



## Featured Article

# Wolf Dispersal in the Rocky Mountains, Western United States: 1993–2008

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**ABSTRACT** Gray wolves (*Canis lupus*) were extirpated from the northern Rocky Mountains (NRM) of the United States by the 1930s. Dispersing wolves from Canada naturally recolonized Montana and first denned there in 1986. In 1995 and 1996, the United States Fish and Wildlife Service reintroduced 66 wolves into central Idaho and Yellowstone National Park. By 2008, there were  $\geq 1,655$  wolves in  $\geq 217$  packs, including 95 breeding pairs in the NRM. From 1993–2008, we captured and radio-collared 1,681 wolves and documented 297 radio-collared wolves dispersing as lone individuals. We monitored dispersing wolves to determine their pack characteristics (i.e., pack size and surrounding pack density) before and after dispersal, their reproductive success, and eventual fate. We calculated summary statistics for characteristics of wolf dispersal (i.e., straight-line distance, age, time of year, sex ratio, reproduction, and survival), and we tested these characteristics for differences between sexes and age groups. Approximately, 10% of the known wolf population dispersed annually. The sex ratio of dispersals favored males (169 M, 128 F), but fewer dispersed males reproduced (28%,  $n = 47$ ) than females (42%,  $n = 54$ ). Fifty-nine percent of all dispersers of known age were adults ( $n = 156$ ), 37% were yearlings ( $n = 99$ ), and 4% were pups ( $n = 10$ ). Mean age at dispersal for males (32.8 months) was not significantly different ( $P = 0.88$ ) than for females (32.1 months). Yellowstone National Park had a significant positive effect on dispersal rate. Pack density in a wolf's natal population had a negative effect on dispersal rate when the entire NRM population was considered. The mean NRM pack size (6.9) from 1993 to 2008 was smaller than the mean size of packs (10.0) from which wolves dispersed during that time period ( $P < 0.001$ ); however, pack size was not in our most supported model. Dispersals occurred throughout the year but generally increased in the fall and peaked in January. The mean duration of all dispersals was 5.5 months. Radio-collared wolves dispersed between Montana, Idaho, and Wyoming to other adjacent states, and between the United States and Canada throughout the study. Mean straight-line distance between starting and ending points for dispersing males (98.1 km) was not significantly different than females (87.7 km;  $P = 0.11$ ). Ten wolves (3.4%) dispersed distances  $> 300$  km. On average, dispersal distance decreased later in the study ( $P = 0.006$ ). Sex, survival rate in the natal population, start date, dispersal distance, and direction were not significant predictors of dispersal rate or successful dispersal. Wolves that formed new packs were  $> 11$  times more likely to reproduce than those that joined packs and surrounding pack density had a negative effect on successful dispersal. Dispersal behavior seems to be innate in sexually mature wolves and thereby assures that genetic diversity will remain high and help conserve the NRM wolf population. © 2017 The Wildlife Society.

**KEY WORDS** *Canis lupus*, dispersal, genetic, gray wolf, Idaho, Montana, mortality, Northern Rocky Mountains, recolonization, Wyoming.

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Wolves have an ability to disperse, find mates, and recolonize empty habitat. Each wolf pack can be considered a “dispersal pump that converts prey into young wolves and spews them far and wide over the landscape” (Mech and Boitani

2003:11). Wolves can disperse distances >850 km (Ballard et al. 1983, Fritts 1983, Boyd et al. 1995) and over inhospitable terrain, even sea ice (Mech and Boitani 2003, Linnell et al. 2005, Wabakken et al. 2007). Only extremely large bodies of water or deserts appear to prevent wolf dispersal (Linnell et al. 2005). Dispersal is critical to wolf population resilience and has allowed wolves to persist throughout much of their historical range worldwide and to recover in areas where they had been extirpated by human persecution (Boitani 2003, Fuller et al. 2003, Adams et al. 2008).

By the 1930s wolves had been deliberately exterminated by humans in the northern Rocky Mountains (NRM) of the United States (Young and Goldman 1944). This area is different from other parts of North America where wolves have persisted (i.e., Alaska and Canada) because wolf habitat within the NRM was highly fragmented by human activity and was surrounded by unsuitable areas (Oakleaf et al. 2006). Although lone, long-distance dispersing wolves from Canada were occasionally documented in the NRM, reproduction was not documented until 1986 (Ream et al. 1989), more than a decade after wolves became protected by the federal Endangered Species Act (ESA). The population grew rapidly after wolves were reintroduced to Yellowstone National Park and central Idaho in 1995 and 1996 (Bangs and Fritts 1996). The NRM wolf recovery goal required maintenance of a metapopulation that never dropped below 30 breeding pairs (defined as 1 adult M and 1 adult F with  $\geq 2$  pups surviving until 31 Dec; Mitchell et al. 2008) and 300 wolves with effective genetic exchange (either human-assisted or from natural dispersal) between the 3 core recovery areas, which included northwestern Montana, central Idaho, and the Greater Yellowstone Area, USA (Fig. 1).

Recovery goals were achieved in 2002, and by 2008 there were  $\geq 1,655$  wolves in the NRM (U.S. Fish and Wildlife Service [USFWS] et al. 2011). Monitoring of radio-collared wolves and genetic testing indicated that the wolf population in NRM was connected to thousands of wolves in western Canada and had genetic diversity as high as those source populations (Forbes and Boyd 1996, 1997; Boyd and Pletscher 1999). Subsequent genetic research detected effective migration throughout the entire NRM (vonHoldt et al. 2010). As part of the wolf restoration effort in NRM, we monitored 1,681 wolves via radio-telemetry from 1993 to 2008. We used a subset of those data, including wolf identification number, sex, date of capture, estimated age at dispersal, dispersal start date, dispersal end date, last known location, origin or natal pack, end pack, dispersal direction, reproduction at destination, and fate to describe dispersal characteristics and to determine which characteristics were predictors of annual dispersal rate and success. We further compared Yellowstone National Park to the rest of the NRM to determine if a national park setting, where a high portion of the wolf population was radio-collared, no livestock was present, and illegal mortality was negligible, affected annual dispersal rate and contributed to dispersal success.

