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dynamic equilibria of animals with environment. Ecol. Monogr. 39:227–244.
SAS INSTITUE INC. 1989. SAS/STAT user's guide. Version 6. SAS Inst. Inc., Cary, N.C. 1686pp.
SMITH, R. J. 1973. Weather in relation to behavior of confined cottontail rabbits. M. S. Thesis, Purdue Univ., Lafayette, Ind. 106pp.
TABER, R. D., AND I. MCT. COWAN. 1969. Capturing and marking wild animals. Pages 277–317 *in* R. H. Giles, Jr., ed. Wildlife management techniques. The Wildl. Soc., Washington, D.C.
TRENT, T. T., AND O. J. RONGSTAD. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. J. Wildl. Manage. 38:459–472.
TRIPPENSEE, R. E. 1934. The biology and management of the cottontail rabbit (*Sylvilagus floridanus mearnsii* Allen). Ph.D. Thesis, Univ. Michigan, Ann Arbor. 217pp.
WALLER, R. A., AND D. B. DUNCAN. 1969. A Bayes Rule for the symmetric multiple comparisons problem. J. Am. Stat. Assoc. 64:1484–1503.

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POPULATION DYNAMICS OF A RECOLONIZING WOLF POPULATION

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Abstract: Breeding populations of wolves (*Canis lupus*) were absent from the western United States for about 50 years following their extirpation by humans in the 1930s. Here we describe the recolonization by wolves of northwestern Montana and southeastern British Columbia, from the initial production of a litter by a pair of wolves in 1982 through the mid-1990s when 3–4 packs produced litters. Sex ratio of captured wolves favored females (38/54 = 70%; $\chi^2 = 8.96$, 1 df, $P < 0.005$). Litter size in early summer ($\bar{x} = 5.3$, SE = 0.4, $n = 26$) and in December ($\bar{x} = 4.5$, SE = 0.5, $n = 26$) were relatively high compared to similar counts in established populations elsewhere. Pack size in May was unrelated to litter size in June ($r_s = -0.13$, 23 df, $P = 0.25$) or the following December ($r_s = -0.12$, 23 df, $P = 0.28$). Annual adult survival rate (0.80) was relatively high in this semi-protected population and was higher among residents (0.84) than among wolves that dispersed (0.66) from the study area ($Z = 2.24$, $P = 0.025$). Although dispersal was common among radiocollared wolves (19/43 = 44%), population growth within the study area averaged 20% per year from 1982 to 1995. Low human-caused mortality rates and maintenance of connectivity for wolves between this small population in the United States and larger populations in Canada will enhance the probability of persistence and expansion of this population.

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Key words: British Columbia, *Canis lupus*, dispersal, endangered species, Glacier National Park, Montana, mortality, natality, population dynamics, sex ratio, wolf

Wolves were extirpated from much of their historic range in North America through intensive human efforts during the 19th and early 20th centuries (Mech 1970). Eradication from Montana was complete by the 1930s, although a few individual animals were killed in later years (Singer 1979, Day 1981, Ream and Mattson 1982). Recolonization by wolves in the western United States began in the late 1970s and was focused in Glacier National Park, Montana (Ream et al. 1985, 1989, 1991). The nearest breeding population at the time was at least 100 km, and may have been 250 km, north in Canada (Ream and Harris 1986).

Several factors facilitated the increase of this wolf population. Wolves were listed as endangered in Montana in 1973 under the Endangered Species Act and were fully protected in southeastern British Columbia (BC) from 1967 until limited hunting was allowed starting in the late 1980s (Pletscher et al. 1991). Glacier National Park (GNP) provided additional security for wolves in the United States. Prey populations were high due to a series of relatively mild

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winters (H. E. Nyberg, Mont. Dep. Fish, Wildl. and Parks, Kalispell, pers. commun.).

Our objectives were to document wolf reproduction, survival, immigration, and dispersal in this population within and near GNP that is apparently a source for wolves repopulating the western United States. We believe results from our study may provide insights into what may occur elsewhere in the region.

