

DISTRIBUTION OF GRAY WOLVES IN RESPONSE TO HABITAT AND HUMAN PRESENCE IN THE ABSAROKA-BEARTOOTH WILDERNESS, MONTANA

Gidske Houge¹, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Post Box 5003, NO-1432 Ås, Norway
Daniel B. Tyers², USDA Forest Service, Gardiner District, Gardiner, Montana 59030-005
Jon E. Swenson, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Post Box 5003, NO-1432 Ås, Norway and Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway

ABSTRACT

Since wolves (*Canis lupus*) were reintroduced into Yellowstone National Park (YNP) in 1995 and 1996, the population has increased and expanded into adjacent areas. In this study, we documented the distribution of wolves in relation to habitat and human presence in the Absaroka-Beartooth Wilderness (ABW) in Montana during the summers of 2005 and 2006, prior to the onset of wolf hunting in 2009, by observing tracks and scat along USDA Forest Service (USFS) trails. Our results indicated that wolves in the ABW 1) were primarily located near the boundary of YNP, 2) did not prefer forested habitats when traveling on trails, 3) did not avoid USFS cabins or outfitter camps, and 4) did not differentiate between permanent cabins and temporary camps.

Key words: Absaroka-Beartooth Wilderness, *Canis lupus*, gray wolf, human-wolf interactions, Montana, sign survey.

INTRODUCTION

Historically, the gray wolf (*Canis lupus*) was persecuted intensively by European settlers in North America (Bangs and Fritts 1996). In 1884, the Territorial Government of Montana initiated wolf bounties as part of an official eradication effort (USDI Fish and Wildlife Service et al. 2006). The last known wolf in Yellowstone National Park (YNP) was shot in 1926 (Smith 2005), and by the 1930s wolf populations had disappeared from Montana, Idaho, and Wyoming (Bangs and Fritts 1996). It was protected by law in 1974 under the federal Endangered Species Act of 1973 (Smith 2005, USDI Fish and Wildlife Service et al. 2006).

Wolves were reintroduced into YNP in 1995 as a nonessential experimental population, i.e., not essential for the survival of the species, so it could be managed with more flexibility (USDI Fish and

Wildlife Service et al. 2006). A total of 31 wolves were captured in Alberta and British Columbia, Canada, and released into YNP in 1995 and 1996 (Smith 2005). At the end of 2006, an estimated 390 wolves were in the Greater Yellowstone Recovery Area (USDI Fish and Wildlife Service et al. 2007). This population of wolves in Montana was removed from the protection of the Endangered Species Act on 4 May 2009, and the State of Montana began a quota-regulated hunting season in the fall of 2009. With the August 5, 2010 federal court decision that reinstated Endangered Species Act protection for wolves in the Northern Rocky Mountains, federal law again guides Montana's management of the state's wolf population.

Key components of wolf habitat include access to sufficient prey throughout the year, suitable and somewhat secluded denning and rendezvous sites, and sufficient space with minimal exposure to humans (USDI Fish and Wildlife Service 1987). Wolves use many different types of habitat,

¹Stømsbuveien 7j, NO-4835 Arendal, Norway

²USDA Forest Service, Interagency Grizzly Bear Study Team, Northern Rockies Science Center, 2327 University Way Ste.2, Bozeman, MT 59715

including nonforested areas such as deserts, prairies, swamps and tundra (Fuller et al. 2003). They are still found in open habitats, for instance in Spain (Fritts et al. 2003, Blanco et al. 2005), but studies from Poland (Jedrzejewski et al. 2004, Jedrzejewski et al. 2005), Italy (Ciucci et al. 1997, Massolo and Meriggi 1998) and North America (Mladenoff et al. 1995, Johnson et al. 2005, Oakleaf et al. 2006) have shown that they prefer forests.

