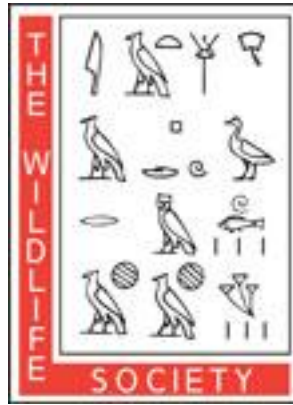


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CHARACTERISTICS OF DISPERSAL IN A COLONIZING WOLF POPULATION IN THE CENTRAL ROCKY MOUNTAINS

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Abstract: Gray wolves (*Canis lupus*) were eradicated from Montana in the 1930s and the adjacent Canadian Rockies by the 1950s, but recolonized these areas in the 1980s. We studied wolf recovery in and near Glacier National Park (GNP), Montana, from 1979 to 1997. During this period, 31 of 58 tagged wolves dispersed. Most wolves (57%) did not make exploratory forays 3 months before permanent separation from their natal pack. Wolves usually left their natal home range quickly (median = 4 days; mode = 1 day) after separating from the pack. Mean dispersal distance was not different ($P > 0.05$) between males (113 km) and females (78 km), excluding an unusually long dispersal of 840 km by a yearling female. Wolves tended to disperse in a northerly direction to areas of higher wolf density. January–February and May–June were peak months for dispersal. Mean dispersal age ($M = 28.7$ months; $F = 38.4$ months) was not correlated with maximum pack size. Twenty percent of dispersers were ≥ 57 months old at dispersal. Sex ratios of dispersers and captured wolves (both 71% F) differed from parity ($P = 0.002$). Annual survival rate ($\bar{x} \pm SE$) for dispersers and bidders (philopatric wolves) did not differ (dispersers = 0.76 ± 0.10 ; bidders = 0.77 ± 0.14). Wolves killed by humans died closer to roads ($\bar{x} = 0.13$ km) than wolves that died from other causes ($\bar{x} = 0.85$ km). Eighty percent ($n = 30$) of wolf mortalities were caused by humans, with proportionately more dispersers (90%) than bidders (60%) dying from human causes. Dispersers produced more litters than bidders. Effects of mountainous terrain and management on wolf recovery are discussed.

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Key words: Alberta, bidder, British Columbia, *Canis lupus*, central Rocky Mountains, colonizing, dispersal, disperser, gray wolf, Montana, mortality, reproduction.

Gray wolves were extirpated from the western United States by the 1930s (Young and Goldman 1944, U.S. Fish and Wildlife Service 1987). Wolf populations were severely reduced in the Canadian Rocky Mountains of southeastern British Columbia and southwestern Alberta in the 1930s and again in the 1950s (Gunson 1983, Tompa 1983). A viable wolf population ceased to exist between Jasper National Park, Alberta, and GNP, Montana, by the late 1950s (Day 1981, Ream and Mattson 1982, Boyd et al. 1995). In the 1970s, wolves began recolonizing this region of Canada and northwestern Montana (hereafter, central Rockies; Ream et al. 1991, Hayes and Gunson 1995, Boyd-Heger 1997). We defined the central Rockies as the geographic area centered on the junction of the Continental Divide, which included the landscape from Banff, Alberta, to Helena, Montana.

The successful recolonization initially occurred via dispersal from source populations north of Banff National Park (BNP), Alberta

(Boyd et al. 1995; P. Paquet, University of Calgary, personal communication), approximately 300 km north of GNP. Wolves are a highly mobile species with dispersals occasionally exceeding 600 km (Van Camp and Gluckie 1979, Fritts 1983, Ballard et al. 1987). Reports of long-distance movements are becoming more common as more wolves are being tagged and telemetry technology is improved. Wolves have substantial genetic variation across North America, but relatively little differentiation among local populations (Kennedy et al. 1991, Wayne et al. 1992, Roy et al. 1994; Forbes and Boyd 1996, 1997), which is additional evidence of frequent, long-distance dispersals and resulting gene flow.

Animals disperse in response to a variety of factors including competition for food and mating opportunities, environmental disruptions, social aggression, and habitat availability (Greenwood 1980, Waser 1985). In social animals such as wolves, dispersal is an important mechanism for population regulation (Lidicker 1975), genetic exchange (Forbes and Boyd 1996, Smith et al. 1997), social organization (Hamilton 1964, Greenwood 1980, Zimen 1982), and colonization (Fritts and Mech 1981,

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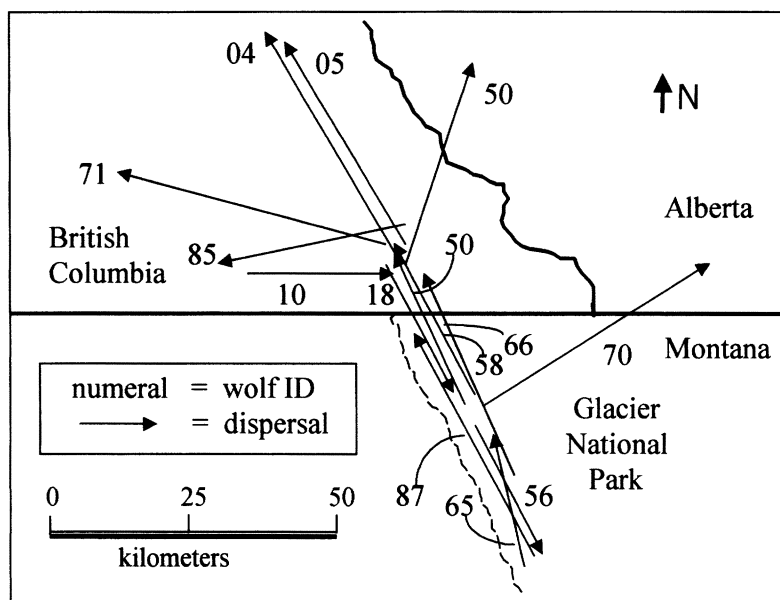


Fig. 1. The intensive study area as defined by dispersals <50 km by 14 gray wolves from the Glacier National Park area, 1985–97.

