Modeling Gray Wolf Habitat in the Northern Rocky Mountains

by

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Abstract:

The reintroduction of the gray wolf into the Northern Rocky Mountains has created many difficult management issues; ranchers fear for their livestock, hunters worry about game populations, ecologists and biologists support the reintroduction, and resource management agencies are caught in the middle. To date (2000), the one hundred plus wolves in the Yellowstone National Park area and approximately 200 more in Idaho and Montana have been monitored and managed using action/reaction techniques. Consequently, as wolves disperse through these areas, little preparation or planning has been conducted due to a lack of information about wolf locations, movements, and habitat preferences.

To improve the management of the gray wolf in the Northern Rocky Mountains, and to assist with pro-active planning, a geographic information system (GIS) was developed to create a wolf habitat suitability model. There were two main objectives to this project: the first was to identify the most effective mapping unit (Idaho Game Management Units, 33x33 km grid, 16x16 km grid) for modeling wolf habitat, and the second was to analyze four landscape variables (land cover, land ownership, road density, elk density) using logistic regression to predict wolf habitat suitability. Habitat models were built using data from Idaho, then the best model was tested using data from Montana and Wyoming for out-of-sample validation.

Results indicated that a 33 x33 kilometer grid worked best for modeling wolf habitat, and that road density and land cover were the most influential landscape variables for determining wolf habitat suitability. Overall accuracies of 83%, 89%, and 75% were achieved for predicting the presence/absence of wolves in Idaho, Montana, and Wyoming, respectively. The resulting habitat suitability maps can assist management agencies in the identification of potential wolf habitats, areas where human/wolf conflicts are likely to occur, and areas that should be considered essential wolf habitat, thus contributing to the improved management and protection of the gray wolf in the Northern Rocky Mountains.

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1.1 Introduction

The gray wolf (*Canis lupus*) historically inhabited most of North America until the wolves were systematically exterminated from most of their original range through hunting, trapping, and poisoning (Mech 1970). By the 1930s, there were no permanent wolf populations remaining in the western United States. There were, however, some long-range dispersers from Canada that were occasionally killed in the northern Rocky Mountains (Nowak 1983). In 1973, the Endangered Species Act required that the federal government use all methods and procedures necessary to restore wolves to suitable habitats. A recovery plan for the wolves was subsequently drafted in 1974 that recommended natural dispersal and relocation be used to restore wolf populations.

The western United States, however, did not produce a litter of wolf pups until 1986 when a pack of wolves from Canada moved south and settled in northwestern Montana (Ream et al. 1989). Seeing that natural dispersal was not working fast enough, the United States Fish and Wildlife Service (USFWS) revised its plan and specified the reintroduction of wolves into Yellowstone National Park (YNP) and central Idaho if a naturally occurring population was not in place by 1992 (USFWS 1987). In the late 1980s as wolves slowly moved south into northwestern Montana there were incidents of livestock depredation that forced intensive management strategies (Bangs 1991, Bangs et al. 1995, Fritts et al. 1995). This was the beginning of a still continuing debate over the reintroduction of gray wolves into the western United States. Those opposed claim that wolves would severely damage livestock and destroy game animal populations. Proponents for the reintroduction of wolves cite that livestock losses would be minimal and compensation would be provided. They also argue that wolves are a natural part of the ecosystem, and their return would help maintain healthy animal populations through natural selection.

As a compromise to these opposing viewpoints, wolves were reintroduced as an "experimental nonessential" species. The "experimental nonessential" status excluded the reintroduced wolves from the Endangered Species Act, enabling wildlife managers to control (relocate or kill) the wolves if they caused problems. In 1995 and 1996, after more than a decade of work, 35 wolves were released into central Idaho and 31 wolves were released into YNP (Figure 1)(Bangs and Fritts 1996).

Wolf Management Areas

No wolves were released into Montana because wolves were already colonizing the area as a result of natural dispersion from Canada. The wolves quickly adapted to their new locations and at the end of 1998 had prospered to a population of approximately 115-120 wolves in 11 packs in the Yellowstone area, as well as an estimated 145-150 wolves in Idaho and about 65 wolves in Montana (Table 1) (USFWS 2000).

The question of how to manage the wolves still remains unanswered; this project was designed to assist in answering that question. A map-based conservation plan could help facilitate human-wolf coexistence by identifying areas where human development trends may create potential conflicts with wolves (Mladenoff et al. 1995, Mladenoff et al. 1997). Determining the correct scale, however, to study an animal that can have a home range from 100 sq km to greater than 2000 sq km (Noss et al.1996) is a difficult task and is critical to creating accurate habitat models. Therefore, the objectives of this research were to:

1) Identify the most suitable mapping unit for modeling wolf habitat.

   This was accomplished by using three different mapping units for analyzing four landscape variables. Mapping units used included the Idaho state Game Management Units (GMU), a 33x33 km grid, and a 16x16 km grid. These mapping units were compared to see if they identified the same habitat variables as important, and whether they identified similar patterns of habitat suitability. The mapping unit that produced the best results using the Idaho data was used for modeling habitat suitability in Wyoming and Montana.

2) Predict probabilities of suitable wolf habitat using logistic regression.

   I analyzed land cover, land ownership, road density, and prey density as they related to the presence/absence of wolves. Wolf habitat was evaluated and modeled for a 108,750 square km area in central Idaho. The landscape variables were entered into a logistic regression equation with wolf presence/absence being the dependent variable. The results of the regression analysis showed the probability of suitable wolf habitat as defined by data from the present wolf locations in Idaho.

Table 1. Minimum Fall Wolf Populations for Northern Rocky Mountain States (1979-1999). From USFWS 2000.

Year	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
NW Montana	2	1	2	8	6	6	13	15	10	14	12	33	29	41	55	48	66	70	56	49	63
Yellowstone*																	21	40	86	112	118
Central Idaho*																	14	42	71	114	141
Total	2	1	2	8	6	6	13	15	10	14	12	33	29	41	55	48	101	152	213	275	322

* No wolves were present in central Idaho or Yellowstone prior to 1995.

1.2. Wolf Ecology

1.2a. Pack Structure

Wolves are social creatures that live in groups called packs, consisting of a mated pair and their offspring from one or more years (Mech 1970). When viewed individually, these packs are fairly independent units. When viewed at a regional scale, however, they appear as a mosaic of interacting sub populations, each influencing and reacting to changes in each other and other ecological variables. Each pack has a social hierarchy, with the alpha male and alpha female (breeding pair) at the top. Below the alpha pair, the others members of the pack assert their positions into the hierarchy; the lowest ranked wolf is referred to as the omega wolf.

The number of individuals within a pack fluctuates greatly, though most packs do not exceed seven members (Mech 1970, Cowan 1947). Mech (1989) reports that there are four factors that influence the number of wolves in a pack: 1) the smallest number of wolves required to effectively track and kill prey, 2) the largest number of wolves that can feed on a prey animal, 3) the social attachment factor, 4) the social competition factor. Frequently in the spring, wolves will disperse in an effort to form their own pack. Males and females are equally likely to disperse, and both sexes of wolves generally disperse when they are two or three years old (Fritts and Mech 1981, Peterson et al.1984, Fuller 1989). When dispersing, the average minimum distance traveled is 133 km, with distances up to 700 km possible (Mech et al. 1998). New packs are formed when two dispersers of opposite sex pair up and occupy a previously unoccupied region.

Each pack establishes and defends a territory that it uses for hunting and day-to-day travels. The size of this territory is influenced by the number of individuals in the pack and the abundance of prey (Mech 1970). Fuller (1989) noted that territory size tended to be smaller in areas where prey biomass was higher. One study in Minnesota noted that a pack of five wolves used an area that ranged from 49 to 135 sq km (Ballenberghe 1975), while another study in Minnesota reported winter pack territory sizes of 150-180 sq km (Fuller et al. 1992). Studies in Alaska report pack territories in Denali ranging from 600 to over 4,000 sq km (Mech et al. 1998); however, it should be noted that the wolf packs in Denali are among the largest on record.

1.2b. Predator/Prey Relations

Living in packs helps the wolf to pursue and kill large prey species, however they still have a relatively low success rate. Observations in Isle Royale National Park noted that out of 131 moose detected by a pack of 15 -16 wolves, 54 escaped “un-tested” and only 6 were killed (Mech 1970). As a result of this low success rate, wolves have adapted to live on a feast/famine diet. Mech (1970) reports having seen wolves consume half a moose in less than two hours, approximately 20 pounds of meat per wolf. Another observation made by Cowan (1947) reports that a pack of three wolves consumed three mule deer and an elk calf in five days. To balance this feasting, wolves often go for many days without eating. This feast/famine cycle allows for wolves to feast, then spend one to two weeks searching for more food before repeating the cycle (Mech 1970).

By adapting to feed on the dominant large ungulate of a given region, wolves were historically able to establish populations in almost every portion of the northern hemisphere (Mech 1970). The wolves in the Great Lakes region in the United States eat primarily deer and moose, while wolves in the Arctic tundra feed primarily on caribou, and wolves in western Canada and the northern Rocky Mountains feed mainly on elk (Mech 1970, Fuller 1989). A study conducted by Ballenberghe (1975) in the Great Lakes region found that 55% of the wolves’ diet was white tailed deer, 13.1% moose, and 9.7% beaver; the remaining 22.2% of their diet was made up of small mammals such as rabbits and mice. The preferred prey of wolves is a learned behavior that they pick up as juveniles from their older pack members. This learned behavior was exemplified in the Ninemile valley of Montana, where a litter of orphaned wolf pups, who were previously raised on whitetail deer, refused to eat two bighorn sheep (Bass 1992).

Wolves are opportunistic predators and will kill whichever animal (within its "search pattern") is easiest catch, and as a result, it is usually the young, old, or sick that are eaten (Mech 1970). Wolves will often give chase to a large herd of prey, and if no vulnerable animals are detected, the wolves will give up the chase and continue searching for more vulnerable prey. Wolves help keep prey populations healthy and strong by eliminating biologically/physically inferior animals before they can breed and pass on their detrimental genes (Mech 1970). Ungulates such as deer and elk have no internal mechanism to limit population size, therefore, they have historically relied on predators to keep their numbers at a level compatible to their food supply. One example of this can be found by looking at the history of the moose on Isle Royale. Moose have inhabited the island for most of the century; however, wolves were not present until 1949 when they crossed the frozen ice of lake Superior. Before the wolves arrived, the moose population soared to between 1000-3000 animals before it crashed in the 1930s as a result of disease and starvation. The moose population grew again, and again the population was drastically reduced as a result of starvation in the 1940s. Since the wolves arrived on the 210 square mile island in 1949, they have killed an estimated 140 moose calves and 83 adult moose per year (Mech 1970), thereby helping to regulate the moose population. It should be noted that wolves not only reduce prey populations, they also stimulate birth rates to create a balance. Observations of the moose populations on Isle Royale before wolves colonized the island in 1949 showed that the occurrence of moose twins were rare (6%) in 1930 as compared to 38% in 1959 (Mech 1970).

As a result of the powerful and adaptive feeding strategy used by wolves, their impact on prey populations is a topic that needs to be addressed. When wolf/prey density ratios are high, wolves are often the primary limiting factor of the prey populations. A study done in Algonquin Provincial Park, Ontario, where the deer population was limited by wolves, found a ratio of about 100-150 deer per wolf or 15,000-22,500 pounds of deer per wolf (Pimlot 1967). Conversely, and more commonly, when wolf densities are low and prey is super abundant, the wolf has little impact on prey populations, indicating that wolves generally do not kill more prey than they can eat. The natural dispersal of wolves to Isle Royale has been an excellent source for monitoring wolf/prey interactions. It appears that the Isle Royale wolf population reacts to, rather than causes, change in the local moose population (Figure 2) (Peterson 1998). A study by Cowan (1947) in the Rocky Mountains of Canada compared wolf and non-wolf areas and found little to no difference in the prey populations, indicating that wolves were not the controlling factor for prey populations. Cowans' study in Canada estimated a prey density of 300-400 animals (bighorn sheep, elk, moose, deer, and caribou) per wolf, or 90,000-120,000 pounds of prey per wolf. A similar study in Wisconsin found that wolves did not limit the growth of deer populations where the deer population density was about 10 deer per square mile, resulting in a ratio of about 350 deer (52,500 lbs) per wolf (Thompson 1952).

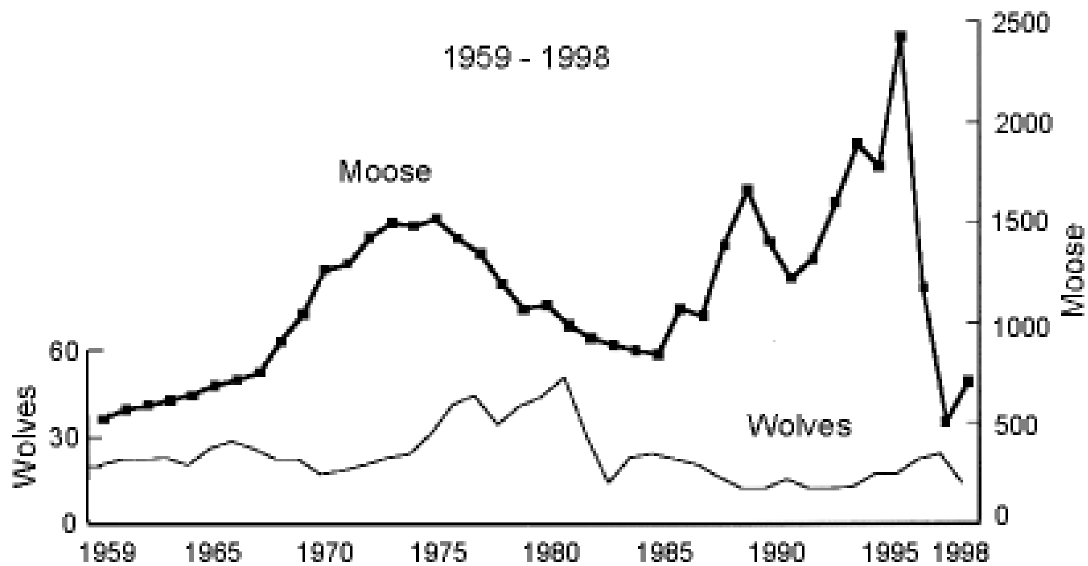

Figure 2. Isle Royale moose-wolf population trends. Moose population estimates from 1959-1985 were based on population reconstructions from dead moose and wolves, while moose and wolf populations estimates from 1986-1998 were based on aerial surveys

(from Peterson 1998).

1.2c. Wolf/Human Relations

When discussing how wolves interact with humans, there are four issues that are usually mentioned, including the possible predation of humans by wolves, competition for game animals, competition for livestock, and persecution of wolves by humans. The stories that have been told about each of these topics differ depending on whom you talk to. Many ranchers and avid hunters will testify wolves should be eliminated because they kill people, decimate game populations, and constantly prey on livestock. Environmentalists often claim the opposite, and assert that wolves should be allowed to repopulate the area.

Most accounts of wolves attacking humans cannot be traced back to any reliable source; they are usually old "trapper stories" or other hearsay accounts. Lee Smits (1963) investigated many of the claims of wolf attacks, and concluded that there has never been a case of a non-rabid wolf deliberately attacking a human in North America. In fact, there is much more evidence supporting the claim that wolves are harmless to humans as demonstrated through the interactions of wolves and wolf researchers. According to Mech (1970) one researcher (Mure) entered a wolf den and stole one of the pups while the other wolves stood nearby barking and whining. Another researcher (Parmelee) also abducted a pup from its den and was followed, but never threatened, by the other wolves all the way back to his camp.

The debate over whether wolves severely damage game populations has been a controversial topic in many areas, especially Minnesota, which, prior to the reintroduction of wolves into Idaho and the Greater Yellowstone Ecosystem (GYE), held the only substantial wolf population in the contiguous United States. While it is true that most of the prey that wolves feed upon are also valued by humans for sport hunting, it is difficult to say if fewer wolves would mean more game. If wolves are the limiting factor for a species, then their absence would likely result in an unstable population similar to the moose on Isle Royale before the wolves arrived. However, in regions where wolves are not the limiting factor, the wolf may have little effect on game populations. As a result of wolves being exterminated from most of their original range, most game populations are currently regulated by hunting and available habitat rather than wolf predation. In Minnesota, a study compared hunter success rates for a region heavily populated by wolves to success rates in adjoining counties with very few wolves. The results showed that there was no difference in hunter success rates in wolf versus non-wolf areas, and therefore, wolves could not be considered serious competitors for game species (Mech 1970).

Livestock depredation is a serious issue in areas where wolves and livestock live in close proximity and/or occupy similar habitats. This is especially true for areas where wolves are re-colonizing, such as Montana where 65% of the state is agricultural land containing about 453,500 cattle and 58,420 sheep (Bangs et al. 1995). The total number of livestock depredations that were reported to Animal Damage Control (ADC) in Montana between 1986 and 1991 show that only a very small portion of livestock deaths were actually caused by wolves (Table 2). Of the 138 cows and 2,394 sheep killed in Western Montana, only 4 cows and 2 sheep were killed by wolves; the remaining depredations were caused by other predators such as coyotes, mountain lions, fox, and bears. Of these six depredation incidents, all of them occurred on private lands between March and May, when young livestock were available and young elk and moose were not (Bangs et al. 1995). In 1999, wolves were responsible for killing 13 cattle and 19 sheep in Montana, 16 cattle and 57 sheep in Idaho, and 4 cows and 13 sheep in Wyoming (USFWS 2000). To compensate ranchers for their livestock losses, Defenders of Wildlife paid out a total of $15,350.00 in 1999 (Table 3).

Human actions can have a detrimental impact on wolf populations. In the past, wolves were completely exterminated from most of their original territory through the use of hunting, trapping, and poisoning for bounty and/or sport. Currently, there is still a hunting/trapping season to control the wolf population in parts of Alaska and Canada. To control wolf populations in the western Provinces and Territories of Canada, a total of 4,025 wolves have been harvested since 1986 (Hayes and Gunson, 1995). In fact, even though there is no legal harvesting in the conterminous states, humans were responsible for 72% of the wolf mortality in western Montana between 1985 and 1992 (Bangs et al. 1995). Since wolves were released into Yellowstone National Park, approximately 73 wolves have died, with 15-20 of these deaths being illegally/accidently caused by humans, and another 11 wolves were legally killed by humans for control purposes (Maughan). Wolves are resilient and adaptable creatures that can survive in a wide variety of habitats; in fact, it appears that it may be a mixture of human tolerance and habitat suitability that ultimately determines where wolves can successfully colonize.