Early studies on the effects of human presence on wolves have shown that they avoid areas where road densities are above a particular threshold value, such as 0.45 (Mladenoff et al. 1995, Mladenoff et al. 1999), 0.58 (Thiel 1985, Jensen et al. 1986, Mech et al. 1988) or 0.70 km/km² (Fuller et al. 1992). Roads serve as an indicator of human presence, and because humans are a major contributor to wolf mortality (Mech 1977, Forbes and Theberge 1992, Wydeven et al. 1992, Boyd and Pletscher 1999), wolves risk being killed by trappers, hunters, or vehicles when they are near roads (Jensen et al. 1986, Mech et al. 1988). More recent studies have moderated this conclusion by indicating that roads with relatively low levels of use can benefit wolves by creating easy paths of travel (Thurber et al. 1994, James and Stuart-Smith 2000, Pedersen et al. 2003, Whittington et al. 2005). Merrill (2000) reported successful wolf reproductions at road densities of 1.42 km/km² and Thiel et al. (1998) found that wolves denned close to areas with high degrees of human activity. These two cases illustrate that the main concern is the attitudes of local people, not the roads themselves (Carroll et al. 2003). Wolves avoid human settlements and buildings in some areas (Theuerkauf et al. 2003a, Jedrzejewski et al. 2004, Jedrzejewski et al. 2005, Kaartinen et al. 2005), but are not affected by them (Pedersen et al. 2003), or may actively seek them out in search of food, in other areas (Fritts et al. 2003). To our knowledge, researchers have not investigated whether wolves differentiate between permanent and temporary structures.

The goal of this study was to document the distribution of wolves in the Absaroka-Beartooth Wilderness (ABW), immediately north of YNP, as indicated by their scats and tracks along USFS trails to test the following hypotheses: 1) Because several studies from North America have found that wolves preferred forested habitat, we predicted that there would be sign on trails more often in forested areas than in areas without forest cover; 2) If wolves actively avoid humans and their activities, we would expect sign less often on trails near outfitter camps and USFS cabins than on trails far from these structures; 3) If wolves habituate more easily to permanent structures, we predicted that wolves would avoid temporary outfitter camps more than permanent USFS cabins.

STUDY AREA

The study was conducted in the ABW, which is located in south-central Montana adjacent to the northern boundary of YNP (Fig. 1). The USFS manages this area, which encompasses portions of three National Forests (Gallatin, Shoshone and Custer) and five Ranger Districts (Gardiner, Beartooth, Big Timber, Clark's Fork, and Livingston). The ABW has a total area of 3819 km², primarily in Montana but with a small portion in Wyoming. The area was officially designated in 1978 as a Wilderness Area under the U. S. Wilderness Act of 1964. Regulations prohibit use or possession of motorized and mechanized equipment, which was intended to minimize disturbance to wildlife and to preserve the wilderness character.

Our effort centered primarily in the Gardiner Ranger District (GRD), which borders YNP and comprises about one-third of the ABW. The GRD has the highest ungulate/prey density in the ABW, is adjacent to YNP, and wolf packs occurred within its boundaries. We also conducted field work in other ABW Ranger Districts, but not as intensively as in the GRD.

The terrain is remote, rugged, mountainous, and consists of deeply incised glacial valleys and high plateaus. Vegetation includes montane forests

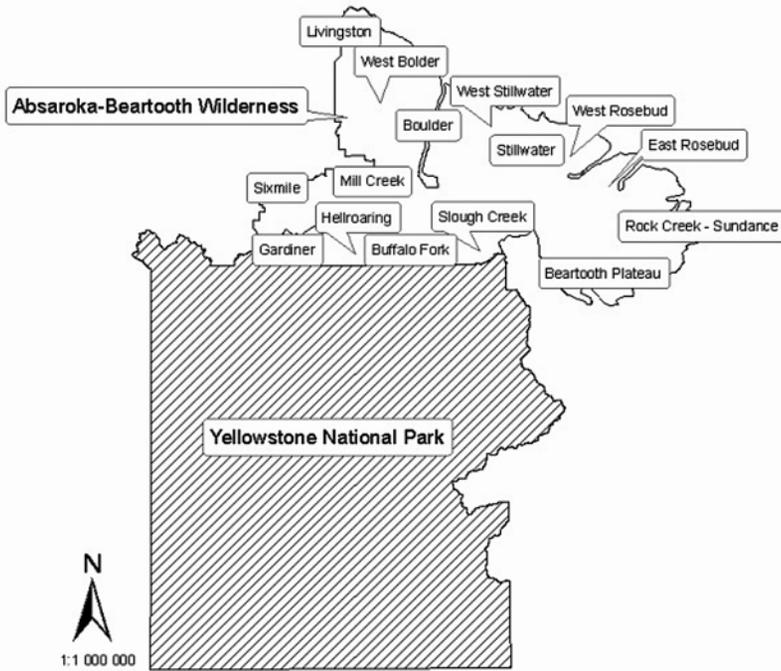


Figure 1. Yellowstone National Park and the Absaroka-Beartooth Wilderness Montana and Wyoming, showing the major drainages within the wilderness area.

