), human activity (Paquet et al. 1996, Woodroffe and Ginsberg 1998), and barriers to movement such as roads (Trombulak and Frissel 2000, Riley et al. 2006). Examples of such long-distance dispersals exist

for pumas (Stoner et al. 2010, Hawley et al. 2016), leopards (Fattebert et al. 2013), and wolves (Ciucci et al. 2009, Andersen et al. 2015).

Wolverines in the conterminous U.S. exist as a demographically vulnerable metapopulation dependent on dispersal between areas of high elevation habitat separated by relatively arid valley bottoms (Cegelski et al. 2006, Gude et al. 2007, Schwartz et al. 2009, Inman et al. 2013). Inman et al. (2013) identified several covariates associated with areas suitable for use by resident adult wolverines (primary habitat) in the conterminous U.S. including steep terrain, deep snow, proximity to high elevation talus fields, proximity to trees, and few roads. In the southern extent of wolverine range in the conterminous U.S., such areas exist in island-like patches in mountain ranges separated by lower elevation valleys and basins unsuitable to occupation by resident wolverines. Wolverines are capable of dispersing through atypical habi-

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tat (Inman et al. 2012) and over great distances (Magoun 1985, Gardner et al. 1986, Flagstad et al. 2004, Aubry et al. 2016). Nevertheless, it is difficult to track dispersing wolverines, especially those making long-distance dispersals outside their natal home range (Vangen et al. 2001). Multiple research studies in the Rocky Mountains have lost radio contact with dispersal-age study animals (Inman et al. 2004, Squires et al. 2006, Copeland and Yates 2008, Murphy et al. 2011) and data chronicling wolverine movements during dispersal events are limited.

Historical evidence suggests wolverines were, or nearly were, extirpated from the conterminous U.S. by about 1930 (Grinnell et al. 1937, Newby and Wright 1955, Aubry et al. 2007), but have recovered within portions of their historic distribution in Washington, Montana, Idaho, and Wyoming. This reestablishment of reproductive populations demonstrates that dispersing wolverines are capable of repopulating previously occupied areas (Newby and Wright 1955, Newby and McDougal 1964, Cegelski et al. 2003, Flagstad et al. 2004, Anderson and Aune 2008). More recently, a remote camera photograph and subsequent genetic analysis of samples from a wolverine in California provided evidence of a long-distance dispersal from currently occupied habitat in the Rocky Mountains to unoccupied habitat in the Sierra Nevada where no verified wolverines had been documented in 86 years (Moriarty et al. 2009). This case illustrates the potential for long-distance wolverine dispersals across atypical habitat, yet does not provide information on the route the animal may have taken. During spring 2009 we monitored the dispersal of M56, a subadult male wolverine, from northwestern Wyoming to northern Colorado. M56 was the first verified wild wolverine documented in Colorado in 90 years (Grinnell 1926, Nead et al. 1985, Aubry et al. 2007, Tanya Shenk, Colorado Division of Wildlife, personal communication). M56 subsequently travelled to and was shot in North Dakota; the first verified wild wolverine in North Dakota in over 200 years (Bailey 1926). Here, we present a detailed account M56's dispersal through atypical habitat from a wolverine population in Wyoming to historic, unoccupied wolverine range in Colorado.

Methods

Capture and Handling

We tracked M56 as part of a larger wolverine ecology study in the Greater Yellowstone Ecosystem of Montana, Idaho, and Wyoming conducted from 2000–2010 (Inman et al. 2012). Over the course of the study, we captured and monitored 38 wolverines (23 female, 15 male). Study area elevations ranged from 1400 to 4200 m. We captured wolverines during winter in log box traps (Copeland et al. 1995, Lofroth et al. 2008) equipped with trap-transmitters (Telonics, TBT-500, Mesa, AZ). We captured juvenile wolverines by hand at den or rendezvous sites (Persson et al. 2006). We used a variable-powered CO₂ pistol (CO₂ PI, Dan-Inject, Knoxville, TN), a syringe pole, or a hand syringe to deliver an initial dose of 8.0 mg/kg ketamine + 0.05 mg/kg medetomidine + 0.40 mg/kg torbugesic (Quigley 2000) or approximately 7.5 mg/kg ketamine + 0.25 mg/kg medetomidine (Fahlman et al. 2008). We surgically implanted wolverines with an intra-peritoneal VHF radio-transmitter (Telonics Imp400L, Imp300L, Mesa, AZ; Advanced Telemetry Systems M1255B, M1250B, M1245B, Isanti, MN). We followed handling procedures approved by the Animal Care and Use Committees of the Hornocker Wildlife Institute/Wildlife Conservation Society (2000-RMW-504, 2000–2006) and Montana Department of Fish, Wildlife and Parks (IACUC 1-2006, FWP2-2010) as permitted by U.S. Department of Agriculture, Animal and Plant Health Inspection Service (Permits 81-R-0015 and 81-R-0018).