Gese and Mech 1991, Boyd et al. 1995). Potential benefits of dispersal include increased reproductive success, decreased probability of inbreeding, release from intraspecific competition for resources, and range expansion (Shields 1987). Potential costs of dispersal include increased mortality in unfamiliar habitat, outbreeding depression, and increased energetic demands during dispersal (Shields 1987).

Ten articles have been published documenting wolf dispersal (Fritts and Mech 1981, Peterson et al. 1984, Ballard et al. 1987, Mech 1987, Fuller 1989, Gese and Mech 1991, Boyd et al. 1995, Wydeven et al. 1995, Ballard et al. 1997, Mech et al. 1998). Additionally, 5 notes have been published documenting unusual wolf dispersal events (Van Camp and Gluckie 1979, Ballard et al. 1983, Fritts 1983, Van Ballenberghe 1983, Mech et al. 1995). However, little information has been published on the role of dispersal in wolf recolonization (Fritts and Mech 1981), particularly in the Rocky Mountains. Our objectives were to examine wolf dispersal patterns and outcomes, and the role of dispersal to wolf recovery in the central Rockies from 1979 to 1997.

STUDY AREA

The core GNP study area (approx 10,000 km²) included GNP and adjacent lands within

50 km of GNP, including southeastern British Columbia, southwestern Alberta, and northwestern Montana (hereafter, GNP; Fig. 1). The GNP area is characterized by long, narrow valley bottoms surrounded by rugged mountains with elevations ranging from 1,020 to 3,600 m. Dense coniferous forests dominated the GNP area, with meadow and riparian areas less common (Koterba and Habeck 1971). The few human residents were present mostly in summer. The extensive study area was defined by the movements of wolves dispersing from GNP and extended from northern British Columbia south to Missoula, Montana, and east–west from the eastern Rocky Mountain Front to westcentral Idaho (Fig. 2). The study area encompassed parts of 2 countries, 2 provinces, 2 states, and numerous jurisdictions within each of these (Pletscher et al. 1991), resulting in a mosaic of land management classifications.

METHODS

Captures

Wolves were captured with modified number 4 Newhouse foothold traps and sedated as described by Mech (1974) and Ream et al. (1991). Pups <20 kg were eartagged only; wolves ≥20 kg were radiocollared and eartagged. Although estimating wolf age is difficult (Ballard et al.

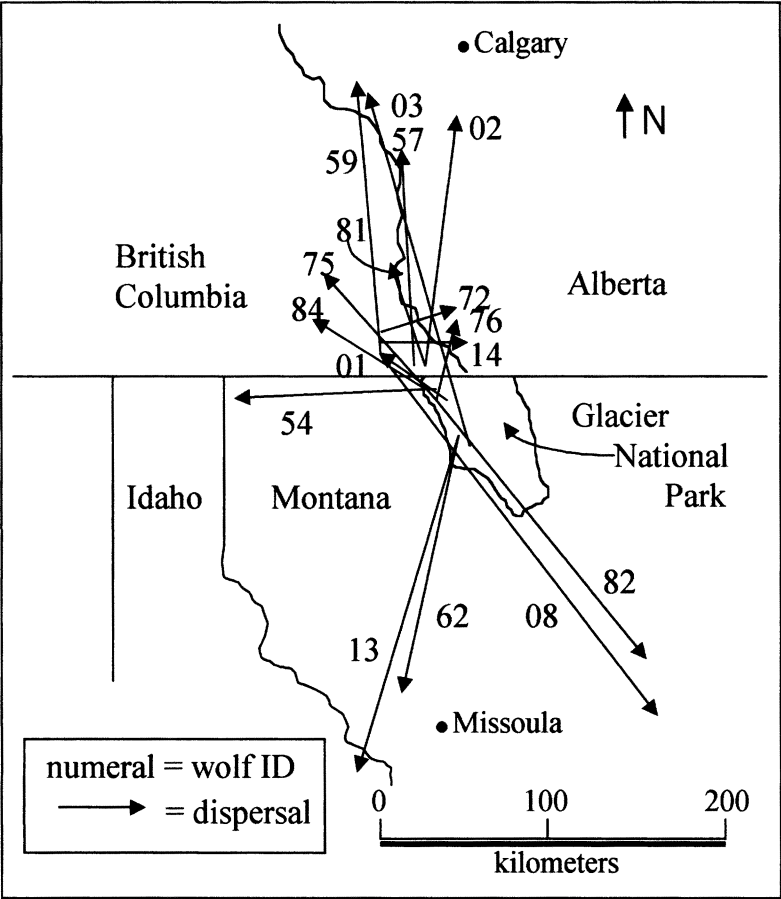


Fig. 2. The extensive study area as defined by dispersals ≥ 50 km by 16 gray wolves from the Glacier National Park area, 1985–97.

1995, Landon et al. 1998), we estimated age by examining tooth eruption and dental wear patterns. We felt this method of estimation was sufficiently accurate because of the intensity with which the colonizing wolves were captured and monitored. Many wolves were captured repeatedly over several years, allowing observers to assess dental wear patterns based on known-aged animals for later comparison to animals of unknown ages. Additionally, many wolves in this population had distinctive pelage color patterns that allowed for individual identification for many months or years before tagging, which provided a minimum age estimate. Adult wolves of questionable age were assigned an age on the younger end of a reasonable range (e.g., a wolf 3–5 yr old was called a 3-yr-old), which may have biased age estimates downward.

Radiotelemetry and Dispersal

Radiocollared wolves were located approximately 3 times/week from the ground and once per week from an airplane. Immigration and emigration were often detected during aerial observations for 2 reasons: (1) Rocky Mountain wolves vary greatly in color from black to white, aiding identification of individuals; and (2) population dynamics of only a few packs were intensively monitored during the recolonization period, enhancing visual familiarity with individuals. We tagged our first study wolf in 1979, but the first predispersal movements were documented in 1985. The first dispersal occurred in 1986. Therefore, dispersal data were collected from 1985 to 1997.