dominated by Douglas-fir (*Pseudotsuga menziesii*), quaking aspen (*Populus tremuloides*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and limber pine (*P. flexilis*), and subalpine forests dominated by subalpine fir (*Abies lasiocarpa*) and whitebark pine (*P. albicaulis*) (Alden et al. 1999, DeBlander 2001). The vegetation at high elevations includes tundra and perennial snowfields. Riparian areas are comparatively limited, but are ecologically important. Carnivorous mammals occurring in this study area include grizzly bears (*Ursus arctos*), black bears (*U. americanus*), mountain lions (*Felis concolor*), lynx (*Lynx canadensis*), wolverine (*Gulo gulo*), wolves, coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*). Ungulate species include elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), bighorn sheep (*Ovis canadensis*), moose (*Alces alces*), and mountain goats (*Oreamnos americanus*).

The varied topography of the Rocky Mountains creates a wide range of weather

conditions and unique local climates (Alden et al. 1999). At high elevations, there is snow from early October to early July, and at lower elevations, from late October to late May (Despain 1990). The annual rainfall in the Rocky Mountains ranges from 18 to 109 cm (Despain 1990).

METHODS

The ABW has about 1437 km of trails, which we delineated into 379 labeled and easily defined segments, generally from one trail junction to another. The trail segments varied between 0.2 to 13.4 km in length and were used by the GRD Forest Service backcountry crew, hikers, etc. between 15 May and 1 November each year. Tasks of the backcountry crew were many, and sampling for wolf sign was done while hiking the trails. The backcountry crew used 278 trail segments in 2005 and 216 in 2006. The backcountry crew recorded the number of wolf scats and tracks representing individual wolves for each segment on each trip. Multiple tracks scattered over a distance were thought to have originated

from one individual if the tracks were going in the same direction within the same trail segment. The crew was trained to identify wolf scats and tracks by Jim Halfpenny, director of “A Naturalist’s World” in Gardiner.

Common ways to differentiate between wolf and dog (*Canis familiaris*) sign, e.g., difference in paw size, movement behavior, amount of hair and bone in scats, are not always reliable (Aronson and Eriksson 1992, Landa 1999). To minimize uncertainty, we considered the frequency by which trail segments were used by hikers with dogs. If the crew encountered hikers with dogs, or the trail was known to be a popular recreation area for people with dogs, we considered the probability of a large canine track belonging to a dog to be high and disregarded all observed sign. However, YNP has a ban on dogs, so we classified sign found on ABW trails originating from YNP as wolf sign.

We distinguished coyote tracks from wolf tracks based on the fact that wolves have larger paws than coyotes (Murray and Lariviere 2002). To differentiate between coyote and wolf scat, we used Halfpenny’s (1986) cutoff diameter and classified all canine scat ≥ 23 mm as wolf scat. The large overlap in diameter (Weaver 1979, Reed et al. 2004, Prugh and Ritland 2005) caused some bias because some of the collected scats could be from coyotes, and small wolf scats would be classified as coyote and not included in the sample.

Sign of wolves was recorded as a binary variable, observed or not. We then created maps using ArcGIS 9.1 and analyzed data using a combination of tools in ArcGIS 9.1, Hawth’s Analysis Tools 3.26 and ET Geo Wizards 9.6. We classified trail segments as forested or nonforested by using vegetation maps provided by the Gallatin National Forest. Permanent structures included three USFS cabins located on Slough Creek, Buffalo Fork and Hellroaring creeks, as well as the Silver Tip Ranch in Slough Creek. Temporary structures included 13 outfitter camps. Outfitter camps were present in the ABW from 2 wks to 4 mos. The

USFS cabins were used between May and November.

We tested the hypotheses with a binary logistic regression (Agresti 2002) using MINITAB 14 Statistical Software (Minitab Inc). When testing hypothesis No. 3 (wolves should be found farther from permanent than temporary structures), we measured the distance from each trail to the nearest structure. When testing hypothesis No. 1 (wolves should prefer forested habitats), we classified the habitat type for each trail according to the dominant vegetation type along its length. To test for other variables, we included the distance to the YNP boundary in the model, using the shortest distance from the center of each trail segment to the boundary of the YNP. We corrected for sampling effort by including the average number of times a trail had been sampled in the model. We used only trail segments within the GRD for this test. Hypotheses were tested using a significance threshold of $P < 0.05$.