Table 2. Summary of average annual sheep and cattle losses reported by Animal Damage Control in Montana 1986-1991. (From Bangs et al. 1995)

Predator	Prey	Total $	Number	% Adult
mountain lion	sheep	3,825	47	18
	cattle	650	1.5	0
coyote	sheep	145,408	2,106	12
	cattle	53,712	127	1
fox	sheep	3,561	64	4
	cattle	71	0.3	0
black bear	sheep	8,893	102	60
	cattle	1,733	3.4	23
brown bear	sheep	777	13.5	68
	cattle	854	1.8	28
dog	sheep	5,880	60	48
	cattle	71	0.5	40
wolf	sheep	263	2.3	65
	cattle	1,336	3.8	39
total losses	sheep	168,607	2,394	15
	cattle	58,427	138	3

Table 3. Livestock depredation/compensation and wolf control records. (from USFWS 2000)

Idaho

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	Total
cattle									0	4	1	10	16	31
sheep									0	24	29	5	57	115
dog									0	0	4	0	5	9
other livestock									0	0	0	0	0	0
$ paid *									0	5185	3761	6855	1787	33688
wolves moved									0	5	0	3	15	23
wolves killed									0	1	1	0	6	8

Wyoming

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	Total
cattle									0	0	5	3	4	12
sheep									0	13	67	7	13	100
dog									1	0	0	4	6	11
other livestock									0	0	0	1	1	2
$ paid *									0	1221	17644	2050	6310	27225
wolves moved									6	8	14	0	0	28
wolves killed									0	1	6	3	9	19

Montana

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	Total
cattle	6	0	3	5	2	1	0	6	3	9	16	9	13	73
sheep	10	0	0	0	2	0	0	0	0	0	30	0	19	61
dog	0	0	0	1	0	0	0	0	2	1	0	0	2	6
other livestock	0	0	0	0	0	0	0	0	0	0	0	0	0	0
$ paid *	3049	0	1730	3700	1250	374	0	1772	1633	1485	10877	1675	7253	34798
wolves moved	0	0	4	4	3	0	0	2	2	10	7	0	4	32
wolves killed	4	0	1	1	0	0	0	0	0	4	14	4	9	37

* Compensation paid by Defenders of Wildlife

1.3. Response to landscape variables

There have been numerous studies that relate how wolves respond to their environment in terms of habitat selection. Human activities have been shown to influence the distribution and survival of wolves (Theil 1985, Fuller et al. 1992, Mladenoff et al. 1995). Wolves were found to occur more often in areas with fewer than 1.54 humans per square km. (Mladenoff et al. 1995). In Minnesota, 88% of the wolves were found in townships that had fewer than 4 humans per square km (Fuller et al. 1992). The absence of wolves from areas with high levels of human activity may be the result of increased mortality rates and/or simply a behavioral avoidance (Carroll et al. 1998). Roads have been used as an effective measurement of human activity in an area, and can therefore be used to identify suitable wolf habitat. Roads, by increasing human contact, have been documented to negatively affect wolf populations at both local and regional scales (Fuller 1989, Thurber et al. 1994, Mladenoff et al. 1995, Mech et al. 1988). Road data can be incorporated into habitat models in a variety of ways, including distance from roads or road density. The distance-from-roads measurement may be more applicable for local studies. Paquet et al. (1997) documented a 500 meter buffer from roads in the Banff area, and Thurber et al. (1994) showed a negative response to roads up to 5 km away in Alaska. The mean road density in areas occupied by wolves is generally lower than in areas not occupied by wolves. In Wisconsin, wolves were generally absent from areas with a road density greater than 0.58km/km^2 (Theil 1985) however, there were exceptions when these areas were located adjacent to a large roadless area (Mech 1989). Similarly, studies in Wisconsin showed that wolves were concentrated in areas with a mean road density less than 0.23 km/sq km, and tolerated areas as high as 0.45 km/sq km; as opposed to a mean road density of 0.74 km from random non-pack areas (Mladenoff et al.1995).

Land ownership is another factor that influences habitat selection, as wolves occur much more frequently on public lands than private (Mladenoff et al. 1995). This preference is probably because public lands generally have lower levels of human disturbance, while private property is often more developed and less accommodating for wolves. Habitat selection is not based solely on avoiding humans; studies indicate wolves also respond to natural landscape variable such as vegetation type, and prey density. In Minnesota, wolves territories had a higher proportion of conifer and conifer mixed woodlands than non wolf areas. Similarly, occupied areas had a lower percentage of agricultural and deciduous forest than occupied land (Mladenoff et al. 1995). Some studies suggest that the main limiting factor for wolves, after human tolerance, is prey availability (Fuller et al. 1992). Other studies, however, have found little to no difference in prey densities in wolf and non-wolf areas (Mladenoff et al. 1995, 1997).

1.4. Recent Modeling Efforts

In recent years, there have been many advances in wildlife modeling techniques, including the use of multivariate analysis, and the enlargement of study areas to broader spatial scales to recognize regional characteristics (Morrison et al. 1998). Researchers have also recognized the need to adjust their models to correspond with the type of threat facing the species of focus. If habitat loss is one of the principal limiting factors, then land cover/land use would be appropriate variables to examine. Similarly, if human contact is limiting a population, roads (correlated to human disturbance) and land use may be appropriate variables to examine.

Logistic regression is a non-parametric, non-linear technique for analyzing independent variables (categorical and continuous data) to predict the probability of a dependent variable. The research done by David Mladenoff et al. (1995, 1998, 1999) serves as an inspiration and foundation for this research. He successfully used logistic regression with a 150 sq km mapping unit (mean pack territory size) to model wolf habitat suitability in the Great Lakes region of the United States. His results indicated that wolves in this region favored mixed conifer forests and wetland forests over agriculture and deciduous forests, public lands to private property, and low road densities (<0.45km/km2). His results also indicated that there was no difference in deer densities when pack and non-pack areas were compared. Boyd-Heger (1997) created a logistic regression model using elevation, slope, and distance to roads, to predict areas of possible wolf colonization. Another study done by De la Vile et al. (1998) used a 100 sq km mapping unit to identify suitable wolf habitat across Greenland and North America (except Florida). His model found that suitable habitat was characterized by low amounts of human disturbance (roads, agriculture) and areas with greater that 40% herbaceous and woody cover. Morrison et al. (1998) state that logistic regression models may be more robust than parametric procedures and have better classification success than discriminant analysis techniques.

Discriminant analysis classifies the independent variables (continuous data) into one of the pre-defined, categorical, dependent variables. Once all the observations are placed into one of the specified groups, comparisons between groups can be used to identify differences and correlations. Boitani et al.(1997) used discriminant function analysis and Mahalanobis distance with a 100 square km mapping unit (mean pack territory size) to model wolf habitat in Italy, and later Corsi et al. (1999) used similar methods to assist in the planning of a nation-wide management plan for the wolf in Italy. Discriminant analysis is a widely used technique; however, it should be noted that this method often performs poorly when using categorical independent variables (Morrison et al. 1998).

There has also been a substantial amount of modeling research concerning the biological and dispersal characteristics of the wolf. Haight et al. (1998) modeled wolf population dynamics in the semi-developed landscape around Lake Superior and concluded that wolves can survive in a fragmented landscape if there are migration corridors to allow for the packs to interact with each other as population sources and sinks. By managing the landscape as a mosaic of preserves and utilized land, the effective management area will be much larger than the sum of the preserves (Fritts and Carbyn 1995). A simulation model was created to model the wolf prey dynamics in the Greater Yellowstone Ecosystem that predicted population trajectories for wolves, elk, mule deer, moose, and bison under different scenarios/options including climate, human hunting impact, and the legal hunting of wolves, among others (Boyce 1995). Results indicated that both climate and hunting harvest influenced prey populations, and that when human-caused mortality was held constant, elk population trends were the dominant influence on wolf populations. Paquet et al. (1997) used a modified “least-cost path” model to identify dispersal barriers in Banff National Park. Dispersal was modeled in a GIS by accounting for attraction to preferred habitats, minus energetic costs (topography), security costs (human exposure), and physical obstructions (lakes, cliffs).

1.5. Suggested Modeling Approaches

The effectiveness of a model is ultimately related to the modeler's ability to identify and generalize the habitat requirements of a species so they can be entered into a GIS (Donovan et al. 1987). Habitat models built around a theoretical design, using qualitative generalizations, don't always work for wide ranging carnivores. Carroll et al.(1998) suggests that regional-scale, empirical, multivariate models built from extensive GIS data sets and satellite imagery be used for modeling habitat. Multivariate models may also be used to help identify significant combinations of environmental variables that impact habitat suitability (Morrison et al. 1998).

To accommodate the large area required to support a population of wolves (multiple packs), modeling efforts should focus on a large spatial area (Noss et al. 1996, Mech 1995, Haight et al. 1998). Focusing on a large spatial area will also provide conservationists and policy makers with more information, allowing them to develop regional management plans. Researchers should also consider the effects of scale (resolution) on habitat relationships. The hierarchy theory is one way to do this. Hierarchy theory recognizes links between process at multiple scales (Allen et al. 1984, Wiens 1989); for example, areas with high road density may limit a population at coarse scales, while vegetation and/or prey may be a greater influence at finer resolutions. One method to identify the best resolution would be to start with a course resolution, then progressively use finer scales until the minimum level of detail needed is identified (Carroll et al. 1998). By integrating multiple models at multiple spatial scales, the modeler may be able to produce more biologically and spatially accurate results.

1.6. Study Area

This study focuses on predicting wolf habitat in the Northern Rocky Mountains; specifically, the Idaho, Montana, and Wyoming tri-state area (Figure 3). This area contains a wide range of topography and vegetation types, making a regional summary difficult, but in general the area can be characterized as being mountainous with a semi-arid, continental climate. Precipitation varies greatly in response to elevation change, ranging from 30 to 122 centimeters (12-48 inches) annually, with slightly higher amounts in the winter months (Marston 1991).

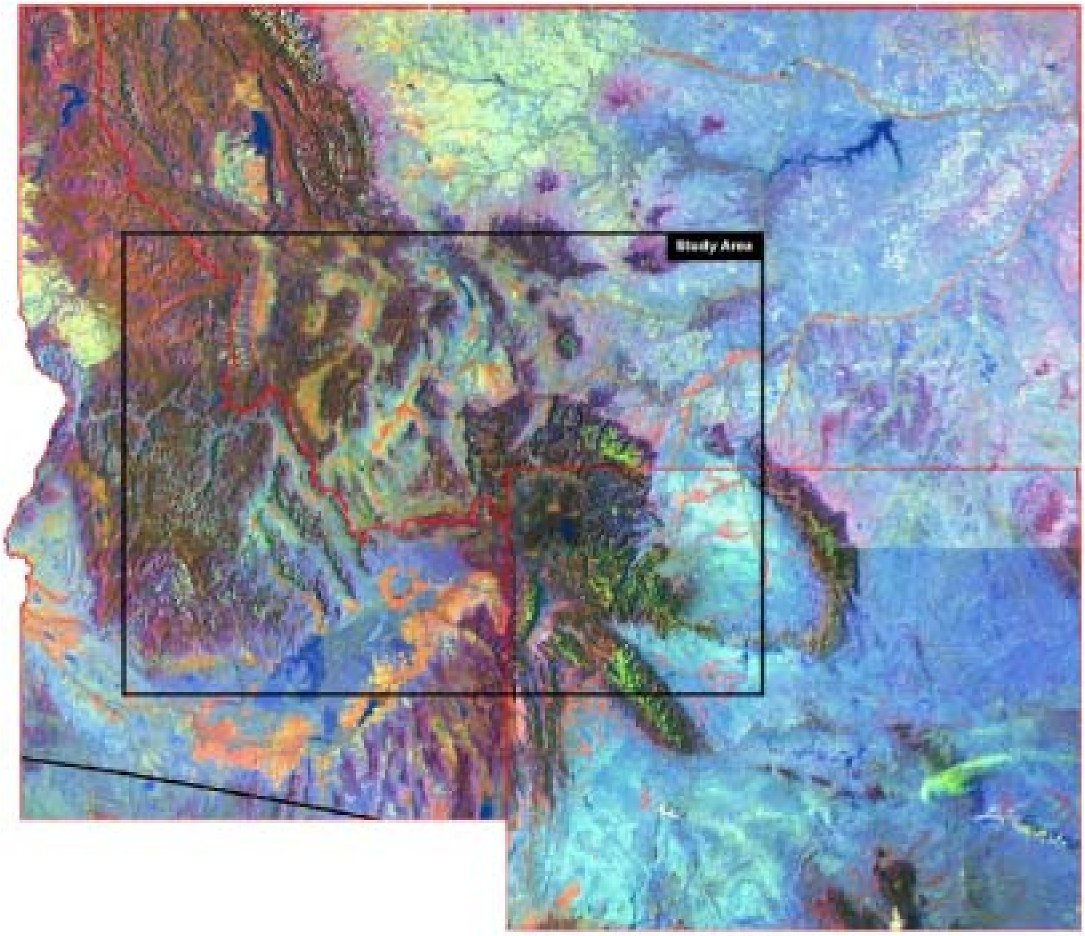

Figure 3.
AVHRR false color composites (2,1,3) from August, 1996, from the "Color Landform Atlas of the United States" by Ray Sterner, http://fermi.jhuapl.edu/states

These factors work together to create a landscape that is characterized by western temperate coniferous forests in the upper, wetter elevations, and sagebrush steppes in the lower, drier elevations. The region is generally sparsely populated by humans with large tracts of remote, often roadless wilderness.

The western portion of the study area contains the rugged mountain region of central Idaho and its 16,000 sq km of designated wilderness. This wilderness supports over 241,000 wild ungulates including mule deer (*Odocoileus hemionus*), white- tailed deer (*Odocoileus*

Virginianus) , elk (*Cervus elaphus*), and moose (*Alces alces*), among others (Bangs and Fritts 1996). This area is used by hunters, who harvest around 33,360 ungulates annually, and ranchers who seasonally graze more than 300,000 head of livestock on federal lands despite annual losses of approximately 12,310 cattle and 9,360 sheep (Bangs and Fritts 1996).

The southeastern portion of the study area includes the Greater Yellowstone Ecosystem. This area, as defined by Marston (1991), is the Yellowstone Plateau and the areas above 2,130 meters (7,000 feet) in the surrounding 14 mountain ranges. Vegetation in the area is heavily influenced by the effects of elevation on temperature and precipitation. This effect stratifies the region into communities that include, from lowest to highest elevation: grassland and shrubland, low elevation forests, middle elevation forests, and upper elevation forests. In the lowest elevations, grasses include wheatgrasses from the genus *Agropyron*, needlegrasses from the genus *Stipa*, Idaho fescue (*Festuca idahoensis*), and various bluegrasses from the genus *Poa*, among others. Shrub steppes are commonly dominated by big sagebrush *(Artemisia tridentata),* with other species such as threetip sagebrush *(Artemisia tripartita)* and rabbitbrush *(Chrysothamnus)* frequently occurring. The lower elevation forests are largely comprised of Douglas fir *(Pseudotsuga menziesii)* which give way to extensive lodgepole pine *(Pinus contorta)* forests in the middle elevations. As elevation continues to increase, the lodgepole pine communities become intermixed with subalpine forest species such as the Engelmann spruce *(Picea engelmannii)*, subalpine fir *(Abies lasiocarpa)*, and whitebark pine *(Pinus albicaulis)*.

1.7. Methods

1.7a. Model design

Habitat suitability models were created using wolf habitat data from Idaho. Idaho was used for the creation of this model because it has a large number of wolves, and the data used as independent variables were readily available. The wolf packs currently in Montana and Wyoming were used for out-of-sample model validation. To validate the model, the most effective Idaho model was applied to Montana and Wyoming, and its ability to correctly identify current wolf locations was assessed. It was important for this model to perform well on out-of-sample data, as this would reinforce its validity and increase its functionality.

1.7b. Mapping resolution

In an effort to identify the optimal resolution to use for modeling suitable gray wolf habitat in the Northern Rocky mountains, Three different mapping units were used. The first unit used was a boundary system created by the state that defines Game Management Units (GMU), the second and third mapping units were generally smaller, and were uniform in size and shape; a 33 x 33 km grid and a 16 x 16 km grid (Figure 4). All three mapping units were used to analyze four independent variables (road density, prey density, land ownership, and land cover) to predict the presence or absence of wolves. Using these three approaches helped to identify which scale was more appropriate for studying wolf habitat in the Northern Rocky Mountains. The GMU's were the initial modeling units for several reasons. Foremost, they were pre-established units for wildlife management, and population counts for elk were readily available for these units. The 33 km grid was selected because it was a good approximation of the average pack territory size and the 16 km grid was selected to see if a smaller mapping unit would bring out subtle variations in habitat parameters.

1.7c. Habitat Suitability Analysis

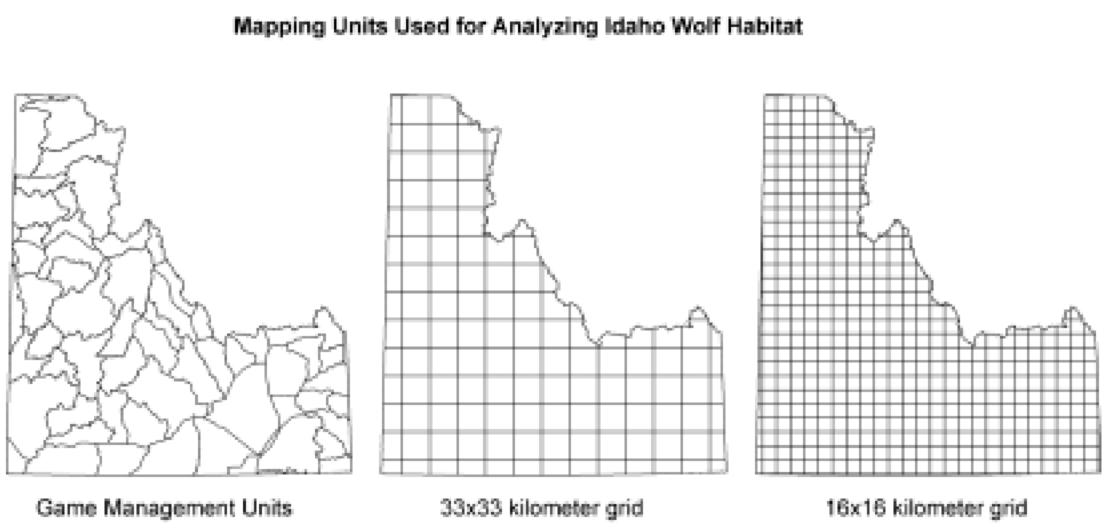

Figure 4. Three different mapping units used in the analysis of Idaho wolf habitat. The mapping unit that performed the best was validated using data from Montana and Wyoming.