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STUDY AREA

Our study was initiated in the Flathead River drainage in the southeast corner of BC and encompassed the adjacent Wigwam River drainage to the west and GNP to the south. In the United States, the Flathead River separates GNP on the east from U.S. Forest Service, state, and private lands on the west. The river valley is 4–10 km wide and about 1,200 m in elevation, rising to forested slopes and steeper, subalpine peaks. The Wigwam River valley is narrower and steeper. Both valleys were dominated by dense coniferous forests interspersed with meadows, marshes, and riparian habitats (Habeck 1970, Krahmer 1989). Lodgepole pine (*Pinus contorta*) was the dominant tree species, associated with spruce (*Picea engelmannii*), larch (*Larix occidentalis*), sub-alpine fir (*Abies lasiocarpa*), and Douglas-fir (*Pseudotsuga menziesii*).

As the wolf population increased, wolves dispersed and the study area grew to include northeastern Idaho, westcentral Montana near Missoula, the Sun River Game Range near Augusta, Montana, and the areas surrounding Banff National Park, Alberta (Ream et al. 1991, Boyd et al. 1995).

The density of humans in the study area was less than 0.005 people/km^2 in BC and less than 0.1 people/km^2 in Montana. Logging, petroleum exploration, and hunting occurred on forest service, state and provincial, and private lands. Three ranchers grazed cattle in the Flathead west of GNP; cattle were not present during winter. No cattle were permitted in the BC portion of the study area. None of these consumptive uses was permitted within GNP where wolves spent most of their time when in the United States.

Ungulate prey of wolves within the study area included white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), moose (*Alces alces*), and mule deer (*O. hemionus*; Boyd et al. 1994). In addition, bighorn sheep (*Ovis canadensis*) occurred in the Wigwam area and snowshoe hare (*Lepus americanus*) and beaver (*Castor canadensis*) inhabited the entire area. Other predators competing for some of the same prey in this ecosystem included grizzly bears (*Ursus arctos*), black bears (*U. americanus*), cougars (*Puma concolor*), coyotes (*Canis latrans*), and humans.

METHODS

We captured wolves and sedated them following techniques described by Mech (1974) and Ream et al. (1991). Wolves >20 kg were radiocollared; smaller wolves were eartagged only. We assumed equal catchability of males and females (Mech 1975).

Radiocollared wolves were located from the ground about 3 times per week and from an airplane about once per week. We determined pack sizes from aerial observations and from track counts along winter travel routes. Pelage color varied from black to light gray, and this factor aided in determining pack sizes during aerial counts by color combination as well as total number observed. We noted possible immigrants during aerial counts using known pack sizes and color combinations.

The first observations of pups generally were made in late June or July while aerially locating radiocollared adults. Some pup mortality may have occurred before initial observation. Pups were distinguished from adults based on size differences and behavioral observations through September. By October, pups and adults were of similar size and differentiation became increasingly difficult; color combinations (black or gray) to identify individuals, and known mortalities and dispersals were then used to track pup survival until December.

We investigated radiocollared wolves that died to determine the cause of mortality. Mortalities of nonradioed wolves were sometimes discovered at these same locations. Other mortalities were found while back-tracking wolves during winter and at den sites following abandonment. Wolves legally harvested from the study area in Canada were reported to us by Canadian officials.

We estimated age- and sex-specific survival rates and survival rates of dispersing and resident wolves for radiocollared and eartagged wolves (Trent and Rongstad 1974) using program MICROMORT (Heisey and Fuller 1985). One of 4 eartagged wolves was excluded because its fate was unknown. Radiocollared wolves that were dispersal-aged or showed typical pre-dispersal movements (from and back to the natal pack territory, generally over a period of weeks) and subsequently disappeared were assumed to have dispersed. Three wolves that did not show pre-dispersal movements were assumed to have dispersed in the first survival and dispersal analysis, and to have been killed illegally in the second analysis. We assigned mortality dates as halfway between the last known live location and the first indication that the wolf had died, unless carcass evidence indicated otherwise.