RESULTS

The monitoring frequency for trail segments decreased from 2005 to 2006 (Table 1) with sampling efforts of 1050 km and 709 km, respectively, but the average number of times a trail was sampled increased from 2005 to 2006. The unadjusted total amount of sign in 2005 was 115; 74 tracks and 41 scats. In 2006, this doubled to 241; 137 tracks and 104 scats. A significantly greater frequency of trail segments (all segments) showed wolf presence in 2006 than 2005 ($\chi^2 = 22.28$, d.f. = 1, $P < 0.001$). In 2005, the majority of sign was located from the eastern part of the Gardiner Basin, eastwards through the Hellroaring, Buffalo Fork and Slough Creek drainages, to the southern part of the Stillwater Drainage and was also high in the southern part of the Beartooth Plateau and the western part of the Boulder Drainage, close to the Mill Creek Drainage. Single cases of wolf sign were registered on four different trail segments on the north-eastern boundary of the ABW. In 2006, the areas with the highest amount of sign shifted

Table 1. Summary statistics for the gray wolf sign survey in the Absaroka-Beartooth Wilderness, south-central Montana, USA (2005-2006).

| | 2005 | 2006 |
|---------------------------------------|------|------|
| No. trail segments | 278 | 216 |
| No. times a trail was traveled | | |
| \bar{X} | 3.08 | 6.24 |
| SD | 2.85 | 6.70 |
| Range | 1-22 | 1-52 |
| Scats/trail segment | | |
| \bar{X} | 0.15 | 0.48 |
| SD | 0.47 | 1.14 |
| Range | 0-3 | 0-6 |
| Tracks/trail segment | | |
| \bar{X} | 0.27 | 0.63 |
| SD | 0.64 | 1.22 |
| Range | 0-4 | 0-6 |

slightly. Sign was greater along the southern boundary of the ABW, i.e., from the middle of the Gardiner Basin, eastwards through the Hellroaring, Buffalo Fork and Slough Creek drainages. There was, however, a gap in the presence of sign between the Gardiner Basin and Hellroaring/Buffalo Fork/Slough Creek drainages. There still was sign in the southern part of the Beartooth Plateau, but the sign in the western part of the Boulder Drainage continued over into the Mill Creek Drainage in 2006. In addition to wolf sign, wolves were observed once and wolves were heard howling four times during 2006 by the backcountry crew.

According to the binary logistic model we used to explain wolf presence in the GRD, wolves did not avoid temporary

Table 2. Logistic regression model explaining gray wolf presence in the Gardiner Ranger District, Absaroka-Beartooth Wilderness, south-central Montana, in 2005 and 2006.

| Predictor | Coefficient | P-value |
|---|-------------|---------|
| Constant | 1.962 | 0.125 |
| Distance to camps/cabins (km) | 0.029 | 0.374 |
| Distance to Yellowstone National Park (km) | -0.091 | 0.013 |
| Camp type (categorical) | 0.239 | 0.687 |
| Forest (categorical) | -1.260 | 0.304 |
| Average number of times a trail segment was traveled | 0.301 | 0.005 |
| Distance camps/cabins (km) * Average number of times a trail segment was traveled | -0.039 | 0.002 |

camp or permanent cabins or differentiate between them, nor did they use forested and nonforested trail segments differently (Table 2). Wolf presence was significantly and negatively correlated with distance to YNP. According to the logistic model, 50 percent probability of finding wolf sign occurred when the trail segment was 21.5 km from the YNP boundary. The variable “average number of times a trail segment was traveled” was added to the model to correct for effort and naturally showed that there was a higher probability of encountering wolf sign if the trail had been traveled often. By including this variable, we corrected for the bias that it otherwise would have caused in the analysis of the effects of the other variables. The interaction term showed that the field crew traveled less on trail segments located far from camps and cabins. The fit of the model was not high, however. A Pearson goodness-of-fit was 0.35, which indicated that the model did not explain much variation in wolf distribution.

DISCUSSION

Track surveys and other noninvasive methods are becoming more popular in wildlife and conservation research, because of few negative effects, such as immobilizing and handling the animals, in addition to being less time-consuming and expensive (Kendall et al. 1992, Smallwood and Fitzhugh 1995, Alexander et al. 2005).