If a radiocollared wolf was not detected during several location attempts, a search flight was

conducted within 300 km of GNP at 3,500–3,700 m above sea level. When dispersed wolves were located outside of our study area or were missing, we gave their radiocollar frequencies to other biologists for monitoring. Dispersed wolves were monitored to determine their pack status, reproductive success, and fates. We analyzed attributes of dispersal including distance, direction, season, age of disperser, sex ratio, temporal and spatial separation from pack, annual survival rate, and reproductive contribution. Data for all characteristics were not available for all dispersed wolves, so sample sizes differ for different analyses.

Wolves were protected as an endangered species in the United States during the study, but they were legally harvested in Alberta and British Columbia. We maintained contact with local residents and agencies to enhance learning of mortalities of dispersed wolves. We investigated all mortalities of tagged wolves and called successful Canadian hunters for accurate information on location, pack association, and reproductive condition of harvested wolves.

Shields (1987:4) defined dispersal as “the movement of an organism or propagule from its site or group of origin to its first or subsequent breeding site or group.” He subdivided dispersal into natal dispersal (movement of a propagule between birthplace or natal group and first breeding site or group) and breeding dispersal (movement between consecutive breeding sites or groups of adult breeders). We defined wolf dispersal as having occurred when a wolf permanently left its natal territory. We defined natal pack as the pack a wolf was a member of when it was captured. Wolves that remained philopatric were classified as bidders (Packard and Mech 1983).

A wolf may remain in its natal home range but separate from the pack for days or weeks before actually dispersing out of the natal home range. We defined temporal separation from the pack as the time a wolf permanently dissociated from its natal pack and remained in its natal home range before actual dispersal. We counted the days between the last time it was located with the pack and the date when it permanently left its natal home range. We defined spatial separation as the situation in which a pack member was disjunct from other pack members but within the pack's home range. We classified wolves as pack hoppers when they made extra-territorial movements (Messier 1985) or were

members of >1 pack in a given season. Temporal separation, spatial separation, and pack hopping were all considered to be predispersal movements.

We correlated dispersal rate and age at dispersal with maximum size of the pack (adults plus pups) a disperser belonged to ≤ 12 months before the dispersal (an index of population density). We included only those dispersers that had been located with members of a pack for at least 1 month before dispersal. We calculated dispersal rate by dividing the number of dispersers in a given year by the maximum number of tagged wolves in the same year (Gese and Mech 1991).

We estimated the center of natal and dispersed home ranges based on the 25% isopleth of the adaptive kernel method (Kie et al. 1994). We used only locations that were >2 days apart per wolf to attain independence between locations. We used the Pythagorean theorem in EXCEL (Microsoft 5.0) to calculate the dispersal distance from the center point of the natal home range to the center point of the dispersed home range. The dispersal of 8 wolves was determined solely by a reported mortality location (radiocollar returned) but little other postdispersal data. We used the mortality location as the dispersal end point for these animals. These wolves may not have completed their dispersal at the time of their death. Therefore, this information may lead to an underestimation of dispersal distances.

To determine direction dispersed, we connected the center point of the natal home range with the center point of the dispersal home range (or mortality point), and measured the resultant azimuth. We categorized the azimuths into 2 directional groups: (1) north = 271–90°; and (2) south = 91–270°. Sample sizes were too small to divide azimuths into more categories or to compare dispersal direction differences between sexes.

Month of dispersal and age at dispersal were estimated by a date halfway between the date a wolf was last located in its natal home range and first located permanently away from its natal home range. Two exceptions to this method of estimation of dispersal month and age were wolves 8502 and 8808, which were captured as pups and eartagged but not radiocollared. Wolf 8502 was shot a year after he was tagged, so we estimated his dispersal date as halfway between 12 months of age and death. We used this es-

time of dispersal date because the youngest dispersal age documented was 12 months, so we presumed 12 months was the earliest age at which a wolf would disperse. Wolf 8808 was first located 57 months after we eartagged him, so we omitted him from age and month of dispersal analyses.

We estimated annual survival rates of dispersers and bidders using program MICRO-MORT (Heisey and Fuller 1985). We assumed a birth date of 15 April, an earliest possible age of dispersal was 12 months, and a choice of bidders at that age to disperse or remain bidders. We calculated radio days for dispersers as the number of days alive postdispersal past 12 months of age, to the last date of transmission or reported mortality, or until the end of this study (31 May 1997). We calculated radio days for bidders as the number of days alive past 12 months of age to the last date of transmission or reported mortality, or until the end of this study. For bidders and dispersers whose exact date of mortality was unknown, we chose the mortality date as halfway between the last known live location and the first confirmation of mortality (Pletscher et al. 1997). Sample sizes were small and mortalities were similarly distributed among intervals, so we pooled data across monthly and yearly intervals (Heisey and Fuller 1985).

We determined breeding contribution for dispersers and bidders based on several assumptions. We assumed wolves would not reproduce until a minimum of 22 months of age (Mech 1970). Females were defined as breeders, based on physical evidence of lactation upon capture (Mech et al. 1993) and dominant or mating behaviors observed from aircraft during radiotelemetry flights. Males were defined as breeders based on testicle size relative to other animals of known breeding status captured the same time of year, and dominant or mating behaviors aurally observed. If wolf A was breeding in year 1, remained with the same pack for years 2 through n , no other breeders of the same sex were detected, and pups were whelped, we assumed wolf A was the breeder in years 2 through n . To ascertain breeding status, we also considered den-site attendance patterns relative to other pack members, and parental exclusion through genetic analyses of family groups (Forbes and Boyd 1996).

We compared reproductive contribution for dispersers and bidders by wolf age. A male that

sired pups or a female that whelped was considered to have reproduced. Each year that a wolf reproduced was recorded as 1 reproductive event (1 litter) for that age. A wolf's reproductive status was omitted from analysis if it was unknown at a given age.

Statistical Tests

All samples were assumed to be random and independent. Whenever possible, we used parametric tests (t -tests) to compare population means. Nonparametric tests (chi-square, Mann-Whitney U) were used when populations failed to meet assumptions of normality and homoscedasticity. All statistical tests were considered significant at $P \leq 0.05$.