Current observations for wolf locations/territories as delineated by Maughan (1999) were digitized using ESRI's Arc/Info software. The presence/absence of wolves from a mapping unit was used to identify preferred landscape conditions for wolves in the Northern Rocky Mountains according to land cover, land ownership, prey density, and road density. Previous studies on wolves and their habitat indicate that each of the selected variables can influence the territory selection of a wolf pack. Most notably, road density has been shown to be inversely correlated to wolf locations (Mech 1989, Mech 1995, Maldenoff et al. 1995, 1997, Theil 1985). Land cover has been shown to have an impact on wolf locations and several studies have also indicated that in areas where prey is scarce, the availability of prey (deer, elk, and moose) is significantly correlated to wolf presence and density in some areas (Fuller et al.1992).

1.7d. Statistics

The descriptive data extracted from the GIS data set (land cover, land ownership, road density, prey density) were statistically analyzed and tested, then used to create a logistic regression model to predict the probability of suitable wolf habitat. To test for significant differences between wolf and non-wolf locations, a T-test was performed to identify differences in road density and elk density, and a chi square test was performed to identify differences in land cover and land ownership. All statistical tests were performed using a $p \leq 0.05$. Logistic regression was then used to analyze all four independent variables to predict the probability of suitable wolf habitat. The variables were entered using a forward step-wise method with a minimum significance level of $p \leq 0.05$ to enter and a minimum of $p \leq 0.1$ to exit the model. Predicted probabilities greater than or equal to 0.5 were classified as potential wolf habitat.

1.8. Relevance

This study addresses several important issues regarding the effective management of the wolves of the Northern Rocky Mountains. By examining multiple mapping resolution, a large spatial extent, and multiple landscape variables, this study brings together many of the habitat modeling techniques recommended by other researchers. Analysis of landscape variables using different mapping resolutions helps to identify the strengths and weaknesses of each, and identifies which mapping unit is the most suitable. The large study area, approximately 280,500 sq km, covering three states and multiple national parks and forests promotes cross jurisdictional and regional planning. The final habitat suitability maps will aid in the identification of suitable wolf habitat so that pro-active planning can be initiated for areas where wolves are likely to occur as populations expand. The maps will make it easier to locate the areas that will likely be inhabited by wolves, areas where wolf/human conflicts are likely to occur, and areas that should be considered as essential wolf habitat

1.9. Literature Cited

Allen, A.W., R. V. O'Neill, and T.W. Hoekstra. 1984. *Interlevel Relations in Ecological*

Research and Management: Some Working Principles from Hierarchy Theory. USDA FS Rocky Mountain Forest an Range Experiment Station. Fort Collins CO. General Technical Report RM-110

Ballenberghe, V. V., A.W. Erickson, and D. Byman. 1975. Ecology of the Timber Wolf in Northeastern Minnesota. *Wildlife Monographs*. No 43.

Bangs, E.E., S.H. Fritts. 1996. Reintroducing the Gray Wolf to Central Idaho and Yellowstone National Park. *Wildlife Society Bulletin*. 24(3):402-413

Bangs, E.E. 1991. Return of a Predator: Wolf Recovery in Montana. *Western Wildlands* 17:7-13.

Bangs, E.E., S.H. Fritts, D.R. Harms, J.A. Fontaine, M.D. Jimenez, W.G. Brewster, and C.C. Niemeyer. 1995. Control of Endangered Gray Wolves in Montana. Pages 127-134 in L.N.Carbyn, S.H. Fritts, D.R. Seip. eds. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute.. Occasional Publication Number 35, Univ. Alberta, Edmonton.

Bass, R. 1992. *The Ninemile Wolves*. Ballantine Books, New York.

Boitani, L., F. Corsi, and E. Dupre. 1997. *Large Scale Approach to Distribution Mapping: The Wolf in the Italian Peninsula*. Oral Presentation, 1997 Annual Meeting for the Society for Conservation Biology, Victoria, Canada.

Boyce, M.S. 1995. Anticipating consequences of Wolves in Yellowstone: Model Validation. Pages 199-210 in L.N. Carbyn, S.H. Fritts, and R.R, Seip, eds. *Ecology and*

Conservation of Wolves in a Changing World. Canadian Circumpolar Institute, University of Alberta, Edmonton Alberta.

Boyd-Hedger, D.K. 1997. *Dispersal, Genetic Relationships, and Landscape Use by Colonizing Wolves in the Central Rocky Mountains*. Ph.D. Thesis. University of Montana, Missoula, Mt. 184 pp.

Carroll, C., P. Paquet, R. Noss, and J. Strittholt. (Draft 1998) *Modeling Carnivore Habitat in the Rocky Mountain Region: A Literature Review and Suggested Strategy*.

Corsi, F., E. Dupre, and L. Boitani. 1999. A Large-Scale Model of Wolf Distribution in Italy for Conservation Planning. *Conservation Biology* 13:1, 150-159

Cowan, I. M. 1947. The Timber Wolf in the Rocky Mountain National Parks of Canada. *Canadian Journal of Research*. 25:139-174

Donovan, L. M, D.L. Rabe et al. 1987. Use of Geographic Information systems to Develop Habitat Suitability Models. *Wildlife Society Bulletin* 15:574-579.

Fritts, S.H., and L.D. Mech. 1981. Dynamics, Movements, and Feeding Ecology of a Newly Protected Wolf Population in Northwestern Minnesota. *Wildlife Monographs* 80. 79pp.

Fritts, S.H., L.N. Carbyn. 1995. Population viability, Nature Reserves, and the Outlook for Gray Wolf Conservation in North America. *Restoration Ecology* 3:26-38.

Fritts, S.H., E.E. Bangs, J.A. Fontaine, W.G. Brewster, J.F. Gore. 1995. Restoring the Wolf to the Northern Rocky Mountains of the United States. Pages 107-125 in L.N.

Carbyn, S.H. Fritts, D.R. Seip. Eds. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute. Occasional Publication Number 35, University of Alberta, Edmonton.

Fuller, T. K. 1989. Population Dynamics of Wolves in North-Centeral Minnesota. *Wildlife Monographs*. 105:1-41.

Fuller, T.K., W.E. Berg, G.L. Radde, M.S. Lanarz, and G.B. Joselyn. 1992. A History and Current Estimate of Wolf Distribution and Numbers in Minnesota. *Wildlife Society Bulletin* 20:42-55

Haight, R.G., D.J. Mladenoff, and A.P. Wydeven. 1998. Modeling Disjunct Gray Wolf Populations in Semi-Wild Landscapes. *Conservation Biology* 12:(4) 879-888.

Hayes, R.D., and J.R. Gunson. 1995. Status and Management of Wolves in Canada. Pages 21-33 in L.N. Carbyn, S.H. Fritts, and D.R. Seip, Eds. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Marston, R.A., J.E. Anderson. 1991. Watersheds and Vegetation of the Greater Yellowstone Ecosystem. *Conservation Biology*. 5(3):338-346.

Maughan, R. 1999. *Ralph Maughan's Wildlife Reports*. http://www.forwolves.org/ralph/

Mech, L. D. 1970. *The Wolf: The Ecology and Behavior of an Endangered Species*. Natural History Press, Garden City, New York

Mech, L. D. 1995. The Challenge and Opportunity of Recovering Wolf Populations. *Conservation Biology* 9(2):270-278.

Mech, L. D. 1989. Wolf Population Survival in an Area of High Road Density. *American Midland Naturalist*. 121:387-389.

Mech, L. D., S.H. Fritts, G.L. Radde, W.J. Paul. 1988. Wolf Distribution and Road Density in Minnesota. *Wildlife Society Bulletin* 16(1)

Mech, L. D., L.G. Adams, T.J. Meier, J.W. Burch, B.W. Dale. 1998. *The Wolves of Denali*. University of Minnesota Press, Minneapolis.

Mladenoff, D.J., T.A. Sickley, R.G. Haight, A.P. Wydeven. 1995. A regional Landscape Analysis and Prediction of Favorable Gray Wolf Habitat in the Northern Great Lakes Region. *Conservation Biology*. 9(2):279-294.

Mladenoff, D.J., R.G. Haight, T.A. Sickley, and A.P. Wydeven. 1997. Causes and Implications of Species Restoration in Altered Ecosystems: A Spatial Landscape Projection of Wolf Population Recovery. *Bioscience*. 47:21-31.

Mladenoff, D.J., 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):1-10pp

Morrison, M.L., B.G. Marcot, R.W. Mannan. 1998. *Wildlife Habitat Relationships: Concepts and Applications*. University of Wisconsin Press.

Noss, R.F., H.B. Quigley, M.G. Hornocker, T. Merill, and P.C. Paquet. 1996. Conservation Biology and Carnivore Conservation in the Rocky Mountains. *Conservation Biology* 10:949-963.

Nowak, R.M. 1983. A Perspective on the Taxonomy of Wolves in North America. Pages 10-19 in *Wolves in Canada and Alaska: their status biology and management*. L.N. Carbyn. editors. Canadian Wildlife Service. Rep. Ser. No. 45, Ottawa.

Paquet, P.C., J. Wierzchowski, and C. Callaghan. 1997. *Assessing Reserve Designs Using a Predictive Habitat Suitability and Movement Model*. Oral Presentation, 1997 Annual Meeting of the Society for Conservation Biology, Victoria, Canada.

Peterson, R O. 1998. *Ecological Studies of Wolves on Isle Royal, Annual Report* 1997-1998. School of Forestry and Wood Products, Michigan Technological University.

Pimlot, D.H. 1967. Wolf Predation and Ungulate Populations. *American Zoology* 7:267-278

Ream R.R., M.W. Fairchild, D.K. Boyd, and A.J. Blakensley. 1989. First Wolf Den in United States in Recent History. *Northwest Naturalist*. 70:39-40.

Smits, L. 1963. King of the Wild. *Michigan Conservation* 32(1) :45.

Thiel, R.P. 1985. Relationship Between Road Density and Wolf Habitat Suitability in Wisconsin. *American Midland. Naturalist*. 113:404.

Thompson, D.Q. 1952. Travel, Range, and Food Habits of Timber Wolves in Wisconsin. *Journal of Mammalogy* 33:429-442.

Thurber, J. M., R.O. Peterson, T.R. Drummer, S.A. Thomasma. 1994. Gray Wolf Response to Refuge Boundaries and Roads in Alaska. *Wildlife Society Bulletin*. 22:61-68.

U.S. Fish and Wildlife Service. 1987. *Northern Rocky Mountain Wolf Recovery Plan*. U.S. Fish and Wildlife Service, Denver, Co. 119pp.

U.S. Fish and Wildlife Service 2000. *Rocky Mountain Wolf Recovery 1999 Annual Report.*

Ville, N. De La, S. H. Cousins, C. Bird. 1998. Habitat Suitability Analysis Using Logistic Regression to Outline Potential Areas for Conservation of the Gray Wolf. *Innovations in GIS: Selected Papers from the Fifth National Conference on GIS Research in UK* . Steve Carter editor. Taylor and Francis Group.

Wiens , J.A.1989. Spatial Scaling in Ecology. *Functional Ecology*. 3:385-397.

Chapter 2. Examining the Impacts of Spatial Resolution on Wolf Habitat Suitability Models

2.1 Introduction

2.2 Wolf Ecology

2.1. Introduction:

Thirty wolves were reintroduced into central Idaho in 1995 and 1996, now there are over 100. The question of how to manage them, however, is still a point of conflict and an issue that remains unanswered. Identifying potential wolf habitat is an important consideration that needs to be included in management techniques so that wolves can be managed in a pro-active rather than a reactive manner. Habitat models should be created only after several important issues have been considered, including: the ecology of the species being modeled, the spatial resolution and extent of the study area, how habitat relationships may change as a function of the mapping unit used, and how the model output could help management decisions.

The purpose of this research was to consider each of these aspects, then attempt to identify the most suitable mapping unit for modeling wolf habitat in the Northern Rocky Mountains. This task was accomplished by using three different mapping units (Idaho state Game Management Units (GMU), a 33x33 km grid, and a 16x16 km grid) for analyzing landscape variables. The mapping units were statistically analyzed and compared to see if they identified the same habitat variables as important, and whether they identified similar patterns of habitat suitability. The mapping unit that produced the best results using the Idaho data was tested using out-of-sample data from Wyoming and Montana.

2.2. Wolf ecology

Wolves are social creatures that live in groups called packs, consisting of a mated pair and their offspring from one or more years (Mech 1970). When viewed individually, these packs are fairly independent units. However, when viewed at a regional scale, they appear as a mosaic of interacting sub-populations, each influencing and reacting to changes in each other and various ecological variables. Each pack has a social hierarchy, with the alpha male and alpha female (breeding pair) at the top. Below the alpha pair, the others members of the pack assert their positions into the hierarchy.

The number of individuals within a pack fluctuates greatly, though most packs do not exceed seven members (Mech 1970, Cowan 1947). Mech (1989) reported that there are four factors that influence the number of wolves in a pack: 1) the smallest number of wolves required to effectively track and kill prey, 2) the largest number of wolves that can feed on a prey animal, 3) the social attachment factor, and 4) the social competition factor. Frequently in the spring, wolves will disperse in an effort to form their own pack. Males and females are equally likely to disperse, and both sexes of wolves generally disperse when they are two or three years old (Fritts and Mech 1981, Peterson et al.1984, Fuller 1989). When dispersing, the average minimum distance traveled is 133 km, with distances up to 700 km possible (Mech et al. 1998). New packs are formed when two dispersers of opposite sex pair up and occupy a previously unoccupied region.

Each pack establishes and defends a territory that it uses for hunting and day to day travels. The size of this territory is influenced by the number of individuals in the pack and the abundance of prey (Mech 1970). Fuller (1989) noted that territory size tended to be smaller in areas where prey biomass was higher. One study in Minnesota noted that a pack of five wolves used an area that ranged from 49 to 135 sq km (Ballenberghe 1975), while another study in Minnesota reported winter pack territory sizes of 150-180 sq km (Fuller et al. 1992). The wolves in this region had an average home range of 768 sq km with Idaho, Montana, and Wyoming wolves averaging 933, 481, and 891 sq km respectively (USFWS 2000). Studies in Alaska report pack territories ranging from 600 to over 4,000 sq km (Mech et al. 1998), however, it should be noted that the wolf packs in Denali are among the largest on record.

2.3. Issues of Scale

As a result of the large pack territory size inhabited by wolves, some special consideration should be given to the possible influence of spatial scale. There are two major components of spatial analysis: the extent, and the grain size (Wiens 1989, Allen et al. 1984). The extent determines the entire area of the study, while the grain is the smallest definable subunit (mapping unit). If a mapping unit represents the average attribute value found within it, then as the mapping unit increases in size, areas with high levels of heterogeneity will be generalized and data will be lost. If the mapping unit simply designates presence or absence of an attribute, then increasing its size will increase the number of occurrences. Studies performed using fine resolution data may show greater detail about the wildlife/habitat relationships, while larger mapping units may help present larger, more general patterns. Many recent wolf modeling efforts have had success using mapping units approximately equal in size to the average pack territory size (Mladenoff 1995, 1998, De La Ville et al.1998, Boitani et al. 1997). It is also important to use the correct spatial extent so that enough information is presented to be useful. Many researchers agree that to accommodate the large area required to support a population of wolves (multiple packs), modeling efforts should also focus on a large spatial area (Noss et al. 1996, Mech 1995, Haight et al. 1998).

Using the correct mapping resolution is important, because different resolutions may show different natural processes and correlations (Wiens 1989). Sometimes the influence of resolution on habitat relationships does not follow a continuous gradient, but instead may be broken down and arranged into domains. A domain is the range of resolutions in which spatial patterns for certain phenomena either do not change, or change very little, as a result of differences in resolution. Spatial domains may be identified by investigating the variance between mapping units. Peaks of unusually high variances may indicate scales at which vegetation naturally aggregates into communities (Greig-Smith 1979). Fractal geometry is another approach that may be used to identify changes in spatial domains. Using this method, a change in the fractal pattern may signal a change in the dominant process or constraint. Since habitat correlations and dominant processes are assumed to be the same within a domain, it can also be assumed that findings at a particular scale may be extrapolated to other scales within the domain.

Scaling issues should become a critical component of ecological research and planning, because the scale at which an organism interacts with the landscape influences how it interprets landscape/habitat variation. Similarly, our ability to detect landscape/habitat variations is a function of the spatial resolution used to sample the landscape. Studies incorporating multiple scales will provide a better understanding of what processes dominate at different scales, and how organisms at different scales interact (Wiens 1989). One method to identify the optimal resolution would be to start with a coarse resolution, then progressively use finer scales until the minimum level of detail needed is identified (Carroll et al. 1998). By integrating multiple models at multiple scales the modeler may be able to produce more biologically and spatially accurate results.

2.4. Study Area

This study focused on predicting gray wolf habitat in the central and eastern portions of Idaho (Figure 1). This location was selected because it is where a total of 35 wolves were reintroduced to in 1995 and 1996, and at the end of 1999 it was inhabited by approximately

140 wolves. This area contains a wide range of topography and vegetation types making a regional summary difficult, but in general the area can be characterized as being mountainous with a semi-arid, continental climate. Precipitation varies greatly in response to elevation change, with slightly higher amounts in the winter months. These factors work together to create a landscape that is characterized by western temperate coniferous forests in the upper, wetter elevations, and sagebrush steppes in the lower, drier elevations. The region is generally sparsely populated with large tracts of remote, often roadless wilderness.

Central Idaho is dominated by a rugged mountainous region and more than 16,000 sq km of designated wilderness. This wilderness area supports over 241,000 wild ungulates including mule deer (Odocoileus hemionus), white- tailed deer (Odocoileus Virginianus), elk (Cervus elaphus), and moose (*Alces alces*) among others, not to mention the mountain lions*(Puma concolor*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*) (Bangs and Fritts 1996). This area is largely used by hunters, who harvest around 33,360 ungulates annually, and ranchers who seasonally graze more than 300,000 head of livestock on federal lands despite annual losses of approximately 12,310 cattle and 9,360 sheep (Bangs and Fritts 1996).