Distribution of wolves

As expected from our hypothesis, a logistic regression analysis corrected for effort indicated that the probability of finding wolf sign in the ABW was higher in the vicinity

of YNP. Given the dispersal capabilities of wolves, it is surprising that wolves had not traveled further into the wilderness area. Wolves have been recorded dispersing long distances, such as 670 (Van Camp and Gluckie 1979), 732 (Ballard et al. 1983), 840 (Boyd and Pletscher 1999) and 886 (Fritts 1983) km. Even though wolves have a great capacity for dispersal, they maximize their chance of breeding rather than maximizing resources (Mech and Boitani 2003). Studies have shown that territorial species are attracted to areas that already are inhabited (Stamps 1988, Smith and Peacock 1990, Ray et al. 1991), presumably because areas that are occupied by conspecifics offer mates and an assurance of good habitat (“cuing”) (Stamps 1988). The colonization rate for wolves in the GYA averages 9.78 km/year, which is considerably lower than would be expected from the high reproductive rate and long distance dispersal of wolves (Hurford et al. 2006) and was consistent with our results. In addition to the drainages located close to YNP, sign also was detected on the southern slope of the Beartooth Plateau and in the Boulder/Mill Creek drainages, perhaps due to the occurrence of reproducing packs in these areas. Single tracks and scats were observed on separate trail segments in 2005. These trail segments were located on the wilderness boundary from the north to the east.

Use of forested and nonforested habitat

Contrary to our hypothesis, we detected no difference in use of forested and nonforested habitats by wolves. This may have been an error due to definitions used in the study because the vegetation maps used in the analysis divided vegetation into only four categories; aspen (forest), conifer (forest), sagebrush grassland (nonforested) and willow (nonforested), which may have been too coarse to allow any patterns of selection to be manifested. Also, trail segments often crossed several vegetation types, but only the dominant vegetation type was recorded for each trail. The dominant vegetation type was usually forest, so the number of trail segments with nonforested

habitat was low compared to the number of trail segments with forest. Although the results did not support our hypothesis and assuming that they were not a statistical error, they did fit well with the fact that wolves are habitat generalists (Fuller et al. 2003) and are limited only by access to a sufficient prey base when not hunted by humans (USDI Fish and Wildlife Service 1987). The method we used possibly did not allow documentation of the true preference for forested and nonforested areas but only showed if wolves used trails more or less in these habitats. Because the trails represent easy paths of travel (Thurber et al. 1994, James and Stuart-Smith 2000, Whittington et al. 2005, Shepherd and Whittington 2006), there is no reason why wolves should leave the trails once they enter a different habitat.

Avoidance of humans

Also contrary to our hypothesis, we found no evidence that wolves either differentiated between temporary outfitter camps and permanent USFS cabins, or avoided camps or cabins. The outfitter camps and USFS cabins in the ABW differed in two main aspects. The cabins are permanent structures, whereas the camps are temporary. Also, the camps are always occupied by one or more people who look after the camp, whereas the cabins are occasionally vacant of people. Our results suggested that wolves view these structures equally.

In a study conducted in the Canadian central Arctic, Johnson et al. (2005) found that wolves selected mineral exploration sites and outfitter camps, probably because of the availability of food rewards. However, with the “leave no trace” policies in the ABW, i.e. packing out all trash, leftover food, and litter, there is little or no food around camps and cabins to attract wolves. Generally, wolves are believed to avoid human contact spatially in areas with low human density, and temporally in areas with high human density (Vilà et al. 1992, Ciucci et al. 1997, Pedersen et al. 2003, Theuerkauf et al. 2003a). In Poland,

where human density is high, wolves avoid being in the same place at the same time as humans (Theuerkauf et al. 2003a, Theuerkauf et al. 2003b). Wam (2003) studied wolf behavior towards humans in densely populated parts of Norway and found that, when approached, wolves ran away with a mean tolerance distance of 257 m. Because our data only included sign to indicate wolf presence, we were unable to determine whether wolves in the ABW avoided humans temporally. In areas with no legal or illegal hunting, however, wolves are thought to be less wary of humans (Thiel et al. 1998, Merrill 2000, McNay 2002, Whittington et al. 2005), and wolves are currently colonizing a wide range of habitats that previously were not thought to be suitable wolf habitat (Mech 1995). A study investigating carnivore responses to big-game hunting on the boundary between ABW and YNP found that wolves did not change their movement patterns during the pre-hunt and hunting periods (Ruth et al. 2003). Because wolves in the ABW and YNP were not hunted by humans during our study, it is reasonable to conclude that wolves do not avoid humans in this area.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

