

**EFFECTS OF WOLVES ON LIVESTOCK CALF SURVIVAL
AND MOVEMENTS IN CENTRAL IDAHO**

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Abstract

We examined interactions between wolves (*Canis lupus*) and domestic calves within a grazing allotment in central Idaho to evaluate the role of wolf predation in calf survival and movements. During the 1999 and 2000 grazing seasons, we radio-marked 231 calves per year, representing 33% of the calf population, on the Diamond Moose Association (DMA) grazing allotment, and monitored their survival and movements relative to wolf distribution. Overall, calf survival was high ($\geq 95\%$), with relatively few mortalities ($n = 13$) among the marked population. Non-predation calf mortality (pneumonia, unknown natural causes, and fire) and wolf-caused calf mortality represented 61% and 31% of deaths, respectively, while coyote predation accounted for the remaining (7%) mortality. Calves selected by wolves were younger than the surviving cohort by an average of 26 days ($P < 0.05$). Calf movement patterns and group size did not vary relative to the level of spatial overlap with wolves, however, vulnerability to predation appeared to be correlated with spatial proximity of calves to wolf home ranges and rendezvous sites. These results suggest that in our study area the overall impact of wolves on calf survival and behavior was modest, and that ranchers could further minimize wolf predation by altering calving periods to favor older calves and minimize spatial overlap between grazing cattle and areas of intense wolf activity.

Introduction

Gray wolves were extirpated from much of western North America due in part to conflicts with domestic livestock (Young and Goldman 1944, Mech 1970). Accordingly, wolf-livestock conflicts were viewed as an important concern of the Northern Rocky Mountain Wolf Recovery Plan (U.S. Fish and Wildlife Service 1987). Wolves dispersed naturally into Montana (Ream et al. 1989), and were reintroduced into Yellowstone National Park and central Idaho (Fritts et al. 1997). The present recovery plan relies on the nonessential experimental designation of wolves in the Greater Yellowstone Area (GYA) and central Idaho to allow for management flexibility designed to mitigate wolf-livestock conflict (U.S. Fish and Wildlife Service 1994). Currently, wolf populations in Wyoming, Montana, and Idaho have caused less livestock damage than initially anticipated (U.S. Fish and Wildlife Service 1987). However, in each of these states some livestock producers who experienced confirmed wolf depredations also reported an increased level of missing calves, which may be attributed to wolf predation (Bangs et al. 1998); areas in Minnesota had similar reports (Fritts 1982). Even with increased monitoring, some wolf kills inevitably remain undetected due to rapid and extensive consumption by wolves and scavengers, rapid carcass decomposition during summer, and the rugged, inaccessible, forested terrain where such kills often occur (Bangs et al. 1998). Thus, there exists a clear need to better understand the direct impact of recolonizing wolves on livestock mortality.

Few data are available on either the factors pre-disposing livestock to predation, or the sub-lethal effect of wolf predation risk on livestock behavior. Some studies have suggested that wolves select disproportionately for domestic livestock calves (Fritts 1982, Fritts et al. 1992, Bjorge and Gunson 1985), while others indicate that livestock depredation

and winter severity may be inversely correlated due to the availability of alternate prey (Mech et al. 1988). In wild ungulates, age (Mech 1970, Peterson 1977, Nelson and Mech 1981), juvenile and maternal nutritional status (Peterson 1977, Mech et al. 1987, Mech et al. 1991, Kunkel and Mech 1994), and maternal age (Ozoga and Verme 1986), all have been identified as factors pre-disposing ungulate prey to wolf predation. It is reasonable to presume that similar patterns characterize wolf selection of domestic livestock prey, although such interactions have yet to be examined quantitatively. Furthermore, colonizing wolves may have subtle impacts on wild ungulates, including possible decreased weight gain among juveniles due to increased vigilance and altered movements patterns related to predation risk (Berger et al. 2001). Similarly, wild ungulate movement patterns and group sizes may affect wolf prey selection (Nelson and Mech 1991, Fritts and Mech 1981, Kunkel and Mech 1994, Carbyn et al. 1993, Carbyn 1997). Cattle could portray similar patterns, provided that wolf predation risk is of sufficient intensity so as to influence their behavior.

The present study was designed to examine three objectives related to wolf-livestock interactions: (1) the cause of death among calves found in areas recolonized by wolves in Idaho; (2) the attributes of the wolf-killed calf cohort and the factors promoting their vulnerability to predation; and (3) the movement and group size responses of calves to wolf predation risk. We predicted that wolves would select calves that were disadvantaged in terms of age and spatial proximity to wolf territories, and that predation risk would increase both herd sizes and movement distances.

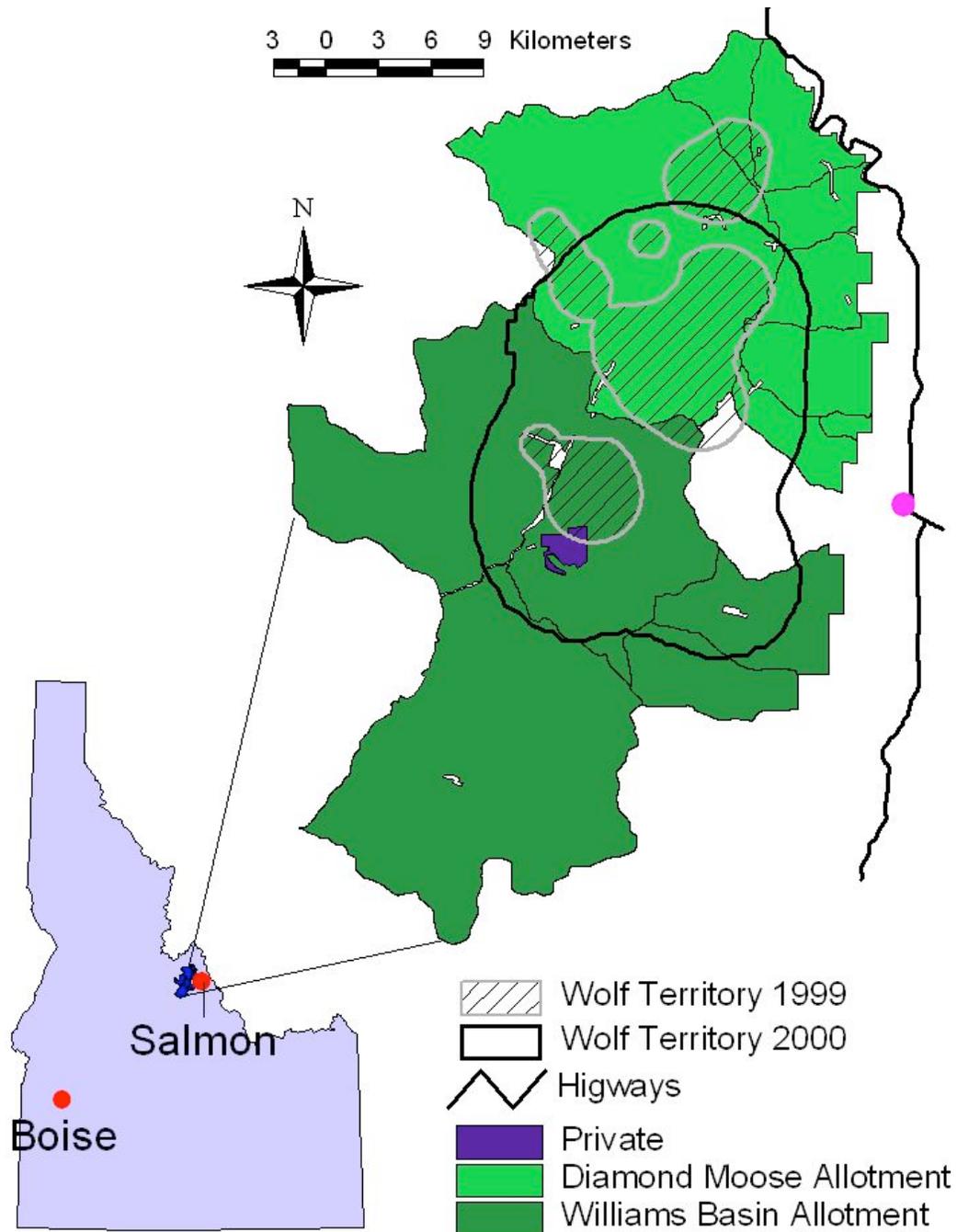
Study Area

The study was conducted on the Diamond-Moose grazing allotment (DMA) in Lemhi County, northwest of Salmon, Idaho (45°11'N, 113°54'W, Figure 1). The landscape is

mountainous with dense coniferous cover, interspersed with small grassy meadows and riparian areas. The allotment contains portions of 5 drainages flowing into the Salmon River, with 5 livestock permittees (Aldous, Bills, McFarland, Slavin, and Wiley) grazing approximately 688 cow/calf pairs annually within the 30,000 hectare allotment (Figure 1). Establishment of the Jureano wolf pack occurred in 1996, with pup production occurring in 1997 (6 pups), 1998 (4), 1999 (9), and 2000 (6). Control actions and subsequent relocations in 1998 reduced pack size to an estimated six wolves going into the 1999-breeding season. Natural mortalities (7 pups), control actions (2 adults killed, 2 pups relocated), illegal mortality (1 adult), and dispersal (2 adults), resulted in the disappearance of all individuals from the Jureano wolf pack by late winter 2000. However, 1 of the dispersing adults returned, with an unknown adult, to form a new pack in the area by spring of 2000. This pack produced pups in the same den, and used the area in a similar fashion, as the 1999 pack (Figure 1). Thus, during the course of the study, livestock on the DMA were exposed to 4-15 wolves occupying the same general area.

Reported cattle losses (deaths and unexplained missing) on Forest Service public grazing allotments within the pack's territory increased during 1996-1998 relative to historic trends (U.S. Forest Service unpublished data). Missing calves comprised the majority of the increase in reported losses, with loss rates for cows and bulls not increasing during the same period. Wolves, mountain lions (*Felis concolor*), bobcat (*Lynx rufus*), black bear (*Ursus americanus*), and coyote (*Canis latrans*) are possible predators upon livestock in the area.

Figure 1. Wolf-cattle study area in central Idaho. Intensive study was conducted on the Diamond Moose Allotment (DMA) in the portions where wolf home ranges overlapped.



Methods

Survival

During the 1999 and 2000 grazing seasons (May-October), ear-tag radio transmitters (Advanced Telemetry Solutions, Isanti, MN) equipped with two-hour mortality switches were attached to 462 calves (231 per year). This sample represents approximately one third of all calves grazed on the allotment. Gender, birth date, mother's age, ear tag number, and livestock permittee were recorded for each marked calf. Calves were monitored daily via radio-telemetry to determine spatial distribution and survival. Calves found to have a transmitter in mortality mode were promptly located and covered in the field to prevent further consumption by scavengers. USDA/APHIS, Wildlife Services (WS) personnel then examined dead calves within one day of initial discovery to determine cause of death (see guidelines by Roy and Dorance 1976, Fritts 1982). A veterinarian performed internal necropsy on carcasses to determine cause of death for non-predation mortalities. All causes of deaths were categorized as predation (wolves or coyotes) or non-predation (pneumonia, unknown natural causes, or fire) to calculate cause-specific mortality rates.

Calf survival was analyzed via Poisson regression, which uses the Poisson distribution as the basis for statistical inference (Selvin 1995). We used a stepwise model building approach that evaluates the relationship between multiple independent variables and a rate, which in our case consisted of the daily mortality rate (Selvin 1995, Murray in press, Wirsing et al. 2002). Calf gender, birth date, mother's age (in years), year and month of study, wolf activity period (high or low, dummy coded for the time period when wolf-cattle interaction occurred on the DMA), and livestock permittee were used as independent

variables and made available for retention in the model. Forward stepwise regression (see Hosmer and Lemeshow 1989) was used to develop our survival models, with the partial likelihood ratio test determining variable retention (level to enter, $P = 0.05$). Akaike's information criterion (AIC) also was calculated for all models to ensure model parsimony; models with a Δ AIC value > 2.0 were considered a significantly better fit than comparison models (Anderson et al. 2000). We used three different mortality categories (all mortalities, only natural mortalities, and only wolf-caused mortalities) as dependent variables in three separate survival analyses, to fully evaluate the attributes of wolf-killed calves relative to the surviving cohort. This was accomplished by right-censoring mortalities that were not of interest in the particular analysis. The final step in model building constituted checking the robustness of each final model via backwards selection. The influence of continuous variables on mortality rate was described using rate ratios (rate ratio = $e^{\text{coefficient}}$), which enables assessment of the relative risk provided by a given variable. Cause-specific calf survival rates were calculated by $[1 - (\text{deaths}/\text{radio days})^{\text{days}}]$, where deaths represented specific causes of death (Trent and Rongstad 1974).

Space use

A random sample of marked calves (20-30) was located on a weekly basis to evaluate their positions relative to weekly aerial locations of radio-collared wolf pack members (1-4 individuals located per week). Calves were located via aerial telemetry and ground locations using a Trimble Global Positioning System unit (3-5 meter accuracy). Cover type (forest, mountain brush, riparian, grass and other), position on slope (bottom, lower slope, mid-slope, upper-slope, ridge top, and bench), percent slope (0-20, 21-40, and >40), aspect (N, E, S, W), and group size associated with the calf (1-10, 11-20, 21-30, and >40) were recorded for each

calf location based on visual observation. Home ranges (95% fixed kernel [FK]) and core use areas (50% FK) with least-squares cross-validation (LSCV, Worton 1995) were constructed to describe spatial distribution of cattle belonging to each permittee, using the animal movement extension in the program Arcview (Hooge et al. 1999, ESRI, Redlands, CA, USA).

Nez Perce Tribal biologists located wolves from the ground 2 to 3 times per week and assigned locations to 1-km² grids overlaid on 1:24,000 topographic maps. Points were then constructed using a geographical information system (GIS) based on the center of the grids containing wolf locations. Combined with aerial locations, this information was used to construct home ranges using the same methods as described above for cattle. All home ranges were constructed with >30 independent locations (Seaman et al. 1999). We compared the amount of home range overlap between individual permittee's cattle and wolves, coupled with wolf kill rate, to assess if degree of overlap pre-disposed calves to wolf predation.