We fit M56 with a global positioning system (GPS) collar programmed to collect locations at various intervals (Lotek Wireless Inc. 3300SL, 6000SL, Newmarket, Ontario, Canada). Based on age at reproductive maturity for female wolverines (Persson et al. 2006) and the age through which dispersal movements typically occur, we classified wolverines of three years or older as adults and wolverines under three years of age as subadults.

Dispersal Observations

We attempted to collect aerial VHF telemetry locations every ten days in M56's natal home range

(December 2008–March 2009), then at least once daily during dispersal movements (April 2009–July 2009), weather permitting. We estimated VHF telemetry error to be approximately 300 m (Inman et al. 2012). We calculated the minimum distance M56 travelled during dispersal using straight-line segments between VHF locations. We calculated a straight-line dispersal distance between the site M56 was first captured and the last VHF location we recorded in Colorado. We calculated a straight-line dispersal distance between the last VHF location we recorded in Colorado and the location where M56 was shot in North Dakota. We calculated three metrics to describe rate of movement during dispersal: average rate of daily movement, average rate of daily movement while travelling, and average rate of daily movement while resting. We calculated the average rate of daily movement by dividing the minimum distance travelled by the number of days the dispersal occurred over. To calculate average rate of daily movement while travelling or resting, we grouped VHF locations into blocks covering roughly 24 hrs of movement (from 21 hr to 27 hr). We classified these blocks of locations as “travelling” if the total distance travelled was > 15 km or as “resting” if the total distance travelled was ≤ 15 km. We then estimated average rate of daily movement for blocks of travelling locations and blocks of resting locations separately (total distance travelled divided by total blocks of locations). Because M56 travelled great distances during some periods and remained relatively stationary within a small cluster of locations during others, we submit that these three metrics give a more comprehensive representation for rate of movement during dispersal than a simple average alone. We classified VHF locations as occurring either inside or outside primary wolverine habitat using maps created by Inman et al. (2013). Additionally, we classified VHF locations according to cover type using data from the U.S. Geological Survey’s Gap Analysis Program (US Geological Survey 2010). We made movement calculations and habitat and land cover classifications using ArcGIS 9.3 (ESRI 2009).

Results

VHF Locations

During the course of our study, we documented dispersal movements for 9 wolverines (4 female, 5 male). Generally, movements from the center of the natal home range did not exceed 200 km (Inman et al. 2012). We began tracking M56 following capture as a subadult in northwestern Wyoming on 20 December 2008 and suspended tracking in northern Colorado on 01 July 2009 (Figure 1). Due to failure of the GPS collar’s VHF transmitter by 08 May 2009, we used the intra-peritoneal VHF radio transmitter for most tracking during the dispersal event. From January to March, VHF locations indicated M56 was using an area of primary wolverine habitat near the capture site at Lava Mountain near the nexus of the Absaroka and Wind River mountain ranges. During two periods, between January and April, M56 was not located during VHF flights (17 January–03 February 2009 and 12 March–05 April 2009). It is possible M56 was making exploratory movements in the first period and began dispersing in the second. M56 likely began dispersing in March. This time frame is consistent with the average age of dispersal of 13 months reported by Vangen et al. (2001) and coincides with a period of improving travel conditions as snow stabilizes (Inman et al. 2012). From 06 April 2009 when we began tracking the dispersal event to 01 July 2009 when we suspended tracking efforts, we recorded 104 VHF locations. During this time, M56 travelled a minimum distance of 710 km, generally focusing movements along higher elevation areas in the landscape rather than taking the most direct route south. The straight-line distance from point of capture to final VHF location in Colorado was 516 km. The average rate of daily movement during dispersal was 8.3 km per day. The average rate of daily movement while travelling was 33.5 km per day (min = 17.8 km, max = 49.3 km, $n = 6$). The average rate of daily movement while resting was 2.9 km per day (min = 0.3 km, max = 10.5 km, $n = 12$).