Age was divided into 2 classes (<3 yr vs. ≥3 yr) because most dispersal and resettling is done by wolves <3 years of age (Gese and Mech 1991, Boyd et al. 1995). We compared survival between sexes, between ages, and between residents and dispersers with z tests. For MICROMORT analysis, the biological year began on 1 April because denning occurred during this month. Initially, each month was considered an interval with a constant daily survival rate. Daily survival rates for each interval were compared, and data from intervals pooled if rates were not significantly different (Heisey and Fuller 1985).

Dispersal in wolves usually is defined as occurring when an animal leaves its natal territory (Gese and Mech 1991). Because we were interested primarily in the population within and adjacent to GNP, we classified wolves as dispersers only if they permanently left the study area.

RESULTS

Sex ratios of all captured wolves favored females (38 F:16 M, 70% F; $\chi^2 = 8.96$, 1 df, $P < 0.005$). We also evaluated sex ratio only among those wolves younger than the minimum known age of dispersal (16 months) to explore the possibility that the skewed sex ratio existed because dispersal differed between the sexes. A weaker bias toward females remained evident in this sample (25 F:14 M, 64% F; $\chi^2 = 3.10$, 1 df, $P = 0.08$). There was no significant difference from parity in our small sample of pups (8 F:5 M, 62% F; $\chi^2 = 0.69$, 1 df, $P > 0.25$).

Observed immigration during the study period was minimal. We documented 2 females (1 in 1986 and 1 in 1987) and 1 male (in 1992) joining known packs. While all may have been immigrants (based on color combinations of missing wolves from the study area), the female in 1987 is the only known immigrant from outside the study area. While we know of no other immigrants, we cannot dismiss the possibility that other wolves immigrated at about the same time resident wolves dispersed or disappeared.

Twenty-six known denning efforts were documented (Table 1). Maximum pup counts ranged from 1 to 9 ($\bar{x} = 5.3$, SE = 0.4, $n = 26$). December pup counts (through 1994) ranged from 0 to 9 ($\bar{x} = 4.5$, SE = 0.5, $n = 26$). Four additional packs had ≥3 adults in them during spring but apparently did not den. No significant relations were found between number of adults in May and maximum pup counts ($r_s = -0.13$, 23 df, $P = 0.25$) or December pup counts ($r_s = -0.12$, 23 df, $P = 0.28$).

Of the 137 pups known to have been born in the study area through 1994, 117 (85.4%) survived until at least December (Table 1). Eight of the 20 (40%) pups that died were known to be human-caused; 3 pups (15%) died of unknown causes at their natal dens, and 9 (45%) disappeared during summer and their fates are unknown.

We examined carcasses from 46 wolf mortalities. Mortalities occurred in all months; of the 43 non-neonatal mortalities, 36 (83.7%) were human-caused (Table 2) and we suspect 2 others were also human-caused. Twenty-two wolves were killed legally in BC and Alberta, and 11 wolves were killed illegally (BC and the U.S.). Only 4 of the non-neonatal mortalities occurred within GNP.

Twenty-nine radiocollared wolves died or were assumed to have died during the study. Survival data were pooled for the study period because of small sample sizes, especially before 1987. Daily survival rates for each monthly interval from April through August and September through March were similar (G^2 test, $P > 0.05$), thus these periods were defined as intervals during which daily survival rates were assumed constant.

Table 1. Production and survival of wolf pups in the northwestern Montana and southeastern BC study area, 1982–94.

Year	Packs	Adults in May	Max. pup count	Pups in Dec
1982	1	2	7	7
1985	1	6	7	7
1986	1	8	5	3
1987	3	5, 3, 2	5, 6, 6	1, 6, 5
1988	3	5–8, 5–7, 3	6, 6, 1	6, 4, 1
1989	2	9–10, 3	2[1], 9	0, 9
1990	3	2, 2–5, 11	6, 6, 2	6, 6, 2
1991	4	7, 5–7, 1, 5	—, 7, 2, 4	—, 7, 2, 1
1992	4	5, 11, 3, 4	5, 2, 6, 7	5, 2, 4, 7
1993	4	10, 5–10, 5, 6	8, 8, 7, —	7, 7, 7, —
1994	3	11, 3, 7	—, 2[2], 5	—, 0, 5
TOTAL			137	117
			$\bar{x}$ = 5.3	$\bar{x}$ = 4.5
			SE = 0.4	SE = 0.5

[1] These pups were found dead at the den (Johnson et al. 1994).
[2] Two pups were heard howling but never seen.