Wolf home ranges for each year were transformed onto a grid, such that each area within the home range could be assigned a specific utilization level by wolves (Hooge et al. 1999, see Roloff et al. 2001). Cattle locations were then overlaid to determine the level of wolf predation risk at each calf location. We then compared calf locations at various wolf predation risk levels to determine if calf movement patterns or cattle group size varied with proximity to core wolf use areas. We used a general linear model (Proc GLM, SPSS Inc. 2000) to analyze calf movement, with daily movement distance as the dependent variable and permittee, year, days between locations (added as a block to remove the influence of decreasing movement distance with increased days between locations), wolf use level (continuous variable, 1%-100% FK) at the initial location of the calf, wolf use level at the

final location of the calf, and the amount of wolf use change between calf locations, as independent variables. Cattle gregarious behavior relative to proximity to wolves was analyzed using log-linear models (Proc Catmod, SAS institute 1996), with estimated group size as the dependent variable and habitat, position on slope, and wolf use level (categorical variable; no wolf use, 99%-90% FK, 89%-60% FK, and < 60% FK), as independent variables. Only locations obtained during the time period when wolves and cattle were both on the DMA (i.e. July-September) were used for movement analysis.

Habitat use

We analyzed habitat selection by cattle and habitats where wolf-killed calves were found on the DMA. We approached this analysis in a hierarchical fashion, by first comparing habitat characteristics at calf locations to available habitat (e.g., locations for Aldous cattle vs. 95% fixed kernel for that herd), then comparing habitat at all mortality sites to that of calf locations, and finally by comparing the habitat characteristics at wolf killed and natural mortality sites to that of calf locations. Mortality sites were compared to the point locations for the herd from which the animal died (e.g. if an Aldous calf was killed by wolves in 1999, availability for that calf was determined from point locations for the Aldous herd during 1999). Selection patterns were compared via χ^2 goodness of fit (Neu et al., 1974) with the program Resource Selection (Leban 1999). Bailey simultaneous confidence intervals determined preference for specific habitat categories when significant selection ($P < 0.05$) was detected (Cherry 1996). We analyzed cover type, aspect, and slope (see above for classification) for point vs. home ranges (availability defined via a USFS land cover map, and 90m Digital Elevation Models). Mortality site analysis included position on slope in addition to the previous comparisons.

Wolf impact on cattle populations

Non radio-marked calf carcasses were found opportunistically by ranchers and examined as described above for collared calves. Wolf-killed calves found by study personnel did not elicit control actions on the wolves, but were compensated for by Defenders of Wildlife (see Fischer 1989). However, calves found independently by ranchers did result in control actions in accordance with established guidelines (U.S. Fish and Wildlife Service 1994). Cause-specific mortality rates of the marked calf population were multiplied by the total number of calves on the DMA ($n = 688$) to estimate the number of calf mortalities that occurred from specific causes during a given year. Detection rates were then calculated by comparing the number of calves estimated to have died from a particular mortality agent to the number recovered during the study. Calf mortalities occurring during the grazing season were separated into calves found by study personnel and those found by ranchers, thus enabling the determination of two separate detection rates. Detection rates were calculated including and excluding calves found by study personnel within the number of calves found to represent maximum and minimum detection rates on the allotment.

Results

Survival

Survival rates of marked calves were high during the 1999 and 2000-grazing season (95 and 98%, respectively), with monthly rates for May – November ranging from 0.98 – 1.00 (Table 1). Cause of death for the 13 marked calf mortalities were: pneumonia (31%), wolf predation (31%), coyote predation (8%), unknown natural mortality (15%), and fire-related mortality (15%).

Table 1. Monthly survival rates for livestock calves on the Diamond Moose Allotment in central Idaho.

Year/month	No. marked	Radio days	Non-Predation deaths	Predation deaths	Monthly Survival rate
1999					
May	231	3932	0	0	1.000
June	234	6851	0	1 ^b	0.996
July	235	6842	1	3 ^c	0.982
August	234	6917	4	0	0.982
September	220	6300	0	0	1.000
October	187	2529	0	0	1.000
November	20	325	0	0	1.000
2000					
May	231	3887	0	0	1.000
June	228	6598	0	0	1.000
July	235	6081	3	0	0.985
August	220	5930	0	1 ^c	0.995
September	201	3587	0	0	1.000
October	105	1014	0	0	1.000
November	11	31	0	0	1.000

^bCoyote predation.

^cWolf predation.

Calf survival models where we included all mortalities and only non-predation mortalities retained wolf activity period ($\chi^2 = 2.793, P < 0.001$, and $\chi^2 = 23.755, P = 0.001$, respectively) as the single significant covariate. Recall that this parameter is a block for the months of July, August and September when wolves and cattle interacted on the DMA. The majority of mortalities (92%) occurred within this time period, regardless of cause of death. The wolf predation model (i.e. right censoring non wolf-caused mortalities) provided a more complex relationship (Table 2). The first parameter to be retained was livestock permittee ($\chi^2 = 8.924, P = 0.005$). All marked calves that were killed by wolves ($n = 4$) were in the Aldous herd, which was located closest to the wolf core use area (see below). Next, wolf activity period was retained in the model ($\chi^2 = 6.584, P = 0.01$). Thus, any parameter subsequently retained in the model was blocked for the time period when wolves and cattle were interacting (i.e. the months of July, August and September). The final parameter retained in the model was birth date of calves ($\chi^2 = 5.04, P = 0.025$), with the coefficient for this parameter indicating that calves born later in the season (i.e. younger aged) were more susceptible to wolf predation. On average, the surviving cohort of calves was 36 days older (wolf killed: March 31 ± 13 days, $n = 4$ [mean birth date \pm SE]; live population: February 23 ± 1.3 days, $n = 445$) surviving than that of the wolf killed cohort. The rate ratio for the age parameter ($e^{0.046} = 1.05$) indicated that for each day older a calf's risk of wolf predation declined by a factor of 5%. Thus, calves that were one month younger were over 4 times ($1.05^{30} = 4.32$) more likely to die from wolf predation. Therefore, our wolf-killed calf survival model revealed that depredated calves belonged exclusively to Aldous, died between July-September, and tended to be younger than average.

Table 2. Parameter estimates for a livestock calf survival model of the Diamond Moose Association in central Idaho (1999-2000) with wolf predations as the dependent variable.

Parameter	Coefficient	95% CI	Δ AIC	<i>P</i>
Significant Parameters				
Intercept	-9.269 ^a			
Permittee	24.479 ^a	-- ^b	5.9	0.005
Wolf activity	24.146 ^a	-- ^b	4.6	0.010
Birthdate (Days)	0.046 ^a	± 0.041	3.0	0.025
Non-Significant Parameters				
Year			-1.0	0.322
Month			-1.0	0.321
Sex (proportion male)			-1.5	0.481
Mother's age (Years)			0.2	0.178

^aCoefficient values are for the time of entry into the model rather than the final model.

^bConfidence intervals were not included for dummy coded variables

Given the above results, it remains unclear if wolves actively select young (i.e. substandard) calves or else if age-specific differences in calf behavior render the younger cohort more vulnerable to predation. To explore these two possibilities, we analyzed locations of young versus older calves (classifications based on means \pm SE of wolf-killed Aldous calves vs. those surviving) with slope, number of cattle in the group, aspect, position, habitat, and spatial overlap with wolves as independent variables. We found that no variables were retained in the logistic regression model (all $P > 0.144$), suggesting that age-specific differences in calf habitat use or social behavior likely were absent. Thus, selection for younger calves was due to either active selection by wolves and/or disparate age-specific escape abilities among calves.

Space use

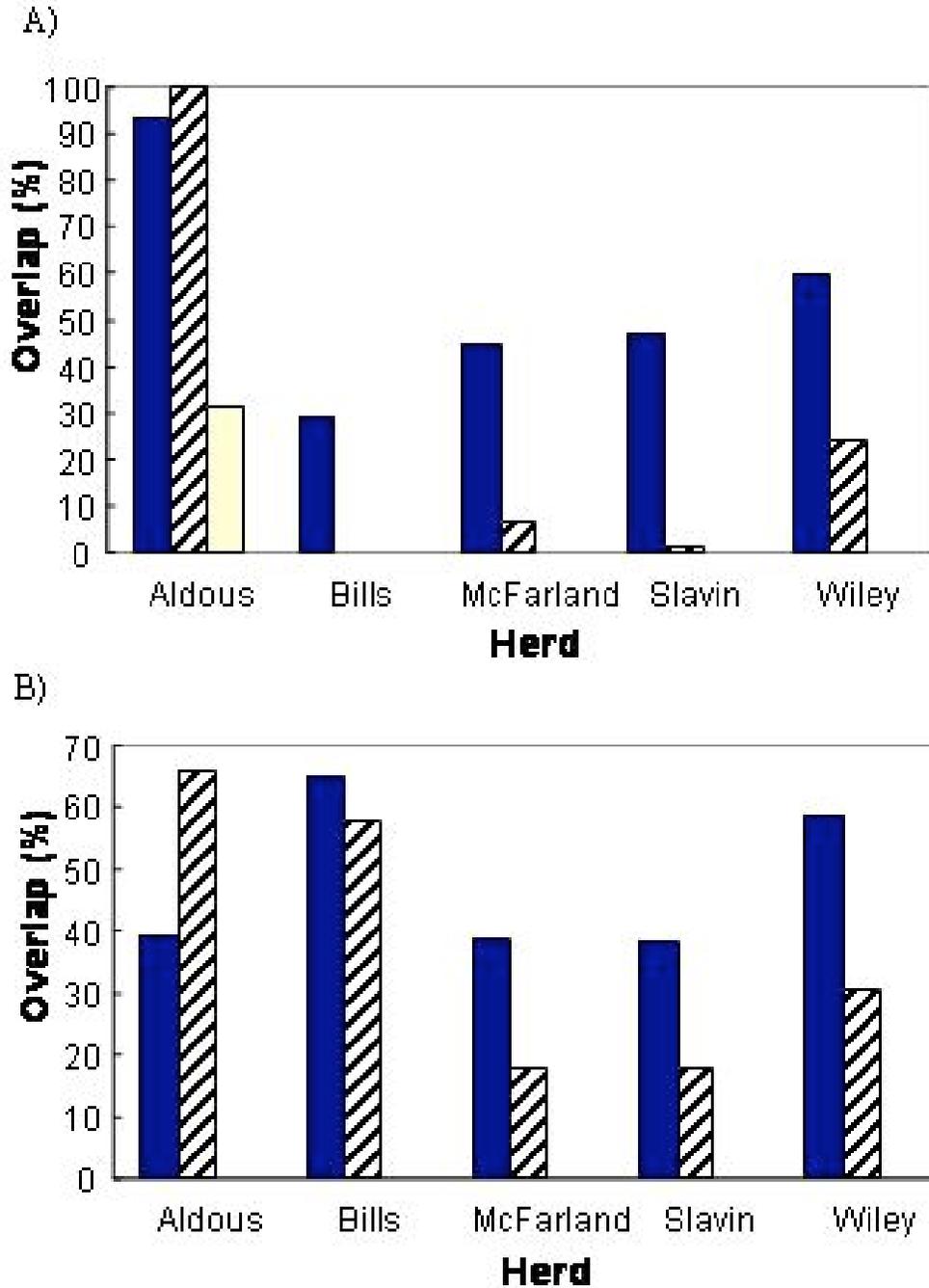
Home range analysis indicated that as wolf and cattle range size was restricted to defined core use areas, only Aldous calves showed an increase in the percent of overlap with wolves (Figure 2). Further, during the 1999-grazing season only Aldous calves had core areas that overlapped with wolves. Thus, Aldous calves likely had highest exposure to wolf predation risk during the period when wolves were most actively killing cattle.

Only two variables influenced calf movement significantly, days to next location ($F = 51.443$, $P < 0.001$) and year ($F = 6.117$, $P = 0.014$). Wolf predation risk (i.e., wolf use level at the initial location of the calf, wolf use level at the final location of the calf, and the amount of wolf use change between locations) and permittee did not influence the distance that calves moved per day (all $P > 0.18$). The observed annual variability in calf movement patterns was the result of reduced calf movement in 2000 (629 meters \pm 76 [mean \pm SE])

relative to 1999 (429 ± 35). Calf movement during 2000 was likely reduced because of a fire in portions of the DMA. Days to next location showed an inverse relationship with movement distance ($r = -0.377$). This difference likely occurred due to decreased resolution between temporally disparate locations, implying that the measure of actual distance moved represented an under estimate with increasing time between locations.

Cattle group size was affected by position on slope ($\chi^2 = 13.13$, $df = 4$, $P = 0.011$) and habitat ($\chi^2 = 16.16$, $df = 6$, $P < 0.001$). Larger groups of cattle were observed near riparian bottoms and in more open habitat. Following the retention of these two variables in the model, wolf utilization levels were not related to cattle group size ($\chi^2 = 3.04$, $df = 6$, $P = 0.803$). These results, combined with the aforementioned movement analysis, suggested that wolf predation had little influence on cattle movement or behavior.

Figure 2. Percent overlap between cattle and the Jureano wolf pack home range for individual permittees on the Diamond Moose Association during the 1999 (A) and 2000 (B) grazing seasons. Dark bars indicate 95% (fixed kernel) cattle utilization overlap with 95% wolf utilization, hatched bars are 95% cattle with 50% wolf, and the white bars are 50% cattle with 50% wolf.



Habitat use

Calf point locations relative to 95% utilization polygons for herds belonging to each of the 5 permittees tended to occur in grass, mountain brush, or riparian land cover types (all $\chi^2 > 171.01$, $P < 0.001$), low slope gradients (0-20%: $\chi^2 = 66.56$ df = 2, $P < 0.001$), and East aspects ($\chi^2 = 11.02$, df = 3, $P < 0.05$). The same analysis also indicated that calves avoided forest cover types ($\chi^2 = 166.29$, df = 4, $P < 0.001$), intermediate slope gradients ($\chi^2 = 151.34$, df = 2, $P < 0.001$), and South aspects ($\chi^2 = 16.371$, df = 3, $P < 0.001$).