We found no evidence that wolves in the ABW selected between forested and nonforested habitats, differentiated between temporary outfitter camps and permanent USFS cabins, or avoided these centers of human activity. The latter may suggest that little illegal hunting of wolves was taking place in the ABW. However, the model gave a relatively poor fit, which suggested that important factors explaining wolf presence were not included in the model. Possible additional factors that are important for the distribution of wolves are location of prey and reproducing wolf packs. Therefore, the model may have been improved by incorporating seasonal distribution of ungulates, locations of active wolf dens, and by including more seasons of data. Our results suggest that, at present, no special

precautions are needed to ensure survival of wolves in the ABW. We recommend that this study be continued to document whether the behavior of wolves in the ABW changes after the advent of hunting in 2009.

ACKNOWLEDGEMENTS

We thank Gerry Bennett, Dick Ohman and Jim Wood for financial support and Heidi Bergsjø, Herbjørg Arntsen, Kristine Ulvund, Jeremy Zimmer, Siri Framness, Craig Olwert, and Hans Ole Ørka for help with the data and the paper. We also thank everyone that worked on the Forest Service trail crew in 2005 and 2006.

LITERATURE CITED

- Agresti, A. 2002. *Categorical data analysis*. John Wiley & Sons, Hoboken, New Jersey.
- Alden, P., B. Cassie, J. Grassy, J. D. W. Kahl, A. Leventer, D. Mathews, and W. B. Zomlefer. 1999. *National Audubon Society field guide to the Rocky Mountain states*. Alfred A. Knopf, New York.
- Alexander, S. M., P. C. Paquet, T. B. Logan, and D. J. Saher. 2005. Snow-tracking versus radio telemetry for predicting wolf-environment relationships in the Rocky Mountains of Canada. *Wildlife Society Bulletin* 33:1216-1224.
- Aronson, Å. and P. Eriksson. 1992. Dyrespor og kunsten å spore. (In Norwegian). J. W. Cappelens Forlag, Oslo, Norway.
- Ballard, W. B., R. Farnell, and R. O. Stephenson. 1983. Long-distance movement by gray wolves, *Canis lupus*. *Canadian Field-Naturalist* 97:333-333.
- Bangs, E. E. and S. H. Fritts. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildlife Society Bulletin* 24:402-413.
- Blanco, J. C., Y. Cortes, and E. Virgos. 2005. Wolf response to two kinds of barriers in an agricultural habitat in Spain. *Canadian Journal of Zoology* 83:312-323.
- Boyd, D. K. and D. H. Pletscher. 1999. Characteristics of dispersal in a

- colonizing wolf population in the central Rocky Mountains. *Journal of Wildlife Management* 63:1094-1108.
- Carroll, C., M. K. Phillips, N. H. Schumaker, and D. W. Smith. 2003. Impacts of landscape change on wolf restoration success: Planning a reintroduction program based on static and dynamic spatial models. *Conservation Biology* 17:536-548.
- Ciucci, P., L. Boitani, F. Francisci, and G. Andreoli. 1997. Home range, activity and movements of a wolf pack in central Italy. *Journal of Zoology* 243:803-819.
- DeBlander, L. T. 2001. Forest Resources of the Custer National Forest. United States Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Despain, D. G. 1990. Yellowstone vegetation. Consequences of environment and history in a natural setting. Roberts Rinehart Publishers, Boulder, Santa Barbara, West Cork.
- Forbes, G. J. and J. B. Theberge. 1992. Influences of a migratory deer herd on wolf movement and mortality in and near Algonquin Park, Ontario. Pp. 303-314 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Alberta, Canada.
- Fritts, S. H. 1983. Record dispersal by a wolf from Minnesota. *Journal of Mammalogy* 64:166-167.
- Fritts, S. H., R. O. Stephenson, R. D. Hayes, and L. Boitani. 2003. Wolves and humans. Pp. 289-316 in L. D. Mech, and L. Boitani, editors. *Wolves. Behavior, ecology, and conservation*. The University of Chicago Press, Chicago and London.
- Fuller, T. K., W. E. Berg, G. L. Radde, M. S. Lenarz, and G. B. Joselyn. 1992. A history and current estimate of wolf distribution and numbers in Minnesota. *Wildlife Society Bulletin* 20:42-55.
- Fuller, T. K., L. D. Mech, and J. F. Cochrane. 2003. Wolf population dynamics. Pp. 161-191 in L. D. Mech, and L. Boitani, editors. *Wolves. Behavior, ecology, and conservation*. The University of Chicago Press, Chicago and London.
- Halfpenny, J. 1986. A field guide to mammal tracking in North America. Johnson Books, Boulder, Colorado.
- Hurford, A., M. Hebblewhite, and M. A. Lewis. 2006. A spatially explicit model for an Allee effect: Why wolves recolonize so slowly in Greater Yellowstone. *Theoretical Population Biology* 70:244-254.
- James, A. R. C. and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management* 64:154-159.
- Jedrzejewski, W., M. Niedzialkowska, R. W. Mysiak, S. Nowak, and B. Jedrzejewska. 2005. Habitat selection by wolves *Canis lupus* in the uplands and mountains of southern Poland. *Acta Theriologica* 50:417-428.
- Jedrzejewski, W., M. Niedzialkowska, S. Nowak, and B. Jedrzejewska. 2004. Habitat variables associated with wolf (*Canis lupus*) distribution and abundance in northern Poland. *Diversity and Distributions* 10:225-233.
- Jensen, W. F., T. K. Fuller, and W. L. Robinson. 1986. Wolf, *Canis lupus*, distribution on the Ontario Michigan border near Sault-Ste-Marie. *Canadian Field-Naturalist* 100:363-366.
- Johnson, C. J., M. S. Boyce, R. L. Case, H. D. Cluff, R. J. Gau, A. Gunn, and R. Mulders. 2005. Cumulative effects of human developments on arctic wildlife. *Wildlife Monographs*:1-36.
- Kaartinen, S., I. Kojola, and A. Colpaert. 2005. Finnish wolves avoid roads and settlements. *Annales Zoologici Fennici* 42:523-532.
- Kendall, K. C., L. H. Metzgar, D. A. Patterson, and B. M. Steele. 1992. Power of sign surveys to monitor population trends. *Ecological Applications* 2:422-430.

