Wolverine, *Gulo gulo*, Home Range Size and Denning Habitat in Lowland Boreal Forest in Ontario

F. NEIL DAWSON¹, AUDREY J. MAGOUN², JEFF BOWMAN³, and JUSTINA C. RAY⁴

¹Ontario Ministry of Natural Resources, RR#1, 25th Side Road, Thunder Bay, Ontario P7C 4T9 Canada; e-mail: neil.dawson@ ontario.ca

²Wildlife Research and Management (WRAM), 3680 Non Road, Fairbanks, Alaska 99709 USA

³Ontario Ministry of Natural Resources, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8 Canada

⁴Wildlife Conservation Society Canada, 720 Spadina Avenue, #600, Toronto, Ontario M5S 2T9 Canada

Dawson, F. Neil, Audrey J. Magoun, Jeff Bowman, and Justina C. Ray. 2010. Wolverine, *Gulo gulo*, home range size and denning habitat in lowland boreal forest in Ontario. Canadian Field-Naturalist 124(2): 139–144.

We conducted the first radio-telemetry study of Wolverines in northwestern Ontario during the winter of 2003-2004 to determine whether home ranges and movements of Wolverines in lowland boreal forest were typical of this species in other ecosystems and to describe reproductive den sites in this habitat type. Seven Wolverines (3 M, 4 F) were radio-tagged and monitored for 31 to 269 (Mean \pm SE = 153 \pm 35) days using a combination of remotely monitored Argos satellite and conventional aerial telemetry. Male and female 95% minimum convex polygon (MCP) home ranges (\pm SE) during December to October were 2,563 (796) km² and 428 (118) km², respectively, for combined VHF and Argos locations. A lactating female had a 95% MCP home range of 262 km². The den site for this female included large boulders and downed trees, similar to dens described for this species in montane ecosystems. Boulder complexes and downed trees may be critical features of wolverine dens in lowland boreal forests. Mean road densities (\pm SE) within 95% MCP and 50% MCP home ranges were 0.43 (0.13) and 0.33 (0.23) km/km², respectively, and our results suggest that road densities may affect selection of home ranges by Wolverines. The Wolverine population was a resident, reproductive population.

Key Words: Wolverine, Gulo gulo, home range, road density, den, Ontario.

Developing strategies for the conservation of Wolverine (Gulo gulo) populations in light of increasing natural resource extraction in remote regions of lowland boreal forest environments is constrained by a lack of basic ecological data in this habitat type. For example, there have been no radio-telemetry studies of this elusive species in Canada east of the Yukon (Banci 1987) and British Columbia (Krebs et al. 2007) with the exception of one study in the central Arctic north of Yellowknife, Northwest Territories (Mulders 2000*). To date, all radio-telemetry studies of Wolverine have taken place in habitats characterized by mountains or tundra (Hornocker and Hash 1981; Gardner 1985; Magoun 1985; Whitman et al. 1986; Banci 1987; Copeland 1996; Mulders 2000*; Krebs et al. 2007; Persson et al. 2009). Dens typically consist of extensive snow tunnels in drifted snow or under boulders, avalanche debris, or windblown trees covered by snow (Magoun and Copeland 1998), which may not occur in lowland boreal forests.

Research findings from montane and tundra habitats cannot necessarily be applied in Ontario or other lowland boreal forest areas of central Canada. Additionally, the relatively low harvest returns in central Canada compared to western North America may be indicative of lower Wolverine densities in central Canada (Slough 2007), suggesting that lowland boreal forest may constitute marginal habitat for Wolverines.

Our objectives were to determine Wolverine home ranges in the lowland boreal forests of central Canada;

whether the study population was a resident, reproductive population; and document characteristics of any den sites encountered. The location of the study area at the northern limit of road development in the boreal forest also provided an opportunity to evaluate how anthropogenic activity (road density) influenced home range placement. We report results of the first radio-telemetry study of Wolverine home ranges in lowland boreal forests in central North America and describe a reproductive den site found in this habitat type.