RESULTS

Captures

We captured and tagged 58 wolves (17 M, 41 F) from 1979 to 1997 in the intensive study area. Additionally, P. Paquet (University of Calgary, Calgary, Alberta, Canada), personnel of the U.S. Fish and Wildlife Service, and M. Jimenez (University of Montana, Missoula, Montana, USA) radiocollared additional wolves outside of our study area, and some of their dispersal data are cited anecdotally.

Twenty-eight wolves dispersed once and 3 wolves dispersed twice, totaling 34 dispersals (Figs. 1, 2). Thirty-one of these wolves permanently left their natal home ranges and were subsequently located in an area disjunct from their former home range. Three additional wolves (8550, 9065, 9066) were classified as dispersers, although they did not meet the above criteria. Females 8550 and 9065 dispersed from their natal packs, maintained a new home range which included a subset of their former home range, reproduced in the new home range, and were never again located with members of their natal packs. Wolf 9065 subsequently made pre-dispersal movements immediately before loss of her radio signal; thus, we assumed she dispersed a second time (Mech et al. 1998). Female 9066 dispersed from her natal pack at 12 months of age and joined a newly formed pair (of which neither was her parent) for 2 months. She exhibited pre-dispersal movements a few days before loss of her radio signal, but she was never located again. An additional 9 wolves that disappeared were excluded from analysis because their radiocollars ceased transmitting and the wolves exhibited no pre-dispersal move-

Table 1. Sex and number of days gray wolves separated from pack before dispersal ($n = 24$) from the Glacier National Park area, 1985–97.

Number of days separated from pack	Males	Females
1	4	3
2	1	1
3	0	3
5	0	1
6	0	2
7	1	0
10	0	3
17	0	1
18	0	1
29	0	1
46	0	1
94	0	1

ments. Omission of these 9 wolves was a conservative approach to including dispersers because some of the 9 excluded wolves most likely dispersed (the majority of known dispersers showed no predispersal movements).

Predispersal Behavior

Most wolves dispersed relatively quickly after separating from their natal pack (Table 1), with males dispersing more quickly than females after separation from the pack ($U = 40.5$, $P = 0.02$, $n = 24$). Ten of 23 (43%) dispersing wolves made forays from the pack and then re-joined the pack within 3 months of permanent separation from the pack. The remaining 13

wolves were always located with other pack members during the 3 months before permanent separation. Before dispersal but after separation from the pack, most wolves remained spatially distant from pack members. The typical pattern of predispersal behavior was for a potential disperser to remain with the pack, suddenly make a permanent break from the pack, wander around in the pack's home range for a few days, and then disperse to a new, disjunct home range.

In 6 instances, packs in the intensive study area temporarily accepted non-pack wolves into their group. The pack-hoppers were females aged 12, 18, 21, 26, 27, and 74 months, respectively, during interpack interactions. The 2 oldest wolves were strangers to the packs they visited, but the younger 4 wolves visited adjacent packs with close relatives. Four of these wolves were observed with >1 pack in a denning season and appeared to belong to multiple packs in a year's time. We documented 2 incidents of extraterritorial movements by entire packs through neighboring packs' territories during December and January.

Dispersal Characteristics

The dispersal rate (Table 2) was not correlated with the previous year's maximum pack size for the disperser's pack ($r = -0.04$, $P = 0.89$, $n = 19$), suggesting that pack size did not influence dispersal rate. Fourteen wolves dispersed

Table 2. Gray wolf population estimates and frequency of tagged wolves ≥ 12 months old that dispersed from the Glacier National Park area, 1982–97.

Year	Maximum ^a population	Maximum pack size	Tagged wolves ^b		Tagged wolves that dispersed ^c	
			<i>n</i>	%	<i>n</i>	%
1982	9	9	0	0	0 ^c	0 ^c
1983	8	8	0	0	0 ^c	0 ^c
1984	7	7	0	0	0 ^c	0 ^c
1985	14	13	2	14	0 ^c	0 ^c
1986	14	13	5	36	3	60
1987	27	10, 9, 8	8	30	3	38
1988	33	14, 11, 3	11	33	3	27
1989	31	11, 10, 8	12	39	2	17
1990	33	13, 11, 8	13	39	3	23
1991	31	14, 9, 7, 3	16	52	5	31
1992	43	14, 11, 10, 9	13	30	1	8
1993	54	19, 18, 10, 6	22	41	4	18
1994	36	14, 11, 11	17	47	5	29
1995	40	16, 16, 7	11	28	1	9
1996	35	19, 10, 5	10	29	2	20

^a Does not include lone wolves.
^b Wolves at least 12 months of age.
^c Data were omitted from dispersal rate analyses because none or relatively few members of the population were tagged.

Table 3. Sex and month of 33 gray wolf dispersals from the Glacier National Park area, 1985–97.

Month dispersed	Males	Females
Jan	1	3
Feb	1	3
Mar	1	1
Apr	0	3
May	2	2
Jun	2	2
Jul	2	1
Aug	0	2
Sep	0	3
Oct	0	2
Nov	0	1
Dec	0	1

<50 km (Fig. 1), and 16 wolves dispersed ≥50 km (Fig. 2). We omitted mapping 4 of 34 dispersals, because the 840 km dispersal of female 8551 (Ream et al. 1991) was considered an outlier; wolves 9065 and 9066 exhibited predispersal movements before cessation of radio transmission and were presumed to have dispersed to unknown end points, and the death site of wolf 9167 was unknown because her radiocollar was found in the garage of an uncooperative hunter. Dispersal distances of males ($n = 10$) and females ($n = 20$) were not different ($U = 171.5$, $P = 0.47$, $n = 30$). The combined mean dispersal distance for males and females was 96.3 km (SE = 14.5), with a range of 15.6–254.9 km.

Wolves tended to disperse in a northerly direction ($\chi^2_1 = 7.26$, $P = 0.01$; Figs. 1, 2); 74% ($n = 31$) of dispersals were northward. Wolves dispersed in all months, with a nonsignificant tendency to disperse in January–February and May–June (Table 3). Males had a nonsignificant tendency to disperse the first half of the year (Jan–Jul), whereas females dispersed in all months.