Interval and annual survival rates were not different (z tests, $P > 0.54$) between males and females (Table 3). Annual survival of wolves ≥3.0 years of age was not different than for wolves <3.0 years old (0.80 vs. 0.74, $P = 0.45$; Table 3).

Annual survival of radiocollared wolves within the study area was significantly greater than survival following dispersal (0.84 vs. 0.66, $P = 0.025$; Table 3). The overall annual survival rate of all radiocollared wolves when dispersal was assumed for the 3 wolves showing no pre-dispersal movements was 0.80 (0.77 when the 3 wolves were assumed to have been illegally killed). The annual rate of known, human-caused mortality (assuming dispersal for the 3 wolves showing no pre-dispersal behavior was 0.07 for illegal and 0.10 for legal mortalities (Table 4).

Table 2. Non-neonatal wolf mortalities in Montana, southeastern British Columbia, and southwestern Alberta 1982–95.

Cause of mortality	No. of mortalities
Human-caused	
Legal	
Shot	22
Research/control action	2
Illegal	
Shot	
Verified	5
Probable	2[1]
Poison	5
Unknown	2[2]
Other causes	
Avalanche[3]	1
Ungulate	1
Wolves	1
Unknown	2
TOTAL	43

[1] One wolf starved following a probable bullet wound; the radiosignal from the second wolf came from a garage.
[2] One was killed during fall hunting season in BC; the other's radiocollar was found in a river near Missoula, Mont.
[3] See Boyd et al. 1992.

From 26 August 1984 through 31 May 1995, 19 of 43 (44.2%) radiocollared wolves dispersed out of the study area. Fourteen (73.7%) of these were females, comparable to the sex ratio of captured wolves (70%).

The number of contiguous packs grew from 1 in 1982 to 4 in 1987. The 1987 hunting season resulted in the demise of 1 pack, and the number of packs in the study area did not reach 4 again until another pack split in 1990. The number of packs remained at 4 through 1993. During 1993, the northernmost pack disappeared. We are currently unsure of the status of this pack, though a pair of tracks were seen in its former territory during May 1995. The pre-denning population grew from 2 wolves in 1982 to a minimum of 23 in 1995, an average finite rate of increase of 1.20 ($r = 0.18$) for the 13 year period. The annual rate of increase ranged from 0.74 to 1.44 with the highest rate occurring in the first years and the lowest rates occurring in the last years. The population density within the study area in 1994 (Singleton 1995) was 35 wolves/1,000 km^2.

Of the 140 wolves known to have been in the study area (the 2 original wolves, 137 pups born, and assuming 1 immigrant), we can account for the fates of 80 (26 in the study area as of Dec 1994, 46 known mortalities, 6 probable pup mortalities, and 2 known dispersers still alive).

Table 3. Survival rates of 52 radiocollared wolves in northwestern Montana for August 1984–May 1995.

	Apr–Aug			Sep–Mar			Annual		
Class	Rate[a]	95% CI	n[b]	Rate[a]	95% CI	n[b]	Rate[a]	95% CI	n[b]
Male	0.97*	0.92–1.00	5765	0.82*	0.72–0.94	8688	0.80*	0.69–0.93	14453
Female	0.95*	0.91–1.00	12745	0.82*	0.74–0.90	17893	0.78*	0.70–0.87	30638
<3.0 yr	0.92$^+$	0.84–1.00	7095	0.81$^+$	0.72–0.91	12107	0.74$^+$	0.64–0.86	19202
≥3.0 yr	0.97$^+$	0.93–1.00	10260	0.82$^+$	0.73–0.92	13018	0.80$^+$	0.71–0.90	23278
Resident	0.98^x	0.94–1.00	12173	0.86^x	0.79–0.93	18282	0.84^x	0.77–0.92	30455
Disperser	0.92^x	0.83–1.00	5333	0.72^x	0.60–0.88	7157	0.66^{xx}	0.53–0.82	12490
Overall[c]	0.96	0.93–1.00	18951	0.83	0.77–0.89	27255	0.80	0.73–0.87	46206
Overall[d]	0.94	0.90–0.99	18510	0.82	0.76–0.89	27573	0.77	0.71–0.85	46083