Of the 104 VHF locations we collected during dispersal, 53 occurred within primary wolverine

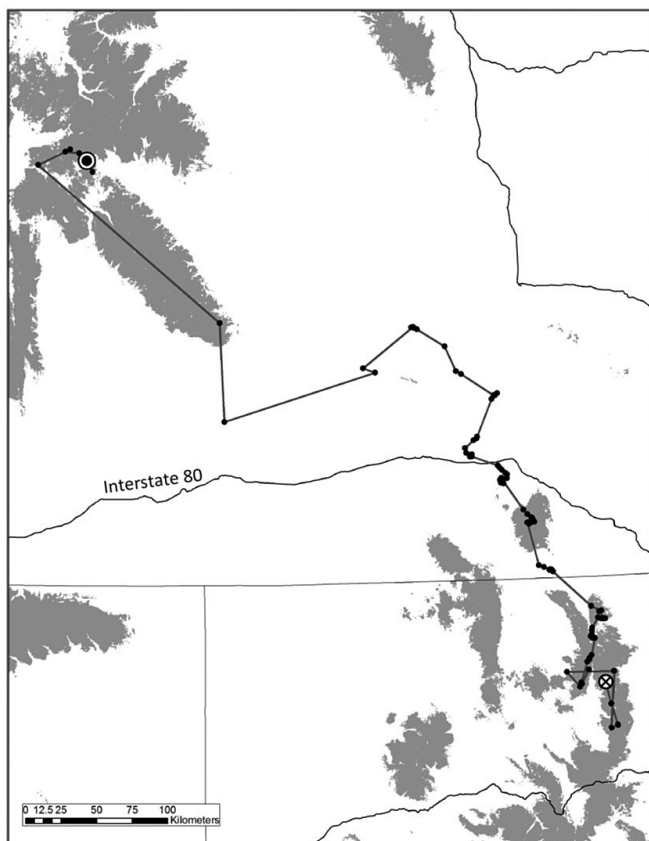


Figure 1. Map of VHF locations (black dots) of wolverine M56 recorded between initial capture in northwest Wyoming on 20 December 2008 (black dot encircled by white) and the final location we collected in Colorado on 01 July 2009 (white dot with black “x”). Primary wolverine habitat (areas suitable for use by resident adult wolverines) is depicted in gray (Inman et al. 2013).

habitat and 51 occurred outside primary wolverine habitat. After locating M56 in primary habitat at the southern end of the Wind River Range on 06 April 2009, M56 travelled at minimum 411 km outside primary habitat across the Wyoming Basin Ecoregion (WBE) before reaching primary habitat on Elk Mountain in southeastern Wyoming on 25 May 2009. The WBE is an arid, intermontane basin in central and southwestern Wyoming dominated by grasslands and shrublands and punctuated by occasional hills and low mountains (Omernik 1987). Land cover types for VHF locations within the WBE included Wyoming big sagebrush ($n = 16$), lodgepole pine ($n = 8$), basin exposed rock/soil

($n = 6$), juniper woodland ($n = 1$), and desert shrub ($n = 1$). VHF locations in lodgepole pine and juniper woodlands occurred on hills or small mountain ranges including the Green, Granite, and Shirley Mountains. Such locations in lodgepole and juniper cover types coincided with clusters of resting locations representing periods when M56 remained relatively stationary over multiple days. One such cluster of resting locations in the Granite Mountains was centered at a cow carcass on a ranch (Figure 2, Figure 3). While travelling through sagebrush, exposed rock and soil, and desert shrub cover types M56 generally took multi-hour, rather than multi-day rest periods. Snow was mostly absent at VHF locations in the WBE with the exception of four locations atop the Shirley Mountains. Snow was largely present at VHF locations concentrated in primary habitat in mountainous areas of Wyoming and Colorado, although patchy in some areas in late May and June.