Dispersal age was not correlated with maximum size of the disperser’s pack during the 12 months before dispersal ($r = 0.003$, $P = 1.00$, $n = 28$). We found no difference between males and females for mean age of dispersal ($U = 138$, $P = 0.54$, $n = 33$). The combined mean age of dispersal for males and females was 35.7 months (SD = 20.2, range = 12–90). Most wolves were tagged as pups or yearlings and did not disperse for several months or years, which provided fairly accurate age estimates. Six wolves were relatively old when they dispersed (57–90 months).

The sex ratio of wolves captured (17 M:41 F; 71% F) favored females ($\chi^2_1 = 9.93$, $P = 0.002$, $n = 58$). The sex ratio for dispersals (10 M:24 F; 71% F) also favored females ($\chi^2_1 = 5.77$, $P = 0.02$) and was not different from the sex ratio of captured wolves ($\chi^2_1 < 0.001$, $P = 0.99$). Thus, males and females dispersed in proportion to the sex ratios of the captured population.

We documented 2 incidents of sibling codispersal. Male 8703 and female 8857 dispersed approximately 1 year apart from the same natal pack and were located together in a new pack 150 km north of their natal home range (Boyd et al. 1995). Male 8703 dispersed from the Camas Pack of GNP in March 1988. He was not located again until July 1989, when he was found with the Highwood Pack in Alberta. His sibling, female 8857, dispersed from the Camas Pack in February 1989 and became the breeding female of the Highwood Pack in spring 1989. These 2 wolves were found together in 1989 before 8703 left the Highwood Pack and dispersed again.

Female 8962 was last located with her natal Camas Pack in GNP on 19 January 1991. Approximately 1 week later, pack-mate male 9013 left the Camas Pack. The 2 were seen in the Ninemile area (170 km south of their natal home range) during April 1991 (R. Thisted, rancher, personal communication). Female 8962 stayed in the Ninemile area and became the breeding female (M. Jimenez, University of Montana, personal communication), while 9013 moved on to Kelly Creek, Idaho. These 2 wolves were first observed in the Ninemile area <2 weeks after the resident wolf pack had been removed because of livestock depredations. Furthermore, 8962 was first observed in the rendezvous site of the previous pack and assumed movements similar to that of the former resident pack.

Postdispersal Behavior and Fates

Thirty mortalities of tagged wolves were recorded during the study (Table 4). Most mortalities were attributed to humans (18/20 dispersers, 6/10 bidders). The majority of bidders resided within protected GNP, and the majority of dispersers lived on provincial and federal lands in Canada where wolves received less protection. Of the nonhuman-caused mortalities for dispersers, 1 wolf was killed by an avalanche (Boyd et al. 1992), and 1 was killed by other wolves. Of the nonhuman-caused mortalities for

Table 4. Month of gray wolf mortalities (n = 30) for dispersers and biders in the Glacier National Park area, 1985–97.

Status	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Disperser	2	1	2	2	0	0	1	2	2	3	3	2
Bider	0	1	2	0	0	0	1	1	1	2	2	0

biders, 1 wolf was killed by an elk (*Cervus elaphus*), 2 were killed by other wolves, and the cause of death for 1 wolf was unknown. Mortalities of several more untagged wolves were documented (Pletscher et al. 1997) but were omitted from these analyses because untagged wolf mortalities would include only biders. Month of mortality for dispersers and biders was similar (Table 4), but sample sizes were too small for analysis. Annual survival rate for dispersers (0.76 ± 0.10) and biders (0.77 ± 0.14) was similar ($Z < 0.001$, $P > 0.50$).

We calculated the mean distance from an anthropogenic linear feature (road or seismic line) for each mortality incident (incidents where >1 wolf was killed at the same time was counted as 1 incident). The mean distance (0.13 km, SD = 0.15, n = 25) from a human linear feature for human-caused mortalities was greater ($U = 318.5$, $P \leq 0.001$, n = 36) than for nonhuman-caused mortalities (0.85 km, SD = 0.87, n = 11). Twenty-one of 25 human-caused wolf mor-

talities occurred within 200 m of a road or seismic line (15 shot, 4 poisoned, 2 trapped).

Thirteen of twenty-three (57%) dispersing wolves found mates the first breeding season after dispersal, and all but 2 of these reproduced that first denning season. The number of known reproductive outcomes for dispersers (n = 58) and biders (n = 61) was similar (Table 5), but dispersers were more likely to reproduce than biders ($\chi^2_1 = 16.95$, $P < 0.001$). The outcome of reproductive events was known for more females (n = 84) than males (n = 35).

Pack Formation

We documented the formation of 13 packs from 1982 to 1997. Ten of these packs became established in areas that had no breeding wolves, which greatly expanded the recolonization process. Three (Sage Creek, South Camas, Spruce Creek) of these 13 packs formed via pack splitting (sensu Meier et al. 1995), whereby the newer pack usurped a portion of the founders' natal home range and expanded into adjacent, unoccupied territory. Some intermingling of newly fissioned packs initially occurred within a few months after pack splitting, but thereafter the packs maintained separate territories.

DISCUSSION

Dispersal Characteristics

The proximate cause of wolf dispersal is unknown. Wolves living in areas with inadequate prey may be subject to nutritional deficiencies and social stress, encouraging dispersal (Zimen 1982, Messier 1985, Ballard et al. 1987). We found no evidence of wolf starvation and no wolf-caused wolf mortalities before 1993. However, ungulate populations in the study area have been declining since at least 1993 (Kunkel 1997), and we subsequently documented 4 incidents of wolves killing wolves (20% of mortalities since 1993; Boyd-Heger 1997). Mortalities caused by intraspecific strife tend to increase in wolf populations stressed by food or space limitations (Mech 1977a, Fritts and Mech 1981, Wydeven et al. 1995, Mech et al. 1998).

Table 5. Production of pups by gray wolves of various ages and sexes, for biders and dispersers, in the Glacier National Park area, 1985–97.