All mortalities ($n = 13$) occurred in areas that were similar in terms of habitat type, percent slope, and aspect (all $P > 0.28$) relative to point locations of calves. However, mortality locations differed in their position on the slope ($\chi^2 = 15.397$, $P < 0.05$), with simultaneous confidence intervals revealing that mortalities occurred more frequently on mid-slope, lower slope, and riparian bottoms than point locations of cattle. Non-predation mortalities ($n = 8$) showed the same pattern as described above. Wolf-killed calf mortalities were marginally more prevalent in forest cover type relative to point locations of calves ($\chi^2 = 8.837$, $P = 0.065$), although the small sample of deaths ($n = 4$) offered limited statistical power. All other comparisons between wolf-killed calf locations and point locations of calves were non-significant (all $P > 0.25$).

Wolf impact on cattle populations

The Jureano Mountain wolf pack was involved in 12 documented calf depredations (8 confirmed, 4 probable) during the two-year study. Six of the twelve depredations (3 confirmed, 3 probable) occurred outside the DMA near a spring homesite of the Jureano Mountain pack (Figure 1), and two of these confirmed calves remained alive after the attack. We estimated that wolves killed a total of 16 calves on the DMA during the two years of the

study (Table 3). Wolf-caused calf mortality detection rates with and without mortalities found by study personnel were 1 of 2.7 and 1 of 8.0 wolf kills, respectively (Table 3). Similarly, detection rates for non-predation mortalities with and without mortalities found by study personnel were 1 of 3.2 and 1 of 11.5 deaths, respectively. Because the DMA was grazed by approximately 700 cow-calf pairs each season, we estimated that wolves killed approximately 1.2% of the calf population each year, while non-predation deaths accounted for 2.3% of the calf population. Accordingly, we concluded that livestock calves constituted a minor source of food for wolves in our area.

Table 3. Cause-specific mortality rates for livestock calves on the Diamond Moose Association (DMA) in central Idaho. Number of calves dead for each cause was estimated by multiplying cause-specific mortality rate (based on marked population, $n = 231$) by the total number of calves grazed on the DMA ($N = 688$). Number missing represents the difference in calf counts from turnout on the range (May) and return from grazing (October-November).

Mortality cause/ Year	No. found by study	No. found by ranchers	Estimated No. dead	No. missing	Estimated mortality rate (%)
Non-Predation	6 ^a	1 ^a	19		2.8
Wolf Predation	3	2	12		1.7
Coyote Predation	1	0	4		0.6
Total (1999)	10	3	35	28	
Non-Predation	1 ^a	1 ^a	4		0.6
Fire	2 ^a	1 ^a	8		1.2
Wolf Predation	1	0	4		0.6
Total (2000)	4	2	16	25	
Grand Total	14	5	51	53	

^aOne calf found dead was discovered by both study personnel and ranchers.

Discussion

Survival

Calf survival rates in our study were characterized by low overall mortality during the 1999 and 2000 grazing season. No mortalities were observed during nine out of fourteen months of the study, and non-predation mortality rate was qualitatively higher than that for wolf-caused deaths. The proportion of calves that died from wolf predation during the study versus other causes was comparable to that found in other studies for wolves (Bjorge and Gunson 1985), and grizzly bears (Anderson et al. 1998).

Other researchers have suggested that wolves select for calves over adult cattle (Fritts 1982, Fritts et al. 1992, Bjorge and Gunson 1985, Gunson 1983), although our study appears to be the first to quantify the influence of calf age on vulnerability to predation. Fritts et al. (1992) indicated that as the grazing season progressed, wolf prey selection patterns seemed to favor younger calves disproportionately; our research supports this observation. Wolf prey selection patterns may be explained via active selection by wolves for individuals that are particularly vulnerable due to smaller size or impaired escape abilities. Alternatively, age-specific differences in calf social behavior, habitat use, or proximity to wolves may explain the observed patterns. Because we failed to detect age-specific differences in group size or habitat use by calves, we surmised that wolves likely selected younger individuals when chasing a group. Another factor in need of consideration is the experience level of individual mothers with wolf predation risk (see Berger 2001). Although the age of the calf's mother was not retained in our survival model for wolf predation (only 2 of 4 calves killed by wolves had mother's age recorded for them), ample evidence exists that both birth date and mother's age affect wild ungulate vulnerability to predation (Keech et al. 2000, Ozoga and Verme

1986, Kunkel and Mech, 1994, Smith and Anderson 1998). Thus, maternal age and experience level, as well as birth date of calves, should be evaluated more fully as potentially pre-disposing livestock to wolf predation.

Considering the low calf mortality rates that we observed, it is unlikely that wolves in the study area subsisted exclusively on cattle during our study. Fritts et al. (1992), Bjorge and Gunson (1985), and Tompa (1983) suggested similar conclusions. Cattle, therefore, likely constitute a secondary prey item, which are killed opportunistically by wolves. While in the field we observed on several occasions wolves and cattle in close proximity (< 500 m) without either predatory attempts or clear avoidance behavior being observed. Accordingly, we suspect that predatory interactions occurred infrequently despite the spatial proximity of wolves to cattle.

Space and habitat use

Analysis of habitat use by cattle on the DMA indicated preferences for several non-forested habitats, 0-20% slope gradients, and East aspects. In general, most wolf kills were located in relatively flat terrain in riparian areas associated with the timbered edges of meadows. However, due to the small statistical power of this analysis, we only found marginal significance, (related to forest cover type), in describing wolf-caused mortalities relative to calf point locations. Spatial overlap of cattle herds and wolves likely influenced calf vulnerability to predation. Cattle owned by Aldous had the greatest degree of spatial overlap and wolf predation relative to the other 4 livestock permittees on the DMA. Further, during the 2000-grazing season, Aldous cattle overlapped less with wolves and had lower wolf-caused calf mortality rates than during 1999. The other four permittees had increased overlap with wolves during 2000 relative to 1999, with no change in wolf-caused calf

mortality rates. However, core area overlap between wolves and individual herds occurred only for the Aldous herd during the 1999-grazing season. Thus, wolf-cattle interactions in the core areas likely resulted in the higher predation rate observed for the Aldous herd during 1999.

Wolf predation risk did not influence cattle movement patterns or group size, suggesting that wolf-caused mortality rates were not sufficiently high so as to influence cattle behavior. Large herd size among cattle could increase vigilance levels, thereby providing greater defense for calves (e.g. Carbyn and Trottier 1987). The absence of an increase in group size as wolf predation risk increased could be due to several factors; (1) calves on the range had aged sufficiently to diminish the advantage of group protection versus foraging efficiency, (2) wolf predation risk was sufficiently low so as not to influence cattle behavior, or (3) exposure of mothers to wolf predatory behavior from 1996 to 2000 may not have been sufficient for them to develop an effective anti-predator strategy (e.g. see Berger et al. 2001). At this juncture we are unable to rigorously test between these scenarios, but future efforts should address in greater detail the potential sublethal effect of wolves on livestock movements, weight gain, and productivity.

Management Implications

The selection for younger calves by wolves suggests that in areas of intensive wolf predation ranchers might reduce their predation losses by either releasing the oldest calves on allotments near wolves, or else by producing calves earlier. Further, it may also be possible for managers to minimize the spatial overlap of wolves and cattle by implementing a system to move cattle away from wolf core areas during periods of intensive activity.

Bjorge and Gunson (1985) were able to recover one out of every 6.7 missing cattle during their study, and suggested that wolf-caused mortalities were difficult to detect. Indeed carcass detection rates were low in our study as well. Thus, current compensation procedures may require adjustment to fully cover losses incurred from wolf depredation. However, DMA carcass detection results may not be applicable in all situations. For example, ranchers found 2 wolf-killed calves, with 1 additional calf missing at the end of a grazing season, on a more open, neighboring, fenced private area. Thus, a compensation program based on detection rates observed in our study would result in overpayment in areas with better accessibility, less timber, and less rugged terrain than the DMA. In general, compensation on private areas should only occur through confirmed wolf kills for several reasons; (1) the increased ability to monitor cattle within fenced pastures, (2) the relatively open nature of private pasture lands, and (3) detection rates only being documented for forested allotments. Further, ranchers may improve their carcass detection by intensively searching timbered edges of meadows during months when wolf and cattle spatial overlap is high and juvenal wild ungulates are more difficult to capture (i.e. July, August, and September).

In general, the overall effect of wolves on the calf population within the DMA was minimal. Control actions during 1999 appeared to effectively reduce the mortality rate of calves in the following year, suggesting that control can be a viable short term management option. Wolf control actions and compensation programs will continue to be inordinately controversial relative to the number of cattle killed by wolves (see Bangs et al., 1998). A modest adjustment in compensation programs may ease the tension of livestock producers and increase tolerance for wolf recovery.

References

- Anderson, C. R., M. A. Ternent, D. S. Moody, M. T. Bruscino, and D. F. Miller. 1998. Grizzly bear-cattle interactions on two cattle allotments in Northwest Wyoming. Wyoming Game and Fish Department, Cheyenne, WY, USA.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912-923.
- Bangs, E. E., S. H. Fritts, J. A. Fontaine, D. W. Smith, K. M. Murphy, C. M. Mack, and C. C. Niemeyer. 1998. Status of gray wolf restoration in Montana, Idaho, and Wyoming. *Wildlife Society Bulletin* 26:785-798.
- Berger, J., J. E. Swenson, and I. Persson. 2001. Recolonizing carnivores and naïve prey: Conservation lessons from Pleistocene extinctions. *Science* 291:1036-1039.
- Bjorge, R. R., and J. R. Gunson. 1985. Evaluation of wolf control to reduce cattle predation in Alberta. *Journal of Range Management* 38:483-487.
- Carbyn, L. N. 1997. Unusual movement by bison, *Bison bison*, in response to wolf, *Canis lupus*, predation. *Canadian Field-Naturalist* 111:461-462.
- _____, and T. Trottier. 1987. Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. *Canadian Journal of Zoology* 65:2072-2078.
- _____, S. M. Oosenbrug, and D. Anions. 1993. Wolves, bison and the dynamics related to the Peace-Athabasca delta in Canada's Wood Buffalo National Park. *Circumpolar Research Series Number 4*. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta, Canada.
- Cherry, S. 1996. A comparison of confidence interval methods for habitat use-availability studies. *Journal of Wildlife Management* 60:653-658.

- Gunson, J. R. 1983. Wolf predation of livestock in western Canada. Pages 102-105 *in* L. N. Carbyn, editor. *Wolves in Canada and Alaska: their status, biology, and management*. Canadian Wildlife Service Report Series 45.
- Hooge, P. N., W. Eichenlaub, and E. Solomon. 1999. The animal movement program. USGS. Alaska Biological Science Center.
- Hosmer, D. W., and S. Lemeshow. 1989. *Applied logistic regression*. John Wiley & Sons, Inc., New York, New York, USA.
- Fischer, H. 1989. Restoring the wolf: Defenders launches a compensation fund. *Defenders* 66(4): 35-39.
- Fritts, S. H. 1982. Wolf depredation on livestock in Minnesota. U.S. Fish and Wildlife Service Resource Publication 145.
- _____, and L. D. Mech. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. *Wildlife Monographs* 80:1-79.
- _____, W. J. Paul, L. D. Mech, and D. P. Scott. 1992. Trends and management of wolf-livestock conflicts in Minnesota. U.S. Fish and Wildlife Service Resource Publication 181.
- _____, E. E. Bangs, J. A. Fontaine, M. R. Johnson, M. K. Phillips, E. D. Koch, and J. R. Gunson. 1997. Planning and implementing a reintroduction of wolves to Yellowstone National Park and central Idaho. *Restoration Ecology* 5:7-27.
- Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management* 64:450-462.

- Kunkel, K. E., and L. D. Mech. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. *Canadian Journal of Zoology* 72:1557-1565.
- Leban, F. A. 1999. Resource Selection Program. Beta version 8.4. University of Idaho, Moscow, Idaho, USA.
- Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Doubleday/Natural History Press, Garden City, New York, New York, USA.
- _____. 1995. What do we know about wolves and what more do we need to learn? Pages 523-526 in L. N. Carbyn, S. H. Fritts, and D. R. Seirp, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta, Canada.
- _____, S. H. Fritts, and W. J. Paul. 1988. Relationship between winter severity and wolf depredations on domestic animals in Minnesota. *Wildlife Society Bulletin* 16:269-272.
- _____, R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationships of deer and moose populations to previous winter snow. *Journal of Animal Ecology* 56:615-627.
- _____, M. E. Nelson, and R. E. McRoberts. 1991. Effects of maternal and grandmaternal nutrition on deer mass and vulnerability to wolf predation. *Journal of Mammalogy* 72:146-151.
- Murray, D. L. In Press. Differential nutritional status and vulnerability to predation in snowshoe hares. *Journal of Animal Ecology*.
- Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in northwestern Minnesota. *Wildlife Monographs* 77:1-53.
- _____, and _____. 1991. Wolf predation risk associated with white-tailed deer movements. *Canadian Journal of Zoology* 69:2696-2699.

- Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 46:541-545.
- Ozoga, J. J., and L. J. Verme. 1986. Relationship of maternal age to fawn-rearing success in white-tailed deer. *Journal of Wildlife Management* 50:480-486.
- Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. National Park Service Science Monograph 11.
- Ream, R. R., M. W. Fairchild, D. K. Boyd, and A. J. Blakesley. 1989. First wolf den in western United States in recent history. *Northwest Naturalist* 70:39-40.
- Roy, L. D., and M. J. Dorrance. 1976. Methods of investigating predation of domestic livestock: a manual for investigating officers. Alberta Agriculture, Edmonton, Alberta, Canada.
- Roloff, G. J., J. J. Millspaugh, R. A. Gitzen, and G. C. Brundige. 2001. Validation tests of a spatially explicit habitat effectiveness model for rocky mountain elk. *Journal of Wildlife Management* 65:889-914.
- SAS Institute. 1996. SAS/STAT user's guide: statistics. Version 6. Fourth edition. Volumes 1 and 2. SAS Institute, Cary, North Carolina, USA.
- Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739-747.
- Selvin, S. 1995. Practical biostatistical methods. Duxbury Press, Belmont, California, USA.
- Smith, B. L., and S. H. Anderson. 1998. Juvenile survival and population regulation of the Jackson elk herd. *Journal of Wildlife Management* 62:1036-1045.
- SPSS Inc. 2000. Systat 10. Statistics 1 and 2. Chicago, Illinois, USA.