We first located M56 in Colorado on 02 June 2009. Three weeks later, a wolverine was photographed in primary habitat within Rocky Mountain National Park (Figure 4). Hair-rubbing along the wolverine’s neck, consistent with wear from a GPS collar, supports

the assumption that the animal was M56. Colorado Parks and Wildlife (CPW) took over monitoring M56 in July of 2009. CPW recorded M56’s last known Colorado location in 2012. On 24 April 2016 M56 was shot in a cow pasture near Alexander, North Dakota in what wildlife authorities determined to be a legal defense of livestock (S. Tucker, North Dakota Game and Fish, personal communication). M56 was identified by the intra-peritoneal VHF radio-transmitter in the abdomen during necropsy. The straight-line distance from the final VHF location we collected on M56 in Colorado and the location where M56 was shot in North Dakota was 826 km.



Figure 2. View of the Granite Mountains (foreground at right) and Green Mountains (background) in the Wyoming Basin Ecoregion taken 08 May 2009 when M56 was relocated in the Granite Mountains via aerial VHF telemetry.



Figure 3. Wolverine M56 (circled) in juniper woodlands in the Granite Mountains taken 08 May 2009 during dispersal through atypical habitat in the Wyoming Basin Ecoregion.

Potential Barriers to Movement

In addition to crossing atypical habitat in the WBE, M56 encountered a number of other potential barriers to movement while dispersing from Wyoming to Colorado. Between capture on 20 December 2008 and 01 July 2009, M56 was located in six National Forests, three BLM Districts, one National Park, Wyoming and Colorado State Lands, and various private lands. M56 crossed nine highways during dispersal including one interstate (I80), two U.S. highways (US287 in Wyoming, US34 in Colorado), and five state highways (WY28, WY220, WY130, WY230, CO14). M56 also



Figure 4. A wolverine, believed to be M56, showing evidence of hair-rubbing consistent with that caused by a GPS collar, photographed in Rocky Mountain National Park on 26 June 2009 (photo courtesy of Ray Rafiti).

travelled within close proximity to areas of human activity at subdivisions near the border between Wyoming and Colorado.

In the case of highways, we were able to make observations during two road crossings. When crossing I80, the largest and highest traffic volume highway along the dispersal route, aerial and ground-based telemetry indicated that M56 crossed between midnight and 0400 on 25 May 2009. At 0831 on the morning of 31 May 2009, we observed from the air as M56 approached state highway WY130 from the north and summited a small rise next to the road. M56 halted as two cars passed. After the cars passed, a motorcycle heading in the opposite direction approached and M56 ran into tree cover away from the road, then continued west and climbed a sheer mountainside, crossing over the crest of the mountains north of the road. M56 eventually continued south across WY130 unobserved at a different location.

In the case of human activity, we observed M56 from the air in close proximity to two areas of human habitation between I80 and the Wyoming-Colorado border. In one case, M56 descended in

elevation on a trajectory to cross a river valley with vehicle activity on the roads. Upon leaving tree cover and approaching the roads, M56 changed direction and moved back towards higher elevation. At this time, M56 either skirted or crossed the edge of a housing development with loose dogs and human activity before climbing back into tree cover. In another instance we observed M56 approach the corner of a cluster of homes surrounded by undeveloped, spruce-fir land cover type. M56 moved approximately 0.5 miles north, away from the development, prior to continuing southeast.