We hypothesized that models of dispersal rates containing characteristics of the individual (e.g., age, sex) and natal pack

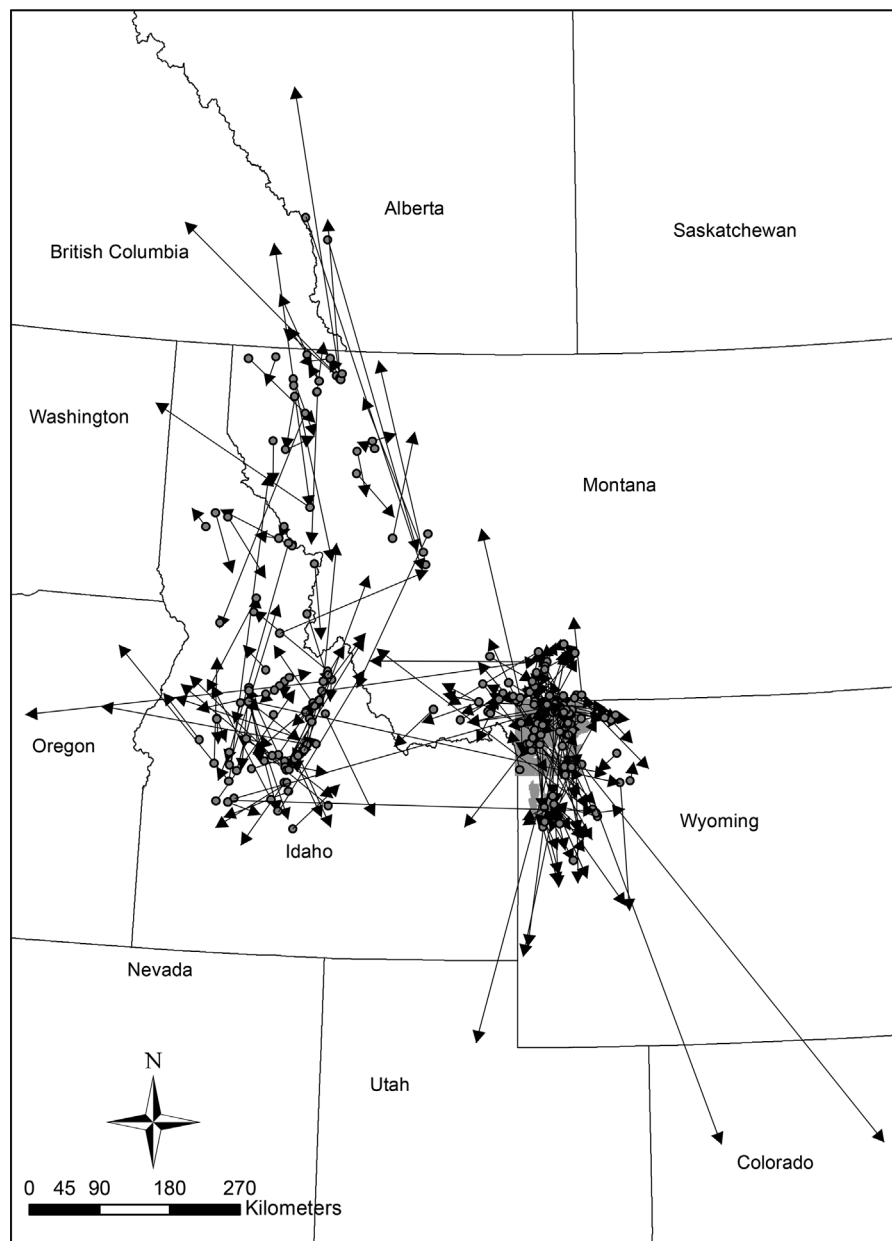
(e.g., pack size) would best predict dispersal rates in the NRM. We hypothesized that an individual-based model (e.g., age, sex, dispersal start date) would be superior to other models of dispersal success and that the distance a wolf dispersed would be a strong predictor of whether they successfully reproduced once they left their natal pack.

## STUDY AREA

Our study area included approximately 373,000 km<sup>2</sup> in the NRM within 7 states of the United States and 2 provinces in Canada (Fig. 1). The core areas of wolf recovery were located in western Montana, northern and central Idaho, and northwest Wyoming. Topography varied throughout the region but was characterized by open valleys surrounded by mountainous forest habitat. Mountain ranges typically ran north-south and at high elevations had a dominant cover of lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and whitebark pine (*Pinus albicaulis*). Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), quaking aspen (*Populus tremuloides*), cottonwood (*Populus* spp.), and willows (*Salix* spp.) were common in the mountains at lower elevations. Areas outside of the mountains tended to be open prairie or high desert shrub, often intensely used for agricultural production of crops, forage, or livestock. Elevation ranged from 200 m to 4,200 m and seasonal temperatures varied from  $-40^{\circ}\text{C}$  to  $35^{\circ}\text{C}$ . Annual precipitation ranged from 25 cm to 150 cm with snowfall beginning in late October and continuing through early April.

The study area was a mixture of private property and public lands managed by various federal, state, Tribal, and provincial land management agencies. The majority of public lands were managed for multiple uses, including livestock grazing. Valley bottoms were often privately owned and used for ranching, farming, and human habitation. Suitable areas for wolf pack persistence were generally mountainous, forested, and publicly owned. Wolf habitat was positively correlated with high elk (*Cervus elaphus*) density, and lower human population and agricultural (primarily sheep) density, which was typical of the 3 primary wolf recovery areas: Northwest Montana, Central Idaho, and the Greater Yellowstone Area (Oakleaf et al. 2006). Landscapes that were not suitable for wolves were flat, open, private or public land, which were extensively grazed for livestock production. Contiguous habitat connected Canada with the Northwest Montana and Central Idaho Recovery Areas but not the Greater Yellowstone Area.

The wolf population steadily grew from only 55 wolves in 1993 to  $>1,655$  wolves in 2008 (USFWS et al. 2011). Wolf prey such as elk, mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and domestic livestock were abundant throughout the NRM. Domestic cattle and sheep grazed year-round on private property and on public grazing allotments from early June to mid-October. Livestock depredations and removal of depredating wolves were common (Bangs et al. 2005, USFWS et al. 2011). Overall, the wolf population in NRM had a 26% annual mortality rate, but dispersers had higher



**Figure 1.** The study area in the northern Rocky Mountains, USA and Canada included 2 countries, 7 states, and 2 provinces. We documented 297 dispersals of radio-collared wolves in the northern Rocky Mountain recovery area from 1993 to 2008. Each vector represents a start and end point of an individual dispersal.

mortality rates (40%/yr) than resident wolves (Smith et al. 2010). Humans caused >80% of wolf mortality and were the primary factor determining wolf distribution and density throughout most of the NRM (Boyd and Pletscher 1999, Bangs et al. 2009, Murray et al. 2010, Smith et al. 2010).