Methods

Our study took place during the winter of 2003-2004 in a 6 600-km² area near Red Lake, Ontario (51°N, 93°W) (Figure 1). Forests were comprised primarily of Black Spruce (Picea mariana) and Jack Pine (Pinus *banksiana*); Trembling Aspen (*Populus tremuloides*) and White Birch (Betula papyrifera) were the major deciduous species present. The area has a gently rolling topography with elevations ranging from 250 to 500 m above sea level, with numerous lakes. Large forest fires (>100 km²) occurred in most decades. The study area was being actively logged using the clearcut silvicultural system with individual cut-blocks varying in size from one to several hundred km². Dominant ungulates in the study area were Moose (Alces americanus) and Caribou (Rangifer tarandus), with small numbers of White-tailed Deer (Odocoileus virginianus) occurring in the southern portion. Primary larger predators in the

area were Gray Wolf (*Canis lupus*), Black Bear (*Ursus americanus*), and Canada Lynx (*Lynx canadensis*).

We captured Wolverines in wooden live-traps (Lofroth et al. 2008) between December 13, 2003 and March 24, 2004. Twenty-five traps were set along a mix of plowed and unplowed logging roads, and baited with road-killed White-tailed Deer and Moose, or trapper-killed Beaver (Castor canadensis) carcasses. We checked traps daily and identified and released any non-target species captured. We immobilized captured Wolverines with tiletamine hydrogen chloride (HCl) and zolazepam HCl (Telazol®; Fort Dodge Animal Health, Fort Dodge, IA) at a dosage of 10 mg/kg (Golden et al. 2002). They were then outfitted with a Kiwi-Sat 101 Argos satellite/very high frequency (VHF) radio collar (Sirtrack Limited, Havelock North, New Zealand). We weighed and sexed each study animal, and estimated its age based on tooth wear and development of teats or testes (Magoun 1985). We marked animals in each ear with uniquely numbered and coloured ear tags, and collected tissue samples for DNA analysis. Each Wolverine was returned to the trap and monitored until it had recovered from the drug. Animal capture and handling followed Ontario Ministry of Natural Resources (OMNR) approved animal handling protocols 03-77 and 04-77.

We received Argos locations daily until the collars stopped transmitting. The Argos platform terminal transmitter (PTT) operated on one of two duty cycles: two collars had a duty cycle of 8 hrs/day each day for a predicted lifespan of 120 days and four collars had a duty cycle of 8 hr/day for the first 30 days, followed thereafter by 8 hr every second day for a predicted lifespan of 310 days. We used only Argos location class (LC) 3, 2, and 1 locations in our analysis due to concerns regarding the inherent error (\geq 1500 m) in the other location classes (Keating et al. 1991).

We used a PA-18 Supercub fixed-wing aircraft to locate collared wolverines from the air, one to three times per day (up to five times for a lactating female) between 25 February and 8 April 2004, weather permitting. We circled the signal location at <100 m AGL until we could determine the location (+/- 100m) of the Wolverine, document the habitat type it occupied and, whenever possible, observe the animal from the aircraft and note its behaviour.

We used the Animal Movement Extension to Arc-View 3.2 (Hooge and Eichenlaub 2000*) to delineate 100%, 95%, and 50% minimum convex polygon (MCP) for each collared Wolverine. Harris et al. (1990) have suggested that MCP is the only technique "strictly comparable between studies". We chose 100 and 95% MCPs as the majority of previous Wolverine studies have reported home ranges using one or both of these metrics. To represent core areas of use we delineated 50% MCPs. MCPs were calculated for VHF locations only (HR) for the six wolverines having \geq 14 locations during the 44-day VHF radio-tracking period. We also compared Argos locations (LC = 3, 2, 1) collected during this 44-day period to the VHF-derived home ranges to determine the degree of overlap between the two. VHF locations were insufficient to calculate home ranges for all study animals, whereas Argos locations were more numerous and covered an extended period of animal monitoring. Consequently, to compare home range size and location for all collared wolverines we used a combination of VHF and Argos location data to delineate home ranges (HR_A) based on 100, 95 and 50% MCPs. Although concern has been expressed about autocorrelated data resulting in negatively biased estimates of home range size (Swihart and Slade 1985), we chose to include all locations for three main reasons. First, the movement rate of Wolverines (8-10 kph [Magoun 1985]) allowed the animals to cross their home range, often many times, during our sampling interval (31–269 days) so that the influence of sampling interval bias was likely negligible. Second, we were interested only in home range size and not quantitative estimates of habitat selection which may be influenced by autocorrelation (Swihart and Slade 1997; Otis and White 1999). Finally, we were concerned that we might lose important biological information if we dropped locations (De Solla et al. 1999).