- Trent T. T., and O. J. Rongstad. 1974. Home range and survival of cottontail rabbits in southwestern Wisconsin. *Journal of Wildlife Management* 38:459-472.
- Tompa, F. S. 1983. Problem wolf management in British Columbia: conflict and program evaluation. Pages 112-119 *in* L. N. Carbyn, editor. *Wolves in Canada and Alaska: their status, biology, and management*. Canadian Wildlife Service Report Series 45.
- U.S. Fish and Wildlife Service. 1987. Northern Rocky Mountain Wolf Recovery Plan. Denver, Colorado, USA.
- _____. 1994. Establishment of a nonessential experimental population of gray wolves in Yellowstone National Park in Wyoming, Montana, and Idaho and central Idaho and southwestern Montana. Final Rule, Nov. 22. *Federal Register* Volume 59, Number 224:60252-60281.
- Wirsing, A. J., T. D. Steury, and D. L. Murray. 2002. A demographic analysis of a southern snowshoe hare population in a fragmented habitat: evaluating the refugium model. *Canadian Journal of Zoology* 80: 169-177.
- Worton, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59:794-800.
- Young, S. P. and E. A. Goldman. 1944. *The wolves of North America*. Dover, New York, New York, and American Wildlife Institute, Washington, D.C., USA.

**HABITAT SELECTION BY RECOLONIZING WOLVES IN THE
NORTHWESTERN UNITED STATES**

BY JOHN K. OAKLEAF

Abstract

Gray wolf populations have persisted and expanded in the northern Rocky Mountains since 1986, while reintroduction efforts in Idaho and Yellowstone have further bolstered the population. However, rigorous analysis of either the availability of wolf habitat in the region, or the specific habitat requirements of local wolves, has yet to be conducted. We examined wolf-habitat relationships in the western U.S. by relating landscape/habitat features found within wolf pack home ranges ($n = 56$) to those found in adjacent non-occupied areas. Logistic regression of occupied versus unoccupied areas revealed that a higher degree of forest cover, lower human population density, higher elk density, and lower sheep density were the primary factors related to wolf occupation. Further, our analysis indicated that relatively large tracks of suitable habitat remains unoccupied, suggesting that wolf populations likely will continue to increase in the region. Analysis of the habitat linkage between the 3 main wolf sub-populations indicates that populations in central Idaho and northwest Montana have higher connectivity, and thus greater potential for exchange of individuals, than does either subpopulation to the Greater Yellowstone Area subpopulation. Thus, for the northern Rocky Mountains to function as a metapopulation for wolves and other carnivores (e.g. lynx, wolverine, and grizzly bears), it will be necessary that dispersal corridors to the Yellowstone ecosystem be established and conserved.

Introduction

By the late 1930's, gray wolf (*Canis lupus*) populations in northwestern U.S. and southwestern Canada had been largely extirpated through human persecution (Young and Goldman 1944; Mech 1970). Following protection under the Endangered Species Act (ESA 1973), wolves began to naturally recolonize portions of the United States, including the northern Rocky Mountains. However, it was not until 1986 that the first successful production of pups by free-ranging wolves was documented in northwestern Montana (Ream and Matson 1982; Ream et al. 1989), and soon thereafter an established population was found to exist in the area (Ream et al. 1991).

Lethal control due to high rates of livestock depredation, as well as dispersal of animals to the Canadian populations, quelled the growth of re-established wolf packs in Montana (Bangs et al. 1998). Yet, approximately 60 wolves were released in Yellowstone and central Idaho during 1995-96, and their populations have increased rapidly (U.S. Fish & Wildlife Service 1987; Fritts et al. 1997; Bangs et al. 1998). The initial recovery objective, establishing a minimum of 30 breeding pairs of wolves evenly distributed among the three recovery areas (central Idaho, the Greater Yellowstone Area, and northwestern Montana) for three successive years, currently is approaching the final year under this directive (U. S. Fish & Wildlife Service 1987). Accordingly, procedures designed to remove wolves from protection afforded by the Endangered Species Act may be initiated in early 2003. Yet, despite this approaching deadline and the possibility that wolf populations in the northwestern U.S. soon will be subject to changes in protection status, little effort has been made to determine the amount of available wolf habitat, potential wolf population limits, or the availability of wolf dispersal corridors in the western U.S.

Previous investigations of wolf habitat selection in the western U.S. have included the analysis of home range data using locations obtained during exploratory wolf movements (Brehme 1997), which could lead to a biased assessment of wolf habitat availability in the area. A related effort used published wolf home range maps derived from computer manipulations (Kelley 2000), but because such efforts typically lack the resolution necessary for strong inference (Schooley 1994), substantive errors could exist in this analysis as well. Thus, it should be a priority to examine wolf habitat selection and availability in the recovery area prior to any change in wolf protection status.

Wolf densities are known to be positively correlated to prey densities (Keith 1983; Fuller 1989; Fuller et al. 1992), indicating that wolves likely select areas with high ungulate density and thus should have higher rates of population growth within such areas. Further investigation of wolf habitat requirements have determined that high densities of both roads and humans were possible impediments to wolf survival, with sustainability thresholds allegedly approaching <0.70 km roads/km² and <4 humans/km² (Theil 1985; Jensen et al. 1986; Mech et al. 1988; Fuller et al. 1992; Harrison and Chapin 1998). These thresholds were found to be even lower in an expanding wolf population in Wisconsin (Mladenoff et al. 1995), indicating that selection for higher quality habitat may occur in an expanding population. Lesser factors also found to influence wolf habitat selection in the latter study included land ownership, land cover type, and various lesser landscape features (Mladenoff et al. 1995). While wolves are known to disperse long distances (Fritts 1983; Ballard et al. 1987; Boyd and Pletscher 1999), currently there appears to be limited interchange of individuals between the three Northern Rockies recovery regions (Boyd and Pletscher 1999; USFWS et al. 2000). It follows that further investigation into possible dispersal corridors

between recovery regions should be beneficial for both understanding how the three subpopulations may function as a metapopulation, and determining areas likely to be used for dispersal and thus in need of protection. Elsewhere, such analyses have identified possible wolf dispersal corridors as well as helped evaluate the possibility for natural wolf recolonization of vacant areas (Harrison and Chapin 1998; Wydeven et al. 1998).

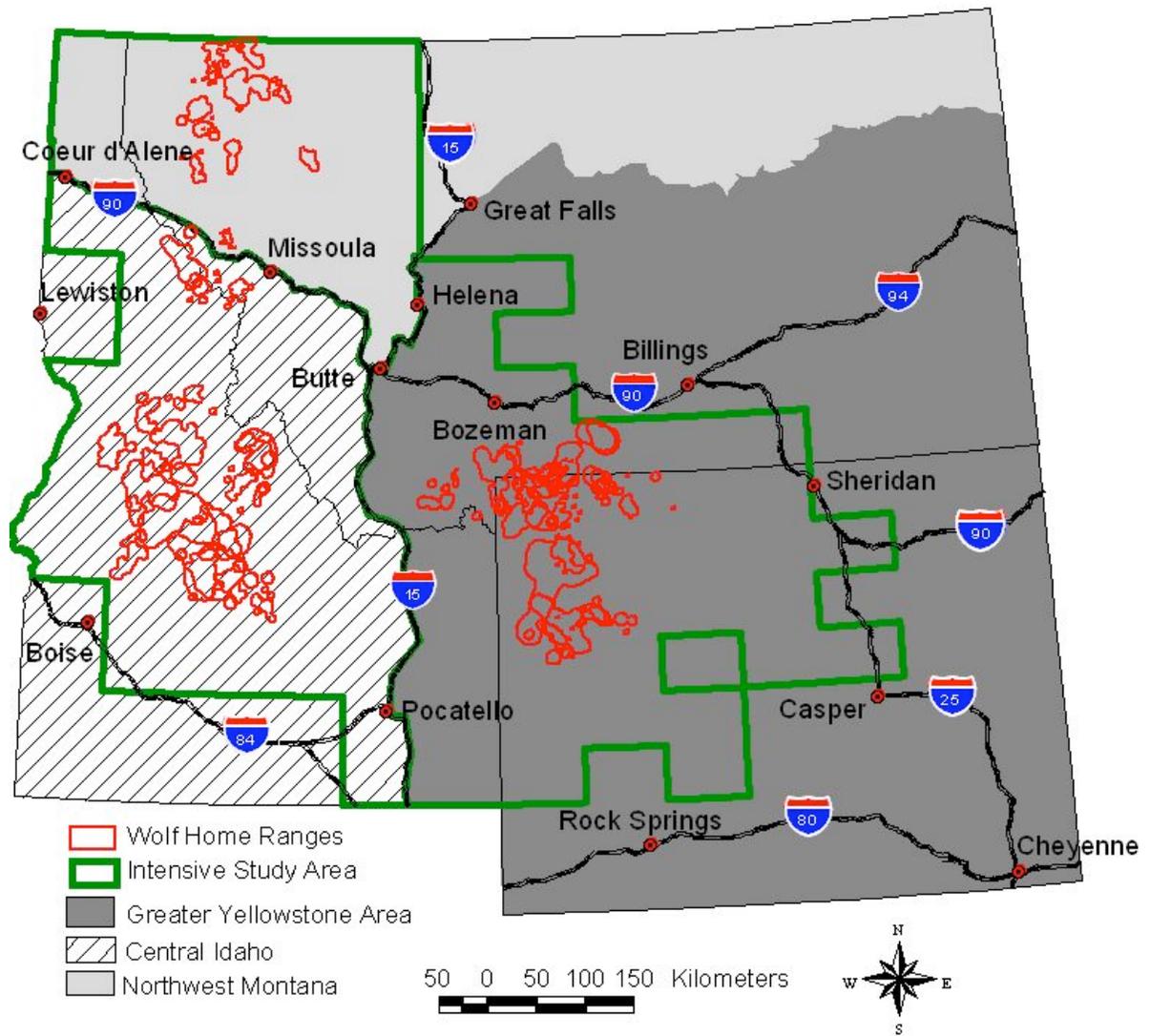
The objectives of the present study were to: (i) determine the current patterns of habitat selection of wolves within the northern Rockies and predict future colonization probabilities within the area, (ii) identify potential dispersal corridors of wolves between the three recovery areas, and (iii) determine if landscape-scale attributes such as availability of natural and domestic prey, or human and road densities, affect wolf pack extinction probability and home range size.

Methods

Study area

The three wolf recovery areas identified by the U.S. Fish and Wildlife Service for the northern Rocky Mountain region are northwestern Montana (NMT), central Idaho (CID), and the Greater Yellowstone Area ([GYA] U.S. Fish and Wildlife Service 1987; Bangs et al. 1998). Each of the recovery areas covers $> 50,000 \text{ km}^2$, with a mixture of primarily public and some private lands in the areas (Figure 1). Elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and moose (*Alces alces*) are the major prey species within these recovery areas. Domestic livestock occur throughout the area, with the exception of National Parks and parts of wilderness areas. Vegetation is characterized by a variety of habitat types, ranging from sage covered foothills to forested mountains.

Figure 1. Study area for the wolf habitat selection in the northern Rocky Mountains



Home ranges

Aerial locations from wolves in each of the three recovery areas were used to develop home ranges for the habitat selection portion of this study (White and Garrott 1990). We based home range polygons upon 1 year of locations evenly distributed across summer and winter seasons for wolves from a given pack (Mladenoff et al. 1995; Wydeven et al. 1995). In order to maximize sample independence, individual locations were only recognized for any radio-marked wolf that was either spatially or temporally separated from other pack members; this approach limited potential pseudoreplication of locations. Wolf home range size has been shown to reach an asymptote at around 30 locations and increasing the number of locations has little effect on the size of the home ranges (Carbyn 1983; Fuller and Snow 1988). Recognizing that some wolf populations in the northern Rockies occur in remote areas and thus are not monitored intensively, we used ≥ 20 locations per year as a threshold of retention in our database. We felt that this approach was justified because Gese et al. (1990) determined that the minimum sample size for home range analysis of coyotes (*C. latrans*) was ≥ 23 locations, which should be comparable to home range analysis for wolves. For our dataset (56 home ranges), 18% ($n = 10$) had between 20-23 locations, 21% ($n = 12$) between 24 and 29 locations, and the remainder had > 29 locations ($n = 24$). We felt that this approach was further justified by the fact that fixed kernel method of home range analysis is preferred by many authors (Seaman et al. 1999; Powell 2000), and that this method performs better than most other estimators when the number of locations is limited (Kernohan et al. 2001). Indeed, fixed kernel home ranges derived from smaller sample sizes typically yield larger home ranges (Seaman et al. 1999; Kernohan et al. 2001), which for habitat selection analysis should result in a more conservative assessment of habitat preference. Thus, home

range polygons were generated at the 95% and 50% levels to represent home range and core use areas by wolves (White and Garrott 1990), using the fixed kernel method (Worton 1989) with least-squares cross-validation (LSCV) as the smoothing option in the animal movement extension in the program Arcview (Hooge et al. 1999; ESRI, Redlands, CA, USA).

Initially, home range sizes were described for the packs in each of the three recovery areas. Within each recovery area an equivalent number of circular non-pack home ranges (controls) were randomly created to mimic wolf home ranges in areas not currently occupied by wolves. Non-pack areas were the size of the average wolf home ranges for the 95% fixed kernel level of their respective recovery area. Both pack and non-pack areas were overlaid on multiple geographic information system (GIS) layers to determine the characteristics of these areas. Although most packs occupied particular home ranges for several years, we only used one wolf pack-year as the basis for the comparison. Selection of the pack-year for each pack was based upon the time period within the dataset which allowed for the greatest number of annual locations to develop the home range, and the pack-year that occurred closest to our reference year (2000).