[a] Rates followed by 2 superscript symbols are significantly different ($P < 0.05$) than rates above them with only 1 of the same superscript.
[b] No. of transmitter-days.
[c] Assuming dispersal of 3 wolves showing no pre-dispersal behavior.
[d] Assuming mortality of 3 wolves showing no pre-dispersal behavior.

DISCUSSION

The sex ratio of offspring in wolves favors males in saturated, high density populations on a relatively low nutritional plane (Mech 1975). Conversely, females would be favored in low density populations where the nutritional plane was higher. The preponderance of females in our expanding population appears to support Mech's hypothesis, though we have few data for pups.

Immigration into a population is difficult to monitor with certainty, even in a population as intensively monitored as ours. We recorded 1 known and 2 possible immigrants following the initial recolonization. Recent genetic findings (Forbes and Boyd 1996) indicate immigration was greater than that suggested by our direct observations.

Pup production in our study area was relatively high compared to studies reviewed by Fuller (1989). The only study with a comparable number of pups produced was a heavily exploited wolf population in southcentral Alaska (Ballard et al. 1987).

Pack size and surviving litter size in canids generally are correlated positively, presumably because pack members help feed pups (Harrington et al. 1983). The one negative correlation was in a study area where the wolf population was declining. We found no significant correlation between pack size and litter size; our results concurred with results from several other studies (Peterson et al. 1984, Ballard et al. 1987, Fuller 1989). Our pack sizes (Table 1) were greater than most of the sizes reported by Harrington et al. (1983), probably because survival rates of both pups and adults were high. These traits may characterize reintroduced and recolonizing populations in the western United States.

Survival for wolves is generally higher within their territories (Messier 1985). Lower survival of dispersing wolves than resident wolves was also reported in Alaska by Peterson et al. (1984) where survival of wolves outside their natal territory was half that of wolves within their territories. The lower rate of survival in dispersing wolves was probably due to travel in unfamiliar areas and a reduced tendency among dispersers to avoid settled areas (Peterson et al. 1984). These factors likely also played a role in our study. Many dispersers in our study left the relative security of GNP and travelled to Canada where wolf hunting and trapping were legal. A result of the recovery of the wolf population in southern Alberta and BC (coinciding with

Table 4. Cause-specific mortality rates of 52 radiocollared wolves in northwestern Montana for August 1984–May 1995.

	Apr–Aug			Sep–Mar			Annual		
Cause	Rate	95% CI	n[a]	Rate	95% CI	n[a]	Rate	95% CI	n[a]
Unknown	0.01	0.00–0.02	18798	0.01	0.00–0.02	27043	0.02	0.00–0.04	45841
Non-human	0.00	0.00–0.00	18798	0.02	0.00–0.05	27043	0.02	0.00–0.05	45841
Illegal	0.02	0.00–0.04	18798	0.06	0.02–0.10	27043	0.07	0.03–0.11	45841
Legal	0.02	0.00–0.04	18798	0.09	0.04–0.13	27043	0.10	0.05–0.15	45841

[a] No. of transmitter-days.

population growth in northwestern Mont.) was a liberalization of wolf hunting and control practices that resulted in the death of 8 of our radiocollared wolves in 1994–95. The survival rate for August 1993–May 1995 was lower than the rate for August 1984–July 1993 (0.61 vs. 0.85, $P = 0.009$). Had the 1994–95 mortalities been excluded from our analysis, survival rates of resident and dispersing wolves would not have differed. No significant differences in survival related to dispersal, however, were found in Minnesota (Fuller 1989).

Our adult and pup survival rates were similar to the highest rates reported in the literature (Fuller 1989). We used Fuller's (1989) linear model to predict an exponential rate of increase based on annual mortality rate and predicted a value of r substantially higher than we found (0.32 vs. 0.18). We believe the difference may be due in part to many of our dispersers leaving the study area, and therefore they and their offspring were not counted. In addition, the relation between mortality rate and r would not remain linear at low annual mortality if pup production declines as pack size increases.