- Kunkel, K. and D. H. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. *Journal of Wildlife Management* 65:520-530.
- Landa, A. 1999. Spor og tegn. Et hefte i bestemmelse av store rovdyr. (In Norwegian). Norwegian Institute for Nature Research (NINA) Norwegian Institute for Cultural Heritage Research (NIKU), Trondheim, Norway.
- Massolo, A. and A. Meriggi. 1998. Factors affecting habitat occupancy by wolves in northern Apennines (northern Italy): a model of habitat suitability. *Ecography* 21:97-107.
- McNay, M. E. 2002. Wolf-human interactions in Alaska and Canada: a review of the case history. *Wildlife Society Bulletin* 30:831-843.
- Mech, L. D. 1977. Productivity, mortality, and population trends of wolves in northeastern Minnesota. *Journal of Mammalogy* 58:559-574.
- Mech, L. D. 1995. The challenge and opportunity of recovering wolf populations. *Conservation Biology* 9:270-278.
- Mech, L. D. and L. Boitani. 2003. Wolf social ecology. Pp. 1-34 in L. D. Mech, and L. Boitani, editors. *Wolves. Behavior, ecology, and conservation*. The University of Chicago Press, Chicago and London.
- Mech, L. D., S. H. Fritts, G. L. Radde, and W. J. Paul. 1988. Wolf distribution and road density in Minnesota. *Wildlife Society Bulletin* 16:85-87.
- Merrill, S. B. 2000. Road densities and gray wolf, *Canis lupus*, habitat suitability: an exception. *Canadian Field-Naturalist* 114:312-313.
- Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great-Lakes region. *Conservation Biology* 9:279-294.
- Mladenoff, D. J., T. A. Sickley, and A. P. Wydeven. 1999. Predicting gray wolf landscape recolonization: Logistic regression models vs. new field data. *Ecological Applications* 9:37-44.
- Murray, D. L. and S. Lariviere. 2002. The relationship between foot size of wild canids and regional snow conditions: evidence for selection against a high footload? *Journal of Zoology* 256:289-299.
- Oakleaf, J. K., D. L. Murray, J. R. Oakleaf, E. E. Bangs, C. M. Mack, D. W. Smith, J. A. Fontaine, M. D. Jimenez, T. J. Meier, and C. C. Niemeyer. 2006. Habitat selection by recolonizing wolves in the Northern Rocky Mountains of the United States. *Journal of Wildlife Management* 70:554-563.
- Pedersen, H. C., S. M. Brainerd, O. Liberg, H. Sand, and P. Wabakken. 2003. Utredninger i forbindelse med ny rovviltmelding. Ulv - Bestandsdynamikk, levedyktighet og effekter av uttak. (Wolf - population dynamics, viability and effects of alpha-individual loss. Abstract in English). Norwegian Institute for Nature Research (NINA). Report 61.
- Prugh, L. R. and C. E. Ritland. 2005. Molecular testing of observer identification of carnivore feces in the field. *Wildlife Society Bulletin* 33:189-194.
- Ray, C., M. Gilpin, and A. T. Smith. 1991. The effect of conspecific attraction on metapopulation dynamics. *Biological Journal of the Linnean Society* 42:123-134.
- Reed, J. E., R. J. Baker, W. B. Ballard, and B. T. Kelly. 2004. Differentiating Mexican gray wolf and coyote seats using DNA analysis. *Wildlife Society Bulletin* 32:685-692.
- Ruth, T. K., D. W. Smith, M. A. Haroldson, P. C. Buotte, C. C. Schwartz, H. B. Quigley, S. Cherry, K. M. Murphy, D. Tyers, and K. Frey. 2003. Large-carnivore response to recreational big-game hunting along the Yellowstone