Sex	Age (yr)	Pups produced?			
		Biders		Dispersers	
		Yes	No	Yes	No
M	2	0	8	0	1
F	2	2	16	2	1
M	3	0	4	1	2
F	3	4	7	4	3
M	4	0	1	3	2
F	4	3	5	3	2
M	5	0	0	4	2
F	5	5	0	4	2
M	6	0	0	4	1
F	6	3	1	5	0
M	7	0	0	1	0
F	7	0	2	2	1
M	8	0	0	1	0
F	8	0	0	2	1
M	9	0	0	0	0
F	9	0	0	1	1
M	10	0	0	0	0
F	10	0	0	1	1
Total M		0	13	14	8
Total F		17	31	24	12
Total M + F		17	44	38	20

Interestingly, we observed a slight, nonsignificant ($\chi^2_1 = 0.28$, $P > 0.50$) decrease in dispersal rate concurrent with decreases in the ungulate population since 1993 (Table 2), with a mean dispersal rate of 29.1% from 1986 to 1992, and 19.0% from 1993 to 1996.

Wolves in our study area existed in disjunct packs, encompassing the ungulate winter ranges that were widely distributed across the landscape. A dispersing wolf in the central Rockies may have decreased chances of encountering prey or potential pack mates to assist with prey capture than dispersers in the more homogeneous landscape of the midwestern United States. Wolf dispersal rates declined slightly in our study area during times of lower ungulate densities. During times of food shortages, wolves in Minnesota reduced movements to conserve energy in a high-density wolf population with more evenly dispersed ungulate winter ranges (Mech 1977b). The need to conserve energy would be even greater in the central Rockies, where wolves likely travel farther between more widely dispersed ungulate winter ranges to find prey. Elsewhere, increased resource competition (lower prey abundance) increased stress in saturated wolf populations, which subsequently increased wolf dispersal rates (Messier 1985, Ballard et al. 1987, Peterson and Page 1988, Gese and Mech 1991).

We compared our data to the 8 most comprehensive articles on wolf dispersal to evaluate differences between colonizing and established populations (Table 6). Mean dispersal distances in our study area were intermediate with those reported in other areas (Table 6). A 20-month-old female (Ream et al. 1991) made the longest dispersal from our study area (840 km), although most documented record dispersals were made by male wolves. Record dispersals from other studies range from 390 to 886 km, with longer dispersals tending to occur in terrain with more topographic relief (Van Camp and Gluckie 1979, Fritts and Mech 1981, Berg and Kuehn 1982, Fritts 1983, Ballard et al. 1987, Gese and Mech 1991, Mech et al. 1995, Mech et al. 1998). Variation in long-distance dispersals may be explained by differences in density of wolves, individual behavioral variation, prey availability, human density, and patchiness of the landscape. Wolves traveling in mountainous landscapes or in areas of low wolf density may travel excessive distances to find suitable habitat, prey, or mates.

Table 6. Gray wolf dispersal data from various North American studies.

Source	Location	Dispersal Age ^a			n	Population status ^b	Dispersal sex (% F)	Capture sex (% F)	Male mean dispersal distance (km)	Female mean dispersal distance (km)
		Pups (n)	Yearlings (n)	Ad (n)						
This study	GNP ^c	1	11	21	33	I,S	71	71	113	78
Fritts and Mech (1981)	Minnesota	0	7	1	8	I	63	59		
Peterson et al. (1984)	Alaska	1	11 ^d	6	18	S	28	48		
Ballard et al. (1987)	Alaska		18 ^e	20	38	D	26	45 ^f	84	114
Fuller (1989)	Minnesota	11	11 ^d	6	28	I		56		
Gese and Mech (1991)	Minnesota	17	40	18	75	D,S,I	48	49	88	65
Wydeven et al (1995)	Wisconsin	1	8	7	16	D,I	63	54	65	144
Ballard et al. (1997)	Alaska	1	7	13	21	I,D	38	49	154	123
Mech et al. (1998)	Alaska	2	24	25	51	S	48	49	83	83

^a Pups <12 months old; Yearlings = 12–24 months old; Adults >24 months old.
^b D = decreasing, I = increasing, S = stable.
^c GNP = Glacier National Park and adjacent areas ≤50 km from GNP, including parts of Montana, British Columbia, and Alberta.
^d Author combined yearlings and 2-year-olds.
^e Author defined as ≤24 months of age.
^f Author reported even sex ratio for yearlings and pups, but adult sex ratios were skewed toward large males due to intentional selection of larger wolves.

Several other dispersals within and near the study area have contributed to recolonization of the central Rockies. For example, a yearling male dispersed 280 km from near Missoula, Montana, to northeastern Washington (M. Jimenez, University of Montana, personal communication). An adult female dispersed 470 km from Peter Lougheed Provincial Park, Alberta, to Deer Lodge, Montana (P. Paquet, University of Calgary, personal communication; J. Fontaine, U.S. Fish and Wildlife Service, personal communication). An adult female fitted with a satellite transmitter in Peter Lougheed Provincial Park, Alberta, moved through southern Alberta, southeastern British Columbia, Browning, Montana, the GNP area, and Kellogg, Idaho, before being shot near Canal Flats, British Columbia (C. Callaghan, University of Guelph, personal communication; P. Paquet, University of Calgary, personal communication). These anecdotal accounts are interesting individual events, and we report them to indicate the tremendous movements that frequently occur by wolves in the central Rockies, and their contribution to wolf recovery. If landscape linkages are maintained and human persecution is minimized, wolves have great potential to recolonize areas far from core wolf populations (Mech 1995).

Direction of dispersal is apparently affected by management policies, availability of lands without conflicting use, and conspecific attraction. Most wolves (74%) in our study dispersed in a northerly direction toward higher-density wolf populations in Canada (original source of GNP colonizers). However, our ability to detect direction of dispersal may have been affected by different management policies for wolves in Canada and the United States. Wolves legally killed in Canada were more likely to be reported or discovered than those illegally killed as an endangered species in the United States. In both countries, the hunter or agency locally responsible for wolf management reported most wolf mortalities to us. Nonetheless, 74% ($n = 34$) of our dispersal discoveries were the result of our locating live animals via radiotelemetry. No dispersals were discovered via illegal mortalities. Another factor that may have affected dispersal direction was the availability of lands to wolves without conflicting human use. Wydeven et al. (1995) reported dispersal from a colonizing wolf population in Wisconsin to higher-density wolf populations in Minnesota (the

original source for Wisconsin colonizers). However, some dispersing wolves travel to areas of low wolf densities and high human densities (Mech et al. 1995, this study). Ray et al. (1991) postulated the theory of conspecific attraction whereby animals disperse preferentially to sites occupied by conspecifics. This theory may explain why most dispersers from GNP moved northward to higher-density wolf populations. Wolves find other wolves by scent-marking and howling (Mech 1970, Peters and Mech 1975, Harrington and Mech 1979). Wolves often travel well-established routes and may detect scent marks long after deposition. Wolves from the same pack dispersed months or years apart, and ended-up in the same area 3 times in our study.