The density of wolves at the end of our study was comparable to the highest densities reported by Fuller (1989:40). We expect more dispersal, to adjacent and distant areas, rather than a further increase in density within currently occupied areas.

Our annual human-caused mortality rate of 0.17 was low compared to the studies reviewed by Fuller (1989; range = 0.15–0.68). The proportion of total mortalities attributed to humans in our study area, however, was high but not unusual (Fuller 1989). In Banff and Kootenay national parks from 1986 to 1993, 28 of 29 wolf mortalities (96.6%) were caused by humans (hit by cars and trains; P. Paquet, Banff Natl. Park, pers. commun.). Thus, despite protection, humans are the most common cause of mortality in many wolf populations.

Cause-specific mortality rates can be biased when a transmitter fails but is returned later when the animal is killed by humans because the transmitter probably would not have been recovered if the death was not human-caused (White and Garrott 1990:225). Five wolves fell into this category. As a result, we may have underestimated nonhuman caused mortality rates.

The dispersal rate we documented (44%) was higher than for any other study we found. Dispersal rates from other studies ranged from 21% in northwestern Minnesota (Fritts and Mech 1981) to 35% in northcentral Minnesota (Fuller 1989). Yearling and pup dispersal rates increased during population increases and declined during stable population phases in Minnesota (Gese and Mech 1991). Increased dispersal and success at pairing also occurred in an expanding wolf population with an ample prey base in Minnesota (Fritts and Mech 1981). The opportunity for dispersing wolves to successfully establish their own pack in unoccupied territory was high during our study and may have been a factor in the high dispersal rate (Boyd et al. 1995).

Dispersal occurred in all directions. Dispersers went north to Canadian national parks and beyond, to the Missoula area, to Idaho (Boyd et al. 1995), to the Rocky Mountain front near Augusta, Montana (J. Fontaine, U.S. Fish and Wildl. Serv., Helena, pers. commun.), and possibly south of Yellowstone National Park (S. Fain, Wildl. Forensic Lab, Ashland, Oreg., pers commun.). By estimating the growth rate of the population of adjacent packs within our study area, we have underestimated the effect of the GNP population on population growth at a larger scale.

Glacier National Park was without a breeding population of wolves from the 1930s until 1986 (Ream et al. 1989), although occasional dispersers were reported throughout that period (Singer 1979). Human actions surrounding the park certainly played a role in this absence (Curnow 1969), but the role of genetic or other biological factors are unknown.

Glacier National Park is likely to remain an important core area for wolves dispersing into the western United States. Wolves have a high reproductive rate, and wolf recovery should proceed relatively rapidly in the Northwestern Montana Recovery area if connectivity with wolf populations further north is maintained and human-caused mortality rates remain relatively low.

LITERATURE CITED

BALLARD, W. B., J. S. WHITMAN, AND C. L. GARDNER. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. 98. 54pp.

BOYD, D. K., P. C. PAQUET, S. DONELON, R. R. REAM, D. H. PLETSCHER, AND C. C. WHITE. 1995. Dispersal characteristics of a colonizing wolf population in the Rocky Mountains. Pages 135–140 *in* L. N. Carbyn, S. H. Fritts, and

D. R. Seip, eds. Ecology and conservation of wolves in a changing world. Can. Circumpolar Inst., Univ. Alberta, Edmonton.

———, R. R. REAM, D. H. PLETSCHER, AND M. W. FAIRCHILD. 1994. Prey taken by colonizing wolves and hunters in the Glacier National Park area. J. Wildl. Manage. 58:289–295.

———, L. SECREST, AND D. H. PLETSCHER. 1992. A wolf (*Canis lupus*) killed in an avalanche in southwestern Alberta. Can. Field-Nat. 106:524–525.

CURNOW, E. 1969. The history of the eradication of the wolf in Montana. M.S. Thesis, Univ. Montana, Missoula. 99pp.