2.5. Methodology

For this project, three mapping units were used to identify regions of suitable habitat for the gray wolves of the northern Rocky Mountains. Idaho State Game Management Units (GMU), a 33x33 km grid, and a 16x16 km grid (Figure 2) were each used to build habitat models using four landscape variables (land cover, land ownership, road density, and elk density). The GMU's, though irregularly sized and shaped, were selected because they were pre-established units for wildlife management in Idaho, and elk population counts were available per management zone. The 33x33 km grid was selected because it was a close approximation of the average pack size in Idaho, and the 16x16 km grid

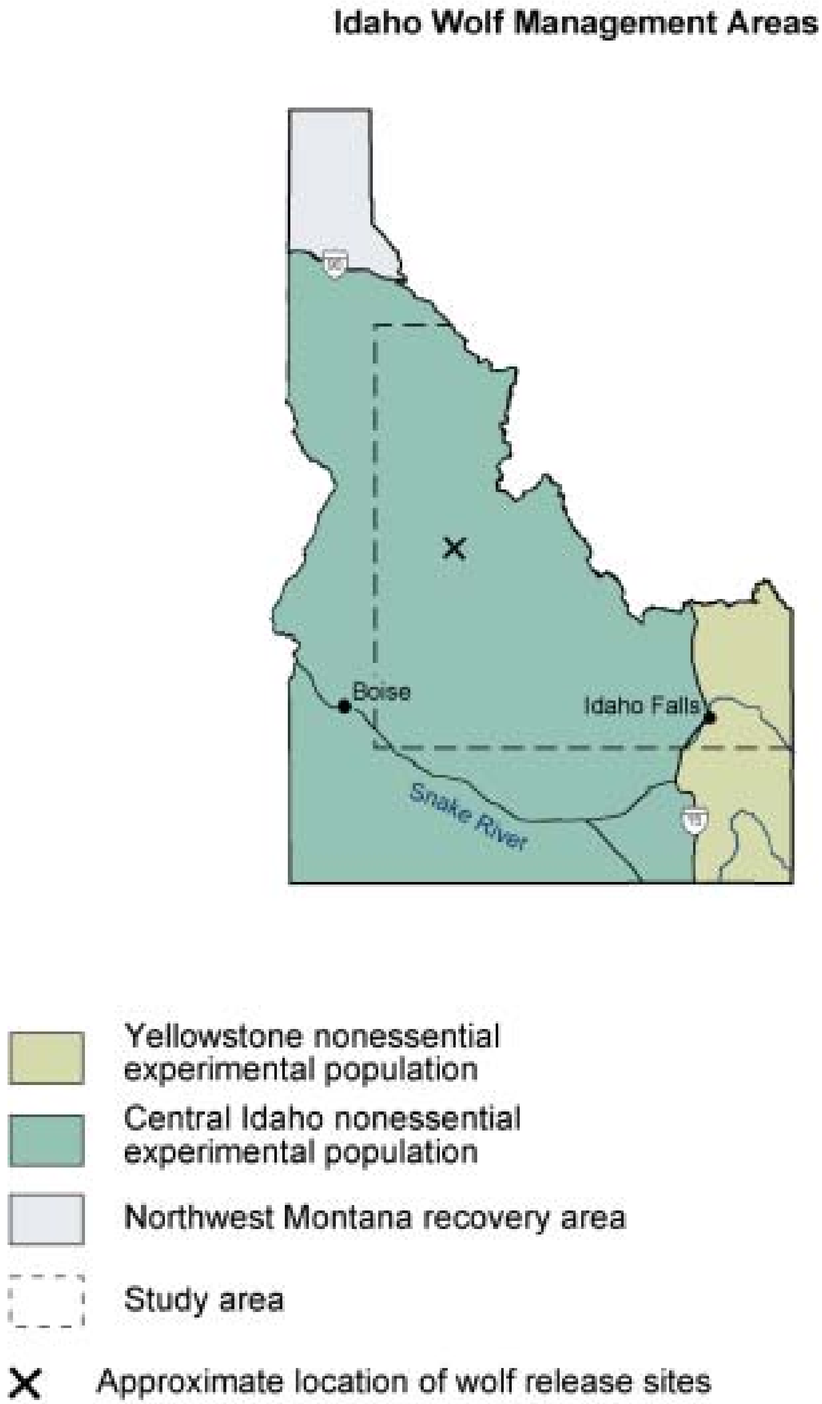

Figure 1. Map identifying the different wolf management zones that affect the reintroduction of the gray wolf as defined by the USFWS.

was created to see if a smaller mapping unit would show different habitat relations and/or different regions as preferred habitat. Both of the grid techniques provide a more uniform sampling scheme that can be more easily applied to other locations.

The data sets used for this research were obtained from a variety of sources. The land cover data were 1:250,000 scale maps developed by the United States Geological Survey (USGS) in the late 1970's. The land cover data uses the Anderson Level II classification scheme and has a minimum mapping area for non-man made features of 16 hectares. The 1:100,000 land ownership data was obtained from the Idaho Department of Water Resources and have a spatial resolution of 16 hectares. Data regarding 1998 elk populations within GMU's were obtained from the Idaho Department of Fish and Game; and road data for Idaho was downloaded from the ESRI Arc USA database.

The land cover and land ownership data was clipped to the Idaho state boundary and converted to a grid, then exported to an image file for analysis. The variables were analyzed, and the majority land cover/land owner within a mapping unit (GMU, 33x33, 16x16) identified. Elk density was calculated using a weighted mean of the number of elk per mapping unit, then divided by the area of the mapping unit.

The road data layer was first edited down to include only the class values corresponding to improved roads (roads that are passable by two wheel drive vehicles). This was done to omit roads not likely to impact wolf habitat such as logging roads, service roads, and trails that are sometimes used by wolves for travel. Next, the vector coverage of the roads was buffered to create a network of four meter wide roads. The width of four meters was chosen to represent the average road width. The total area of roads contained within each mapping unit was then calculated, which was then divided by the area of the mapping unit to produce road density.

The current wolf locations as delineated by Maughan (1999) were used as training sites for identifying suitable wolf habitat. Sampling units that intersect with a portion of a wolf pack were designated as suitable wolf habitat (1), and cells that did not intersect with known wolf packs were be labeled as unsuitable habitat (0). This method provided a reasonable measure of what constitutes suitable and/or preferred habitat

It should be remembered, however, that this is a new and expanding wolf population;

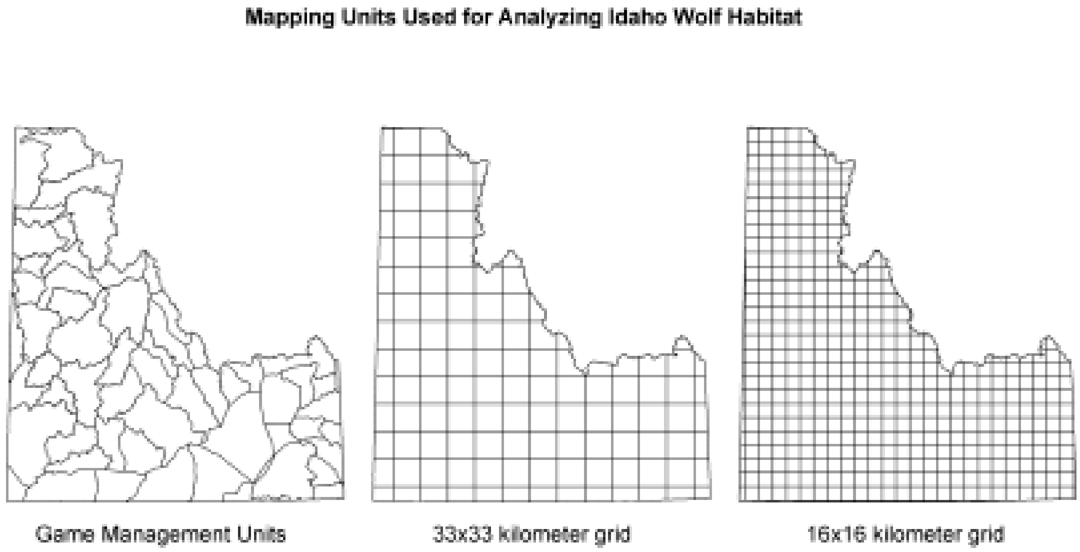

Figure 2. Three different mapping units used in the analysis of Idaho wolf habitat. The mapping unit that performed the best was validated using data from Montana and Wyoming.

therefore, the absence of wolves does not necessarily mean that the habitat is unsuitable for wolves. The resulting attribute classes in each of the sampling unit coverages were: unit number, unit area, road area, road density, majority land cover, majority owner, number of elk, elk density, and wolf presence/absence (1,0).

The data were analyzed using correlation and regression techniques to identify any differences between wolf and non-wolf grid cells. The variables were next analyzed using logistic regression to calculate the probability of each mapping unit being suitable wolf habitat. Mapping units with a probability value greater than 50% were assigned to the suitable wolf habitat class. To identify the most suitable mapping unit for modeling wolves in the Northern Rocky Mountains' the results of multiple statistical tests were compared among all three mapping units. The different mapping units were also examined to identify any differences in the importance of certain variables at different spatial resolutions, indicating the presence of spatial domains in wolf/landscape relationships. The most suitable mapping unit was identified, and used for out-of-sample validation in Montana and Wyoming.

2.6. Results

The strength of the relationship between known wolf locations and the four landscape variables is presented in Tables 1, 2, 3. Chi square analysis of the data assessed using GMU's revealed significant differences in both the land ownership and land cover characteristics between wolf and non-wolf areas. These differences were statistically significant at $p \leq 0.007$ for land cover and $p \leq 0.004$ for land ownership. When analyzed using the 33 km and the 16 km grids, the difference between land cover and land ownership characteristics in wolf and non-wolf areas was more pronounced. Using the 33 and 16 km grids, a highly significant difference in land cover and land ownership ($p \leq 0.000$) was found between wolf and non-wolf areas. A similar pattern was found when road density and elk density were analyzed using a T-test. The data mapped using the GMU's identified a statistically significant difference in road density ($p \leq 0.007$), but no significant difference in elk density was found between wolf and non-wolf areas ($p \leq 0.105$). The 33 km grid showed significant differences in both road density ($p \leq 0.000$) and elk density ($p \leq 0.004$) between wolf and non-wolf areas; while the 16 km grid identified both road density and elk density as having statistically significant differences ($p \leq 0.000$) different between wolf and non-wolf locations.

The correlation of the landscape variables with the presence of wolves showed both similarities and differences between mapping units. The 33 km grid identified road density and elk density as the two variables most correlated to wolf presence/absence with coefficients of $r = -0.47$ and 0.25, respectively. The negative relationship between wolf presence and road density indicates that as road density increases, the probability of suitable wolf habitat decreases. Conversely, the positive relationship with elk density indicates that as elk density increases, so does the probability of suitable wolf habitat. Correlations done with data at the GMU level identified road density and land cover as the most correlated variables ($r = -0.39$ and 0.30, respectively). The 16 km grid was the only mapping unit that identified elk density as the most correlated variable with a r value of 0.283; road density was the second highest correlated ($r = -0.28$).

The change in mapping resolution affected how the habitat variables were represented across the landscape, which in turn affected how suitable wolf habitat was defined. Most notably affected were road density measurements (Figure 3). The GMU's showed that the average road densities were 0.77 and 1.24 km/sq km for wolf and non-wolf mapping units, respectively. When analyzed using the slightly smaller 33 km grid, mean road densities of 0.33 and 0.69 km/sq km were found in wolf and non-wolf locations. Finally, when the average road density was calculated for wolf and non-wolf locations using the 16 km grid, values of 0.17 and 0.09 km/sq km were observed. It appears that as the mapping resolution becomes finer, the estimates of road density for wolf areas steadily decreases while the road density for non-wolf areas steadily increases. When the variables were entered into the logistic regression equation, the GMU model identified road density and land ownership as the most important variables for predicting wolf habitat suitability with an r^2 value of 0.49. The 33 km and the16 km models both used road density and land cover as the predictors of suitable wolf habitat, and had r^2 values of 0.62 and 0.41 respectively.

Table 1. Results of statistical analysis for each of the three mapping units examined.

Statistics	**GMU**	**33x33 km grid**	**16x16 km grid**
Chi square			
Land cover	.01	.00	.00
Land ownership	.00	.00	.00
t-test			
Road density	.01	.00	.00
Elk density	.11	.00	.00

Table 2. Results of correlation analysis between landscape variables and wolf presence (r).

Correlation	GMU	33x33 km grid	16x16 km grid
most correlate	road density -0.39	road density. -0.47	elk density 0.28
	land cover .030	elk density 0.25	road density -0.28
	elk density. 0.08	land cover 0.20	land cover 0.19
least correlated	landowner -0.07	landowner -0.13	landowner -0.08

Table 3. Results of regression analysis and accuracy assessment

	GMU	33x33 km grid	16x16 km grid
Variables entered into logistic regression	road density land ownership	road density land cover	road density land cover
model r^2	0.49	0.62	0.41
Accuracy			
predicted presence	38.9%	70.6%	13.8%
predicted absence	88.2%	87.4%	98.3%
overall	75.4%	83.0%	84.3%

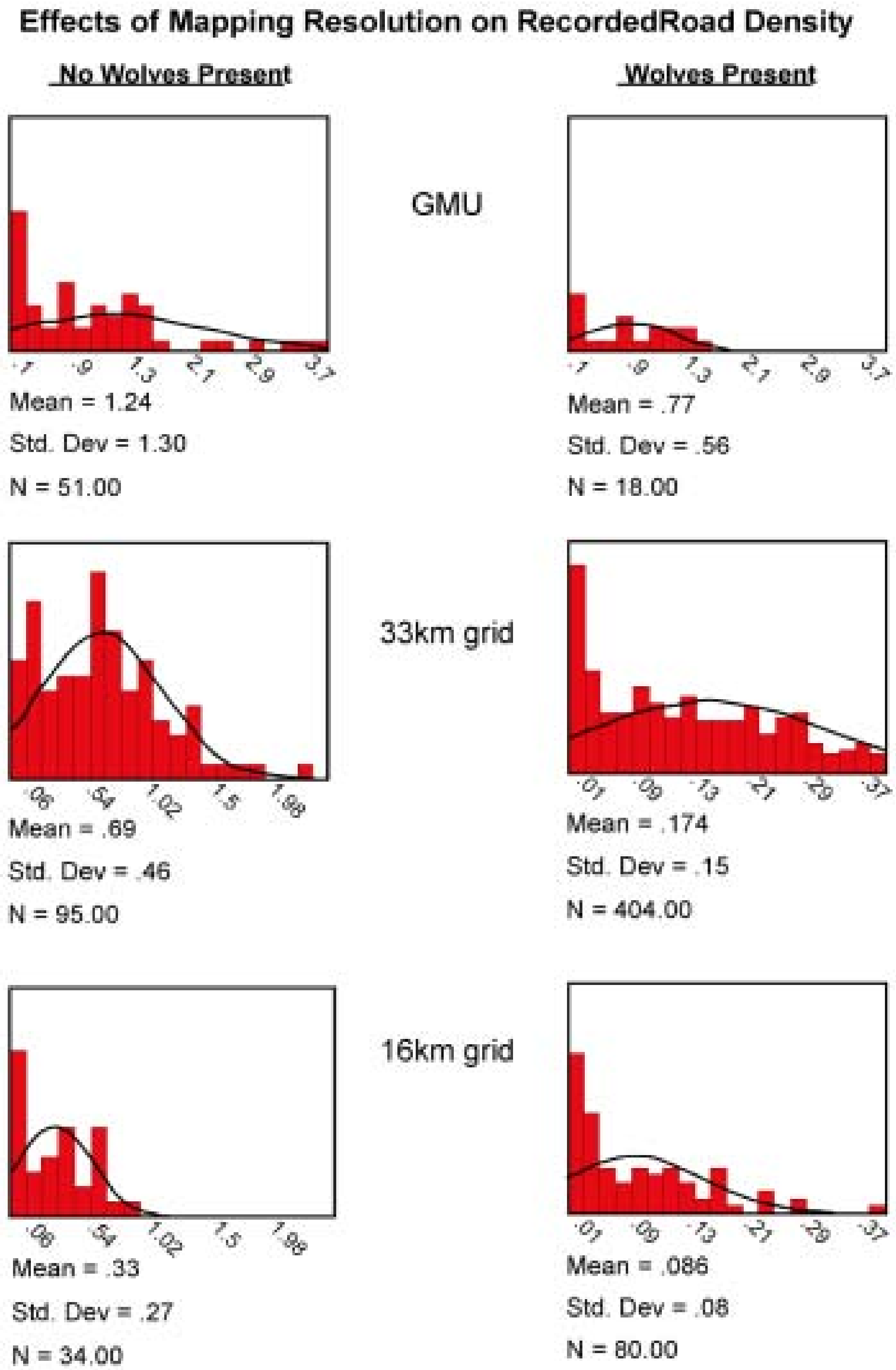

Figure 3. The resolution of the mapping unit influences the percieption of how wolves respond to road density. The GMU's (the largest mapping unit) reported the largest road density valuses for both wolf and non-wolf locations. Similarily, the 16 km grid (the smallest mapping unit) reported the lowest values for wolf and non-wolf locations

The probability values for each mapping unit were mapped and the final accuracy was assessed for each of the models using an error matrix to compare predicted presence/absence to the known presence/absence of wolves in a mapping unit (Figure 4). The 16 km grid performed the worst of the three models in terms of identifying suitable wolf habitat as defined by the presence of wolves. There were 80 mapping units that contained wolves in Idaho; however, the model only identified 18 as suitable, and only 11 of these corresponded to known wolf locations for an accuracy of 13.8%. The GMU model performed slightly better with an accuracy of 38.9%. Of the 18 GMU's containing wolves, only seven were correctly identified as suitable wolf habitat. In contrast to the other two models, the 33 km grid model did a much better job of correctly identifying current wolf locations. Of the 34 grid cells that contained wolves, the model correctly labeled 24 of them as suitable wolf habitat for an accuracy of 70.6%.