GIS layers

Road density, topography, land ownership, ungulate density, livestock density, vegetation characteristics, and human density layers comprise the GIS layers used to analyze wolf habitat selection (Table 1). Slope and elevation data were derived from digital elevation models (DEM's), while road density information (km of roads/km²) was separated into three variables: (1) the density of roads passable by a 2-wheel-drive vehicle (Mech et al. 1988), (2) the density of 4-wheel-drive roads, and (3) total density of 2- and 4-wheel drive roads.

Table 1. GIS data layers used to construct wolf habitat models and the type of data analysis performed with each layer.

Layer	Resolution	Data Source	Analysis Type ^b
Baileys Ecoregions		USFS ^a	A
Road density	90 m	ID ^c , WY ^d , MT ^e	A, B, C, E
Human density	Block groups	USBC ^f	A, B, C, D, E
Protection Status	90 m	GAP ^g	A, B, C, E
Land Ownership	90 m	GAP	A, B, C, E
Slope	90 m	USGS ^h	B, C, E
Elevation	90 m	USGS	B, C, E
Land Cover ⁱ	90 m	GAP	B, C, D, E
Ungulate Density	GMU	Harvest ^j	B, C, D, E
Cattle Density	County	USDA	B, C, D, E
Sheep Density	County	USDA	B, C, D, E
Wolf Home Ranges		USFWS ^k	A, B, C, D, E

^aU.S. Forest Service

^bA=1:100,000 quadrangle study area definition, B=Conservative logistic regression of use and non-use, C=Liberal logistic regression of use and non-use, D=Dispersal corridor analysis, E=Pack persistence analysis

^cIdaho Department of Water Resources

^dWyoming Spatial Data and Visualization Center

^eNatural Resource Information System

^fU.S. Bureau of Census

^gNational GAP

^hU.S. Geological Survey

ⁱLand Cover was reclassified into 7 percent cover classifications (Forest, Shrub, Desert, Human, Grass/Agriculture, Riparian/water, and Other)

^jBased on ungulate game harvest data collect by state Fish and Game agencies

^kData collected by U.S. Fish and Wildlife Service, Yellowstone National Park, and Nez Perce Tribe, home ranges were composed by the authors.

Ungulate density information was based on unpublished harvest statistics provided by the states of Idaho, Montana, and Wyoming, while livestock density was based upon U.S. Department of Agriculture statistics for counties. Total cattle (non-dairy) and sheep were averaged across a five-year period (1995-2000) for each county, and linked with a county layer to generate livestock densities for the region. Wilderness and national parks were excluded from counties to ensure that livestock density estimates encompassed only areas where grazing occurred. Land ownership was divided into 4 classifications based on national GAP data (private, federal, state, and water), while vegetation cover was reclassified into 7 types based on national GAP data (forest, shrub, urban, desert, grass/agriculture, riparian/water, and other [rock and ice]). For the purposes of our analysis of factors promoting pack persistence (see below), we used urban/agriculture and grass as classifications rather than grass/agriculture and urban. This allowed for vegetation cover with similar wolf mortality risk to be grouped in the persistence analysis, and vegetation cover with similar landscape features to be grouped in the habitat analysis.

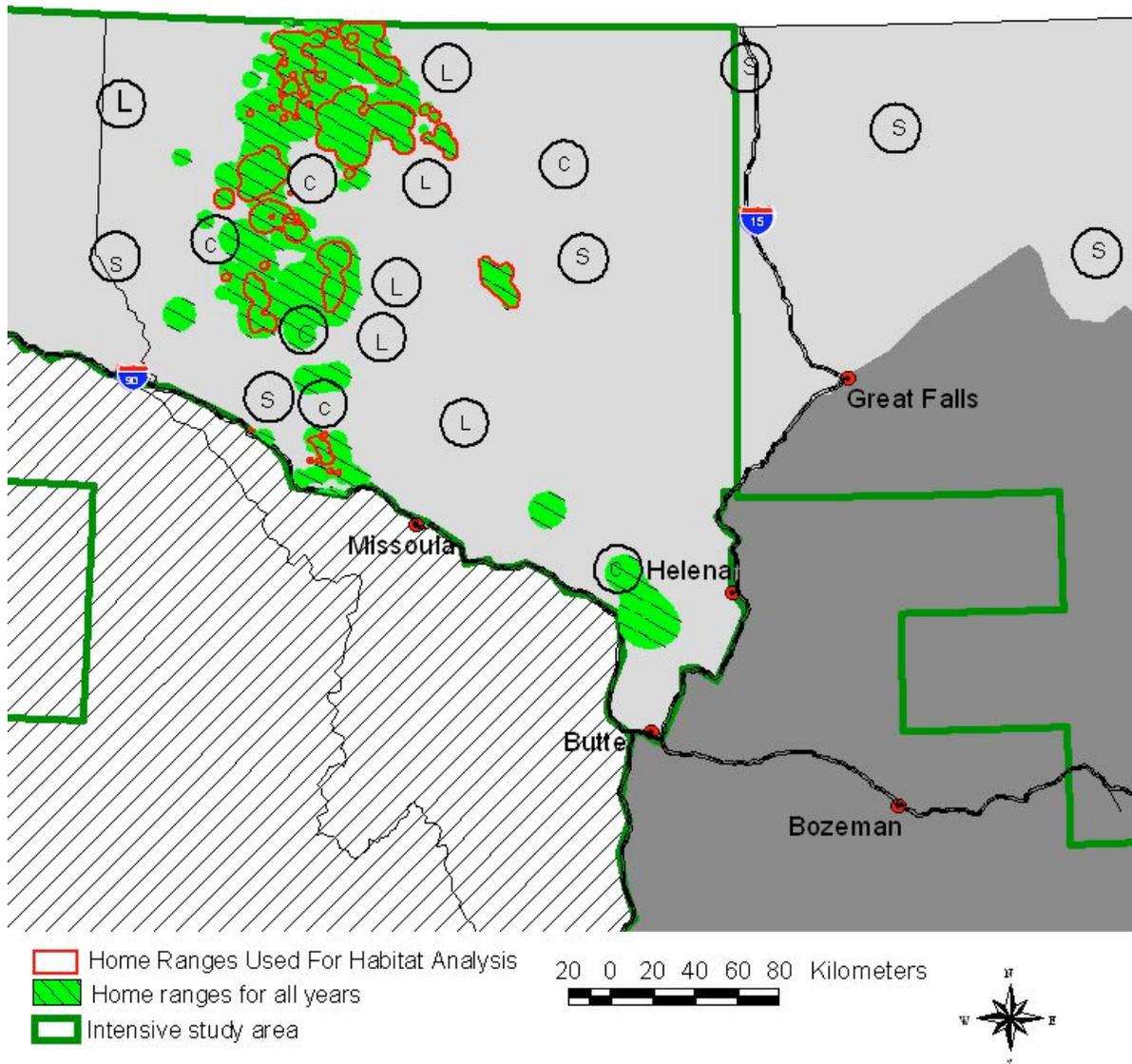
We did not use population estimates for game management units (GMU) to describe ungulate densities because population estimation techniques and intensity of monitoring varied for states, GMU's, and ungulate species. Instead, we compared available aerial flight population estimates for GMU's with various recorded harvest statistics (e.g. days per harvest, percent successful harvest, etc.), to arrive at an index for ungulate density that could be applied across jurisdictions. Using stepwise linear regression, we confirmed that total harvest was the most strongly correlated index for both mule deer ($r = 0.71$, $t = 4.776$, $P < 0.001$, residual mean standard error (RMSE) = 0.763, $n = 25$) and elk ($r = 0.64$, $t = 9.309$, $P < 0.001$, RMSE = 0.624, $n = 126$) density estimates. Accordingly, total harvest was averaged

for a five year period (1995-2000) across each GMU and then described as high, medium, or low based on the quartiles of distribution for all GMU's. Areas where hunting was not permitted or the state agency did not have information (e.g. National Parks and reservations) were classified based on the average of the GMU's along their respective border.

Habitat selection analysis

Habitat analysis can be greatly influenced by the extent of the study area chosen to represent available habitat (Huston 2002; McClean et al. 1998; Garshelis 2000). We chose to examine areas used by wolf packs versus those currently unused (controls) across several spatial scales. First, we defined our intensive study area by allowing control areas to occur anywhere within the recovery area (Figure 2), and used logistic regression comparing habitat attributes for wolf packs versus unused areas (controls). This step allowed for an intensive study area boundary to be generated with scientific reasoning, rather than an arbitrary definition of study area extant that has been identified as problematic in habitat analysis by several authors (McClean et al. 1998; Garshelis 2000). Further, this analysis provided a simple preliminary model of wolf habitat selection in the region. Several landscape scale GIS layers were used as the basis for comparisons between use and non-use areas (Table 1). Attributes identified as important in this analysis were then placed within a 1:100000 quadrangle grid to define a study area boundary for which reasonable comparisons for wolf habitat selection could occur (Figures 1 and 2). Two factors were significant in this comparison. First, all wolf packs contained a majority of the temperate-steppe-mountain division of the Bailey's ecoregion layer (Bailey 1983). This variable was a categorical variable, thus, in the regression there were two empty cells (e.g., no wolf packs occurred in temperate-desert or temperate-steppe ecoregions).

Figure 2. A schematic comparison of areas used by wolves versus unused controls in the habitat selection analysis. Non-use areas are represented by the circles with the letter inside representing the type of habitat analysis performed (S = intensive study area design, C = conservative logistic regression, L = liberal logistic regression). Note that the conservative non-use areas were only restricted from wolf home range years that were used in the analysis while the liberal and study area non-use polygons were restricted from any area that wolves had occupied regardless of the specific year the home range was generated. Further, study area non-use polygons were allowed to occur anywhere within the northwest Montana recovery area in order to define study area boundaries, while the other non-use areas were restricted to occur only within the intensive study area.



Logistic regression creates unreliable coefficient estimates with large standard errors with empty cells in a categorical variable (Hosmer and Lemeshow 2000). Thus, we simply considered any 1:100000 quadrangle which contained a portion of the temperate steppe mountain regime as part of the intensive study area. Protection status was the only other variable identified as significant ($t = 3.965$, $P < 0.001$, change in Aikike's Information Criterion [$_{-}AIC$] = -22.04, $n = 112$). To be conservative, we selected any remaining 1:100000 quadrangle that had a probability of wolf occurrence ≥ 0.25 according to the following formulae:

$$\text{logit}(p) = -4.575 + 1.531(\text{protection status}) \quad (1)$$

$$p = e^{\text{logit}(p)} / 1 + e^{\text{logit}(p)} \quad (2)$$

After defining the study area, we proceeded with a more refined habitat analysis, in which non-use area was restricted to our above defined intensive study area. Logistic regression (Hosmer and Lemeshow 2000) was performed between use and non-use areas, with AIC_c values > 2.0 used to determine parameter retention (Anderson et al. 2000). We defined two non-use levels for comparison; (1) a conservative model in which non-use areas were only exclusive of pack areas for the year in which wolf home ranges were being considered as "used" areas, and (2) a liberal model in which non-use areas were exclusive of all wolf-year home ranges (Figure 2). For example, if a particular wolf pack was selected for the year 2000 home range calculation (and thus considered a "used" area), in the conservative model the control area could occur anywhere outside of that particular home range (except in another wolf home range used in the analysis, or outside of the intensive study area). In contrast, for the liberal model the control area for comparison could occur only where the wolf pack had never occurred during the entire monitoring period (i.e. 1995-

2001). Thus, the conservative model considered control (unused) areas as those not being used by wolves in the year of the analysis, while in the liberal model controls occurred in areas apparently never having been used by wolves. Because of the tendency for the conservative model to select controls interstitially between packs, the liberal model likely provided greater variability between used versus unused areas due to greater geographic separation between use and non-use areas.

Continuous variables that were retained in the model were checked for linearity via the quartile method (Hosmer and Lemeshow 2000). Variables that showed slight deviations from linearity were checked for possible biologically relevant transformations (e.g. categorical, cut points, and quadratic) that could improve the model (Hosmer and Lemeshow 2000). Finally, all 2-way and 3-way interactions between significant variables were tested for possible inclusion in the model. Final models were tested with the Hosmer and Lemeshow goodness-of-fit test statistics (HL Stat) to ensure model fit and appropriate data transformations (Hosmer and Lemeshow 2000). Probabilities of wolf occurrence were calculated for each wolf home range and non-use area. Sensitivity (proportion of used areas predicted to be used), specificity (proportion of non-use areas predicted to be non-use), false positive rate (proportion of predicted use areas that were non-use), false negative rate (proportion of predicted non-use areas that were used), were described for the final regression models (Hosmer and Lemeshow 2000; Manen et al. 2000). The cut point between use and non-use was defined at the 0.50 probability level. To further evaluate model robustness, we tested each model against 8 wolf home ranges that were excluded from model development due to small sample sizes of locations (mean = 13.875 +/- 0.972 [SE] locations). Probabilities were generated across the landscape in 1:24000 quadrangle cells

(the appropriate resolution [e.g. the approximate size of one home range] for wolf occupancy), and in 9 km² cells (the appropriate resolution for dispersal corridors). Wolves generally can disperse across habitat that is poorer than that required for colonization (Harrison and Capin 1998), thus dispersal corridors were identified by wolf presence probabilities ≥ 0.30 in the 9 km² cell grid. By relaxing our colonization standards, we conformed to the practice of favoring less stringent standards to determine dispersal habitat (see Harrison and Chapin 1998).

Additional statistical tests used herein included Kruskal-Wallis tests (Sokal and Rolf 1981) for comparing between wolf use and non-use control areas and a one sample t-test comparing between pack habitat characteristics versus those found in the intensive study area. Finally, a paired t-test between 95% fixed kernel home ranges and 50% fixed kernel core use areas was conducted to examine landscape/habitat features that differed between core versus non-core portions of wolf home ranges. Comparisons between core use areas and home ranges were considered to represent a conservative assessment of potential differences between the two scales of analysis, because 50% cores were a portion of the 95% home ranges.