A bootstrap analysis (100 replications) was conducted using the Animal Movement Extension to ArcView 3.2 (Hooge and Eichenlaub 2000*) to determine the asymptote of the number of locations required for home range calculations. Rather than using a visual estimate, we considered the asymptote to have been reached at the point at which all subsequent home range simulations were within 10% of the final bootstrap HR and HR_A simulation for that study animal. The asymptote for 95% MCPs was reached at a mean $(\pm SE)$ value of 23.4 (± 1.7) (range = 18–27) locations for HR calculations and $38.5 (\pm 5.3)$ (range = 27-63) locations for HR_A calculations. Study animals F02 (HR_{A}) and M02 (HR) had too few locations to reach an asymptote and their home ranges are reported but not included in mean home range calculations.

We calculated road densities using a GIS for the 100, 95 and 50% HR_{A} MCPs of each Wolverine. We used the road data available in the provincial roads layer and Forest Resource Inventory (FRI) 1:20 000 digital maps which included primary though tertiary logging roads (OMNR, unpublished data).

We radio-tracked one lactating female up to 5 times per day during March and April 2004 to locate her reproductive den site (Magoun 1985, Magoun and Copeland 1998). We visited the den site on the ground in June 2004. During our radio-tracking flights, we circled this female repeatedly in an attempt to observe any kits that might be with her.

Results

We captured and collared seven Wolverines (four females, three males) during 1088 trap-nights (TN).

Animal	Estimated	Number of Days	NT	100%	95%	50%
	Age (yrs)	Located	N	MCP	MCP	MCP
F01	1	30	33	316	235	41
F02 ¹	1	0	0	_	_	_
F03	1	24	27	495	453	38
F04	3+	14	29	348	332	3
Mean				386	340	27
(SE)				(55)	(63)	(12)
M01	2	29	39	1898	1434	247
M02	1	13	15	2509	2509^{2}	182
M03	3–4	29	40	1685	1308	209
Mean				1791	1371	228
(SE)				(106)	(63)	(19)

TABLE 1. Home range size (HR) based on minimum convex polygons (MCP) derived from all VHF radio telemetry locations for the period 25 February – 8 April 2004 for radio-collared Wolverines (*Gulo gulo*) in northwestern Ontario, Canada.

¹ F02 was killed prior to the VHF monitoring period.

 2 Due to the low number of locations for this animal analysis results for 95 MCP was the same as for 100 MCP and all results for M02 are not included in the mean HR calculations

TABLE 2. Approximation of home range size (HR_A) based on minimum convex polygons (MCP) derived from a combination of Argos satellite/VHF derived locations for Wolverines (*Gulo gulo*) in during December 2003 to October 2004 in northwestern Ontario, Canada.

			HR_{A} (km ²)			Road Density (km/km ²)			
Animal	Period	Days Monitored	Ν	100% MCP	95% MCP	50% MCP	100% MCP	95% MCP	MCP 50%
F01	Dec. 14 – Apr. 19		44	431	365	141	0.489	0.551	0.433
F02 ¹	Dec. 25 – Jan. 25	31	15	301	301 ²	28	1.148	1.148	1.683
F03	Feb. 7 – Oct. 14	251	68	750	656	171	0.119	0.135	0.089
F04	Mar. 23 – Jun 16	85	86	551	262	10	0.315	0.373	0.000
Mean (SE)				577	428	107	0.518	0.552	0.551
				(93)	(118)	(49)	(0.223)	(0.216)	(0.389)
M01	Jan. 15 – Oct. 9	269	50	2506	2117	196	0.147	0.174	0.018
M02	Feb. 24 - May 20	87	45	4340	4109	337	0.454	0.441	0.008
M03	Feb. 28 – Oct. 3	219	61	1783	1463	317	0.363	0.201	0.100
Mean (SE)				2876	2563	283	0.321	0.272	0.042
				(761)	(796)	(44)	(0.091)	(0.085)	(0.029)

¹ F02 was killed prior to the VHF monitoring period, therefore all locations are Argos LC= 3, 2, 1

² Due to the low number of locations for this animal analysis results for 95 MCP was the same as for 100 MCP and all results for F02 are not included in the mean HR_A calculations

Our capture rate for Wolverines was 0.83 per 100 TN, including two recaptures. The mean (SE) mass for females was 9.9 (0.4) kg and for males 13.6 (0.6) kg. All but two captured individuals appeared to be year-lings or sub-adults, based on tooth wear. One female (F04) was lactating at the time of her capture on 23 March.