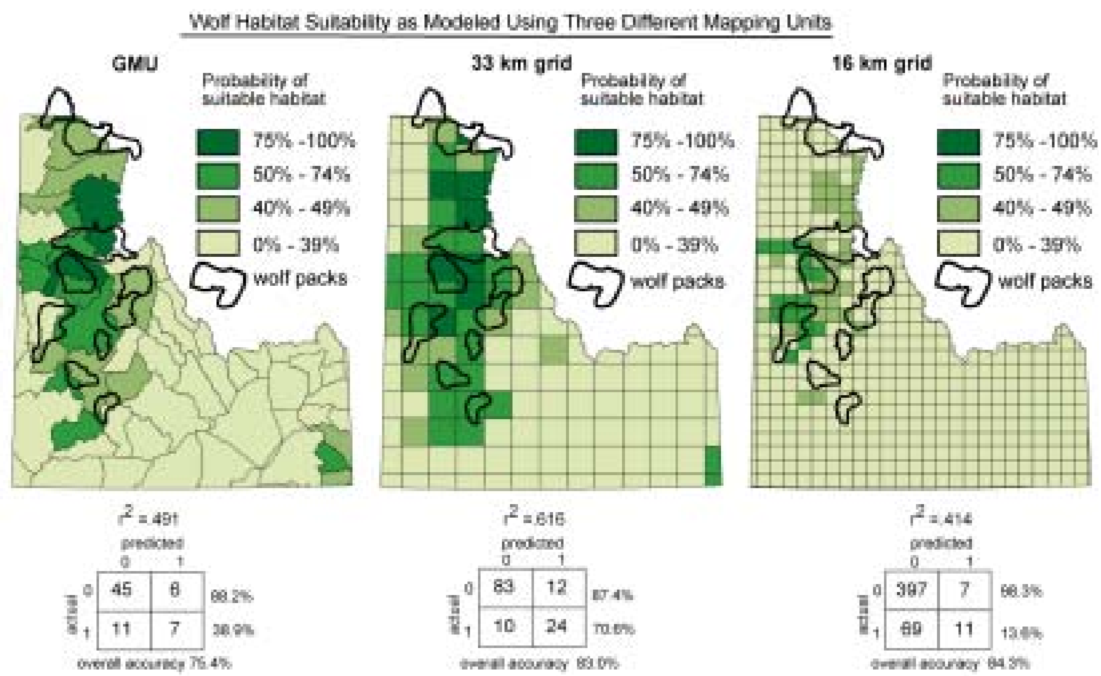

Figure 4. Predicted probability of suitable wolf habitat in Idaho using three mapping units. The 33 km grid produced the best results and was used for out of sample validation in Montana and Wyoming.

All three mapping units did a relatively good job of identifying areas of unsuitable wolf habitat. The GMU model correctly labeled as unsuitable habitat 45 of the 51 management units that did not have wolves present for an accuracy of 88.2%. The 33 km model correctly identified 83 of the 95 mapping units that did not have wolves present (87.4%), and the 16 km model had an accuracy of 98.3% for classifying areas without wolves as unsuitable habitat.

2.7. Discussion and Conclusions:

Looking at the error matrices, it appears that over-classification of unsuitable habitat was a problem for both the GMU and the 16 km model. As a result of over-predicting unsuitable habitat, the accuracy for unsuitable habitat was increased, while the accuracy of predicting suitable habitat was decreased. This issue of over-predicting did not seem to be as much of a problem for the 33 km model that achieved a balance of suitable/ unsuitable habitat prediction accuracies, with both accuracies over 70%.

An important aspect to consider when looking at a model's ability to correctly identify suitable habitat is that this is a new and expanding wolf population. The absence of wolves does not necessarily indicate unsuitable habitat. Therefore, the labeling of a mapping unit as suitable habitat when it is not currently occupied by wolves is not necessarily an incorrect classification, and may result in artificially low accuracy reports.

The large spatial area required by wolves negates the possibility of managing a wolf population in a single large reserve. A more realistic and practical method would be to use zoning to create a network of smaller reserves connected by corridors. Zoning has been found to be an effective method for managing large carnivores in areas of multiple land uses (Mech 1995, Noss and Harris 1986). Haight et al. (1998) modeled wolf population dynamics in the semi-developed landscape around Lake Superior and concluded that wolves can survive in a fragmented landscape if there are migration corridors to allow for the packs to interact with each other as population sources and sinks.

The complex landscape of the study area (multiple land use) could be divided into a matrix of sub-units, each with a particular management practice. Remote regions identified as highly suitable habitat could receive the most protection. Buffers surrounding the core area provide a larger area for the animals to live in, and serve as a gradient between areas of high and low protection. Connectivity is also a very important issue because the large area required to support a population of wolves (multiple packs) is larger than any single reserve/buffer combination. There needs to be a network of corridors that connect the core reserves to allow the sub populations to interact. By managing the landscape as a mosaic of preserves and land utilized by humans, the effective management area will be much larger than the sum of the preserves and allow for large areas to be managed as a unit, even though the area may contain conflicting land uses (Fritts and Carbyn 1995, Noss et al.1996). Perhaps the identification of habitat suitability levels throughout the region can help wildlife mangers develop a zonal management strategy to satisfy both the people that want to preserve wilderness areas and those that want to use the land for the grazing of livestock.

2.8. Literature Cited

Ballenberghe, V. V., A.W. Erickson, and D. Byman. 1975. Ecology of the Timber Wolf in Northeastern Minnesota. *Wildlife Monographs*. No 43.

Bangs, E.E., S.H. Fritts. 1996. Reintroducing the Gray Wolf to Central Idaho and Yellowstone National Park. *Wildlife Society Bulletin*. 24(3):402-413

Boitani, L., F. Corsi, and E. Dupre. 1997. *Large Scale Approach to Distribution Mapping: The Wolf in the Italian Peninsula*. Oral Presentation, 1997 Annual Meeting for the Society for Conservation Biology, Victoria, Canada.

Carroll, C., P. Paquet, R. Noss, and J. Strittholt. (Draft 1998) *Modeling Carnivore Habitat in the Rocky Mountain Region: A Literature Review and Suggested Strategy*.

Cowan, I. M. 1947. The Timber Wolf in the Rocky Mountain National Parks of Canada. *Canadian Journal of Research*. 25:139-174

Fritts, S.H., and L.D. Mech. 1981. Dynamics, Movements, and Feeding Ecology of a Newly Protected Wolf Population in Northwestern Minnesota. *Wildlife Monographs* 80. 79pp.

Fuller, T. K. 1989. Population Dynamics of Wolves in North-Centeral Minnesota. *Wildlife Monographs*. 105:1-41.

Fuller, T.K., W.E. Berg, G.L. Radde, M.S. Lanarz, and G.B. Joselyn. 1992. A History and Current Estimate of Wolf Distribution and Numbers in Minnesota. *Wildlife Society Bulletin* 20:42-55

Greig-Smith. 1979. Pattern in Vegetation. *Journal of Ecology*. 67, 755-779.

Haight, R.G., D.J. Mladenoff, and A.P. Wydeven. 1998. Modeling Disjunct Gray Wolf Populations in Semi-Wild Landscapes. *Conservation Biology* 12(4)878-888.

Marston, R.A., J.E. Anderson. 1991. Watersheds and Vegetation of the Greater Yellowstone Ecosystem. *Conservation Biology*. 5(3):338-346.

Maughan, R. 1999. *Ralph Maughan's Wildlife Reports*. http://www.forwolves.org/ralph/

Mech, L. D. 1970. *The Wolf: the Ecology and Behavior of an Endangered Species*. Natural History Press, Garden City, New York

Mech, L. D. 1995. The Challenge and Opportunity of Recovering Wolf Populations. *Conservation Biology* 9(2):270-278.

Mech, L. D. 1989. Wolf Population Survival in an Area of High Road Density. *American Midland Naturalist* 121:387-389.

Mech, L. D., L.G. Adams, T.J. Meier, J.W. Burch, B.W. Dale. 1998. *The Wolves of Denali.* University of Minnesota Press, Minneapolis.

Mladenoff, D.J., T.A. Sickley, R.G. Haight, A.P. Wydeven. 1995. A regional Landscape Analysis and Prediction of Favorable Gray Wolf Habitat in the Northern Great Lakes Region. *Conservation Biology*. 9(2):279-294.

Mladenoff, D.J., 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):1-10pp

Noss, R.F., H.B. Quigley, M.G. Hornocker, T. Merill, and P.C. Paquet. 1996. Conservation Biology and Carnivore Conservation in the Rocky Mountains. *Conservation Biology* 10:949-963.

Paquet, P.C., J. Wierzchowski, and C. Callaghan. 1997. *Assessing reserve Designs Using a Predictive Hjabitat Suitability and Movement Model*. Oral Presentation, 1997 Annual Meeting of the Society for Conservation Biology, Victoria, Canada.

Peterson, R.O. 1998. *Ecological Studies of Wolves on Isle Royal, Annual Report 1997-1998.* School of Forestry and wood Products, Michigan Technological University.

Peterson, R.O., J.D. Woolington, T.N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs*. 88:52p.

U.S. Fish and Wildlife Service 2000. *Rocky Mountain Wolf Recovery 1999 Annual Report*.

Ville, N. De La, S. H. Cousins, C. Bird. 1998. Habitat Suitability Analysis Using Logistic Regression to Outline Potential Areas for Conservation of the Gray Wolf. *Innovations in GIS: Selected Papers from the Fifth National Conference on GIS Research in UK* . Steve Carter editor. Taylor and Francis Group.

Wiens , J.A.1989. Spatial Scaling in Ecology. *Functional Ecology*. 3:385-397.

Chapter 3. Using Logistic Regression to Model Wolf Habitat Suitability in the Northern Rocky Mountains

3.1. Introduction

The gray wolf (*Canis lupus*) historically inhabited most of North America (Mech 1970) until pioneers and later the federal government systematically exterminated the species. By the 1930s, there were no permanent wolf populations remaining in the western United States. There were, however, some long-range dispersers from Canada that were occasionally killed in the northern Rocky Mountains (Nowak 1983). In the late 1980s as wolves slowly moved south into northwestern Montana there were incidents of livestock depredation that forced intensive management strategies (Bangs 1991, Bangs et al. 1995, Fritts et al. 1995). This was the beginning of a still continuing debate over the reintroduction of gray wolves into the western United States. In 1995 and 1996, after more than a decade of work, 35 wolves were released into central Idaho and 31 wolves were released into Yellowstone National Park (Bangs and Fritts 1996). No wolves were released into Montana because wolves were already colonizing the area through natural dispersal from Canada. The wolves quickly adapted to their new locations and have prospered to a total population of 115-120 wolves in the Yellowstone area, as well as 145-150 wolves in Idaho and about 65 wolves in Montana (Table 1) (USFWS 2000).

This research was designed to assist in the management of the re-colonizing wolves by using logistic regression to analyze land cover, land ownership, road density, and prey density as they relate to the presence/absence of wolves. The resulting output maps relate the probability of suitable wolf habitat per mapping unit as defined by data from the present wolf locations in Idaho. The regression coefficients from the Idaho model was then tested using out-of-sample data from Wyoming and Montana. These habitat suitability maps will make it easier to locate the areas that will likely be inhabited by wolves, areas where wolf/human conflicts are likely to occur, and areas that should be preserved as wilderness and essential wolf habitat.

Table 1. Minimum Fall Wolf Populations for Northern Rocky Mountain States (1979-1999). From USFWS 2000.

Year	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99
NW Montana	2	1	2	8	6	6	13	15	10	14	12	33	29	41	55	48	66	70	56	49	63
Yellowstone*																	21	40	86	112	118
Central Idaho*																	14	42	71	114	141
Total	2	1	2	8	6	6	13	15	10	14	12	33	29	41	55	48	101	152	213	275	322

* No wolves were present in central Idaho or Yellowstone prior to 1995.

3.2. Ecology

Wolves are social creatures that live in packs consisting of a mated pair and their offspring from one or more years (Mech 1970). When viewed individually, these packs are fairly independent units. When viewed at a regional scale, however, they appear as a mosaic of interacting sub-populations, each influencing and reacting to changes in each other and other ecological variables. The number of individuals within a pack fluctuates greatly, though most packs do not exceed seven members (Mech 1970, Cowan 1947). Frequently in the spring, wolves will disperse in an effort to form their own pack. Males and females are equally likely to disperse, and both sexes of wolves generally disperse when they are two or three years old (Fritts and Mech 1981, Peterson et al.1984, Fuller 1989). When dispersing, the average minimum distance traveled is 133 km, with distances up to 700 km possible (Mech et al. 1998). New packs are formed when two dispersers of opposite sex pair up and occupy a previously unoccupied region.

Each pack establishes and defends a territory that it uses for hunting and day-to-day travels. The size of this territory is influenced by the number of individuals in the pack and the abundance of prey (Mech 1970). Fuller (1989) noted that territory size tended to be smaller in areas where prey biomass was higher. One study in Minnesota noted that a pack of five wolves used an area that ranged from 49 to 135 sq km (Ballenberghe 1975), while another study in Minnesota reported winter pack territory sizes of 150-180 sq km (Fuller et al. 1992). Studies in Alaska report pack territories ranging from 600 to over 4,000 sq km (Mech et al. 1998), however, it should be noted that the wolf packs in Denali are among the largest on record.

When discussing how wolves interact with humans, there are four issues that are usually mentioned, including the possible predation of humans by wolves, competition for game animals, competition for livestock, and persecution of wolves by humans. Most accounts of wolves attacking humans cannot be traced back to any reliable source; they are usually hearsay accounts based on rumor and fear. Lee Smits (1963) investigated many of the claims of wolf attacks and concluded that there has never been a case of a non-rabid wolf deliberately attacking a human in North America. In fact, there is much more evidence supporting the claim that wolves are harmless to humans as demonstrated through the interactions of wolves and wolf researchers. According to Mech (1970) one researcher (Mure) entered a wolf den while the parents were nearby and stole one of the pups while the other wolves stood nearby barking and whining. Another researcher (Parmelee) also abducted a pup from its den and was followed, but never threatened, by the other wolves all the way back to his camp.

The debate over whether wolves severely damage game populations has been a controversial topic in many areas, especially Minnesota, which, prior to the reintroduction of wolves into Idaho and the Greater Yellowstone Ecosystem (GYE), held the only substantial wolf population in the contiguous United States. In Minnesota, a study compared hunter success rates for a region heavily populated by wolves to success rates in adjoining counties with very few wolves. The results showed that there was no difference in hunter success rates in wolf versus non-wolf areas, and therefore wolves could not be considered serious competitors for game species (Mech 1970).

Livestock depredation is a serious issue for areas where wolves and livestock live in close proximity and/or occupy similar habitats. This is especially true for the Rocky Mountain wolf recovery region, specifically Idaho, Montana and Wyoming. Montana has approximately 65% of the state used for agricultural lands which contain about 453,500 cattle and 58,420 sheep (Bangs et al. 1995). The total number of livestock depredations that were reported to Animal Damage Control (ADC) in Montana between 1986 and 1991 show that only a very small portion (0.70 %) of livestock deaths were actually caused by wolves (Bangs et al. 1995). Of the 138 cows and 2,394 sheep killed in Western Montana, only 4 cows and 2 sheep were killed by wolves; the remaining depredations were caused by other predators such as coyotes, mountain lions, foxes, and bears. The Annual Rocky Mountain Wolf Report (USFWS 2000) provided summary statistics for all the wolf depredation, wolf control, and financial compensation that occurred in each of the three wolf recovery states. The data indicate that in the three states combined, since 1987, wolves have killed 116 cattle, 276 sheep, and 26 dogs. In response to these depredations, 64 wolves have been killed, 83 captured and relocated, and a total of $95,711.00 has been paid out in livestock compensation to ranchers (Table 2).

Table 2. Livestock depredation/compensation and wolf control records.
(from USFWS 2000)

Idaho

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	Total
cattle									0	4	1	10	16	31
sheep									0	24	29	5	57	115
dog									0	0	4	0	5	9
other livestock									0	0	0	0	0	0
$ paid *									0	5185	3761	6855	1787	33688
wolves moved									0	5	0	3	15	23
wolves killed									0	1	1	0	6	8

Wyoming

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	Total
cattle									0	0	5	3	4	12
sheep									0	13	67	7	13	100
dog									1	0	0	4	6	11
other livestock									0	0	0	1	1	2
$ paid *									0	1221	17644	2050	6310	27225
wolves moved									6	8	14	0	0	28
wolves killed									0	1	6	3	9	19

Montana

	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	Total
cattle	6	0	3	5	2	1	0	6	3	9	16	9	13	73
sheep	10	0	0	0	2	0	0	0	0	0	30	0	19	61
dog	0	0	0	1	0	0	0	0	2	1	0	0	2	6
other livestock	0	0	0	0	0	0	0	0	0	0	0	0	0	0
$ paid *	3049	0	1730	3700	1250	374	0	1772	1633	1486	10877	1675	7253	34798
wolves moved	0	0	4	4	3	0	0	2	2	10	7	0	4	32
wolves killed	4	0	1	1	0	0	0	0	0	4	14	4	9	37

* Compensation paid by Defenders of Wildlife

Human actions can have a detrimental impact on wolf populations. In the past, wolves were completely exterminated from most of their original territory through the use of hunting, trapping, and poisoning for bounty and/or sport. In fact, even though there is no legal harvesting in the conterminous states, humans were responsible for 72% of the wolf mortality in western Montana between 1985 and 1992 (Bangs et al. 1995). Since wolves were released into Yellowstone National Park, approximately 73 wolves have died, with 15-20 of these deaths being illegally or accidently caused by humans, and another 11 wolves were legally killed by humans for control purposes (Maughan 1999). Wolves are resilient and adaptable creatures that can survive in a wide variety of habitats; in fact, it appears that it may be human tolerance of wolves, rather than habitat suitability that limits where wolves can colonize.

3.3. Response to landscape variables

There have been numerous studies that relate how wolves respond to their environment in terms of habitat selection. Human activities have been shown to influence the distribution and survival of wolves (Theil 1985, Fuller et al. 1992, Mladenoff et al. 1995). Wolves were found to occur more often in areas with a less than 1.54 humans per square km (Mladenoff et al. 1995). In Minnesota, 88% of wolves were found in townships that had less than 4 humans per square km (Fuller et al. 1992). The absence of wolves from areas with high levels of human activity may be the result of increased mortality rates and/or simply a behavioral avoidance (Carroll et al. 1998).

Roads have been used as an effective measurement of human activity in an area, and can therefore be used to identify suitable habitat. Roads, by increasing human contact, have been documented to negatively affect wolf populations at both local and regional scales (Fuller 1989, Thurber et al. 1994, Mladenoff et al. 1995,1997, Mech 1989, Mech 1995, Mech et al. 1988). The mean road density in areas occupied by wolves is generally lower than in areas not occupied by wolves. Wolves were generally absent from areas with a road density greater than 0.58km/km^2 (Theil 1985); however, there were exceptions when these areas were located adjacent to a large roadless area (Mech 1989). Similarly, studies in Wisconsin showed that wolves were concentrated in areas with a mean road density of less than 0.23 km/sq km, and tolerated areas as high as 0.45 km/sq km, as opposed to a mean road density of 0.74 km from random non-pack areas (Mladenoff et al.1995).

Land ownership is another factor that influences habitat selection, as wolves occur much more frequently on public lands than private (Mladenoff et al. 1995). This preference is probably because public lands generally have lower levels of human disturbance, while private property is often more developed and less accommodating for wolves. Habitat selection is not based solely on avoiding humans; studies indicate wolves also respond to natural landscape variables such as vegetation type and prey density. In Minnesota, wolves' territories had a higher proportion of conifer and conifer mixed woodlands than non-wolf areas. Similarly, occupied areas had lower percentages of agricultural and deciduous forest than occupied land (Mladenoff et al. 1995). Some studies suggest that the main limiting factor for wolves, after human tolerance, is prey availability (Fuller et al. 1992). Other studies, however, have found little to no difference in prey densities in wolf and non-wolf areas (Mladenoff et al. 1995, 1997).