## METHODS

### Radio-Collared Wolves

We captured wolves ( $\geq 20$  kg and  $> 5$  months of age) in summer using foothold traps (Mech 1974, Ream et al. 1991) and darted or net-gunned wolves from helicopters in winter (Ballard et al. 1987, Kreeger 1996). We physically examined captured wolves and collected blood or tissue samples for

future DNA analysis. All capture activities followed standard USFWS guidelines and handling procedures, and complied with guidelines established by the American Society of Mammalogists. Wolves are born in early to late April and we estimated wolf age by examining dental wear patterns and tooth eruption (Ballard et al. 1995, Gipson et al. 2000). We classified wolves into 3 age groups: pups (young-of-the-year  $< 12$  months old), yearlings (12–24 months old), and adults ( $> 24$  months old; Gese and Mech 1991). We fitted most wolves with very high frequency (VHF) and occasionally global positioning system (GPS) radio-collars (Telonics, Mesa, AZ, USA; Televilt, Lindesberg, Sweden; and Lotek Engineering, Newmarket, Ontario, Canada) and released them on site. All radio-collars contained a mortality sensor. Our dispersal analyses were based on VHF telemetry

locations that provided the start and end points for each dispersal event. Our data could not ascertain the actual distance traveled or routes of dispersing wolves.

We monitored radio-collared wolves from aircraft or from the ground using radio-telemetry  $\geq 1$  time/month. Immigration and emigration were usually detected by telemetry but sometimes through the recovery of dead wolves. When we lost radio contact with individual wolves, we continued searching in the immediate area and we exchanged missing collar frequencies with biologists working in different areas within or near the NRM so they could scan for missing wolves during routine telemetry flights. In addition, we flew high elevation telemetry flights multiple times each year to search for missing frequencies. This enhanced our ability to determine the timing, location, fate, pack status, and reproductive success of dispersing wolves.

### Dispersal Characteristics

We defined dispersal as the permanent emigration of a wolf from its natal home range to a new area (Howard 1960, Gese and Mech 1991) or when a wolf permanently left the home range of a pack in which it was a member when it was originally captured and radio-collared (Gese and Mech 1991, Boyd and Pletscher 1999). We monitored dispersing wolves until they died or until their signal was lost and determined home ranges by plotting minimum convex polygons (Mohr 1947).

We recorded the month when we detected dispersal, and estimated the duration and straight line distance (using the Path, with Distances and Bearings extension for ArcView 3. x; <http://www.jennessent.com/arcview/path.htm>, accessed 11 April 2011) of each dispersal from the last known radio-location in the wolf's natal or original home range (start point) to the first location in a newly established home range (end point). We tested for differences in dispersal distance by year using a generalized mixed effects model with area as a random effect. We performed analyses using the lme4 package in Program R (Version 3.3.0; The R Foundation for Statistical Computing 2016). We determined dispersing wolves were settled in an area when they were consistently traveling with at least one other wolf and holding a territory. We assumed wolves formed new packs or joined existing packs based on observations made from the ground or during aerial telemetry flights. Mortality locations were end points where dispersing wolves died.

Our data identified the start and end points of dispersals but did not describe travel routes taken by wolves. We made general assumptions of the actual dispersal direction based on where dispersals ended ( $n = 287$ ). We calculated the bearing (degrees) between the start and end points for each dispersal using Path, with Distances and Bearings, and then converted degrees to radians. We calculated mean direction, vector strength (i.e., mean resultant length), and circular range. We also evaluated preference for a particular dispersal direction using a Rayleigh test of uniformity. Given we had only the start point and end point, dispersal direction was the bearing between start point and end point. We performed these analyses using circular (Agostinelli and Lund 2013) and CircStats (Agostinelli and Lund 2002) packages within the

R statistical programming language (R Development Core Team 2014).

We did not have sufficient data to describe monthly dispersal rates, but we calculated annual dispersal rate by dividing the number of radio-collared dispersing wolves within a given year by the number of radio-collared wolves in that same year as in previous studies (Gese and Mech 1991, Boyd and Pletscher 1999).

We defined successful dispersal as a dispersing wolf that reproduced (Shields 1987). We made various assumptions in determining breeding status of dispersers. We assumed wolves would not reproduce until 22 months of age (Mech 1970). We identified males as breeders based on testicle size in comparison to other wolves of known breeding status captured at the same time of year (Kreeger 2003), and observed dominant or mating behavior. We identified females as breeders, based on evidence of lactation during handling (Mech et al. 1993), observed dominant or mating behavior, and den-site behavior relative to pups and other pack members (Mech and Boitani 2003).

### Statistical Analysis

We monitored dispersing wolves to determine their pack characteristics (i.e., pack size and surrounding pack density) before and after dispersal, their reproductive success, and eventual fate. We acquired pack data from annual USFWS reports that estimated pack status and size on 31 December of each year (USFWS et al. 2011). Sample sizes differed because data for all characteristics were not available for all dispersed wolves. We calculated summary statistics for the following characteristics of wolf dispersal: straight-line distance, age, time of year, sex ratio, reproduction, and survival. We tested these characteristics for differences between sexes and age groups. We assumed samples to be random and independent, and used  $t$ -tests to compare population means when possible. We used non-parametric tests (Chi-square and Mann-Whitney  $U$ ) when populations failed to meet assumptions of normality. We performed descriptive statistical analyses and basic statistical analyses using Microsoft Excel. We performed other analyses using Statistix 8.0 (Analytical Software, Tallahassee, FL, USA). We considered statistical tests significant at  $P \leq 0.05$ .