Discussion

Cases of wolverines dispersing long-distances (Magoun 1985, Gardner et al. 1986, Flagstad et al. 2004, Aubry et al. 2016) and recolonizing unoccupied habitat (Vangen et al. 2001, Moriarty et al. 2009) have been documented in multiple studies. M56's dispersals to Colorado and North Dakota further confirm the great distances some wolverines may travel when dispersing. The dispersal distances of 516 km (Wyoming to Colorado) and 826 km (Colorado to North Dakota) are the first observations of straight-line dispersal distances exceeding 500 km reported for wolverines. The dispersal to Colorado serves as an example of the capacity for wolverines to recolonize unoccupied habitat as well. How often a dispersal of this nature occurs is unknown, although chance detections of wolverines outside of occupied habitat in Michigan (Shaw and Ford 2012), California (Moriarty et al. 2009), Colorado (Figure 4), Utah (Associated Press 2014), and North Dakota (Stephanie Tucker, North Dakota Game and Fish, personal communication) in the past 13 years suggest it is not exceedingly rare.

In addition to the great distances travelled, the route M56 took through atypical habitat in the WBE, often in the absence of snow and across potential barriers to movement, is noteworthy. This evidence that connectivity is currently adequate for a wolverine to disperse from occupied habitat in Wyoming to unoccupied habitat in Colorado reveals the possibility of population expansion. Inman et al. (2013) estimated that the block of primary habitat in the Southern Rockies of Colo-

rado and New Mexico could account for 21% of the wolverine population in the conterminous U.S., were all areas of primary habitat occupied. Were a reproductive wolverine population to become established in the Southern Rockies it could increase the size of the conterminous U.S. wolverine metapopulation significantly. Despite M56's successful dispersal, recovery of a population in Colorado by wild wolverines dispersing from the north seems unlikely. Female wolverines have not yet been documented dispersing similar distances or across arid valley bottoms similar to movements made by this male (Vangen et al. 2001, Inman et al. 2012). Nevertheless, this event suggests occasional gene flow between more northern populations and any potential, future Colorado population is possible.

Despite the evidence this dispersal provides of possible connectivity between primary habitat in Wyoming and Colorado, it is likely potential barriers to movement will only increase over time. The human population is growing in wolverine range within the conterminous U.S., and further expansion of exurban housing developments and road systems could compromise connectivity. Our observations of M56 encountering potential barriers such as roads and areas of human habitation suggest these landscape features may have affected the route M56 followed as well as the timing of movements. Wolverine have been known to avoid roads and areas of human activity in other instances (Hash 1987, Banci 1994). Detailed movement data need to be collected to determine what levels of roadway traffic volumes and housing development densities wolverines will move across and through. These data would be difficult to obtain, but developing guidelines for placement, size, and spacing of housing developments may be crucial to preserving connectivity for dispersing wolverines in the conterminous U.S. Furthermore, the fact that these long-distance dispersals took place across multiple states and over land managed by several different agencies and private entities underscores the need for cooperative, transboundary management of wolverines in the conterminous U.S. Because the wolverine metapopulation relies upon dispersal between somewhat isolated patches of primary

habitat, land management agencies and the public must consider how to maintain or enhance connectivity if they wish to conserve wolverines at this southernmost extent of their range.