3.4. Past Modeling Approaches

In recent years there have been many advances in wildlife modeling techniques, including the use of multivariate analysis, and the enlargement of study areas to broader spatial scales to recognize regional characteristics (Morrison et al. 1998). Logistic regression is a non-parametric, non-linear technique for analyzing independent variables (categorical and continuous data) to predict the probability of a dependent variable. It has been used by numerous researchers for modeling wildlife habitat. Mladenoff et al. (1995, 1997, 1998) successfully used logistic regression with a 150 sq km mapping unit (mean pack territory size) to model wolf habitat suitability in the Great Lakes region of the United States. His results indicated that wolves in this region favored mixed conifer forests and wetland forests over agriculture and deciduous forests, public lands to private property, and low road densities ($<0.45 km/km^2$). His results also indicated that was no difference in deer densities when pack and non-pack areas were compared. Boyd-Heger (1997) created a logistic regression model using elevation, slope, and distance to roads to predict areas of possible colonization. Another study done by De la Vile et al. (1998) used a 100 sq km mapping unit to identify suitable wolf habitat across Greenland and North America (except Florida). His model found that suitable habitat was characterized by low amounts of human disturbance (roads, agriculture) and areas with greater that 40% herbaceous and woody cover. Morrison et al. (1998) stated that logistic regression models may be more robust than parametric procedures, and have better classification success than discriminant analysis techniques.

3.5. Suggested Modeling Approaches

The effectiveness of a model is directly related to the modelers ability to identify and generalize the habitat requirements of a species so they can be entered into the model (Donovan et al. 1987). Theoretical models such as the Habitat Suitability Index, which use qualitative generalizations don’t always work for wide ranging carnivores (Carroll et al.1998). Future modeling attempts should be based on empirical models built from extensive GIS and remote sensing data sets enabling researchers to examine large (regional) areas (Carroll et al. 1998). There is a growing consensus that to accommodate the large area required to support a population of wolves (multiple packs), modeling efforts should focus on a large spatial area (Noss et al. 1996, Mech 1995, Mladenoff 1997, Haight et al. 1998).

In addition to examining a large study area, a map-based conservation plan may help facilitate human-wolf coexistence by identifying areas where human development trends may create potential conflicts with wolves (Mladenoff et al. 1995, Mladenoff et al. 1997). To make the most of highly fragmented and complex landscapes, it is becoming increasingly important to develop zonal management policies based on multiple land uses. By managing the landscape as a mosaic of preserves and non-protected land, the effective management area will be much larger than the sum of the preserves (Fritts and Carbyn 1995).

3.6. Study Area

This study focuses on predicting wolf habitat in Northern Rocky Mountains, specifically, the Idaho, Montana, Wyoming tri-state area (Figure 1). This area contains a wide range of topography and vegetation types, making a regional summary difficult, but in general the area can be characterized as being mountainous with a semi-arid, continental climate. Precipitation varies greatly in response to elevation change, ranging from 30-122 centimeters (12 to 48 inches) annually (Marston 1991), with slightly higher amounts in the winter months. These physical factors work together to create a landscape that is characterized by western temperate coniferous forests in the upper, wetter, elevations, and sagebrush steppes in the lower, drier, elevations. The region is generally sparsely populated with large tracts of remote, often roadless wilderness.

Central Idaho is dominated by a rugged mountainous region and more than 16,000 sq km of designated wilderness. This wilderness area supports over 241,000 wild ungulates including mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus Virginianus*) , elk (*Cervus elaphus*), and moose (*Alces alces*), among others, not to mention the mountain lions *(Puma concolor*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*) (Bangs and Fritts 1996). This area is widely used by hunters, who harvest around 33,360 ungulates annually, and ranchers, who seasonally graze more than 300,000 head of livestock on federal lands despite annual losses of approximately 12,310 cattle and 9,360 sheep (Bangs and Fritts 1996).

The southeastern portion of the study area includes the Greater Yellowstone Ecosystem (GYE). This area, as defined by Marston (1991), is the Yellowstone Plateau and the areas above 2,130 meters (7,000 feet) ft. in the surrounding 14 mountain ranges. Vegetation in the area is heavily influenced by the effects of elevation on temperature and precipitation.

Wolf Management Areas

This effect stratifies the region into communities that include, from lowest to highest elevation: grassland and shrubland, low elevation forests, middle elevation forests, and upper elevation forests. In the lowest elevations, grasses include wheatgrasses from the genus *Agropyron*, needlegrasses from the genus *Stipa*, Idaho fescue (*Festuca idahoensis*), and various bluegrasses from the genus *Poa*, among others. Shrub steppes are commonly dominated by big sagebrush *(Artemisia tridentata*), with other species such as threetip sagebrush (*Artemisia tripartita*) and rabbitbrush (*Chrysothamnus*) frequently occurring. The lower elevation forests are largely comprised of Douglas fir (*Pseudotsuga menziesii*) which give way to extensive lodgepole pine (*Pinus contorta*) forests in the middle elevations. As elevation continues to increase, the lodgepole pine communities become intermixed with subalpine forest species such as the Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and whitebark pine (*Pinus albicaulis*).

3.7. Methodology

Three mapping units were initially used to model wolf habitat in Idaho in an attempt to identify the best mapping resolution for modeling wolf habitat. The results of that study concluded that a 33km grid functioned best for modeling wolf habitat in the Northern Rocky Mountains. As a result, a 33x33 km grid was used in this study to extract data regarding each of the four landscape variables (Figure 2). The land cover and land ownership data were clipped to the Idaho state boundary and converted to a grid, then exported to an image file for analysis. The variables were analyzed and the majority land cover/land owner within a mapping unit identified. Elk density was calculated using a weighted mean of the number of elk per mapping unit, then divided by the area of the mapping unit.

The road data were first edited to include only the class values corresponding to improved roads, roads that are passable by two wheel drive vehicles. This was done to omit roads not likely to impact wolf habitat such as logging roads, service roads, and trails. Next, the vector coverage of the roads was buffered to create a network of four meter wide roads. The width of four meters was chosen to represent the average road width. The total area of roads contained within each mapping unit was then calculated, which was then divided by the area of the mapping unit to produce road density.

33 Kilometer Grid

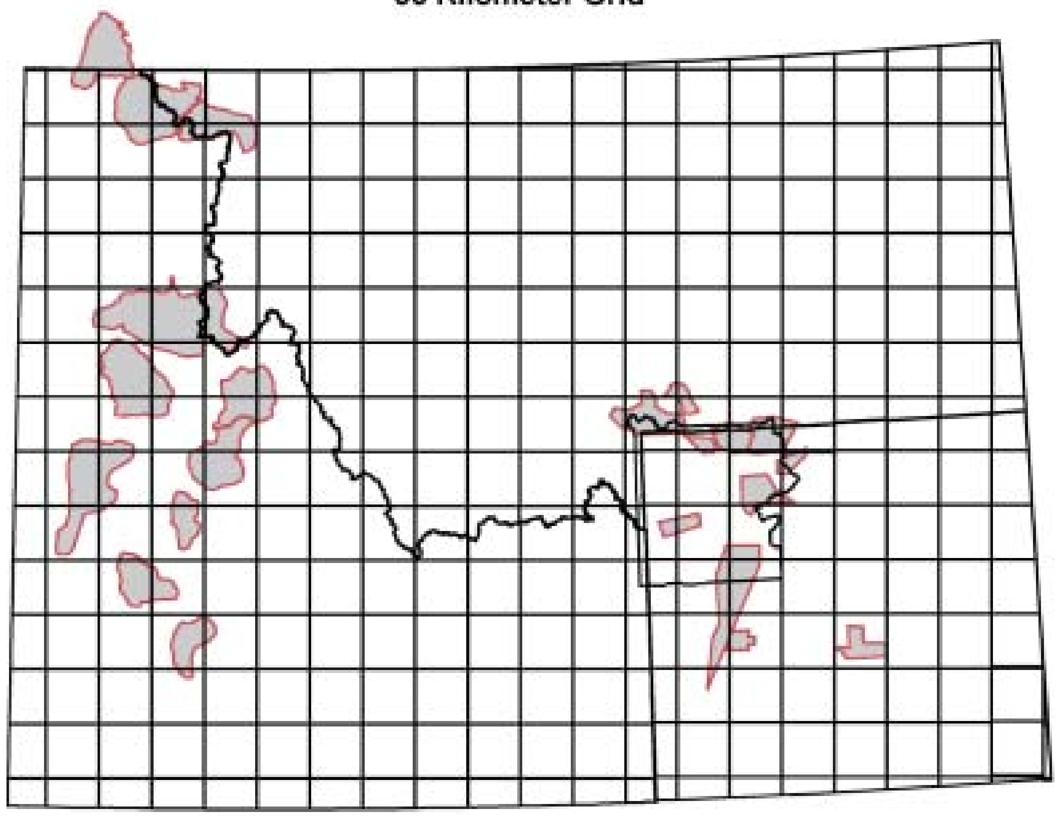

Figure 2. Map showing the 33 kilometer grid over the portions of Idaho, Montana, and Wyoming included in this study and known wolf pack territories

The current wolf locations as delineated by Maughan (1999) were used as training sites for identifying suitable wolf habitat. Sampling units that intersect with a portion of a wolf pack territory were designated as suitable wolf habitat (1), and cells that did not intersect with known wolf packs were labeled as unsuitable habitat (0). This method provided a reasonable measure of what constitutes suitable and/or preferred habitat It should be remembered, however, that this is a new and expanding wolf population; therefore, the absence of wolves does not necessarily mean that the habitat is unsuitable for wolves. The resulting attribute classes in each of the sampling unit coverages were: unit number, unit area, road area, road density, majority land cover, majority owner, number of elk, elk density, and wolf presence (1) or absence (0).

The data extracted from the GIS coverages were statistically analyzed and tested for significant differences between wolf and non-wolf locations. A t-test was performed to identify differences in road density and elk density, and a chi square test was performed to identify differences in land cover and land ownership. All statistical tests were performed using an alpha value of 0.05. The four landscape variables were then entered into a logistic regression model in a forward step-wise manner with a minimum significance value of .05 to enter and a minimum of .1 to exit the model. Predicted probabilities greater than or equal to 0.5 were identified as potential wolf habitat.

Classification accuracy was assessed using an error matrix to compare mapping units identified as suitable habitat to mapping units known to contain wolves. After this initial modeling of Idaho, the model was tested using out-of-sample data from Montana and Wyoming. The 33 km grid was applied to land cover data from Montana and Wyoming, and road density and majority land cover were calculated as described earlier. The resulting data per mapping unit were entered into the Idaho logistic regression equation using the equation: prob=((1)/(1+e $^{-z}$)). The resulting probability values were examined and values >.5 were classified as suitable wolf habitat. As before, the accuracy for each state was assessed using an error matrix to compare habitat suitability to known wolf locations. The three wolf habitat probability maps (Idaho, Montana, Wyoming) were joined to examine the regional pattern of predicted wolf habitat suitability.

3.8. Results

Statistical analysis of land cover and road density for all three states showed very similar patterns (Table 3). Chi square analysis of the land cover and land ownership variables showed a significant difference between wolf and non-wolf area ($p \leq 0.000$). Wolf locations were dominated by coniferous or coniferous/deciduous mix forests owned by either the state or national government. Similarly, when a t-test was applied to road density and elk density data, it was found that there was a significant difference between wolf and non-wolf areas ($p \leq 0.000$ and $p \leq 0.004$, respectively). Wolves occurred in areas with low road density (generally less than 0.45km/sq km), and areas with higher elk density.

Table 3. Results of statistical and regression analysis for each of the three states examined.

Statistics	Idaho	Montana	Wyoming
Chi square			
Land cover	.01	.01	.00
t-test			
Road density	.01	.00	.00
Correlation			
	road density -0.47	road density -0.20	road density -0.32
	land cover 0.20	land cover 0.17	land cover 0.31
Accuracy			
predicted presence	70.6%	60.0%	93.7%
predicted absence	87.4%	91.0%	68.6%
overall	83.0%	88.9%	74.6%

When all four variables were entered into the logistic regression mode using a forward step-wise approach, road density was the first of two variables to enter, with a significance value of 0.000, and an r^2 value of 0.36. The second variable to enter the regression analysis was land cover, which entered with a significance value of 0.0001, and raised the r^2 value to 0.616. Mapping units with a probability value of greater then 0.50 were classified as suitable wolf habitat. The accuracy was assessed using a classification error matrix to provide the overall accuracy as well as information on the type of classification errors that were made. The model correctly identified 24 locations as being suitable for wolves and 83 locations as being unsuitable for wolves. There were 12 errors of commission, in which the model incorrectly identified 12 sites as suitable wolf areas when in fact there were no wolves present, and 10 errors of omission in which the model incorrectly predicted the areas as non-suitable areas when in reality there were wolves present. The overall accuracy of the Idaho model was calculated to be 83.0%.

The out-of-sample data from Montana and Wyoming were analyzed and found to show somewhat similar wolf/habitat relationships as the Idaho data. In Montana there was a significant difference in road density (p≤0.015), while there was no significant difference (p≤0.199) in land cover between wolf and non-wolf mapping units. Wyoming showed the opposite of Montana, with a significant difference in land cover (p≤0.042), but not road density (p≤0.220). Accuracy assessment using error matrices showed that the Idaho regression model performed approximately as well using out-of-sample data, with overall accuracies of 89.0% in Montana and 74.6% in Wyoming (Figure 3). Overall, 285 of the 340 mapping units were correctly classified (83.8%). Forty mapping units were incorrectly classified as suitable habitat when in reality there were no wolves currently present. Only 15 mapping units where wolves were known to occur were incorrectly classified as unsuitable habitat. Closer examination revealed that 6 of the 15 mapping units incorrectly classified as unsuitable habitat had probability values between 0.4 and 0.5, and nearly all of the incorrectly identified locations occurred at transition zones between areas classified as suitable and unsuitable habitat.

3.9. Discussion and Conclusions

The findings of this research suggest that wolf habitat can be successfully modeled

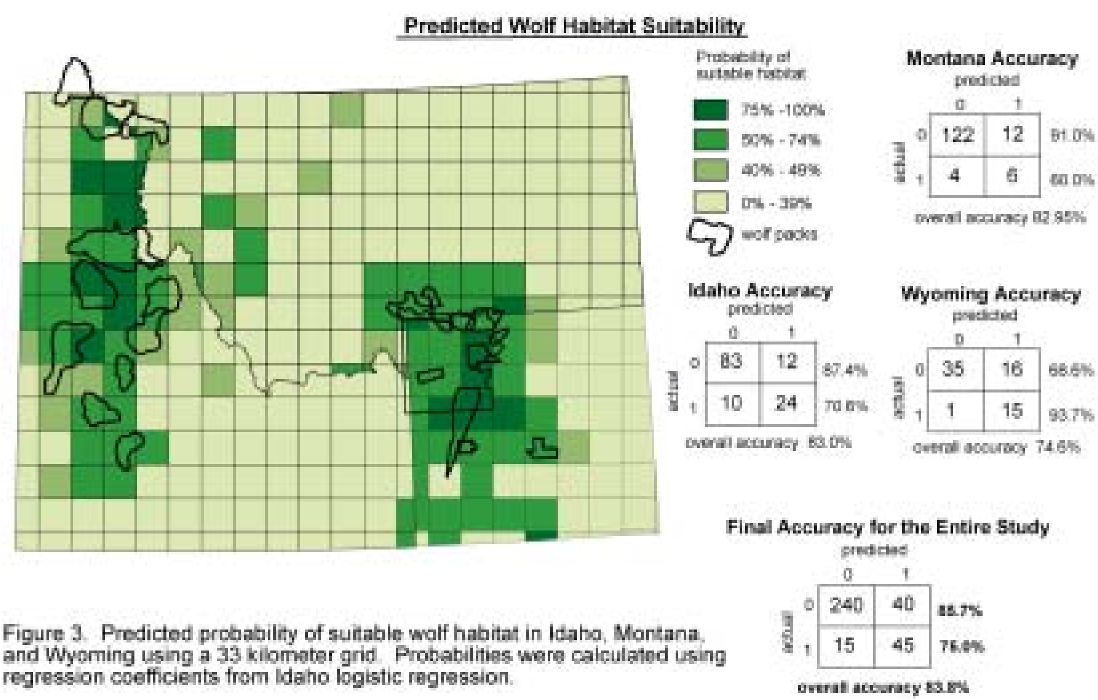

Figure 3. Predicted probability of suitable wolf habitat in Idaho, Montana, and Wyoming using a 33 kilometer grid. Probabilities were calculated using regression coefficients from Idaho logistic regression.

using road density and land cover when mapped at a resolution approximately equal to the average pack territory size. The regression formula generated using data from Idaho produced satisfactory results when applied to out-of-sample data from Montana and Wyoming. One difficulty with assessing the accuracy of these models lies in the fact that this is a new and expanding wolf population. Because of this, the absence of wolves in an area does not necessarily indicate that the area is unsuitable. As a result, errors of commission may be artificially high, thus making the overall accuracy difficult to interpret.

Identifying suitable wolf habitat is an important step in managing wolf populations throughout the region. It helps wildlife managers have a better idea of where wolves may disperse to as populations increase in the future, and may assist with the creation of management zones and pro-active planning. By identifying areas of suitable habitat, areas of potential conflict can be identified, and population sources/sinks can be considered. For example if there is a disjunct area of suitable habitat surrounded by private ranch property, this may be an area to closely monitor for conflicts. Similarly, large remote areas of highly suitable habitat may be protected to serve as a source population for neighboring areas with high mortality rates.

In general, this research showed similar habitat relationships as other studies conducted in different parts of North America. The wolves of the northern Rocky Mountains preferred publicly owned landscapes dominated by coniferous forests with low road densities and high prey densities. The similarity in results helps to reinforce the general pattern of wolf habitat selection, and suggests that there may be little difference in habitat preferences between different sub-species of wolves. This research can provide a beginning point for more in-depth and exploratory analysis into the ecology of the newly reintroduced gray wolves of the northern Rocky Mountains. Future efforts may benefit by examining landscape complexity (fragmentation) or interspecies relations. Wildlife habitat modeling has become increasingly popular as a means of monitoring and managing wildlife and landscapes. By identifying and predicting suitable wolf habitat in the northern Rocky Mountains, it is hoped that policy makers will be able to make more informed decisions.