We used multiple linear regression in SPSS 23 (IBM Corporation, NY, USA) to compare 5 models predicting wolf dispersal rates in the NRM (Ramsey and Schafer 2002). We log-transformed natal pack size to meet normality assumptions (Ramsey and Schafer 2002) and we used values from Smith et al. (2010) for estimates of survival rates in the animal's natal population. Lastly, we calculated surrounding pack density in the natal population as the number of packs present annually divided by the recovery area ( $\text{km}^2$ ). We then scaled pack density estimates to  $1,000 \text{ km}^2$  for comparisons. We used  $R^2$  to assess model fit and considered variables with  $P \leq 0.05$  to be powerful predictors of dispersal rates. We used multiple logistic regression and 5 competing models to predict whether a dispersing wolf successfully bred or not. These models included the animal's age, sex, natal pack size, survival rate in the natal population, pack density in the natal



population, month dispersal began, distance traveled, direction of dispersal, and whether the animal joined or formed new pack. We used receiver operating characteristic to assess model fit, and odds ratios to determine which variables were the most powerful predictors of successful breeding (i.e., those with odds ratios that did not overlap 1.0). For models predicting dispersal rate and models predicting whether a dispersing wolf successfully bred or not, we used an information-theoretic framework to compare candidate models (Hosmer and Lemeshow 2000, Burnham and Anderson 2002). We considered models with the lowest AIC to have the most support and models within 2 AIC equally supported by the data.

## RESULTS

We captured and radio-collared 1,681 wolves from 1993 through 2008. The sex ratio of 858 (51%) males and 823 (49%) females that we captured was not significantly different from parity ( $\chi^2_1 = 0.73$ ,  $P = 0.393$ ). We estimated age at capture for 1,536 wolves: 599 (39%) adults, 345 (22%) yearlings, and 592 (39%) pups. We documented 297 dispersals of lone individuals (Fig. 1). Dispersers within the NRM originated from Montana ( $n = 56$ ), Idaho ( $n = 78$ ), Wyoming outside Yellowstone National Park ( $n = 38$ ), and Wyoming inside Yellowstone National Park ( $n = 125$ ).

The sex ratio for 297 recorded dispersals (169 M, 128 F) favored males ( $\chi^2_1 = 5.70$ ,  $P = 0.017$ ). We estimated the age at dispersal for 265 wolves. Fifty-nine percent of dispersers were adults ( $n = 156$ ) and 37% yearlings ( $n = 99$ ). Only 4% were pups ( $n = 10$ ; 5 M, 5 F). Pup dispersal was lower than expected based on the proportion of radio-collared wolves ( $\chi^2_2 = 136.29$ ,  $P < 0.001$ ) and we excluded pups from further analysis. Mean age of male dispersers was  $32.8 \pm 19.1$  (SD) months (range = 9–103) and was not significantly different from the mean age of  $32.1 \pm 19.0$  months (range = 8–112) for female dispersers ( $U = 7,148$ ,  $P = 0.88$ ).

In the NRM (outside Yellowstone National Park), dispersals began in all months and peaked in January, July, and September (Fig. 2). Thirty-three percent ( $n = 42$ ) of all dispersals in the NRM (outside Yellowstone National Park) occurred between October and February. Dispersals began in all months in Yellowstone National Park but peaked in late fall and early winter (Fig. 3). Fifty-seven percent

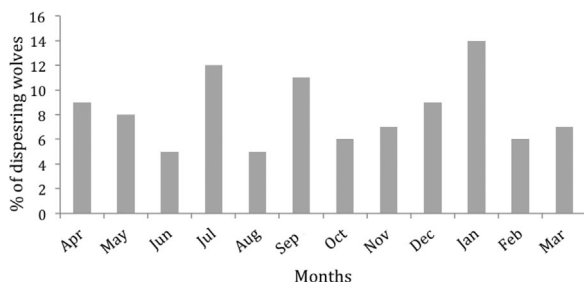
( $n = 64$ ) of all dispersals in Yellowstone National Park occurred between October and February.

For dispersals with known start and end dates ( $n = 182$ ), mean duration of dispersals during our study was  $5.5 \pm 6.8$  months (range = 1 day–26 months). There was no significant difference in the time it took dispersing yearlings (3.9 months) or adults (5.7 months) to form new packs ( $t_{93} = 1.48$ ,  $P = 0.141$ ) or in the time it took yearlings (7.0 months) or adults (4.9 months) to join existing packs ( $t_{57} = 1.18$ ,  $P = 0.242$ ; Table 1). There was no significant difference in the mean time it took dispersing males (5.0 months) and females (5.2 months) to form new packs ( $t_{95} = 1.99$ ,  $P = 0.869$ ) or for males (6.1 months) and females (6.8 months) to join existing packs ( $t_{27} = 2.05$ ,  $P = 0.911$ ).

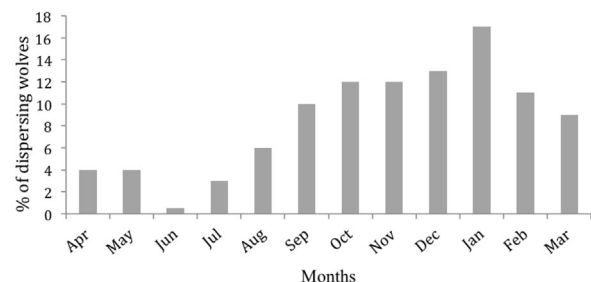
Mean dispersal distance for males ( $n = 160$ ) was  $98.1 \pm 99.9$  km and was not significantly different from the mean dispersal distance for females ( $n = 121$ ), which was  $87.7 \pm 101.9$  km ( $U = 10,768$ ,  $P = 0.107$ ; Fig. 4). The mean dispersal distance was longer for yearlings (120.1 km) than adults (69.8 km;  $t_{148} = 1.98$ ,  $P = 0.005$ ; Fig. 5). Included in our analysis were 3 long-distance dispersals to Oregon, 2 to Colorado, 1 to Utah, 1 to Washington (USA), 4 to British Columbia, and 2 to Alberta (Canada). We recorded 2 dispersals from Alberta to Montana. Ten wolves (3.4%) dispersed distances  $>300$  km (Figs. 4, and 5 1). Average dispersal distance decreased over the course of our study ( $\beta = -4.19$ ; 95% CI =  $-7.42$  to  $-0.84$ ;  $t = -2.51$ ,  $P = 0.006$ ).