Habitat associations with population dynamics

Whenever possible, habitat selection models should be correlated with local population dynamics (Garshelis 2000; Heglund 2002). Thus, we examined wolf demographic patterns (pack persistence and home range size) relative to our predicted probability values within the habitat selection model, as well as in comparison to a variety of landscape/habitat characteristics of wolf home ranges. Pack persistence models were built using logistic regression with the dependent variable based on the pack's extinction status

(see methods described previously for the habitat selection analysis). General linear models were used to investigate the correlation between home range size and (1) year of home range, (2) number of wolf pack borders within 10 kilometers of a given pack's border (i.e. an index of density dependence constraints on home range size), (3) number of wolves per pack at the start and end of the year, (4) pup production, (5) colonization probabilities derived from our liberal model, and (6) various habitat features described previously. Recovery area was entered as the first term in this model to ensure that biologically meaningful independent variables were evaluated irrespective of the specific recovery area. For the present analysis, we decided to use all available wolf-year home ranges within the home range size analysis. Despite possible pseudoreplication using this method, we felt that there could exist considerable annual variability in pack home range size, pup production, pack size, and number of adjacent packs, thereby justifying a year-by-year approach to this analysis.

Results

Habitat selection

Polygons were established for each of the 64 wolf packs included in the analysis, which totaled 198 pack years. However, only 56 packs in 154 pack years had an adequate number of locations (≥ 20) for home ranges to be generated. Our data analysis revealed that the average number of annual locations per home range was 36 ($n = 58$), 33 ($n = 27$), and 60 ($n = 69$) for CID, NMT, and the GYA areas, respectively. Core use areas differed significantly from home ranges for slope and elevation variables, with core use areas being characterized by lower elevation and slope (Table 2).

Table 2. Mean (+/- SE) landscape variable characteristics for wolf pack territories (95% Fixed Kernel) and core use areas (50% fixed kernel [$n = 56$]), conservative and liberal definitions for non-use areas ($n = 56$), and the northern Rocky Mountain study region.

Variable	Pack Territories	Pack Core Use	Non-Use Conservative	Non-Use Liberal	Study Area
Land Cover (%)					
Urban	0.07(0.02)	0.06(0.03)	0.23(0.09)	0.31(0.11)	0.26 ^b
Grass/Agriculture	11.76(1.48)	11.72(2.17)	17.41(1.65) ^a	23.51(2.51) ^a	23.14 ^b
Shrubs	13.71(1.54)	13.13(1.82)	24.24(3.04)	30.70(3.45) ^a	23.78 ^b
Desert	0.10(0.06)	0.00(0.00)	7.22(2.58) ^a	2.32(1.07) ^a	2.49 ^b
Forest	68.21(2.06)	67.42(2.57)	42.36(3.83) ^a	34.59(3.69) ^a	43.08 ^b
Other (Rock/Ice)	2.38(0.49)	2.04(0.53)	5.37(1.25) ^a	4.57(0.79)	3.55 ^b
Riparian/Water	3.78(0.45)	5.23(1.18)	3.17(0.36)	4.00(0.81)	3.70
Land Ownership (%)					
Federal	83.67(3.24)	81.59(3.81)	73.30(2.84) ^a	65.04(3.48) ^a	65.27 ^b
Private	13.60(2.96)	15.89(3.50)	22.27(2.54) ^a	27.91(3.08) ^a	28.94 ^b
State	1.98(0.57)	1.57(0.63)	3.89(0.72) ^a	5.74(1.15) ^a	4.79 ^b
Water	0.67(0.22)	0.87(0.44)	0.34(0.10)	1.30(0.68)	1.00
Density ^c					
2-wheel-drive roads	0.44(0.06)	0.44(0.07)	0.62(0.05) ^a	0.64(0.05) ^a	6.48 ^b
4-wheel-drive roads	0.10(0.02)	0.12(0.03)	0.06(0.01) ^a	0.08(0.02)	0.09
Human	0.43(0.07)	0.33(0.06)	2.26(0.98) ^a	2.41(0.78) ^a	2.44 ^b
Sheep	0.24(0.04)	0.25(0.06)	1.06(0.18) ^a	1.09(0.15) ^a	1.01 ^b
Cattle	2.50(0.34)	2.63(0.41)	6.02(0.48) ^a	6.61(0.53) ^a	5.71 ^b
Coded variables ^d					
Mule Deer	1.64(0.07)	1.66(0.08)	1.84(0.08)	1.88(0.08) ^a	1.86 ^b
White-tailed Deer	1.60(0.10)	1.61(0.10)	1.69(0.11)	1.52(0.10)	1.67
Elk	2.20(0.09)	2.22(0.09)	1.70(0.11) ^a	1.68(0.11) ^a	1.84 ^b
Protection Status	2.46(0.11)	2.50(0.12)	2.98(0.08) ^a	2.99(0.09) ^a	3.04 ^b
Topography					
Slope	11.64(0.42)	10.34(0.58) ^c	9.88(0.74)	8.66(0.68) ^a	9.22 ^b
Elevation	2025.7(60.9)	1981.9(66.2) ^c	1848.0(70.6) ^a	1820.2(60.3) ^a	1799.7 ^b

^aKruskal-Wallis test compared with pack territories was significant for the variable at $P < 0.05$

^bSingle sample t test compared with pack territories was significant for the variable at $P < 0.05$

^cDensity measured as km/km² for road variables and no./km² for human, cattle, and sheep

^dCoded variables were weighted averages for the area and went from low (1) to high (3) for elk, mule deer, and white-tailed deer. Protection status was coded with four categories with high protection receiving a value of 4.

^ePaired t-test significant ($P < 0.05$) in comparisons between the variable and pack territories.

Univariate analysis identified several landscape characteristics that were significantly related to the presence of wolves within the intensive study area (Table 2), suggesting that a large number of possible models could potentially describe areas in which wolves are likely to occur. However, when we conducted a stepwise multiple regression, relatively few variables were retained in the models, with both the conservative and liberal models yielding similar results in terms of specific variables retained (Table 3). Indeed, both models showed a positive relationship between wolf presence and both forest cover and elk density variables. Similarly, each model identified a negative correlation between human density and livestock densities (cattle for the conservative model and sheep for the liberal model). A negative relationship with other (rock and ice) cover was only identified for the conservative model. Variables in both models conformed to the assumption of linearity, and both the conservative and liberal final models performed well in model fit tests (conservative: $R^2 = 0.472$, HL stat = 5.633, $P = 0.583$, $df = 7$, liberal: $R^2 = 0.491$, HL stat = 8.444, $P = 0.295$, $df = 7$). The final formulas for the conservative and liberal model are described in Table 3.

The results from each of these formulas were placed in formula 2 (see methods section) to generate probabilities for all used and non-used areas, to further examine model performance. The conservative and liberal models both performed well with regards to sensitivity (44 of 56 [0.79], and 49 of 56 [0.88] wolf use areas predicted correctly, respectively) and specificity (44 of 56 [0.79] and 46 of 56 [0.82] non-use areas predicted correctly, respectively). In contrast, false positive and false negative rates were relatively low and ranged from 0.21 to 0.12 for the models. In addition, each of the models predicted site occupation for 7 out of 8 wolf packs that were not used to develop the models.

Table 3. Parameter estimates for significant variables in a conservative and liberal logistic regression model for wolf habitat selection in the northern Rocky Mountain wolf population. Models were based on 56 wolf home ranges compared with 56 non-use areas.

Parameter	Coefficient	<i>SE</i>	Odds Ratio	ΔAIC_c^a	<i>P</i> ^a
Conservative Model					
Constant	-1.292	1.470			0.379
Cattle Density	-0.377	0.120	0.686	31.036	0.002
Forest Cover	0.031	0.015	1.032	9.702	0.035
Human Density	-0.790	0.381	0.454	8.376	0.038
Elk	1.000	0.446	2.719	3.420	0.025
Other Cover ^b	-0.115	0.054	0.891	2.550	0.032
Liberal Model					
Constant	-4.457	1.722			0.010
Forest Cover	0.057	0.018	1.059	45.994	0.002
Human Density	-0.871	0.326	0.326	11.566	0.007
Elk	1.351	0.474	3.862	7.170	0.004
Sheep Density	-1.735	0.789	0.176	3.020	0.030

^a ΔAIC_c values were calculated at the time of entry of the parameter while *P* values are based on the full models.

^bOther cover represents rock and ice.

Upon further model examination and assessment, we selected the liberal model for all subsequent analysis due to its (1) slightly improved ability to predict areas where wolves occur, (2) increased R^2 value, (3) greater parsimony. To assess the amount of habitat available in the three recovery areas, probabilities for the liberal model were generated in a 1:24000 quadrangle grids (Figure 3) and 9 km² grids (Figure 4). We found that the CID recovery region had the greatest amount of preferred wolf habitat (probability ≥ 0.5 ; 77,596 km²), while the GYA (45,900 km²) and the NMT (44,929 km²) recovery areas had similar amounts of preferred wolf habitat (Table 4). However, the NMT region contained a greater percentage of area encompassed by preferred habitat (54%) than did either the CID (52%), or the GYA (25%) regions. Also, when wolves are delisted from the ESA, wolf management will be initiated by the three states and our model predicted that at that time the jurisdictional breakdown of preferred wolf habitat will change to 72,012 km², 69,490 km², and 28,725 km² for Idaho, Montana, and Wyoming, respectively (Table 4).

Dispersal corridor analysis detected a solid linkage between the NMT and CID recovery areas, with large dispersal corridors comprised of suitable habitat connecting the core habitat areas in both regions (Figure 4). Further, there appears to be appropriate dispersal habitat in western Idaho to allow for wolf dispersal into Oregon and Washington states. However, the GYA recovery region appears to be poorly linked to the other populations through relatively narrow and rather disjunct corridors of appropriate habitat (Figure 4).

Figure 3. The probability of wolf occupancy predicted for the northern Rocky Mountain recovery region. Maps were derived using 1:24,000 quadrangles

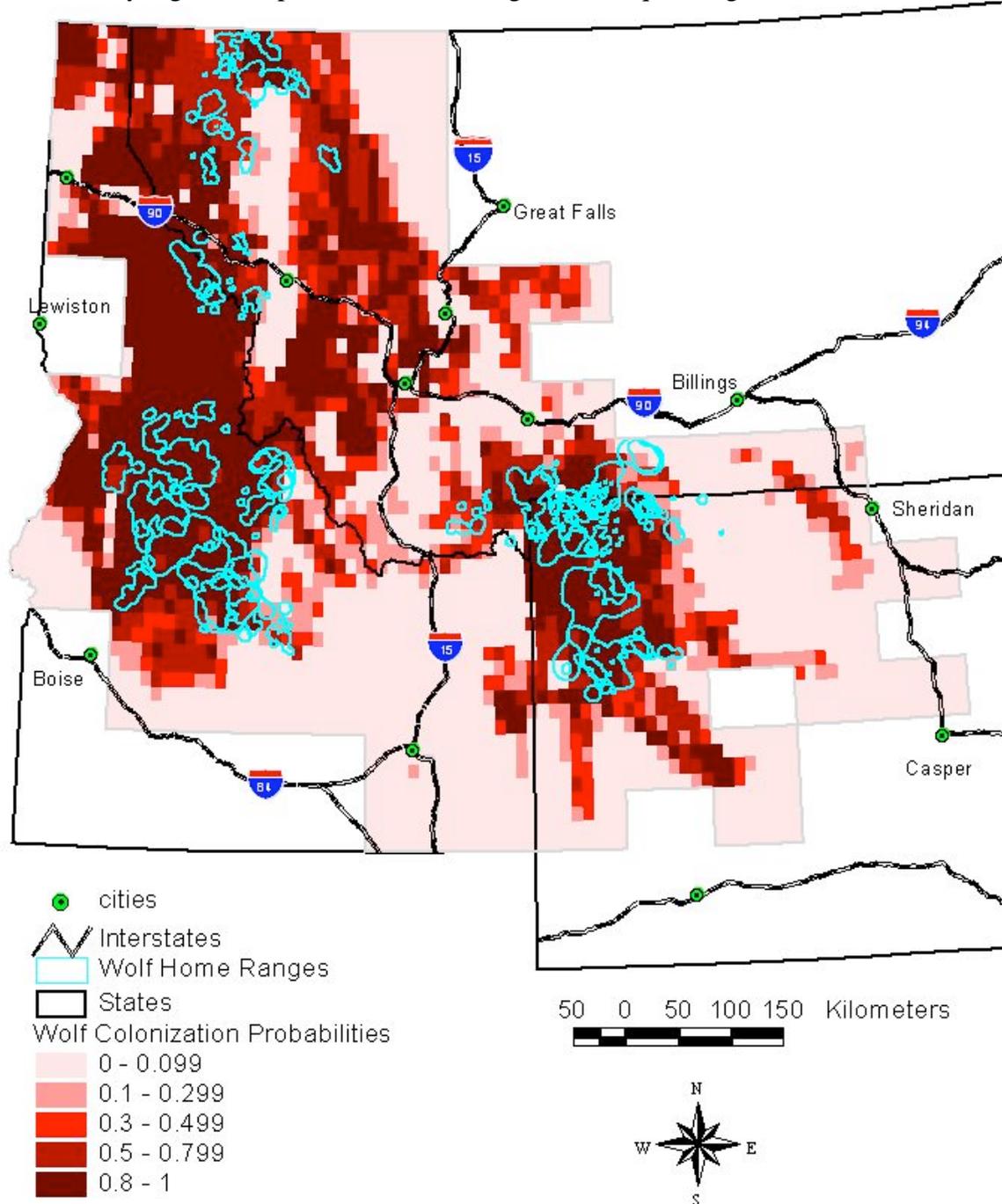


Figure 4. Possible wolf dispersal corridors defined between 3 wolf subpopulations of the northern Rocky Mountains wolf recovery region.