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Literature Cited

- Andersen, L. W., V. Harms, R. Caniglia, S. D. Czarnomska, E. Fabbri, B. Jędrzejewska, G. Kluth, A. B. Madsen, C. Nowak, C. Pertoldi, E. Randi, I. Rinhardt, and A. V. Stronen. 2015. Long-distance dispersal of a wolf, *Canis lupus*, in northwestern Europe. *Mammal Research* 60:163-168.
- Anderson, N. J., and K. E. Aune. 2008. Fecundity of female wolverine in Montana. *Intermountain Journal of Sciences* 14:17-30.
- Associated Press. 2014. Utah wolverine sighting first documented in 30 years. *The Washington Times*, July 2. Available online at <http://www.washingtontimes.com/news/2014/jul/2/images-document-wolverine-in-uinta-mountains/> (accessed 06 September 2017).
- Aubry, K. B., K. S. McKelvey, and J. P. Copeland. 2007. Distribution and broadscale habitat relations of the wolverine in the contiguous United States. *Journal of Wildlife Management* 71:2147-2158.
- Aubry, K. B., J. Rohrer, C. M. Raley, and S. Fitkin. 2016. Wolverine distribution and ecology in the North Cascades ecosystem: Final Progress Report (February 9, 2016). US Forest Service, Pacific Northwest Research Station, Olympia, WA. Available online at http://wolverinefoundation.org/wp-content/uploads/2011/02/NorthCascadesWolverineStudy_Final-Progress-Report2012-2016.pdf (Accessed 1 May 2017).
- Bailey, V. 1926. A biological survey of North Dakota. *North American Fauna* 49:1-226.
- Banci, V. 1994. Wolverine. In L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski (technical editors), *The Scientific Basis for Conserving Forest Carnivores: American Marten, Fisher, Lynx, and Wolverine in the Western United States*. General Technical Report RM-254. US Forest Service Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. Pp. 99-127.
- Cegelski, C. C., L. P. Waits, and N. J. Anderson. 2003. Assessing population structure and gene flow in Montana wolverines (*Gulo gulo*) using assignment-based approaches. *Molecular Ecology* 12:2907-2918.
- Cegelski, C. C., L. P. Waits, 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.
- Ciucci, P., W. Reggioni, L. Maiorano, and L. Boitani. 2009. Long-distance dispersal of a rescued wolf from the northern Apennines to the western Alps. *Journal of Wildlife Management* 73:1300-1306.
- 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 R. E. Yates. 2008. Wolverine population assessment in Glacier National Park, comprehensive summary update. The Ecology and Management of Wildlife and Habitats, RWU 4201, USDA Forest Service, Rocky Mountain Research Station, Missoula, MT.
- ESRI. 2009. ArcGIS version 9.3. Environmental Systems Research Institute, Redlands, CA.
- Fahlman, Å., J. M. Arnemo, J. Persson, P. Segerström, and G. Nyman. 2008. Capture and medetomidine-ketamine anesthesia of free ranging wolverines. *Journal of Wildlife Diseases* 44:133-142.
- Fattebert, J., T. Dickerson, G. Balme, R. Slotow, and L. Hunter. 2013. Long-distance natal dispersal in leopard reveals potential for a three-country metapopulation. *South Africa Journal of Wildlife Research* 43:61-67.
- Flagstad, O., E. Hedmark, A. Landa, H. Brøseth, J. Persson, R. Andersen, P. Segerström, and H. Ellegren. 2004. Colonization history and noninvasive monitoring of a reestablished wolverine population. *Conservation Biology* 18:676-688.
- Gardner, C. L., W. B. Ballard, and R. H. Jessup. 1986. Long distance movement by an adult wolverine. *Journal of Mammalogy* 67:603.
- Grinnell, G. B. 1926. Some habits of the wolverine. *Journal of Mammalogy* 7:30-34.
- Grinnell, J., J. S. Dixon, and J. M. Linsdale. 1937. *Furbearing Mammals of California*. University of California Press, Berkeley.
- Gude, P. H., A. J. Hansen, and D. A. Jones. 2007. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. *Ecological Applications* 17:1004-1018.
- Hash, H. 1987. Wolverine. In M. Novak, J. Baker, M. Obbard, and B. Malloch (editors), *Wild Furbearer Management and Conservation in North America*. Ontario Ministry of Natural Resources, Toronto. Pp. 575-585.
- Hawley, J. E., P. W. Rego, A. P. Wydeven, M. K. Schwartz, T. C. Viner, R. Kays, K. L. Pilgrim, and J. A. Jenks. 2016. Long-distance dispersal of a subadult male cougar from South Dakota to Connecticut documented with DNA evidence. *Journal of Mammalogy* 97:1435-1440.
- Inman, R. M., B. L. Brock, K. H. Inman, S. S. Sartorius, B. C. Aber, B. Giddings, S. L. Cain, M. L. Orme, J. A. Fredrick, B. J. Oakleaf, K. L. Alt, E. Odell, and G. Chapron. 2013. Developing priorities for metapopulation conservation at the landscape scale: Wolverines in the western United States. *Biological Conservation* 166:267-286.
- Inman, R. M., M. L. Packila, K. H. Inman, A. J. McCue, G. C. White, J. Persson, B. C. Aber, M. L. Orme, K. L. Alt, S. L. Cain, J. A. Fredrick, B. J. Oakleaf, and S. S. Sartorius. 2012. Spatial Ecology of wolverines at the southern periphery of distribution. *Journal of Wildlife Management* 76:778-792.
- Inman, R. M., R. R. Wigglesworth, K. H. Inman, M. K. Schwartz, B. L. Brock, and J. D. Rieck. 2004. Wolverine makes extensive movements in the Greater Yellowstone Ecosystem. *Northwest Science* 78:261-266.
- Lofroth, E. C., R. Klafki, J. A. Krebs, and D. Lewis. 2008. Evaluation of live-capture techniques for free-ranging wolverines. *Journal of Wildlife Management* 72:1253-1261.
- Magoun, A. J. 1985. Population characteristics, ecology and management of wolverines in northwestern Alaska. Dissertation, University of Alaska, Fairbanks.
- Moriarty, K. M., W. J. Zielinski, A. G. Gonzales, T. E. Dawson, K. M. Boatner, C. A. Wilson, F. V. Schlexer, K. L. Pilgrim, J. P. Copeland, and M. K. Schwartz. 2009. Wolverine confirmation in California after nearly a century: native or long-distance immigrant? *Northwest Science* 83:154-162.
- Murphy, K., J. Wilmot, J. Copeland, D. Tyers, and J. Squires. 2011. Wolverines in greater Yellowstone. *Yellowstone Science* 19:17-24.
- Nead, D. M., J. C. Halfpenny, and S. Bissell. 1985. The status of wolverines in Colorado. *Northwest Science* 8:286-289.
- Newby, F. E., and P. L. Wright. 1955. Distribution and status of the wolverine in Montana. *Journal of Mammalogy* 36:248-253.
- Newby, F. E., and J. J. McDougal. 1964. Range extension of the wolverine in Montana. *Journal of Mammalogy* 45:485-486.
- Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* 10:949-963.
- Omernik, J. M. 1987. Ecoregions of the conterminous United States. Map (scale 1:7,500,000). *Annals Association of American Geographers* 77:118-125.
- Paquet, P. C., J. Wierzchowski, and C. Callaghan. 1996. Effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. In J. Green, C. Pacas, L. Cornwell, and S. Bayley (editors), *Ecological Outlooks Project: A Cumulative Effects Assessment and Futures Outlook of the Banff Bow Valley*, Department of Canadian Heritage, Ottawa, ON.
- Persson, J. A., Landa, R. Andersen, and P. Segerström. 2006. Reproductive characteristics of female wolverines (*Gulo gulo*) in Scandinavia. *Journal of Mammalogy* 87:75-79.
- Quigley, K. 2000. Hornocker Wildlife Institute immobilization and biological sampling protocols. Hornocker Wildlife Institute, Moscow, ID.
- Riley, S. P., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. *Molecular Ecology* 15:1733-1741.