Wolves dispersed in all compass directions (Fig. 6). Mean direction of dispersal was  $194^\circ$  (95% CI =  $118$ – $290^\circ$ ), vector strength was 0.072, and circular range was 351. Results indicated there was no preferred dispersal direction (Rayleigh test,  $r = 0.072$ ,  $P = 0.23$ ).

Mean pack size for dispersing yearlings (10.5) and adults (9.7;  $t_{186} = 1.1$ ,  $P = 0.292$ ) and for dispersing males (10.2) and females (9.7;  $t_{255} = 0.72$ ,  $P = 0.473$ ) was not significantly different. Male yearlings dispersed from mean pack sizes of  $11.2 \pm 6.9$  and yearling females dispersed from similar mean pack sizes of  $9.7 \pm 4.5$  ( $t_{93} = 1.23$ ,  $P = 0.223$ ). Mean pack size for adult males was  $9.6 \pm 5.1$ , which was not significantly different from the mean pack size of  $9.9 \pm 5.8$  for adult females ( $t_{148} = 0.34$ ,  $P = 0.737$ ; Table 2). The mean size of packs in which dispersal occurred ( $10.0 \pm 5.5$ ; range = 2–37) was significantly larger than the mean overall yearly NRM



**Figure 2.** Wolf dispersal by month in Montana, Idaho, and Wyoming, USA, 1993–2008 ( $n = 128$ ).



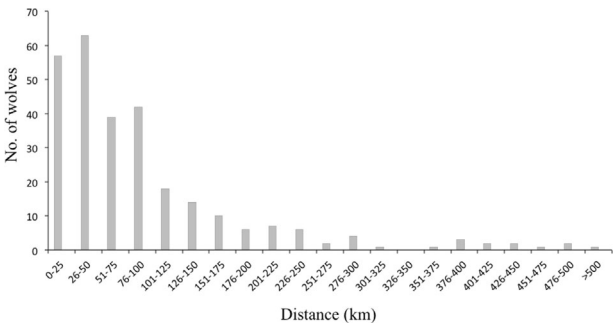
**Figure 3.** Wolf dispersal by month in the Yellowstone National Park, USA, 1993–2008 ( $n = 113$ ).

**Table 1.** Mean time (months) between dispersing and forming a new pack or joining an existing pack for 3 age groups of wolves in the northern Rocky Mountains, USA, 1993–2008.

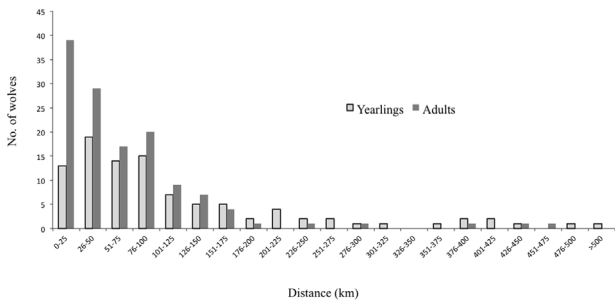
Age class	Sex	Formed new packs			Joined existing packs		
		$\bar{x}$	SD	<i>n</i>	$\bar{x}$	SD	<i>n</i>
Pups	M			0	6.6	9	2
	F	4.9	5.3	4			1
Yearlings	All	3.9	4.9	36	7	8.6	34
	M	4.4	5	14	7.3	8.8	27
	F	3.7	4.9	22	6	8.4	7
Adults	All	5.7	7.1	63	4.9	5.6	33
	M	5.2	6.4	31	4.7	6	25
	F	6.3	7.7	32	5.7	4.6	8

pack size ( $6.9 \pm 4.0$ ; range = 2–37;  $t_{1,335} = 10.1$ ,  $P < 0.001$ ; Tables 2 and 3).

Adult males ( $n = 94$ ) dispersed at a higher rate than adult females ( $n = 62$ ;  $\chi^2_1 = 6.635$ ,  $P = 0.010$ ), but yearling males ( $n = 54$ ) and females ( $n = 45$ ) dispersed at equal rates ( $\chi^2_1 = 0.817$ ,  $P = 0.366$ ). The overall dispersal rate for wolves in NRM was 10% (Table 3). The best model for predicting annual wolf dispersal rates contained variables related to the wolf's natal population (Table 4). The dominant predictors of dispersal rates were pack density within the animal's natal population ( $P < 0.001$ ) and whether the wolf was part of the Yellowstone National Park population ( $P < 0.001$ ). Dispersal rates declined as surrounding pack density increased. We estimated the dispersal rate decreased 4% (95% CI = 3–5) for every 1-unit (i.e., pack) increase in packs/1,000 km<sup>2</sup>. Age also had a negative effect on dispersal although it was not in the best fitting model and its effect ( $P = 0.04$ ) was not as powerful as other influential variables. The dispersal rate was 11% (95% CI = 10–13%) higher for animals originating inside Yellowstone National Park. Even though mean size of packs in which dispersal occurred was larger than the mean overall yearly NRM pack size, pack size was not in our most supported model for dispersal rate. We could not support our hypothesis that models containing variables related to the individual and its natal pack would predict dispersal rates because age, sex, and natal pack size were not significant predictors of dispersal rates (Table 4). Our management



**Figure 4.** Dispersal distance of wolves ( $n = 281$ ) in the northern Rocky Mountains, USA, 1993–2008. Dispersal distance for males (98.1 km,  $n = 160$ ) was not significantly different from females (87.7 km,  $n = 121$ ).

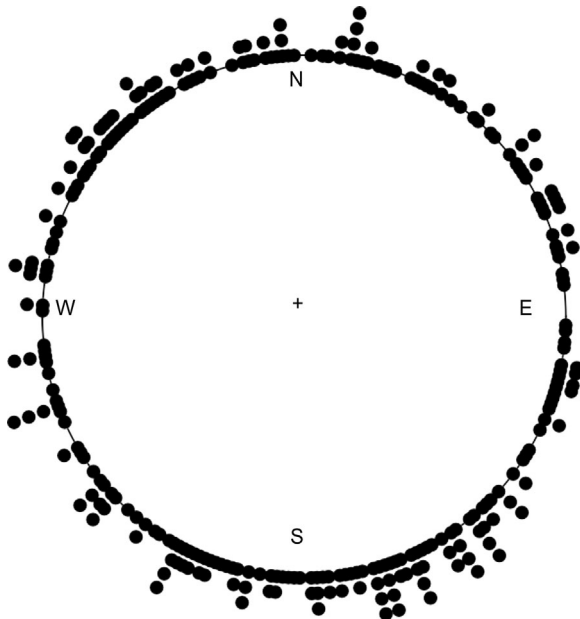


**Figure 5.** Mean dispersal distance of yearling wolves (120.1 km,  $n = 98$ ) was significantly greater than for adults (69.8 km,  $n = 131$ ) in the northern Rocky Mountains, USA, 1993–2008.

model, containing only variables that could be influenced by management, had poor overall fit.