A total of 3369 Argos locations for all Wolverines was received in the following location classes (LC): LC3 = 2.1%; LC2 = 2.6%; LC1 = 4.9%; LCA = 11.8%; LCB = 22.5%; LC0 = 2.8% and LCZ = 53.4%. Argos LC 3, 2 and 1 fixes were available for five of the seven Wolverines during the 44-day VHF monitoring period. Study animal F02 was killed prior to the monitoring period, and no fixes in these LCs were obtained from Wolverine M01 during this period. Of the 32 Argos fixes obtained from the remaining 5 Wolverines during the VHF monitoring period, 28 (87.5%) were within the VHF-derived 100% MCP for the appropriate animal. The distances of the four locations falling outside the 100% MCP were 0.6 km for study animal F03, 2.3 km for F04, and 3.5 and 8.2 km for M02.

Male home range estimates based on both VHF locations only (HR; Table 1) and a combination of VHF and Argos locations (HR_A. Table 2) were substantially larger than estimates for females in all cases; mean values for males were about 4.5 times larger than for females (Table 1, Figure 1). The lactating female F04 had the smallest HR_A for both 95 and 50% MCP home ranges (Table 2).

We documented three, and possibly four, mortalities among the collared animals. Study animals F01 and F02 were incidentally trapped 13 months and 31 days after collaring, respectively. We detected no mortality of male Wolverines during the study; however, M02 was killed by a vehicle on 22 January 2009, 100 km E of his last known location and 18 km S of his capture site. The fate of F04 was unclear; we located her collar and some animal remains about 100 m apart 4 months after she was collared, and there were signs of both Wolf and Black Bear in the vicinity. We were unable to determine if the remains were those of F04, or if she simply shed her collar.

We compared road densities $(\pm SE)$ within the 100, 95, and 50% MCP HR_A (Table 2). Road density averaged 0.43 (0.13) km/km² within 95% MCP HR_{Λ} and 0.33 (0.23) km/km² within 50% MCP HR_A. A Wilcoxon's signed-rank test demonstrated that road densities were not significantly lower within the 50% MCP HR, (z = -1.18, p = 0.237). It is notable, however, that 95 and 50% MCP home ranges for the 2 female Wolverines incidentally killed by trappers had the highest road densities among our study animals (95% MCP = 0.55and 1.15 km/km², 50% MCP = 0.43 and 1.68 km/km²). Excluding these two animals, mean road densities (SE) within the 95 and 50% MCPs were 0.27 (0.06) and 0.04 (0.02) km/km², respectively, and were significantly different (z = -2.02, P = 0.043). The road density within the one denning female's (F04) 50% MCP HR_{Δ} was 0.

Study animal F04 was confirmed to be a reproductive female when lactation was noted at the time of her capture on 23 March 2004. We subsequently located her den site and observed her bringing food to the den and moving a kit between two structures at the den site. Three different structures used at this den site were located approximately 300 m from each other on a hill in second-growth timber. FRI data described the stand as 60% Black Spruce, 30% Jack Pine, and 10% poplar (Trembling Aspen), 12 m in height, 70% stocking, and 83 years of age. This stand was located within the perimeter of a 104 km² burn that occurred in 1956 (OMNR, unpublished data). One structure at the den site consisted of a complex of large boulders approximately 60 m long and 30 m wide. The largest boulder was about 4 m in diameter and there were many large spaces under the boulders. Another structure, near the top of the hill at the edge of a small opening in the forest, consisted of fallen trees covered with snow. The third structure was in a dense stand of trees and could not be observed from the aircraft. Only the boulder structure was visited on the ground after the snow melted. The hill where the den site was located was 7 km from the nearest forestry road and cutblock, 5 km from a lightly used mining trail, and approximately 10 km from active logging.

Discussion

For six of our study animals, the 95% MCP HR based on VHF locations only were within the limits for VHF-derived home range estimates reported by other researchers, regardless of how home range size was calculated (see: Mulders 2000*; Krebs et al. 2007; Persson et al. 2009). For all of our study animals, home range estimates (HR_A) based on a combination of VHF and Argos locations indicate that home range sizes for Wolverines in lowland boreal forest in Ontario are similar to those in other habitat types. Moreover, the larger size of male home ranges compared to those of females and the overlap in male and female home ranges (Figure 1) were consistent with patterns reported from other areas (Banci 1994).