- National Park and Absaroka-Beartooth Wilderness boundary. *Wildlife Society Bulletin* 31:1150-1161.
- Shepherd, B. and J. Whittington. 2006. Response of wolves to corridor restoration and human use management. *Ecology and Society* 11:1.
- Smallwood, K. S. and E. L. Fitzhugh. 1995. A track count for estimating mountain lion *Felis concolor californica* population trend. *Biological Conservation* 71:251-259.
- Smith, A. T. and M. M. Peacock. 1990. Conspecific attraction and the determination of metapopulation colonization rates. *Conservation Biology* 4:320-323.
- Smith, D. W. 2005. Ten years of Yellowstone wolves, 1995-2005. *Yellowstone Science* 13:7-33.
- Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. *American Naturalist* 131:329-347.
- Theuerkauf, J., W. Jedrzejewski, K. Schmidt, and R. Gula. 2003a. Spatio-temporal segregation of wolves from humans in the Bialowieza Forest (Poland). *Journal of Wildlife Management* 67:706-716.
- Theuerkauf, J., W. Jedrzejewski, K. Schmidt, H. Okarma, I. Ruczynski, S. Sniezko, and R. Gula. 2003b. Daily patterns and duration of wolf activity in the Bialowieza Forest, Poland. *Journal of Mammalogy* 84:243-253.
- Thiel, R. P. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. *American Midland Naturalist* 113:404-407.
- Thiel, R. P., S. Merrill, and L. D. Mech. 1998. Tolerance by denning wolves, *Canis lupus*, to human disturbance. *Canadian Field-Naturalist* 112:340-342.
- Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin* 22:61-68.
- USDI Fish and Wildlife Service. 1987. Northern Rocky Mountain Wolf Recovery Plan. United States Fish and Wildlife Service.
- USDI Fish and Wildlife Service, Nez Perce Tribe, National Park Service, Montana Fish Wildlife and Parks, Idaho Fish and Game, and USDA Wildlife Services. 2006. Rocky Mountain Wolf Recovery 2005 Annual Report. C.A. Sime and E. E. Bangs, eds. United States Fish and Wildlife Service. 130 pp.
- USDI Fish and Wildlife Service. 2007. Rocky Mountain Wolf Recovery 2006 Annual Report. C.A. Sime and E. E. Bangs, eds. United States Fish and Wildlife Service. 235 pp.
- Van Camp, J. and R. Gluckie. 1979. Record long-distance move by a wolf (*Canis lupus*). *Journal of Mammalogy* 60:236-237.
- Vilà, C., V. Urios, and J. Castroviejo. 1992. Observations on the daily activity patterns in the Iberian wolf. Pp 335-340 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Alberta, Canada.
- Wam, H. K. 2003. Wolf behaviour towards people - the outcome of 125 monitored encounters. Master's Thesis Agricultural University of Norway, Ås, Norway.
- Weaver, J. L. 1979. Comparison of coyote and wolf scat diameters. *Journal of Wildlife Management* 43:786-788.
- Whittington, J., C. C. St Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications* 15:543-553.
- Wydeven, A. P., R. N. Schultz, and R. P. Thiel. 1992. Monitoring of a recovering gray wolf population in Wisconsin, 1979-1991. Pp. 147-156 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Alberta, Canada.

Received 19 July 2009

Accepted 15 July 2010