Of the 166 dispersing wolves that survived dispersal, 97 (58%) dispersers paired with another dispersing wolf to form new packs and 69 (42%) joined existing packs ( $\chi^2_1 = 4.709$ ,  $P = 0.030$ ). There was no difference between the frequency of males ( $n = 95$ ) forming new packs ( $n = 42$ ) or joining existing packs ( $n = 53$ ;  $\chi^2_1 = 1.27$ ,  $P = 0.259$ ). However, males joined existing packs more often than females ( $\chi^2_1 = 10.79$ ,  $P = 0.001$ ), and completed dispersal most often in January and February. Females ( $n = 71$ ) formed new packs ( $n = 55$ ) or joined existing packs ( $n = 16$ ) more frequently in January, March, and May. More females formed new packs than joined existing packs ( $\chi^2_1 = 21.42$ ,  $P < 0.05$ ). Forty-seven males (28%) and 54 females (42%) became breeders.

Our global model for predicting successful dispersal had the most support, although we could not unequivocally disregard



**Figure 6.** Circular plot showing patterns of wolf dispersal direction in the northern Rocky Mountains, USA, 1993–2008. Dispersal direction is Euclidian direction between start point and end point. Each dot represents an individual wolf.

**Table 2.** Pack size the year in which the dispersal event occurred for dispersing wolves in the Northern Rocky Mountains, USA, 1993–2008. There were no significant differences among categories related to mean pack size.

	All dispersers	All dispersers		Pups		Yearlings		Adults	
	M and F	M	F	M	F	M	F	M	F
<i>n</i>	257	143	114	5	7	52	43	86	64
$\bar{x}$	10	10.2	9.7	11.4	8	11.2	9.7	9.6	9.9
SD	5.5	5.8	5.2	1.3	3.7	6.9	4.5	5.1	5.8
Min.	2	2	2	10	2	3	3	2	2
Median	9	9	9	12	9	10	9	8	9
Max.	37	37	37	13	12	37	19	23	37

our model based only on individual characteristics (Table 5). As pack density increased, the odds of successful dispersal declined 10% for every 1-unit (i.e., 1 wolf pack/1,000 km<sup>2</sup>) increase in pack density. Furthermore, the odds of successful dispersal were >11 times higher for wolves that formed packs than those who joined packs given that other variables in the model remained constant (Table 6). Sex, start date, pack size, distance dispersed, and direction were not influential variables in whether a wolf successfully dispersed. The coefficient for survival rate in the natal population, although negative, did not have a statistically significant influence on the odds of successful dispersal.

## DISCUSSION

Wolf dispersals in our study area occurred throughout the year, but increased gradually in the fall and peaked in early winter prior to breeding season. Dispersing wolves followed this pattern more consistently in Yellowstone National Park than in the rest of the NRM. We attributed this difference to natural regulation in the Yellowstone National Park wolf population and higher levels of anthropogenic mortality in the rest of the NRM. Agency control and illegal take outside national parks may disrupt pack structure and cause some remaining pack members to disperse.

Our values for dispersal duration were probably over-estimations because they relied on the accurate detection of when the dispersing wolf left the pack in which it was originally marked in, and when it arrived and settled in a new

area. Given the infrequency of relocation (monthly), our ability to ascertain these data were coarse.

Our dispersal data did not describe travel routes taken by wolves. Therefore, we made assumptions of the dispersal direction based on where dispersals ended. Our data were insufficient to identify specific barriers on the landscape that might impede dispersal. We predicted that the mountainous topography of the Rocky Mountains would influence dispersal of NRM wolves. However, our data indicate wolves in this study did not disperse in a preferred direction, with dispersal events in nearly every direction (circular range = 351). In contrast, Boyd et al. (1995) concluded wolf dispersal in Glacier National Park, USA, and Banff National Park, Canada, was influenced by mountain ranges and valleys trending north-south. Wolves tended to disperse north from Glacier National Park or southeastwardly from Banff National Park toward established wolf populations. Phillips et al. (2003) documented wolves dispersing south and west into areas with fewer wolves but abundant prey and vacant habitat. Although our data did not allow fine-scale evaluation of initial dispersal direction, we posit that given the nature of this study (i.e., recovering wolf population, abundant open territory in the early recovery period, abundant prey), the wide range of directions is an accurate representation of wolf dispersal in the NRM.

Our methods underestimated the actual distance and areas traversed by dispersing wolves because we calculated straight-line distances between start and end points. For

**Table 3.** Wolf population estimates in the northern Rocky Mountains, USA, and number and percent of radio-collared wolves and number and percent of radio-collared dispersers, 1998–2008.

Yr	Min. population	$\bar{x}$ pack size	No. radio-collared wolves		No. radio-collared dispersers	
			<i>n</i>	%	<i>n</i>	%
1998	275	9.2	123	45	15	12
1999	337	9.2	158	47	15	9
2000	437	7.2	176	40	22	13
2001	563	7.3	190	34	21	11
2002	663	6.9	194	29	25	13
2003	761	6.6	228	30	23	10
2004	846	7.0	231	27	30	13
2005	1,016	6.9	230	23	25	11
2006	1,300	6.7	274	21	26	9
2007	1,513	6.7	299	20	21	7
2008	1,645	6.4	339	21	32	9

**Table 4.** Regression models, variables, model fit ( $R^2$ ), and model selection criteria (Akaike's Information Criterion [AIC]) used to predict dispersal rates of gray wolves in the northern Rocky Mountains (NRM), including Yellowstone National Park (YNP), USA, 1995–2008. A (+) symbol indicates the variable was included in the model and significant, whereas a (–) indicates the variable was included in the model but not significant.