The 95% HR_A home range for the lactating female (F04) in this study was near the upper limit of home range size for reproductive females using similar data sets (see Mulders 2000*; Krebs et al. 2007; Persson et al. 2009). The presence of a lactating female in our study area and the results of a subsequent aerial survey for Wolverine tracks in a larger area centered on our study area (Magoun et al. 2007), indicated that the Wolverine population in our study area was a resident, reproductive population near the southern edge of the species' distribution in Ontario.

The presence of snow-covered boulders and fallen trees at F04's reproductive den site is not surprising given the description of typical reproductive dens from other study areas (Magoun and Copeland 1998). However, the occurrence of large boulder complexes is much more limited in our study area than in montane habitats where reproductive dens have been described. Moreover, because the boreal forest does not support the deep, wind-hardened snowdrifts used for reproductive dens in tundra (Magoun 1985), structures within the snow layer such as trees and boulders are likely to be critical features of Wolverine dens in lowland boreal forests. Given the potential importance of boulder complexes in our study as reproductive den sites for Wolverines in lowland boreal forest, we recommend that the distribution and characteristics of these boulder complexes be documented in future studies of potential Wolverine habitat.

Our results also suggest that road densities may affect selection of home ranges by Wolverines, in accordance with the broader distribution patterns of this species in the area (Magoun et al. 2007; Bowman et al. 2010). Although Wolverines are generally reported to prefer undeveloped areas, we could find no studies that reported road densities within Wolverine home ranges (Banci 1994; May et al. 2006). Habitat modeling work by Carroll et al. (2001) reported that Wolverine occurrences were negatively associated with

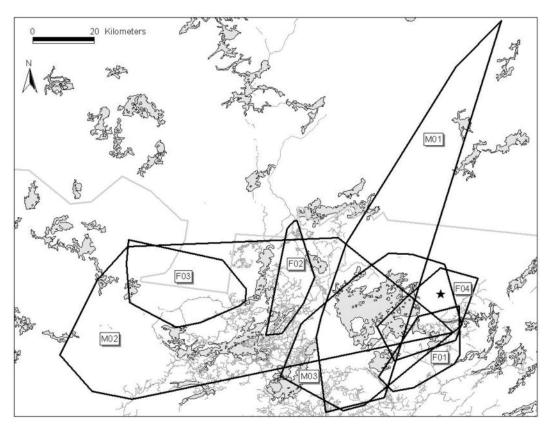


FIGURE 1. Locations of 100% MCP home ranges for 3 male (M) and 4 female (F) Wolverines (*Gulo gulo*) in Ontario, Canada. Locations were derived with a combination of Argos satellite and VHF radio telemetry during December 2003 to October 2004. The road network (mostly logging roads) is depicted by solid gray lines and lakes are shown in gray. The star indicates the location of female F04's den. The thick gray line crossing at approximately the mid point indicates the northern limit of commercial logging.

road densities >1.7 km/km². However, Rowland et al. (2003) suggested that this threshold may be lower, because Wolverine abundance estimates in their watershed-scale models varied between low road densities (<0.44 km/km²) and moderate road densities (0.44 – 1.06 km/km²). Results from our study in lowland boreal forests of central Canada are consistent with their predictions for the interior northwest area of the United States (Rowland et al. 2003). The mean road density for 95% MCP HR_A for all Wolverines in this study was 0.43 km/km², and for the two Wolverines whose home ranges had higher road densities than the suggested threshold of 0.44 km/km², the risk of mortality due to anthropogenic factors appeared to increase.

Roads may also have an important influence on den site selection. May (2007) found that the mean distance (SE) from natal dens to public and private roads was 7461 (206) m and 3058 (120) m, respectively. The reproductive den of Wolverine F04 in our study was 7 km from an active logging road and 5 km from a lightly used mining trail. In central lowland boreal forests maintaining low road densities (<0.44 km/km²) and large areas of undisturbed forest to provide isolated denning sites may be particularly important to Wolverines because they cannot select high-elevation alpine habitats to reduce predation risk and human disturbance (Krebs et al. 2007), as do populations in the West. Further study of movements and den-site selection by Wolverines in this region is needed to determine if Wolverines adjust their movements and home ranges to accommodate changes in land use patterns.

Acknowledgments

Project funding was provided by the Ontario Living Legacy Trust Fund, Wildlife Conservation Society Canada, The Wolverine Foundation, Inc., and the Ontario Ministry of Natural Resources. We could not have accomplished our fieldwork without the dedicated support of field technicians Richard Klafki and Shannon Walshe who were with the project both years. Geoff and Catherine Lipsett-Moore were instrumental in project set-up and design. Additional field technicians who provided valuable support were Marek Klich, Laura Bruce, and Tim Carter. We also thank Dr. Heather Reid who served as our advising veterinarian. The support of staff at the Red Lake OMNR office and from the Red Lake and Ear Falls trappers was also greatly appreciated. Additional thanks to K. B. Aubry and T. Jung for their constructive review comments on the manuscript.