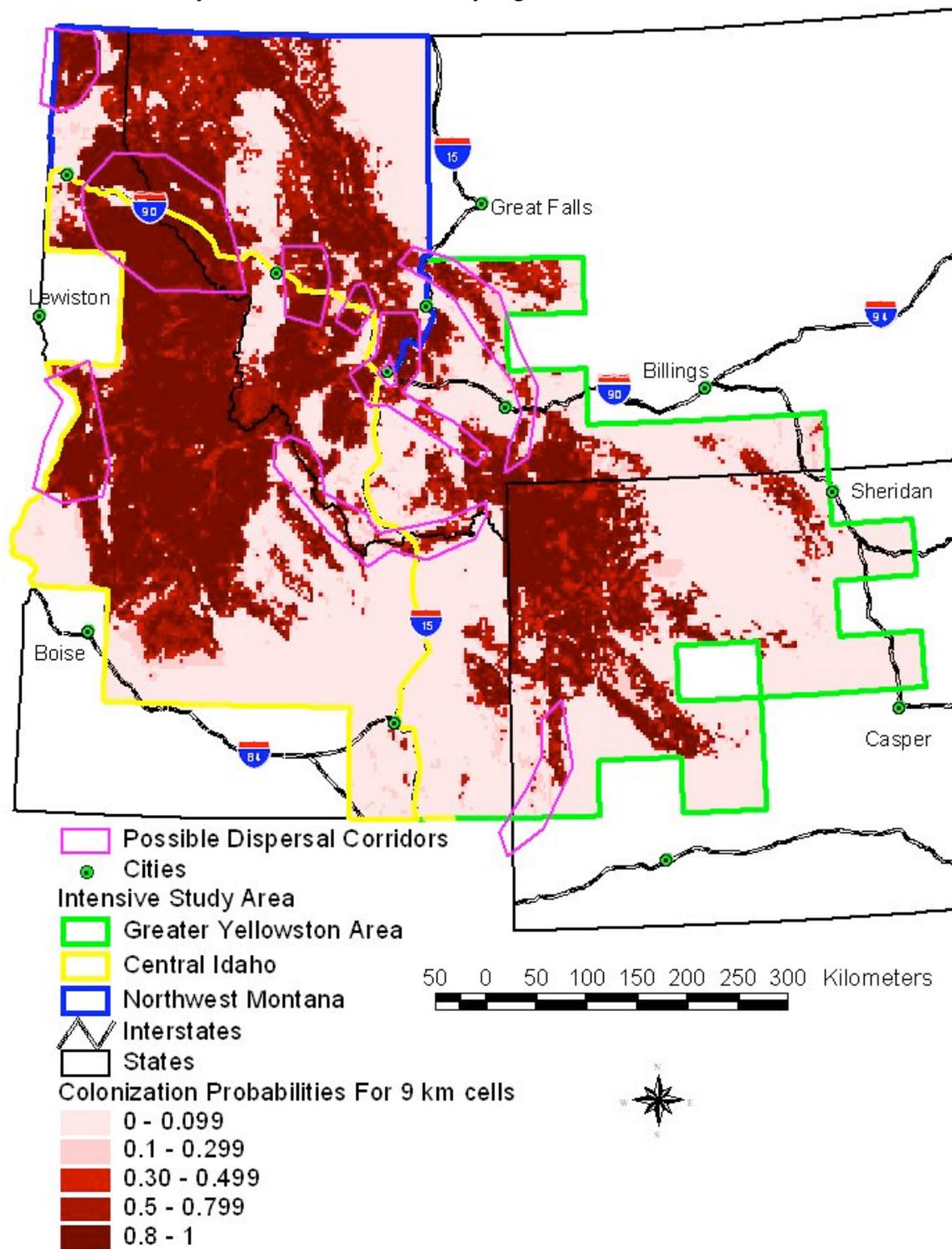


Table 4. Area (km²) of wolf colonization probabilities based on a logistic regression model within the intensive study region (see Figure 1) for current recovery areas (northwest Montana [NMT], Greater Yellowstone Area [GYA], and Central Idaho [CID]) and individual states (Montana, Wyoming, and Idaho).

Probability	NMT	GYA	CID	Montana	Wyoming	Idaho
>0.90	14,382	22,144	47,219	23,086	16,604	44,992
0.75-0.90	18,330	11,023	17,394	25,875	5,647	15,672
0.50-0.74	12,217	12,734	12,983	20,529	6,473	11,347
0.25-0.49	7,182	14,748	8,938	15,557	7,139	8,356
0.10-0.24	5,097	14,703	8,688	13,772	6,322	8,302
0.00-0.09	25,895	111,351	55,248	58,480	59,723	72,403

Habitat associations with population dynamics

Wolf home range area averaged $1295.824 \text{ (km}^2\text{)} \pm 129.51 \text{ (SE)}$, 599.367 ± 104.67 , and 813.88 ± 119.76 for each of the CID, NMT, and the GYA recovery areas, respectively. Grouped t-test between log transformed home range sizes revealed that wolf home ranges in CID were larger than those in either NMT ($t = 4.962$, $P < 0.001$, $n = 85$) or the GYA ($t = 4.548$, $P < 0.001$, $n = 127$), while packs from NMT and GYA were similarly sized ($t = -1.056$, $P = 0.294$, $n = 96$). Thus, we first blocked for recovery area in subsequent analyses of home range size. Home range size was influenced by a variety of independent variables, including an inverse correlation with elk, shrub vegetation cover, year of home range, pup production, and white-tailed deer variables (Table 5). In contrast, home range size was positively correlated with human density, 4-wheel-drive road density, other (rock/ice) vegetation, the number of packs that were found to be adjacent to a particular pack, and the percent slope within the pack territory.

Pack persistence analysis for the 56 (43 extant, 13 extinct) wolf packs identified a relatively simple model in which federal ownership (coefficient = 0.040, $t = 2.863$, $P = 0.004$, $\text{_AIC}_c = 6.246$) and agriculture/urban vegetation (coefficient = -0.739, $t = -2.049$, $P = 0.04$, $\text{_AIC}_c = 2.506$) were the only two variables retained in the model. However, federal ownership was related to extinction probability in a non-linear fashion and thus required a quadratic formula to accurately model the survival equation. Yet, we noted that private land ownership was highly negatively-correlated with federal ownership ($r = -0.98$), and that private ownership was nearly retained as the first parameter in the model ($t = -2.529$, $P = 0.011$, $\text{_AIC}_c = 5.464$). Ancillary analysis of private ownership indicated that a non-linear

relationship failed to provide superior explanatory power. Further, agriculture/urban vegetation was again retained in the model as the second parameter after private ownership ($\Delta AIC_c = 2.24$). Finally, the model containing federal ownership was statistically indistinguishable from that with private ownership ($\Delta AIC = 1.048$). Thus, for simplicity, we used the model with private ownership to describe pack persistence.

$$\text{logit}(p) = 2.364 + (-0.041 * \text{Percent Private Ownership}) + (-0.708 * \text{Percent Agriculture/Urban Vegetation}) \quad (3)$$

This model performed well in model fit test (HL stat = 7.3, $P = 0.505$, $df = 8$), and correctly predicted 6 out of 8 packs excluded from model development due to small sample sizes. Although not retained in the final persistence model, wolf colonization probabilities were significantly related to persistence prior to inclusion of private ownership within the model ($t = 2.254$, $P = 0.024$, $\Delta AIC_c = 3.416$, $n = 56$). Because colonization probability was not retained in the model, the probability for pack persistence was multiplied by the probability of wolf colonization to examine the areas where wolves are likely to colonize and persist in the future (Figure 5). Extinction probabilities could potentially limit wolf packs near the edges of each of the three recovery areas (compare Figure 5 to 3). However, only a 1% decline in total preferred wolf habitat was observed by selecting areas with a ≥ 0.5 probability of persistence and colonization of areas.

Table 5. Parameters retained in a general linear model analysis of home range size of wolves in the northern Rocky Mountains.

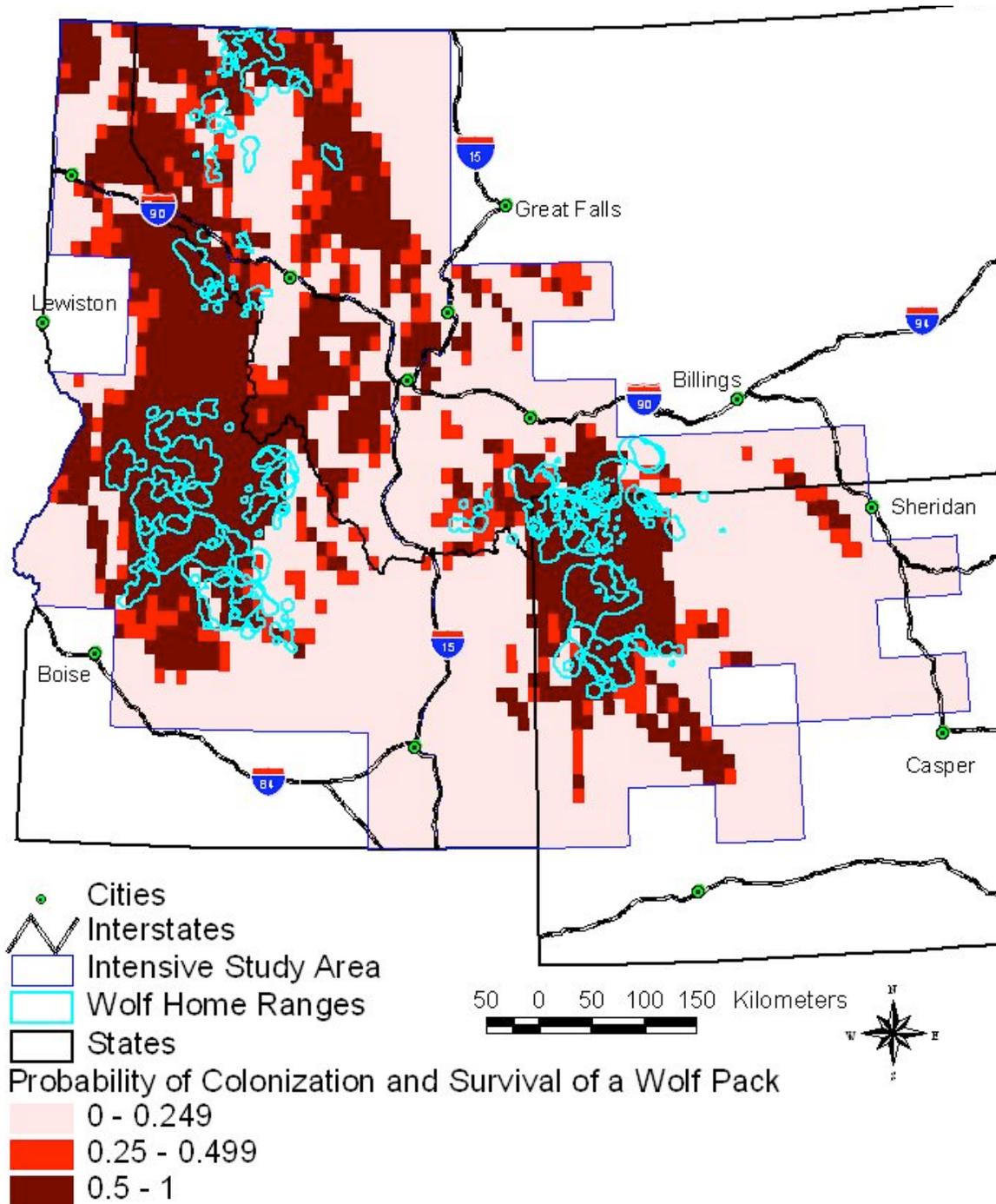
Parameter ^a	Coefficient	<i>SE</i>	<i>F</i>	<i>P</i>	<i>_AIC_C</i>
Study Area ^b	.	.	4.293	0.016	21.581
Elk	-0.694	0.265	6.840	0.010	10.358
Shrub Vegetation (%)	-0.018	0.005	12.739	0.000	8.394
Human Density (no./ km ²)	0.339	0.089	14.462	0.000	7.091
4-Wheel-Drive Roads (km/km ²)	3.073	0.857	12.859	0.000	6.353
Year	-0.110	0.030	13.228	0.000	4.443
Pups (yes or no)	-0.287	0.163	3.096	0.081 ^c	5.602
Number of Packs Adjacent	0.112	0.046	5.804	0.017	3.507
Other (Rock/Ice) vegetation (%)	0.055	0.022	6.126	0.015	4.556
White-tailed Deer	-0.355	0.132	7.232	0.008	3.279
Slope (%)	0.050	0.024	4.291	0.040	2.226

^aParameters are at the position in the table that corresponds to their time of entry into the model. Recovery area was forced as the first parameter retained in the model

^bCategorical variables with > 2 categories do not contain coefficient values

^cThis variable was significant at the time of entry into the model, but was changed by the entry of subsequent parameters into the model.

Figure 5. Probability of colonization and persistence of wolf packs in the northern Rocky Mountains based on probabilities from logistic regression habitat and persistence models. The overall probability was derived from multiplying the two probabilities together. Any probability > 0.25 is considered quality habitat because the animals would have > 0.5 probability of colonization and persistence in that particular area.



Discussion

Wolf habitat preferences and population consequences

Predicting habitat selection for a generalist predator with an expanding population is particularly challenging, and may involve a myriad of assumptions and potential problems (Mladenoff et al. 1995). In general, wolves potentially could live in any area where human tolerance and prey populations are adequate to support viable numbers (Mech 1970; Keith 1983; Fuller 1989). For instance, the presence of wolves in the northeastern United States has been principally described by landscape scale attributes (2-wheel-drive roads density) related to human mortality risk (Mladenoff et al. 1995; Harrison and Chapin 1998; Mladenoff and Sickley 1998; Wydeven et al. 1998). This relationship is based upon the apparently low wolf survival and colonization rates in areas of high road density (Theil 1985; Mech et al. 1998; Fuller et al. 1992; Mladenoff and Sickley 1998; Wydeven et al. 2001) The widely-accepted model by Mladenoff et al. (1995) has been effective in predicting future colonization of wolves in Michigan and Wisconsin (Mladenoff and Sickley 1998; Mladenoff et al. 1999). Yet, this model was originally based on a small sample size ($n = 28$) relative to that commonly required for development of robust logistic regression models (Hosmer and Lemeshow 2000). Also, the model developed by Mladenoff et al. (1995) may not be best suited for predicting wolf occupancy in areas where landscape/habitat features differ considerably from those found in the original study site. Our analysis should be more appropriate for examining wolf-habitat relationships in the western U.S. because it is based on a larger sample of observations and relates relevant habitat attributes to wolf colonization and persistence within the local landscape. Indeed, we determined that the Mladenoff et al.