Model	Age	Sex	(log) natal pack size	$S_{np}$ <sup>a</sup>	Pack density <sub>np</sub> <sup>b</sup>	In YNP or in NRM	$R^2$	AIC	$\Delta$ AIC
Natal population				–	+	+	0.64	–970.74	0.00
Natal pack			–			+	0.56	–940.07	30.67
Individual	+	–				+	0.56	–884.04	86.70
Individual + natal pack	+	–	–			+	0.56	–866.81	103.93
Management			+	–	+		0.06	–710.54	260.20

<sup>a</sup> Survival rate for individuals from Smith et al. (2010).

<sup>b</sup> Packs in natal population/1,000 km<sup>2</sup> annually.

example, a radio-collared yearling wolf from Montana dispersed in September 2008 and died in Colorado in March 2009. Its straight line dispersal distance was approximately 650 km, but the GPS location data showed it had actually traveled >4,750 km through 5 states (Montana, Wyoming, Idaho, Utah, and Colorado; L. Rich and M. Mitchell, University of Montana, personal communication). A wolf in Sweden with a GPS collar traveled a straight-line distance of >1,092 km with an actual travel distance of over >10,000 km in just under a year (Wabakken et al. 2007). We did not calculate the straight-line distance between the centers of the original and newly established home ranges because accurate home range data for most new packs were not available. Home ranges of wolves in NRM are typically so large that this method would bias estimated straight-line dispersal distances.

As wolf habitat became increasingly occupied by resident packs, we predicted dispersing wolves would travel farther to find vacant habitat to start new packs. However, average dispersal distance decreased later in our study. The greater number of packs on the landscape may have provided more opportunities for dispersing wolves to find social openings in existing packs. Wolves continued recolonizing areas between resident packs.

Increased human-caused mortality (illegal take and agency lethal control) removed individual wolves and entire packs, and thereby provided a constant source of vacant habitat for

wolves to recolonize. However, long-distance dispersals still occurred at low wolf density even when vacant habitat was nearby. For example, genetic testing showed that an uncollared wolf shot just south of Yellowstone National Park in 1992, prior to reintroduction, came from northwest Montana or southern Canada (S. Fain, USFWS, personal communication). At that time, there were only 41 wolves in the NRM, and the closest pack was 484 km away, northwest of Missoula, Montana (USFWS et al. 2011).

Dispersal rates in our study were negatively correlated with pack density and positively correlated with whether the animal had originated from Yellowstone National Park. We did not find a significant effect of pack size on dispersal rates, however, other biologists have documented positive relationships between dispersal rate and pack size. Hayes and Harestad (2000) suggested that dispersal rates were positively correlated with pack size in a recovering wolf population in the Yukon, Canada. Boyd and Pletscher (1999) did not report a correlation between dispersal rate and the previous year's maximum pack size. Mech and Boitani (2003) summarized Peterson and Page (1983) noting that dispersal rates increased and were inversely related to pack size during times when prey abundance was low on Isle Royale in Lake Superior, USA.

An average of 10% of the known wolf population in NRM dispersing annually is among the lower documented rates in North America (Fuller et al. 2003). Our estimated dispersal

**Table 5.** Model structure, –2 log-likelihood (–2LL), number of parameters ( $K$ ), Akaike's Information Criterion Value (AIC), change ( $\Delta$ ) in AIC value, Akaike weight ( $w_i$ ), and receiver operating characteristic (ROC) of models predicting successful gray wolf dispersal in the northern Rocky Mountains, USA, 1995–2008.

Model <sup>a</sup>	–2LL	$K$	AIC	$\Delta$ AIC	$w_i$	ROC <sup>b</sup>
Global						
Age + sex + pack size + $S_{np}$ + pack density <sub>np</sub> + start month + distance + direction + joined or formed new pack	52.70	10	72.70	0.00	0.64	0.76
Individual						
Age + sex + start month + distance + direction + joined or formed pack	60.87	7	74.87	2.17	0.22	0.83
Individual + pack						
Age + sex + pack size + start month + distance + direction + joined or formed new pack	60.86	8	76.86	4.16	0.08	0.75
Natal population						
$S_{np}$ + pack density <sub>np</sub> + start month + distance + direction + joined or formed new pack	63.74	7	77.74	5.04	0.05	0.82
Natal pack						
Pack size + start month + distance + direction + joined or formed new pack	69.87	6	81.87	9.17	0.01	0.83

<sup>a</sup>  $S_{np}$  = survival rate for individuals from Smith et al. (2010); pack density<sub>np</sub> = packs in natal population/1,000 km<sup>2</sup> annually.

<sup>b</sup> ROC values >0.70 indicate acceptable discrimination, >0.80 indicates excellent discrimination.



**Table 6.** Logistic regression parameters and odds ratios from the top model (global) describing successful gray wolf dispersal in the northern Rocky Mountains, USA, 1995–2008. Females were the reference category for sex and existing packs was the reference category for formed new packs.

Parameter	Estimate	SE	Odds ratio	Odds ratio lower 95% CI	Odds ratio upper 95% CI
Constant	5.66	18.71			
Age	0.05	0.02	1.05	1.00	1.10
Sex	−0.23	0.92	0.80	0.13	4.83
Pack size	0.85	1.67	2.34	0.09	61.76
Survival rate	−5.59	23.87	0.00	0.00	0.00
Start month	−0.08	0.10	0.92	0.76	1.12
Distance	−0.14	1.01	0.87	0.01	6.31
Direction	0.00	0.00	1.00	1.00	1.01
Pack density	−2.30	0.91	0.10	0.02	0.60
Formed new pack or joined existing pack	2.42	0.94	11.27	1.78	70.98

rate calculations may have been biased low because we recorded data that described the number of active radio-collars each year, but we did not have data describing the number of active radio-collars each month. Therefore, the denominator we used for our rate estimator (no. wolf/yr) was inflated relative to what it would have been if we had used the sum of wolf-days, weeks, or months. Unfortunately we did not have data available at a finer temporal scale for this analysis.

We radio-collared 592 pups during our study, yet they rarely dispersed. Dispersal of pups has been documented (Fuller 1989, Gese and Mech 1991, Packard 2003, Phillips et al. 2003, Adams et al. 2008), but it is uncommon for pups <11 months old to disperse (Ballard et al. 1987, Fuller 1989, Gese and Mech 1991, Mech et al. 1998, Hayes and Harestad 2000). Our low pup dispersal rate may have occurred because the recolonizing population was expanding rapidly, and a high rate of human-caused mortality probably resulted in a high proportion of pups that rarely dispersed in the NRM.