DAY, G. L. 1981. The status and distribution of wolves in the northern Rocky Mountains of the United States. M.S. Thesis, Univ. Montana, Missoula. 130pp.

FORBES, S. H., AND D. K. BOYD. 1996. Genetic variation of naturally colonizing wolves in the Central Rocky Mountains. Conserv. Biol. 10: 1082–1090.

FRITTS, S. H., AND L. D. MECH. 1981. Dynamics, movements, and feeding ecology of a newly-protected wolf population in northwestern Minnesota. Wildl. Monogr. 80. 79pp.

FULLER, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. 105. 41pp.

GESE, E. M., AND L. D. MECH. 1991. Dispersal of wolves in northeastern Minnesota, 1969–1989. Can. J. Zool. 69:2946– 2955.

HABECK, J. R. 1970. The vegetation of Glacier National Park. Natl. Park Serv., and Univ. Montana, Missoula. 123pp.

HARRINGTON, F. H., L. D. MECH, AND S. H. FRITTS. 1983. Pack size and wolf pup survival: their relationship under varying ecological conditions. Behav. Ecol. Sociobiol. 13:19–26.

HEISEY, D. M., AND T. K. FULLER. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. J. Wildl. Manage. 49:668–674.

JOHNSON, M. R., D. K. BOYD, AND D. H. PLETSCHER. 1994. Serologic investigations of canine parvovirus and canine distemper in relation to wolf (*Canis lupus*) pup mortalities. J. Wildl. Dis. 30:270–273.

KRAHMER, R. W. 1989. Seasonal habitat relationships of white-tailed deer in northwestern Montana. M.S. Thesis, Univ. Montana, Missoula. 104pp.

MECH, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Nat. Hist. Press, Garden City, N.Y. 384pp.

———. 1974. Current techniques in the study of elusive wilderness carnivores. Proc. Int. Congr. Game Biol. 11:315–322.

———. 1975. Disproportionate sex ratios of wolf pups. J . Wildl. Manage. 39:737–740.

MESSIER, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to social status and prey abundance. Can. J. Zool. 63:1068–1077.

PETERSON, R. O., J. D. WOOLINGTON, AND T. N. BAILEY. 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Monogr. 88. 52pp.

PLETSCHER, D. H., R. R. REAM, R. DEMARCHI, W. G. BREWSTER, AND E. E. BANGS. 1991. Managing wolf and ungulate populations in an international ecosystem. Trans. North Am. Wildl. Nat. Resour. Conf. 56:539–549.

REAM, R. R., M. W. FAIRCHILD, D. K. BOYD, AND A. BLAKESLEY. 1989. First wolf den in western U.S. in recent history. Northwest. Nat. 70:39–40.

———, ———, ———, AND D. H. PLETSCHER. 1991. Population dynamics and home range changes in a colonizing wolf population. Pages 349–366 *in* R. B. Keiter and M. S. Boyce, eds. The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale Univ. Press, New Haven, Conn.

———, AND R. HARRIS. 1986. Wolf movements in southern Alberta. Natl. Geogr. Res. 21:405–409.

———, ———, J. SMITH, AND D. K. BOYD. 1985. Movement patterns of a lone wolf, *Canis lupus*, in unoccupied wolf range, southeastern British Columbia. Can. Field-Nat. 99:234–239.

———, AND U. MATTSON. 1982. Wolf status in the northern Rockies. Pages 362–381 *in* F. H. Harrington, and P. C. Paquet, eds. Wolves of the world. Noyes Publ., Park Ridge, N.J.

SINGER, F. J. 1979. Status and history of timber wolves in Glacier National Park, Montana. Pages 19–42 *in* E. Klinghammer, ed. The behavior and ecology of wolves. Garland STPM Press, New York, N.Y.

SINGLETON, P. H. 1995. Winter habitat selection by wolves in the North Fork of the Flathead River Basin, Montana and British Columbia. M.S. Thesis, Univ. Montana, Missoula. 116pp.

TRENT, T. T., AND O. J. RONGSTAD. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. J. Wildl. Manage. 38:459–472.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio- tracking data. Acad. Press, San Diego, Calif. 383 pp.

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