- 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* 90:3222-3232.
- Shaw, E. P., and J. Ford. 2012. The Lone Wolverine: Tracking Michigan's Most Elusive Animal. University of Michigan Press, Ann Arbor.
- Squires, J. R., D. H. Pletscher, T. J. Ulizio, and F. F. Ruggiero. 2006. The association between landscape features and transportation corridors on movements and habitat-use patterns of wolverines, final report June 2006, Montana Department of Transportation Project No. 8171. Missoula, MT.
- Stoner, D. C., W. R. Rieth, M. L. Wolfe, M. B. Mecham, and A. Neville. 2008. Long-distance dispersal of a female cougar in a basin and range landscape. *Journal of Wildlife Management* 72:933-939.
- Sweanor, L. L., K. A. Logan, and M. Hornocker. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. *Conservation Biology* 14:798-808.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18-30.
- US Geological Survey. 2010. Gap analysis program, National land cover, version 1. US Geological Survey, Boise, ID. Available online at <https://gapanalysis.usgs.gov/gaplandcover/> (accessed 22 January 2010).
- Vangen, K. M., J. Persson, A. Landa, R. Anderson, and P. Segerström. 2001. Characteristics of dispersal in wolverines. *Canadian Journal of Zoology* 79:1641-1649.
- Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. *Conservation Biology* 10:964-976.
- Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280:2126-2128.

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