(1995) model performed poorly for our area relative to our model (percent of use and non-use areas predicted incorrectly was 31% for the Mladenoff et al. (1995) model versus 15% for our model). This suggests that in general caution should be employed when attempting to use such predictive models for areas with substantially different habitat types.

Our model detected negative correlations between wolf occupancy and anthropogenic factors (human density and sheep density) and positive correlations with environmental factors (forest cover and elk). Each significant variable appears to be intuitively relevant to wolf survival and pack persistence, except sheep density. Yet, it seems likely that retention of this latter parameter is related to lethal control of individual wolves following depredation events, and thus preventing pack formation in these areas. Similarly, human density likely functions as an indication of high wolf mortality in areas of increased human presences. Elk are considered the primary prey item for wolves within the region (Bangs et al. 1998), thus, selection of areas with increased elk densities is of particular biological relevance for wolf survival, production, and habitat use.

Other models designed to predict wolf density as a function of prey density (e.g., Fuller 1989) must be used guardedly because they tend to be developed using wolf populations that are subject to density-dependent constraints rather than those that are expanding to new habitat. We feel that wolves are unlikely to fully saturate potential areas of colonization in the northwestern U.S. due to the patchy distribution of preferred habitat and the heterogeneous distribution of their primary prey (elk) in the region. Because relatively large tracks of unoccupied areas of preferred habitat continue to exist within each of the three recovery areas (although available habitat is reduced in the GYA), wolf numbers are likely to continue increasing in the future. State agencies currently planning to assume wolf

management responsibilities post-delisting should consider how new jurisdictional boundaries will affect the amount of estimated preferred habitat within each of the states. Under these guidelines, Wyoming should consistently have the fewest number of packs within the system because of the small amount of preferred habitat relative to that in Idaho and Montana.

Dispersal

Wolves are able to travel through relatively poor habitat in order to colonize new areas (Mech et al. 1995; Merrill and Mech 2000). However, such dispersal corridors are less than desirable because they expose dispersers to higher mortality risk and thus can result in poor connectivity between populations. Our dispersal habitat model was based on colonization probabilities, with a relatively low colonization threshold (> 0.3) used to characterize corridors. We determined that wolf populations in NMT and CID recovery areas appear to be linked by contiguous tracts of quality habitat; several wolves (8, with 2 contributing offspring) already are known to have successfully dispersed between these regions (J. Fontaine, unpublished data). In contrast, the linkage between the GYA and other recovery areas is more suspect, and this pattern is consistent even when the threshold for dispersal habitat is reduced substantially (> 0.1 probability of colonization, see Figure 4). This finding is supported by the fact that limited documented dispersal has occurred between the GYA and the remaining recovery areas. In fact, 3 of the 4 documented dispersals between the GYA and other recovery areas resulted in either death or relocation of the disperser. However, recently a successful dispersal has been documented from Idaho to the GYA, implying that dispersals to/from the GYA remain possible. However, for the northern Rocky Mountain wolf population to function as a metapopulation, it will be necessary that

dispersal corridors be considered as critical habitat in need of aggressive conservation. This may be somewhat problematic because much of the land between wolf recovery areas is privately-owned. Future use of GPS transmitters for the assessment of dispersal corridors and movement patterns of wolves in the western U.S. should be beneficial.

Habitat associations with population dynamics

Across their geographic range, wolf home range size differences appear to be principally related to prey densities (Keith 1983; Fuller 1989; Fuller et al. 1992). We found that wolf home range sizes in the northern Rocky Mountains were larger than those reported for many other regions, but they also were comparable to those reported for Alaska (see Table 1 in Fuller and Murray 1998). While it is notable that disparity occurred between home range sizes in Idaho versus the other two northern Rockies areas, this difference may be related to the lower density of prey (principally elk) in central Idaho, compared to the high ungulate biomass in the GYA or the high white-tailed deer density in Montana.

Home range size was related to several independent parameters; most notably, the observed negative correlations with elk, shrub vegetation, and white-tailed deer indicate that higher prey densities relate to decreasing home range size. Negative correlations between home range size and year could relate to temporal habitat saturation, but more likely are associated with increased intraspecific competition with time. The production of pups likely causes wolf packs to restrict movements during the summer while pups are young, and thus results in smaller wolf home ranges. Surprisingly, increases in the number of wolf packs adjacent to a home range resulted in larger home ranges; however, this is simply a result of large home range areas being adjacent to more wolf packs. This parameter was likely a poor indication for density of wolves.

Pack extinction rates appeared to be correlated with colonization probabilities for wolves suggesting that our colonization model accounted for areas that wolves were likely to remain extant through time. Interestingly, only two parameters were retained within the pack persistence model (private ownership, and agriculture/human vegetation cover). These parameters likely relate more to common wolf management practices rather than natural processes. Livestock depredations and subsequent control actions probably are more prevalent on private land (Bangs et al. 1998; Mack et al. 2002). In the future, survival analysis for individual radio-collared wolves should further elucidate the relationship between various anthropogenic factors and wolf mortality risk.

Our results naturally lead to the prediction that wolf numbers are likely to continue increasing in the northern Rocky Mountains due to the availability of high-quality preferred habitat and adequate dispersal corridors between sub-populations. At the present time, it does not appear that factors such as low survival or productivity will limit these populations in areas of preferred habitat. Further, potential corridors exist that could facilitate wolf dispersal into adjacent states (Utah, Oregon, and Washington). Indeed, at least one wolf from current established populations is either thought or known to have dispersed to each of these states (Joe Fontaine, U.S. Fish and Wildlife Service, unpublished data). However, in order to better predict potential wolf habitat occupancy, dispersal, and potential for population growth in the western U.S., it remains necessary to pursue additional habitat assessment in currently unoccupied states.

References

- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912-923.
- Bailey, R. G. 1983. Delineation of ecosystem regions. *Environmental Management* **16**:239-248.
- Ballard, W. B., G. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildlife Monographs* **98**:1-54.
- Bangs, E. E., S. H. Fritts, J. A. Fontaine, D. W. Smith, K. M. Murphy, C. M. Mack and C. C. Niemeyer. 1998. Status of gray wolf restoration in Montana, Idaho, and Wyoming. *Wildlife Society Bulletin* **26**:785-798.
- Boyd, D. K. and D. H. Pletscher. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. *Journal of Wildlife Management* **63**:1094-1108.
- Brehme, C. 1997. Landscape-level modeling of potential gray wolf habitat in the northern Rockies. M.S. Thesis. University of Idaho, Moscow.
- Carbyn, L. N. 1983. Management of non-endangered wolf populations in Canada. *Acta Zoologica Fennica* **174**: 239-243.
- Fritts, S. H. 1983. Record dispersal by a wolf from Minnesota. *Journal of Mammalogy* **64**:166-167.
- Fritts, S. H., E. E. Bangs, J. A. Fontaine, M. R. Johnson, M. K. Phillips, E. D. Koch and J. R. Gunson. 1997. Planning and implementing a reintroduction of wolves to Yellowstone National Park and central Idaho. *Restoration Ecology* **5**:7-27.

- Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs* **105**:1-41.
- Fuller, T. K. and W. J. Snow. 1988. Estimating wolf densities from radiotelemetry data. *Wildlife Society Bulletin* **16**:367-370.
- Fuller, T. K., and D. L. Murray. 1998. Biological and logistical explanations of variation in wolf population density. *Animal Conservation* **1**:153-157.
- Fuller, T. K., W. E. Berg, G. L. Radde, M. S. Lenarz, and G. B. Joselyn. 1992. A history and current estimate of wolf distribution and numbers in Minnesota. *Wildlife Society Bulletin* **20**:42-55.
- Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection and importance. Pages 111-164 in L. Boitani and T. K. Fuller, editors. *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York.
- Gese, E. M., D. E. Anderson, and O. J. Rongstad. 1990. Determining home range size of resident coyotes from point and sequential locations. *Journal of Wildlife Management* **54**:501-506
- Harrison, D. J., and T. G. Chapin. 1998. Extent and connectivity of habitat for wolves in eastern North America. *Wildlife Society Bulletin* **26**:767-775.
- Heglund, P. J. 2002. Foundations of species-environment relations. Pages 35-42 in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. *Predicting species occurrences: issues of accuracy and scale*. Island Press, Washington, D. C.

- Hooge, P. N., W. Eichenlaub, and E. Solomon. 1999. The animal movement program. USGS. Alaska Biological Science Center.
- Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression: second edition. John Wiley & Sons, Inc., New York.
- Huston, M. A. 2002. Critical issues for improving predictions. Pages 7-21 in J. M. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington, D. C.
- Jensen, W. R., T. K. Fuller, and W. L. Robinson. 1986. Wolf, (*Canis lupus*), distribution on the Ontario-Michigan border near Sault Ste. Marie, Ontario. Canadian Field Naturalist **100**:363-366.
- Keith, L. B. 1983. Population dynamics of wolves. Pages 66-77 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta.
- Kelley, W. N. 2000. Slope use by wolves in montane environment. Master Thesis, University of Idaho, Moscow.
- Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of Animal Space Use and Movements. Pages 125-187 in J. J. Millspaugh, and J. M. Marzluff, editors. Radio Tracking and Animal Populations. Academic Press, San Diego.
- Mack, C. M., I. Babcock, and J. Holyan. 2002. Idaho wolf recovery program: recovery and management of gray wolves in central Idaho. Nez Perce Tribe. Lapwai, Idaho.
- Manen, F. T., B. A. Crawford, and J. D. Clark. 2000. Predicting red wolf release success in the southeastern United States. Journal of Wildlife Management **64**:895-902.

- McClellan, S. A., M. A. Rumble, R. M. King, and W. L. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. *Journal of Wildlife Management* **62**:793-801.
- Mech, L. D. 1970. *The wolf: the ecology and behavior of an endangered species*. Doubleday/Natural History Press, Garden City, New York.
- Mech, L. D., S. H. Fritts, G. L. Radde, and W. J. Paul. 1988. Wolf distribution and road density in Minnesota. *Wildlife Society Bulletin* **16**:85-87.
- Mech, L. D., S. H. Fritts, and D. Wagner. 1995. Minnesota wolf dispersal to Wisconsin and Michigan. *American Midland Naturalist* **113**:368-370.
- Merrill, S. B., and L. D. Mech. 2000. Details of extensive movements by Minnesota wolves (*Canis lupus*). *American Midland Naturalist* **144**:428-433.
- Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in northern Great Lakes region. *Conservation Biology* **9**:279-294.
- Mladenoff, D. J., and T. A. Sickley. 1998. Assessing potential gray wolf restoration in the northeastern United States: a spatial prediction of favorable habitat and potential population levels. *Journal of Wildlife Management* **62**:1-10.
- Mladenoff, D. J., T. A. Sickley and A. P. Wydeven. 1999. Predicting gray wolf landscape recolonization: logistic regression models vs. new field data. *Ecological Application* **9**:37-44.
- Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65-110 in L. Boitani and T. K. Fuller, editors. *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York.

- Ream, R. R. and U. I. Mattson. 1982. Wolf status in the northern Rockies. Pages 362-381 in F. H. Harrington and P. C. Paquet, editors. *Wolves of the world: perspectives of behavior, ecology, and conservation*. Noyes, Park Ridge, New Jersey.
- Ream, R. R., M. W. Fairchild, D. K. Boyd, and A. Blakesley. 1989. First wolf den in western United States in recent history. *Northwest Naturalist* **70**:39-40.
- Ream, R. R., M. W. Fairchild, D. K. Boyd, and D. H. Pletscher. 1991. Population dynamics and home range changes in a colonizing wolf population. Pages 349-366 in R. B. Keiter and M. S. Boyce, editors. *The Greater Yellowstone ecosystem: redefining America's wilderness heritage*. Yale University Press, New Haven, Connecticut.
- Schooley, R. L. 1994. Annual variation in habitat selection: patterns concealed by pooled data. *Journal of Wildlife Management* **58**:367-374.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W.H. Freeman and Company. New York.
- Seaman, D. E., J. J. Millsbaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* **63**:739-747.
- Thiel, R. P. 1985. Relationship between road density and wolf habitat suitability in Wisconsin. *American Midland Naturalist* **113**:404-407.
- U.S. Fish & Wildlife Service, Nez Perce Tribe, National Park Service, and USDA Wildlife Services. 2000. *Rocky Mountain Wolf Recovery 1999 Annual Report*. Helena, Montana.
- U.S. Fish & Wildlife Service. 1987. *Northern Rocky Mountain Wolf Recovery Plan*. Denver, Colorado.

- White, G. C. and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press Incorporated, New York.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. *Ecology* **70**:164-168.
- Wydeven, A. P., R. N. Schultz, and R. P. Thiel. 1995. Monitoring of a recovering gray wolf population in Wisconsin. Pages 169-175 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta.
- Wydeven, A. P., T. K. Fuller, W. Weber, and K. MacDonald. 1998. The potential for wolf recovery in the northeastern United States via dispersal from southeastern Canada. *Wildlife Society Bulletin* **26**:776-784.
- Wydeven, A. P., D. J. Mladenoff, T. A. Sickley, B. E. Kohn, R. P. Thiel, and J. L. Hansen. 2001. Road density as a factor in habitat selection by wolves and other carnivores in the Great Lakes region. *Endangered Species* **18**:110-114.
- Young, S. P. and E. A. Goldman. 1944. The wolves of North America. Dover, New York, American Wildlife Institute, Washington, D.C.