The temporal pattern of wolf dispersal appeared catalyzed by social or nutritional influences. Wolf dispersal peaked in January–February and again in May–June (Table 3). January–February is a period of courtship and breeding, and therefore a time of increased aggression (Zimen 1982, Packard et al. 1983) that may encourage dispersal. Season of dispersal varies greatly in the literature, but most authors reported dispersal peaks during the breeding season (Peterson et al. 1984, Ballard et al. 1987, Mech 1987, Fuller 1989, Gese and Mech 1991, Ballard et al. 1997, Mech et al. 1998). However, Fritts and Mech (1981) reported 50% ($n = 8$) of dispersals occurred in fall (Sep–Dec), and 50% ($n = 8$) occurred in the breeding season (Jan–Mar).

Ungulates are most vulnerable to wolves during late winter and early spring (Mar–Apr). Lower dispersal rates reported during this period may reflect an abundance of available food resources and a time of relatively low stress between breeding and denning seasons. Potential dispersers may experience increased social distancing from the dominant animals during the early weeks of pup rearing (May–Jun), when parents increase the level of social interactions with each other and their new pups. This additional distancing by dominant animals rearing pups may account for the second pulse of dispersal observed in our study.

Yearlings have 2 dispersal choices in areas of abundant prey: (1) disperse early in life and take advantage of favorable environmental conditions (Fritts and Mech 1981), or (2) become bidders to obtain the benefits associated with a large pack (our study). Factors affecting this choice included pack size, density of interspe-

cific competitors, distance to nearest potential mate, landscape features, and frequency of encounter with resident territorial packs, which may result in mortality of the trespasser.

Fritts and Mech (1981) found that most dispersers were yearlings in a colonizing wolf population with abundant prey in northwestern Minnesota. These relatively young dispersers were maximizing their fitness by dispersing early in life during a time of favorable conditions. This area harbored relatively low-density populations of potential competitors, including coyotes (*Canis latrans*) and black bears (*Ursus americanus*).

Wolves in our study area coexisted with several mid- and large-sized carnivores including coyote, lynx (*Lynx canadensis*), mountain lion (*Felis concolor*), black bear, grizzly bear (*Ursus arctos horribilis*), wolverine (*Gulo gulo*), and numerous avian and mammalian scavengers. This plethora of carnivores may have decreased food appropriation opportunities for lone dispersers and encouraged biding behavior. Thus, as young wolves mature they may stay with their natal pack longer to benefit from pack membership, resulting in an increased mean age of dispersers. A higher percentage of dispersing wolves in our study area were adults than reported elsewhere (Table 6). Younger wolves may have remained with the pack longer in the GNP area because benefits of biding (security, food procurement) outweighed hazards of dispersal (unknown risks, potentially increased mortality). Bider benefits may have included carcass defense against other packs and grizzly bears, ease of capturing large prey by cooperative hunting, and advantage in numbers during interpack trespass encounters. In December 1995, the 17-member South Pack trespassed into the 7-member North Pack's home range in GNP and killed the alpha male of the North Pack. An additional wolf was found dead nearby; it was not radiocollared, but was likely a North Pack member. This interpack strife occurred at a large white-tailed deer (*Odocoileus virginianus*) wintering area, supporting observations by Messier (1985) and Forbes and Therberge (1995) of pack extraterritorial movements to exploit deer.

In areas of low prey abundance and higher wolf density, younger wolves apparently disperse at a higher rate than adults. Messier (1985), Ballard et al. (1987), and Gese and Mech (1991) reported a higher rate of yearling

dispersal during times of lower prey density. Wolves in northeastern Minnesota (Mech 1977a) dispersed from a saturated wolf population at a younger age than colonizing wolves in our study. Gese and Mech (1991) stated that dispersal of adults was unaffected by changes in the saturated wolf population level.

Assuming equal survival of males and females, and equal capture vulnerability, the sex ratios of captured wolves of all age groups should reflect pup sex ratios. The sex ratio favored females for both captures and dispersers (Table 6), and we found no sex bias in the dispersal rate of wolves (assuming the sex ratio of the captured sample represents the population at large). This trend also was observed in other colonizing or increasing wolf populations in Minnesota (Fritts and Mech 1981, Fuller 1989) and Wisconsin (Wydeven et al. 1995). Sex ratios that were even or slightly favored males (Table 6) were reported in stable or decreasing wolf populations (Peterson et al. 1984, Ballard et al. 1987, Gese and Mech 1991, Ballard et al. 1997, Mech et al. 1998). Mech (1975) suggested that wolves in saturated populations (stable to decreasing) with marginal nutrition produce a disproportionate number of male pups, and wolves from populations with lower wolf density had equal sex ratios or a disproportionate number of female pups. An increased number of females would potentially increase the growth rate of the population, but there does not appear to be a significant pattern of sex-biased dispersal in wolves for most long-term studies (Table 6).

Movements and Dispersal Behavior

Single dispersing wolves usually found other wolves soon after they left their natal home range (\bar{x} = 66 days, range = 2–202), despite noncontiguous pack distribution and a low-density wolf population. Fritts and Mech (1981) reported mean time from dispersal to pairing was 16.5 days (range = 8–30) in a colonizing population. Gese and Mech (1991) reported the mean time from dispersal to pairing was 112 days (range = 2.2–5.1 months) in a saturated population. Messier (1985) described dispersal as a lengthy and dynamic process that occurred over many months or years in a saturated wolf population in relatively homogeneous terrain. We observed the opposite: wolves engaged in very few extraterritorial movements relative to other studies. Once wolves permanently sepa-

rated from their pack, they dispersed relatively quickly. Fritts and Mech (1981) also observed rapid dispersal and rapid pairing in a colonizing population in northeastern Minnesota. Recolonizing, low-density wolf populations may present dispersers with lower probabilities of finding mates nearby and may encourage more rapid long-distance dispersal to find mates. The noncontiguous pack distribution in mountainous terrain may further encourage dispersing wolves to keep traveling once dispersal has begun. The heterogeneous, linear nature of mountainous terrain causes patchy distribution of ungulates, in turn causing wolves to move farther and more quickly through the landscape in search of food.