3.10. Literature Cited

Ballenberghe, V. V., A.W. Erickson, and D. Byman. 1975. Ecology of the Timber Wolf in Northeastern Minnesota. *Wildlife Monographs*. No 43.

Bangs, E.E., S.H. Fritts. 1996. Reintroducing the Gray Wolf to Central Idaho and Yellowstone National Park. *Wildlife Society Bulletin*. 24(3):402-413

Bangs, E. 1991. Return of a Predator: Wolf Recovery in Montana. *Western Wildlands* 17:7-13.

Bangs, E., S.H. Fritts, D.R. Harms, J.A. Fontaine, M.D. Jimenez, W.G. Brewster, and C.C. Niemeyer. 1995. Control of Endangered Gray Wolves in Montana. Pages 127-134 in L.N.Carbyn, S.H. Fritts, D.R. Seip. eds. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute. Occasional Publication Number 35, University of Alberta, Edmonton.

Boyd - Hedger. 1997. *Dispersal, Genetic Relationships, and Landscape Use by Colonizing Wolves in the Central Rocky Mountains*. Ph.D. Thesis. University of Montana, Missoula, Mt. 184 pp.

Carroll, C, P. Paquet, R. Noss, and J. Strittholt. (Draft 1998) *Modeling Carnivore Habitat in the Rocky Mountain Region: A Literature Review and Suggested Strategy*.

Cowan, I. M..1947. The Timber Wolf in the Rocky Mountain National Parks of Canada. *Canadian Journal of Reeearch*. 25:139-174

Donovan, L. M, D L. Rabe et al. 1987. Use of Geographic Information systems to Develop Habitat Suitability Models. *Wildlife Society Bulletin* 15:574-579.

Fritts, S.H., and L.D. Mech. 1981. Dynamics, Movements, and Feeding Ecology of a Newly Protected Wolf Population in Northwestern Minnesota. *Wildlife Monographs* 80.

79pp.

Fritts, S.H., L.N. Carbyn. 1995. Population viability, Nature Reserves, and the Outlook for Gray Wolf Conservation in North America. *Restoration Ecology* 3:26-38.

Fritts, S.H., E.E. Bangs, J.A. Fontaine, W.G. Brewster, J.F. Gore. 1995. Restoring the Wolf to the Northern Rocky Mountains of the United States. Pages 107-125 in L.N. Carbyn, S.H. Fritts, D.R. Seip. Eds. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute Occasional Publication Number 35, University of Alberta, Edmonton.

Fuller, T. K. 1989. Population Dynamics of Wolves in North-Centeral Minnesota. *Wildlife Monographs*. 105:1-41.

Fuller, T.K., W.E. Berg, G.L. Radde, M.S. Lanarz, and G.B. Joselyn. 1992. A History and Current Estimate of Wolf Distribution and Numbers in Minnesota. *Wildlife Society Bulletin* 20:42-55

Marston, R.A., J.E. Anderson. 1991. Watersheds and Vegetation of the Greater Yellowstone Ecosystem. Conservation Biology. 5(3):338-346.

Maughan, R. 1999. *Ralph Maughan's Wildlife Reports*. http://www.forwolves.org/ralph/

Mech, L. D. 1970. *The Wolf: the Ecology and Behavior of an Endangered Species*. Natural History Press, Garden City, New York

Mech, L. D. 1995. The Challenge and Opportunity of Recovering Wolf Populations. *Conservation Biology* 9(2):270-278.

Mech, L. D. 1989. Wolf Population Survival in an Area of High Road Density. *American*

Midland Naturalist 121:387-389.

Mech, L. D., S.H. Fritts, G.L. Radde, W.J. Paul. 1988. Wolf Distribution and road Density in Minnesota. *Wildlife society Bulletin* 16(1)

Mech, L. D., L.G. Adams, T.J. Meier, J.W. Burch, B.W. Dale. 1998. *The Wolves of Denali*. University of Minnesota Press, Minneapolis.

Mladenoff, D.J., T.A. Sickley, R.G. Haight, A.P. Wydeven. 1995. A regional Landscape Analysis and Prediction of Favorable Gray Wolf Habitat in the Northern Great Lakes Region. *Conservation Biology*. 9(2):279-294.

Mladenoff, D.J., R.G. Haight, T.A. Sickley, and A.P. Wydeven. 1997. Causes and Implications of Species Restoration in Altered Ecosystems: A Spatial Landscape Projection of Wolf Population Recovery. *Bioscience*. 47:21-31.

Mladenoff, D.J., 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):1-10pp

Morrison, M.L., B.G. Marcot, R.W. Mannan. 1998. *Wildlife Habitat Relationships: Concepts and Applications*. University of Wisconsin Press.

Nowak, R.M. 1983. A perspective on the Taxonomy of Wolves in North America. Pages 10-19 in *Wolves in Canada and Alaska: their Status, Biology and Management*. L.N. Carbyn. editor. Canadian Wildlife Service. Rep. Ser. No. 45, Ottawa.

Peterson, R.O., J.D. Woolington, T.N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs*. 88:52p.

Smitts, L. 1963. King of the Wild. *Michigan Conservation*. 32(1):45.

Thiel, R.P. 1985. Relationship Between Road Density and Wolf Habitat Suitability in Wisconsin. *American Midland Naturalist*. 113:404.

Thurber, J. M., R.O. Peterson, T.R. Drummer, S.A. Thomasma. 1994. Gray Wolf Response to Refuge Boundaries and Roads in Alaska. *Wildlife Society Bulletin*. 22:61-68.

U.S. Fish and Wildlife Service 2000. *Rocky Mountain Wolf Recovery 1999 Annual Report.*

Ville, N. De La, S. H. Cousins, C. Bird. 1998. Habitat Suitability Analysis Using Logistic Regression to Outline Potential Areas for Conservation of the Gray Wolf. *Innovations in GIS: Selected Papers from the Fifth National Conference on GIS Research in UK* . Steve Carter editor. Taylor and Francis Group.

Chapter 4. Summary and Conclusions for Modeling Gray Wolf Habitat Suitability

4.1. Introduction

The gray wolf (*Canis lupus*) historically inhabited most of North America until the wolves were systematically exterminated from most of their original range through the use of hunting, trapping, and poisoning. By the 1930's, there were no permanent wolf populations remaining in the western United States (Mech 1970). In 1973, the Endangered Species Act required the federal government to use all methods and procedures necessary to restore wolves to suitable habitats. The western United States, however, did not produce a litter of wolf pups until 1986 when a pack of wolves from Canada moved south and settled in northwestern Montana (Ream et al. 1989). In the late 1980's, as wolves slowly moved south from Canada into northwestern Montana, there were incidents of livestock depredation that forced intensive management strategies to be developed (Bangs 1991, Bangs et al. 1995, Fritts et al. 1995). This was the beginning of a continuing debate over the reintroduction and management of gray wolves in the western United States.

In 1995 and 1996, after more than a decade of work, 35 wolves were released into central Idaho and 31 wolves were released into Yellowstone National Park (YNP) (Bangs and Fritts 1996). No wolves were released into Montana because wolves were already colonizing the area as a result of natural dispersal from Canada. The wolves quickly adapted to their new locations. By the end of 1999, they had prospered to a population of approximately 118 wolves in the Yellowstone area, as well as an estimated 141 wolves in Idaho, and about 63 wolves in Montana (USFWS 2000).

The question of how to manage the wolves still remains unanswered; this project was designed to assist in answering that question. A map-based conservation plan could help facilitate human-wolf co-existence by identifying areas where human development trends may create potential conflicts with wolves (Mladenoff et al. 1995, Mladenoff et al. 1997). By identifying areas of suitable wolf habitat, wildlife managers can predict where wolves may disperse to as populations continue to grow, thereby helping to manage the wolves in a pro-active rather than reactive manner.

4.2. Scale and Wolf Modeling

Wolves are social creatures that live in packs consisting of a mated pair and their offspring from one or more years (Mech 1970). When viewed individually, these packs are fairly independent units. When viewed at a regional scale, however, they appear as a mosaic of interacting sub-populations, each influencing and reacting to changes in each other and ecological variables. The number of individuals within a pack fluctuates greatly, though most packs do not exceed seven members (Mech 1970, Cowan 1947). The wolf packs in Idaho, Montana, and the Greater Yellowstone Ecosystem (GYE) are slightly larger and average 11.1, 7.1, and 9.2, wolves respectively (USFWS 2000). Each pack establishes and defends a territory of varying size that it uses for hunting and day to day travels. Mech (1970) stated that the size of a wolf pack's territory is influenced by the number of individuals in the pack and the abundance of prey. Fuller (1989) noted that territory size tended to be smaller in areas where prey biomass was higher. One study in Minnesota noted that a pack of five wolves used an area that ranged from 49 to 135 sq km (Ballenberghe 1975), while another study in Minnesota reported winter pack territory sizes of 150-180 sq km (Fuller et al 1992). Studies in Denali National Park, Alaska report pack territories ranging from 600 to over 4,000 sq km (Mech et al. 1998); however, it should be noted that the wolf packs in Denali are among the largest on record. The wolves in Idaho, Montana, and Yellowstone National Park (YNP) are reported to have average territory sizes of 933, 891, and 481 sq km, respectively (USFWS 2000).

As a result of the large area covered and the variability in territory size, special consideration should be given to identifying the optimal spatial resolution and spatial extent for modeling wolf habitat. According to Wiens (1989), there are two major components of spatial analysis: the extent, and the grain size (resolution). The extent determines the entire area of the study, while the grain is the smallest definable subunit (mapping unit) within the area. Many researchers agree that to accommodate the large area required to support a population of wolves (multiple packs), modeling efforts should focus on a large spatial area (Noss et al. 1996, Mech 1995, Haight et al. 1998). Focusing on a large spatial area will provide conservationists and policy makers with more information that allows them to develop regional management plans that include multiple states and land management practices.

In terms of identifying the optimal mapping unit resolution for modeling, the modeler should consider the implications of using different resolutions. Given that a mapping unit represents the average value for an attribute within it, as mapping unit size is increased, areas with high levels of heterogeneity will be generalized and data will be lost. If a mapping unit simply designates presence or absence of an attribute, then increasing the size of the mapping unit will increase the number of occurrences. Studies performed using fine resolution data may show greater detail about wildlife/habitat relationships, while larger mapping units may help present larger, more general patterns. Using the correct scale is important, because different scales may show different natural processes and correlations (Wiens 1989). Studies incorporating multiple scales will provide a better understanding of what process(es) dominate at different scales, and how organisms and processes at different scales interact (Wiens 1989). One method to identify the optimal resolution would be to start with a course resolution, then progressively use finer scales until the minimum level of detail needed is identified (Carroll et al. 1998). By integrating multiple models at multiple scales, the modeler may be able to produce more biologically and spatially accurate results.

4.3. Wolf Habitat Relationships

There have been numerous studies that relate how wolves respond to their environment in terms of habitat selection. Human activities have been shown to influence the distribution and survival of wolves (Theil 1985, Fuller et al. 1992, Mladenoff et al. 1995). Wolves were found to occur more often in areas with less than 1.54 humans per square km (Mladenoff et al. 1995). In Minnesota, 88% of the wolves were found in townships that had less than 4 humans per sq km (Fuller et al. 1992). The absence of wolves from areas with high levels of human activity may be the result of increased mortality rates and/or simply a behavioral avoidance (Carroll et al. 1998).

Roads have been used as an effective measurement of human activity in an area, and therefore can be used to identify suitable habitat. Roads, by increasing human contact, have been documented to negatively affect wolf populations at both local and regional scales (Fuller 1989, Thurber et al. 1994, Mladenoff et al. 1995, Mech et al. 1988). The mean road density in areas occupied by wolves is generally lower than in areas not occupied by wolves. Wolves were generally absent from areas with a road density greater than .58 km/km^2 (Theil 1985); however, there were exceptions when these areas were located adjacent to a large roadless area (Mech 1989). Similarly, studies in Wisconsin showed that wolves were concentrated in areas with a mean road density less than 0.23 km/sq km, and tolerated areas as high as 0.45 km/sq km, as opposed to a mean road density of 0.74 km from random non-pack areas (Mladenoff et al.1995).

Land ownership is another factor that influences habitat selection because wolves have been found to occur much more frequently on public lands than private (Mladenoff et al. 1995). Habitat selection is not based solely on avoiding humans; studies indicate wolves also respond to natural landscape variable such as vegetation type and prey density. In Minnesota, wolf pack territories had a higher proportion of conifer and conifer/mixed woodlands than non-wolf areas. Similarly, occupied areas had a lower percentage of agricultural and deciduous forest than occupied land (Mladenoff et al. 1995). Some studies suggest that the main limiting factor for wolves, after human tolerance, is prey availability (Fuller et al. 1992). However, other studies have found little to no difference in prey densities in wolf and non-wolf areas (Mladenoff et al. 1995, 1997).

4.4. Study Area

This study focused on predicting wolf habitat in the Northern Rocky Mountains; specifically, the Idaho, Montana, and Wyoming tri-state area (Figure 1). This area contains a wide range of topography and vegetation types making a regional summary difficult, but in general the area can be characterized as being mountainous with a semi-arid, continental climate. Precipitation varies greatly in response to elevation change, with precipitation increasing with higher elevations. Average precipitation ranges from 30-122 centimeters (12 to 48 inches) annually, with slightly higher amounts in the winter months (Marston 1991). These factors work together to create a landscape that is characterized by western temperate coniferous forests in the upper, wetter elevations, and sagebrush steppes in the lower, drier elevations.

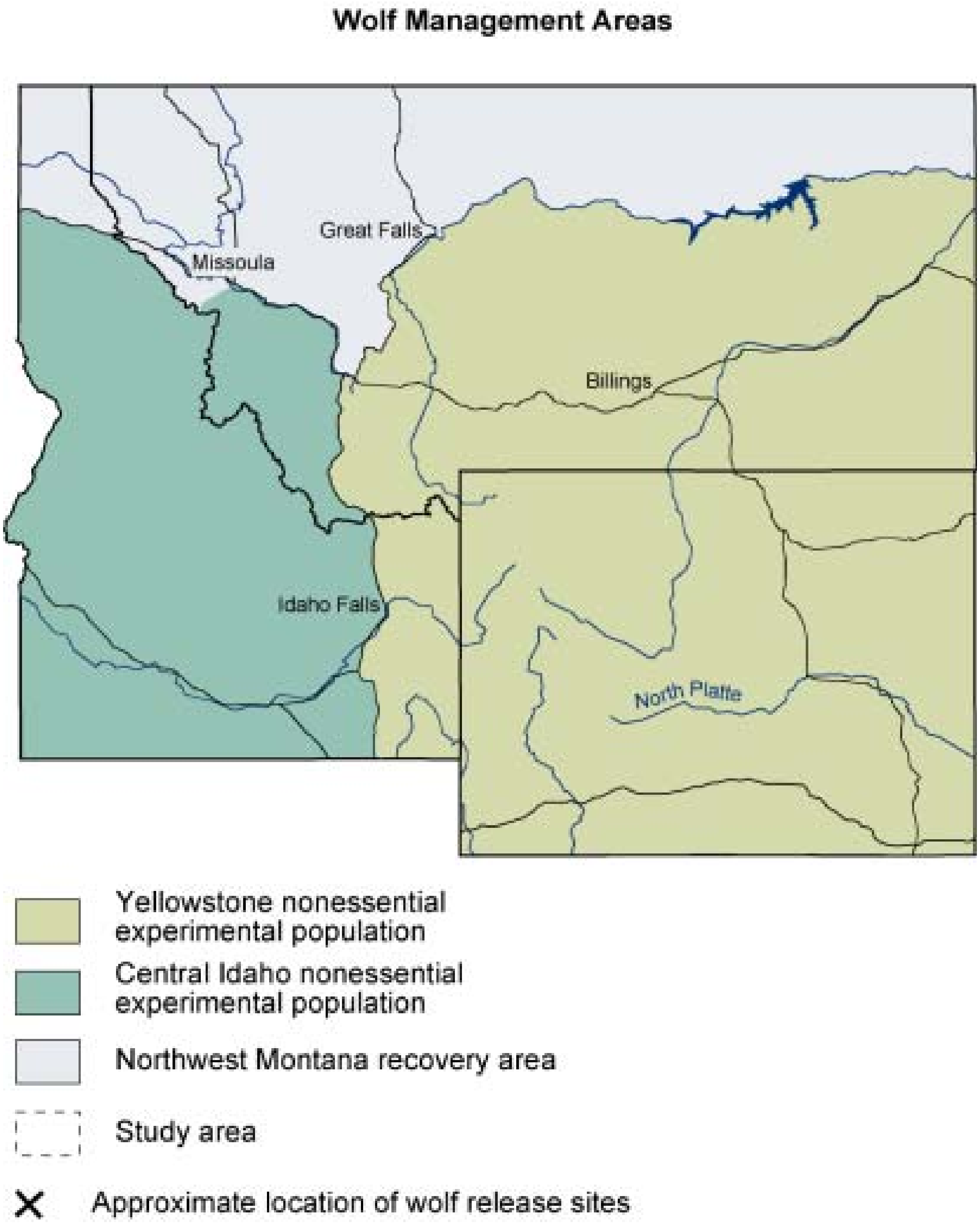

Figure 1. Map identifying the different wolf management zones that affect the reintroduction of the gray wolf as defined by the USFWS.

The region is generally sparsely populated with large tracts of remote, roadless wilderness. The western portion of the study area contains the rugged mountain region of central Idaho and its 16,000 sq km of designated wilderness. This wilderness supports over 241,000 wild ungulates including mule deer (*Odocoileus hemionus*), white- tailed deer (*Odocoileus Virginianus*) , elk (*Cervus elaphus*), and moose (*Alces alces*) among others (Bangs and Fritts 1996). This area is widely used by hunters, which harvest around 33,360 ungulates annually, and ranchers who seasonally graze more than 300,000 head of livestock on federal lands despite annual losses of approximately 12,310 cattle and 9,360 sheep (Bangs and Fritts 1996).

The southeastern portion of the study area includes the Greater Yellowstone Ecosystem (GYE), which Marston (1991) defines as the central Yellowstone plateau, and areas above 2,130 meters (7,000 feet) in the surrounding 14 mountain ranges. Vegetation in this area is heavily influenced by the effects of elevation on temperature and precipitation. This effect stratifies the region into communities that include, from lowest to highest elevation: grassland and shrub land, low elevation forests, middle elevation forests, and upper elevation forests.