Documents Cited (marked * in the text)

- Hooge, P. N., and B. Eichenlaub. 2000. Animal movement extension to ArcView. Alaska Science Center – Biological Science Office, USGS. Anchorage, Alaska, USA.
- Mulders, R. 2000. Wolverine ecology, distribution, and productivity in the Slave Geological Province. Final Report to the West Kitikmeot/Slave Study Society. Department of Resources, Wildlife and Economic Development, Government of the Northwest Territories, Yellowknife, Northwest Territories, Canada. 90 pages.

Literature Cited

- **Banci, V.** 1987. Ecology and behaviour of wolverine in Yukon. M.Sc. thesis, Simon Fraser University, Burnaby, British Columbia, Canada. 178 pages.
- Banci, V. 1994. Wolverine. Pages. 99-127 in The scientific basis for conserving forest carnivores: American marten, fisher, lynx and wolverine in the western United States. *Edited by* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, L. J. Lyon, and W. J. Zielinski USDA Forest Service, General Technical Report RM-254, Fort Collins, Colorado, USA.
- Bowman, J., J. C. Ray, A. J. Magoun, D. S. Johnson, and F. N. Dawson. 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. Canadian Journal of Zoology. 88: 454-467.
- Carroll, C., R. F. Noss, and P. C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications 11: 961-980.
- **Copeland, J. P.** 1996. Biology of the wolverine in central Idaho. M.Sc. thesis, University of Idaho, Moscow, Idaho, U.S.A. 138 pages.
- De Solla, S. R., R. Bonduriansky, and R. J. Brooks. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. Journal of Animal Ecology 68: 221-234.
- Gardner, C. L. 1985. The ecology of wolverines in southcentral Alaska. M.Sc. thesis, University of Alaska, Fairbanks, Alaska, USA. 82 pages.
- Golden, H. N., B. S. Shults, and K. E. Kunkel. 2002. Immobilization of wolverines with Telazol from a helicopter. Wildlife Society Bulletin 30: 492-497.
- Harris, S., W. J. Cresswell, P. G. Forde, W. J. Trewhella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20: 97-123.

- Hornocker, M. G., and H. S. Hash. 1981. Ecology of the wolverine in northwestern Montana. Canadian Journal of Zoology 59: 1286-1301.
- Keating, K. A., W. G. Brewster, and C. H. Key. 1991. Satellite telemetry: performance of animal-tracking systems. Journal of Wildlife Management 55: 160-171.
- Krebs, J. A., E. C. Lofroth, and I. Parfitt. 2007. Multiscale habitat use by wolverines in British Columbia. Journal of Wildlife Management 71: 2180-2192.
- 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. Ph.D. dissertation, University of Alaska, Fairbanks, Alaska, USA. 197 pages.
- Magoun, A. J., and J. P. 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.
- May, R., A. Landa, J. van Dijk, J. D. C. Linnell, and R. Andersen. 2006. Impact of infrastructure on habitat selection of wolverines *Gulo gulo*. Wildlife Biology 12: 285-295.
- May, R. 2007. Spatial ecology of wolverines in Scandinavia. Ph.D. dissertation, Norwegian University of Science and Technology, Trondheim, Norway. 192 pages.
- Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63: 1039-1044.
- Persson, J., P. Wedholm, and P. Segerström. 2009. Space use and territoriality of wolverines (*Gulo gulo*) in northern Scandinavia. European Journal of Wildlife Research 56: 49-57.
- 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.
- Slough, B. G. 2007. Status of the wolverine *Gulo gulo* in Canada. Wildlife Biology 13(Suppl.2): 76-82.
- Swihart, R. K., and N. A. Slade. 1985. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49: 1019-1025.
- Swihart, R. K., and N. A. Slade. 1997. On testing for independence of animal movements. Journal of Agricultural, Biological, and Environmental Statistics 2: 48-63.
- Whitman, J. S., W. B. Ballard, and C. L. Gardner. 1986. Home range and habitat use by wolverines in southcentral Alaska. Journal of Wildlife Management 50: 460-462.

Received 15 January 2010 Accepted 3 August 2010