Was Dispersal a Successful Strategy?

Wolf dispersal initiated recolonization in the central Rockies and was critical to recovery. Prey abundance, social strife, and breeding opportunities undoubtedly influenced dispersal attempts and their outcomes. These proximate factors may vary between ecosystems in severity and consequences. However, the ultimate function of dispersal, increased reproductive success, remains the same for dispersers everywhere.

Potential bias may have been introduced and favored detection of breeding status for dispersed wolves and not bidders because packs newly formed by a disperser were generally smaller than natal packs, and reproductive activity may have been easier to detect for dispersers. Confirming reproductive status is easier for females than males because females have stronger den-site fidelity than males due to lactation demands and permanence of mammary development postlactation, whereas testicle size varies with season and status. However, pseudolactation may complicate the evaluation of female reproduction (Mech and Seal 1987, Mech et al. 1993).

Only the alpha male and female breed in most wolf packs (Mech 1970). If mortality rates are relatively high for dispersers or breeding opportunities are limited, an individual can increase inclusive fitness by remaining a bidder and provisioning related offspring. However, we found equal survival rates for dispersers and bidders, and dispersers produced more offspring than did bidders (Table 5). It would seem advantageous for nonbreeders to disperse younger so as to increase their number of reproductive

years. However, wolves may have honed their survival and pup-rearing skills in their familiar natal home range in the protected habitat of GNP by remaining home longer before dispersing. Gese and Mech (1991) found that the probability of successful breeding following dispersal increased with age at dispersal. If the predispersal learning time were shortened, perhaps postdispersal reproductive success would be lower.

Wolf recovery is continuing in the central Rockies, with dispersing wolves recently repopulating areas of British Columbia, Alberta, Idaho, and Montana. Recolonizing wolves were often tolerant of visiting non-pack members, a situation uncommon in established wolf populations (Mech 1970). However, Meier et al. (1995) documented 8 cases of strange wolves joining established packs in a stable wolf population in Denali National Park, Alaska. Colonizing wolves may have a less rigid social system, so foreign wolves may be allowed to visit or become pack members more easily (Ballard et al. 1987). Dispersing wolves found mates or joined packs relatively quickly after leaving their former home range, augmenting wolf recovery.

Southwestern Alberta serves as an example of a recolonized area becoming a source and then a sink for wolves. The wolf populations in southwestern Alberta greatly increased during the 1980s and became a source for dispersals to Montana. Anti-wolf sentiment grew rapidly in southwestern Alberta during the early 1990s, however, resulting in removal of approximately 95% of the population between Peter Lougheed Provincial Park and GNP (45 wolves killed 1994–95; C. Callaghan, University of Guelph, personal communication; P. Paquet, University of Calgary, personal communication). This heavily exploited region of Alberta became a sink for dispersing wolves from Montana and British Columbia. Concurrently, wolf densities in Montana increased to the point that Montana became a source to recolonize Alberta. However, numerous long-distance dispersals and successful reproduction have allowed continued recolonization throughout the central Rockies.

MANAGEMENT IMPLICATIONS

By 1996, 8 wolf packs had colonized northwest Montana via dispersal (2 in GNP, 6 elsewhere). Additionally, 35 wolves from Canada were reintroduced to central Idaho and 31 were reintroduced to Yellowstone National Park

(YNP) in 1995–96 (Bangs and Fritts 1996, Fritts et al. 1997), aiding recovery efforts demographically and genetically (Forbes and Boyd 1996). All 3 areas are approaching the delisting goal of 10 breeding pairs for 3 successive years in each of the 3 recovery areas (northwest Montana, central Idaho, greater Yellowstone area; U.S. Fish and Wildlife Service 1987). The combination of recolonization and reintroduction should greatly enhance the rate of wolf recovery as long as dispersal occurs between recovery areas to maintain genetic variation and promote population viability.

Wolf recovery is not assured, however, and may be significantly impacted by stochastic environmental events and political pressures. Approximately 40–50% of the white-tailed deer population in northwest Montana died during an unusually severe winter in 1996–97. This decrease in deer availability may have contributed to record-high levels of livestock depredations, resulting in increased lethal control of wolves (Bangs et al. 1999). Subsequently, the number of breeding wolf pairs in northwest Montana declined from 8 to 6 by 1998 (Bangs et al. 1999). As of March 1999, wolves dispersing from YNP have not survived to reproduce outside YNP (D. Smith, Yellowstone National Park, personal communication). Although the YNP effort has been lauded as a restoration success, the connectivity of dispersers between YNP and other wolf populations has yet to be demonstrated. Dispersal between the YNP wolf population and wolves in Montana and Idaho will enhance recovery and attainment of management goals. Managers can affect recovery positively by maintaining landscape connectivity and by minimizing wolf mortalities caused by humans.

Dispersal was a successful strategy for wolf recolonization in the central Rockies and paramount to wolf recovery. Colonizing wolves moved over large-scale landscapes rather than defined corridors, and these rather indeterminate connections are important to continued recovery. The majority of colonizers in the western United States have appeared outside of parks and wilderness areas. Managers should be aware that the proverbial “wolf at the door” has become a reality in places not perceived as wolf habitat. Human changes on the landscape (e.g. habitat alterations that increase white-tailed deer populations) have created defacto wolf habitat in areas where wolf–human conflicts

may threaten recovery. Stochastic events and human intolerance may jeopardize the survival of these semi-isolated packs. As Fritts and Carbyn (1995:26) surmised, “there is no threshold population size or proven reserve design that guarantees long-term survival for a gray wolf population”.

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