Males dispersed at a higher rate than females in our study as they have in other areas (Ballard et al. 1983, Peterson et al. 1984, Wabakken et al. 2007). However, equal dispersal rates between males and females have also been reported (Peterson et al. 1984). This result may reflect a difference in life-history strategies between the sexes; subordinate females have been shown to be more likely to inherit breeding positions in their natal packs (vonHoldt et al. 2008).

Dispersing wolves typically find mates and start new packs (Rothman and Mech 1979, Fritts and Mech 1981, Ballard et al. 1987), or are adopted into existing packs (Fritts and Mech 1981, Van Ballenberghe 1983, Peterson et al. 1984, Messier 1985, Mech 1987). Adopted wolves frequently replace lost breeders (Fritts and Mech 1981, Mech and Hertel 1983, Peterson et al. 1984, Stahler et al. 2002), whereas other wolves join packs but never become breeders (Fritts and Mech 1981, Peterson et al. 1984, Ballard et al. 1987, Mech 1991, Meier et al. 1995). We determined that males more often joined existing packs compared to the frequency at which females joined existing packs, which was similar to the findings of other studies (Peterson et al. 1984, Messier 1985, Meier et al. 1995). Dispersed females were much easier to observe at den or rendezvous sites, creating a potential bias that underestimated the number of males that joined existing packs and became breeders. Our data also depended on functioning radio-collars that might have been biased to more readily detect breeding soon after dispersal

(new pairs) than delayed breeding (joining an existing pack and waiting for a breeding opportunity to become available).

The most powerful variables predicting successful dispersal in the NRM were whether a dispersing wolf formed a new pack or joined an existing pack, age at dispersal, and pack density (Table 6). Wolves that formed new packs were more likely to successfully breed than those that joined existing packs. Adoption into wolf packs is hazardous for dispersing wolves because the potential for intraspecific strife and mortality is high (Mech 1994, Mech et al. 1998). In contrast, if vacant habitat exists, wolves are adept at locating mates (Mech and Boitani 2003), and forming a new pack may be less hazardous and lead to increased fitness (i.e., successful reproduction). The survival rate of wolves in the natal population did not influence the odds of success once a wolf dispersed. A relatively low survival rate in the natal population may indicate years where surviving individuals are in poorer health, thus the odds of successful dispersal may be lower once they leave their natal territory.

Contrary to our expectations, dispersal distance did not affect dispersal success. We suggest that the strong positive effect of establishing one's own pack outweighed the costs associated with the longer dispersal distances typically required to find vacant habitat. However, extra-long distance dispersing wolves (>300 km) may reduce their chances of finding a mate or joining an existing pack if they disperse far from core population centers because fewer wolves might be found on the peripheries of wolf distribution. For example, a lone uncollared wolf from NRM was killed in South Dakota and another was documented in Arizona before eventually being killed in Utah. Dispersing NRM wolves established reproducing packs in Oregon and Washington. Wolves from Oregon have expanded wolf distribution into northern California, but no packs of NRM wolves have been confirmed east or south of Wyoming.

Wolves routinely disperse in response to competition and aggression related to food availability and breeding opportunity within their pack (Mech and Boitani 2003). Wolves disperse at different ages because of limited food resources (Fritts and Mech 1981, Ballard et al. 1987, Mech 1987, Fuller 1989, Gese and Mech 1991), and often postpone dispersal in areas of high prey availability (Ballard

et al. 1987). Dispersal rates may increase when food is scarce (Peterson and Page 1983, Messier 1985). During our study, we recorded few wolf mortalities due to food-stress or starvation (Smith et al. 2010). Abundant wild prey may have contributed to an older mean dispersal age of 32 months in the wolf population in NRM. Theoretically, the average age of dispersal of wolves in NRM could become younger if prey becomes limited. The presence of abundant livestock and wild prey, and high rates of mortality by agency control, illegal take, and public harvest throughout the NRM make it unlikely that the wolf population would become food limited. Possible exceptions might be relatively small areas like Yellowstone National Park or the central Idaho wilderness where wolf density and distribution may remain limited by natural factors related to prey abundance and social regulation. As the wolf population turns over more rapidly from higher rates of human-caused mortality from regulated harvest in addition to agency control, an even younger age structure in the population and increased level of social openings might cause a shift in the proportion of wolves that disperse as yearlings (Brainerd et al. 2008). Managers can expect increased human-caused mortality will result in a slightly younger aged wolf population, more social openings in existing packs, more vacant habitat, and more dispersal outside the winter pre-breeding time period. None of these factors, however, will inhibit successful dispersal.

Wolves can successfully disperse at different times of the year through hostile, unsuitable areas (Linnell et al. 2005). Young and old wolves, of both sexes, disperse for various lengths of time and distances. Most wolves disperse from their natal pack by the age of 3 years (Gese and Mech 1991, Mech et al. 1998). Their phenomenal dispersal ability helps explain why wolves can recolonize distant, vacant habitat relatively quickly and why wolf populations are so resilient even as human-caused mortality increases (Mech and Boitani 2003, Adams et al. 2008). This innate behavior and the proximity of large blocks of habitat in the NRM assures that population viability will be maintained in NRM wolves.

## MANAGEMENT IMPLICATIONS

Dispersal is the main mechanism by which wolves recolonize areas with high human-caused mortality and as mortality increases, will be increasingly important in maintaining viable populations. Therefore, managers should continue to stay aware of any changing environmental conditions or factors such as physical barriers or disease that could inhibit dispersal. Dispersing wolves originating inside Yellowstone National Park, and possibly larger packs in general, had a positive effect on dispersal rate, thereby emphasizing the importance of maintaining source wolf populations in protected areas such as national parks or refugia in large tracts of public lands. The swift recovery of gray wolves in the NRM demonstrates the effectiveness of dispersal as a mechanism for growth where habitat exists. As such, augmenting gray wolf recovery to nearby states may be uneconomical and unnecessary where wolves can effectively disperse on their own. However, managers seeking to reestablish wolf populations where habitat is limited and

disconnected from other wolf populations may need to consider translocation (Carroll et al. 2006).

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