4.5. Methodology

For this project, three mapping units were used to identify regions of suitable habitat for the gray wolves of the Northern Rocky Mountains. Idaho State Game Management Units (GMU), a 33x33 km grid, and a 16x16 km grid (Figure 2) were each used to build a habitat model using four landscape variables (land cover, land ownership, road density, and elk density). The land cover and land ownership data were processed, and the majority land cover/ land owner within a mapping unit was identified. Elk density was calculated using a weighted mean of the number of elk per mapping unit divided by the area of the mapping unit; and road density was calculated by buffering the roads to a width of four meters, then the total area of roads within each mapping unit was divided by the area of the mapping unit.

Mapping Units for Analyzing Idaho Wolf Habitat

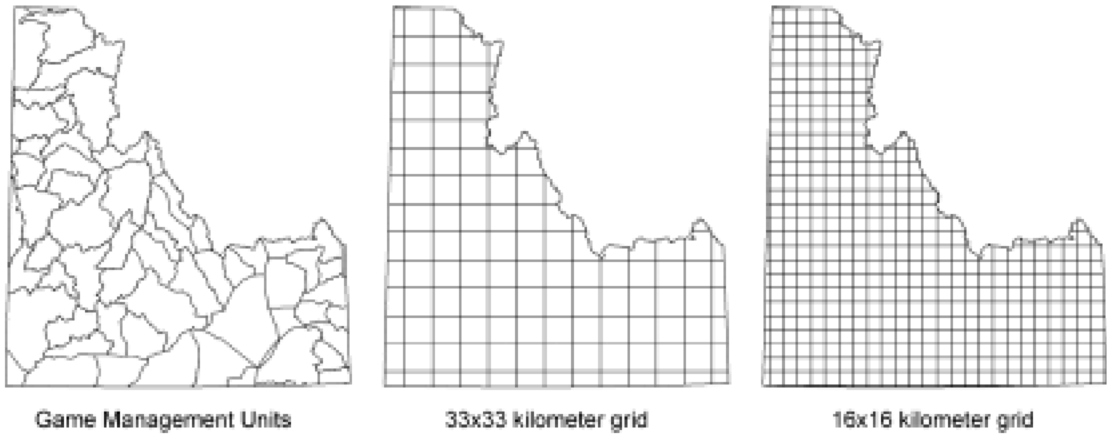

Figure 2. Three different mapping units used in the analysis of Idaho wolf habitat. The mapping unit that performed the best was validated using data from Montana and Wyoming.

The current wolf locations, as identified by Maughan (1999), were obtained and used as training sites for identifying suitable wolf habitat. It should be remembered, however, that this is a new and expanding wolf population; therefore, the absence of wolves does not necessarily mean that the habitat is unsuitable for wolves. The resulting database for each of the sampling unit coverages contained the following attributes: unit number, unit area, road area, road density, majority land cover, majority owner, number of elk, elk density, and wolf presence (1) or absence (0).

The data were analyzed using correlation and regression techniques to identify any differences between wolf and non-wolf grid cells. The variables were next analyzed using logistic regression to calculate the probability of each mapping unit being suitable wolf habitat. Mapping units with a probability value greater than 50% were assigned to the suitable wolf habitat class. To identify the most suitable mapping unit for modeling wolves in the Northern Rocky Mountains, the results of the statistical tests were compared among all three mapping units. Once the most suitable mapping unit was identified, it was used to model suitable wolf habitat in Montana and Wyoming using the above procedures for out-of-sample validation.

4.6. Results

Statistical analysis identified significant differences at the .01 level between wolf and non-wolf locations for land cover, land ownership, and road density using each of the three mapping units. Additionally, the 33 km and 16 km grids identified a significant difference in elk density between wolf and non-wolf locations. When the variables were entered into the logistic regression equation, the GMU model identified road density and land ownership as the most important variables for predicting wolf habitat suitability with an r^2 value of 0.49. The 33 km and the 16 km models both used road density and land cover as the predictors of suitable wolf habitat and produced r^2 values of 0.62 and 0.41 respectively.

Accuracy was assessed for each of the mapping units using an error matrix to compare predicted presence/absence to known presence/absence of wolves (Figure 3). Therefore, the accuracy reflects both correctly identified wolf presence and wolf absence.

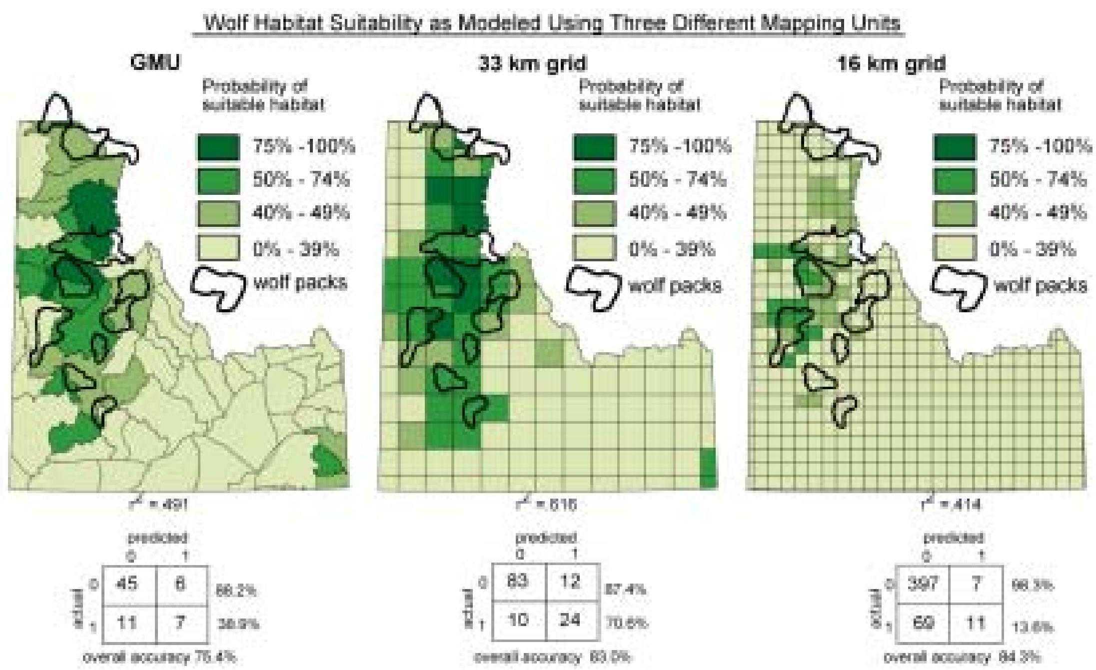

Figure 3. Predicted probability of suitable wolf habitat in Idaho using three mapping units. The 33 km grid produced the best results and was used for out of sample validation in Montana and Wyoming.

The 16 km grid performed the worst of the three models for of identifying suitable wolf habitat as defined by the presence of wolves. There were 80 mapping units that contained wolves in Idaho, however the model only identified 18 as suitable, and only 11 of these corresponded to known wolf locations for an accuracy of 13.8%. The GMU model performed slightly better with an accuracy of 38.9%. Of the 18 GMU's containing wolves, only seven were correctly identified as suitable wolf habitat. In contrast to the other two models, the 33 km grid model did a much better job of correctly identifying current wolf locations. Of the 34 grid cells that contained wolves, the model correctly labeled 24 of them as suitable wolf habitat for an accuracy of 70.6%.

Looking at the error matrices, it appears that over-classification of unsuitable habitat was a serious problem for both the GMU and the 16 km grid model. As a result of over-predicting unsuitable habitat, the accuracy for unsuitable habitat was increased, while the accuracy of predicting suitable habitat was decreased. Over-predicting suitable habitat did not seem to be as much of a problem for the 33 km model which achieved a balance of suitable/unsuitable habitat predictions accuracies, with both accuracies over 70%.

The 33 km grid functioned the best for modeling wolf habitat in Idaho, and was selected for out-of-sample validation in Montana and Wyoming. The 33 km grid performed equally well using out-of-sample data, indicating that it was a successful model (Figure 4). When the model was applied to data from Montana, it had an overall accuracy of 88.88%, with 60.0% accuracy for predicting wolf presence, and 91.0% accuracy for predicting wolf absence. In Wyoming, the model produced an overall accuracy of 74.6%, with 68.6% accuracy for predicting wolf presence and 93.7% accuracy for wolf absence. Again, it appears that the cut-off probability of 0.5 has resulted in an over classification of unsuitable habitat. However, it was not to the same extent as with the GMU or the 16 km grid mapping units.

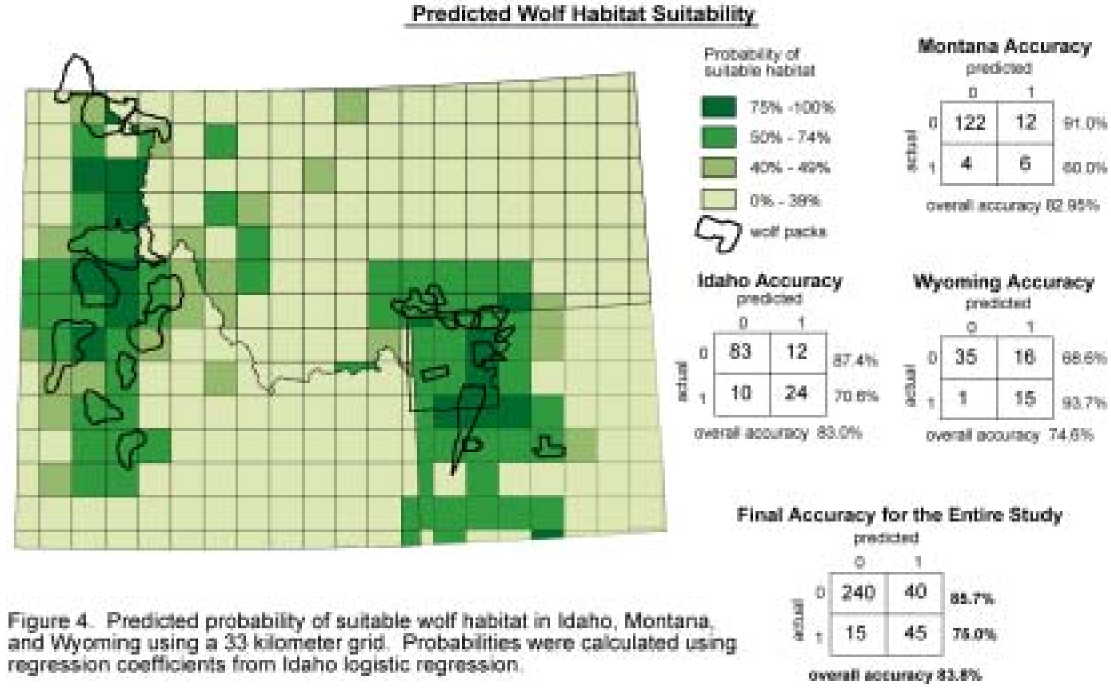

Figure 4. Predicted probability of suitable wolf habitat in Idaho, Montana, and Wyoming using a 33 kilometer grid. Probabilities were calculated using regression coefficients from Idaho logistic regression.

When all three states were viewed as a whole, the 33 km model had an overall accuracy rate of 83.8%. Of the 60 grid cells where wolves were known to exist, the model correctly identified 45 of them (75.0%), and of the 280 cells that did not contain wolves, the model correctly labeled 240 of them as unsuitable habitat (85.7%). It is important to remember when looking at the model's ability to correctly identify suitable habitat that this is a new and expanding wolf population. The absence of wolves does not necessarily indicate unsuitable habitat. Therefore, the labeling of a mapping unit as suitable habitat when it is not currently occupied by wolves was not necessarily an incorrect classification.

4.7. Conclusions

The reintroduction of wolves into the Northern Rocky Mountains has been a success, so far. The fact that wolves are highly adaptable and resilient animals has allowed them to take advantage of their new habitat and increase their numbers from 66 in 1995 to over 200 by the end of 1999. The wolves' success and rapid growth have both positive and negative aspects that are likely to impact public attitude and wildlife management strategies in the coming years.

As the wolf population grows, there will probably be a proportional increase in human-wolf conflicts, and since humans are the leading cause of wolf mortality, public support of the wolves is crucial to their recovery. The regions of Idaho, Montana, and Wyoming that wolves currently occupy are a complex mixture of national parks, national forests, public land, and private property.

To successfully manage wildlife populations in this mosaic of land uses, there will probably need to be an equally complex management strategy. The creation of management zones may be a key strategy to maintain a balance between wildlife conservation and human land use practices. Hopefully, the results of this research can help to identify what areas are the most important to protect for wolves and other species, and what areas should receive limited protection.

The wolf habitat relationships documented in this study are in general agreement with the findings of other wolf habitat studies conducted by other researchers. Wolves were found to prefer national forest/park property dominated by coniferous forests with a low road density. The mean road density in grid cells occupied by wolves was 0.32 as compared to the much higher mean road density from grid cells where wolves were not present of 0.63. Most (75%) of the wolves in this study occurred in sample units with a road density less than 0.54 km per sq km; although, there was one sample unit in Montana occupied by wolves that had a road density of 1.37 km/sq km (Figure 5). These numbers are similar to those found by Mladenoff (1995) which reported that wolves in Minnesota preferred areas with a road density less than 0.45. The ecological similarities between the gray wolf of the northern Rocky Mountains and the timber wolf of the Great Lakes may be a noteworthy point to consider. If the general habitat characteristics of different sub-species of wolves are similar, then wildlife managers in wolf reintroduction areas may be able to confidently draw from the biological and managerial history of regions that already support a population of wolves.

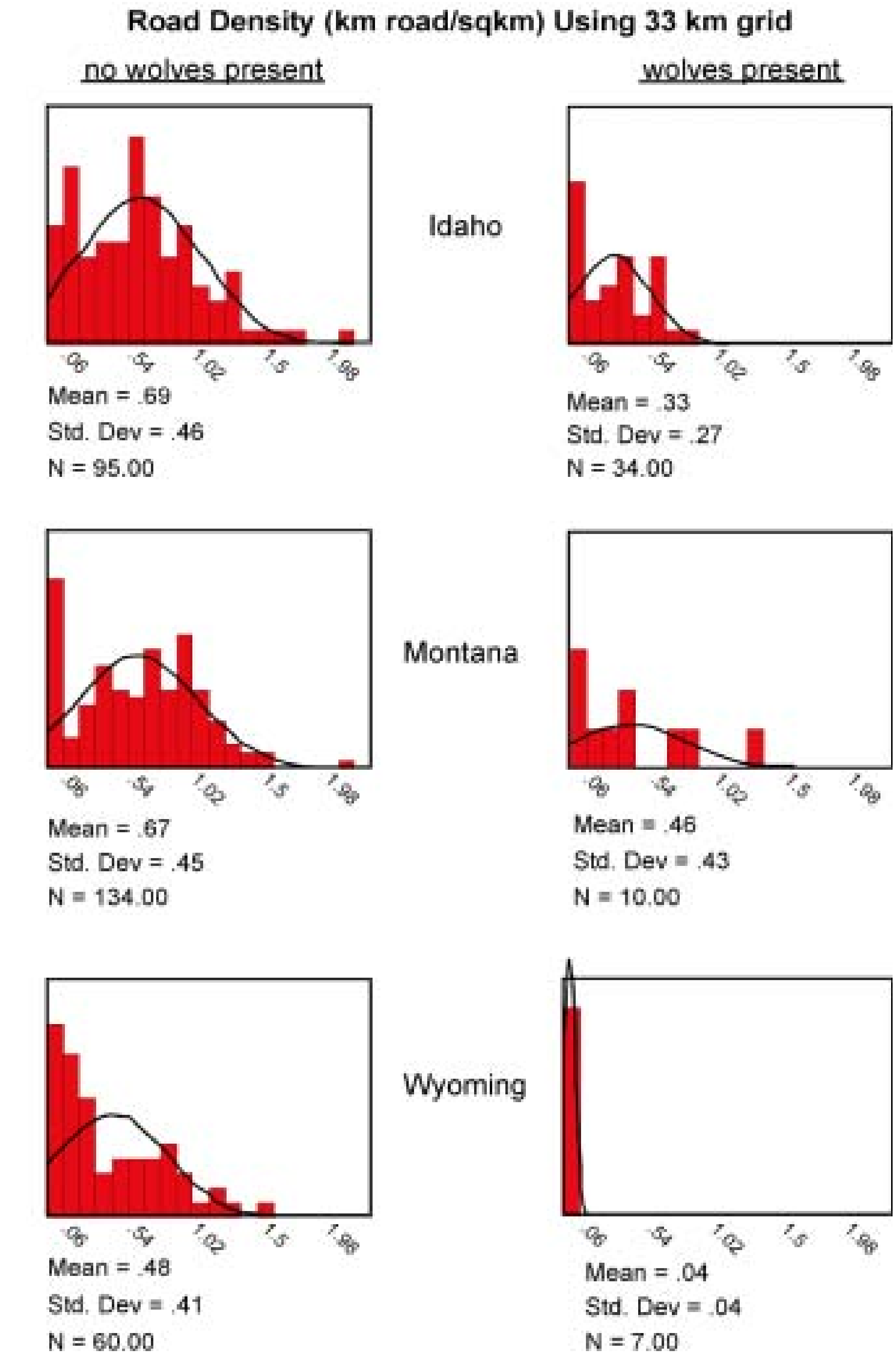

Figure 5. When the 33 km grid was used to analyze road density in Idaho, Montana, and Wyoming, all three states showed a substantial difference in road densiy between wolf and non-wolf grid cells

4.8. Literature Cited

Ballenberghe, V. V., A.W. Erickson, and D. Byman. 1975. Ecology of the Timber Wolf in Northeastern Minnesota. *Wildlife Monographs*. No 43.

Bangs, E. 1991. Return of a Predator: Wolf Recovery in Montana. *Western Wildlands* 17:7-13.

Bangs, E.E., S.H. Fritts. 1996. Reintroducing the Gray Wolf to Central Idaho and Yellowstone National Park. *Wildlife Society Bulletin*. 24(3):402-413.

Bangs, E., S.H. Fritts, D.R. Harms, J.A. Fontaine, M.D. Jimenez, W.G. Brewster, and C.C. Niemeyer. 1995. Control of Endangered Gray Wolves in Montana. Pages 127-134 in L.N.Carbyn, S.H. Fritts, D.R. Seip. eds. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Inst.. Occas. Publ. No.35, Univ. Alberta, Edmonton.

Carroll, C., P. Paquet, R. Noss, and J. Strittholt. (Draft 1998) *Modeling Carnivore Habitat in the Rocky Mountain Region: A Literature Review and Suggested Strategy*.

Cowan, I. M.. 1947. The Timber Wolf in the Rocky Mountain National Parks of Canada. *Canadian Journal of Research* 25:139-174.

Fritts, S.H., E.E. Bangs, J.A. Fontaine, W.G. Brewster, J.F. Gore. 1995. Restoring the Wolf to the Northern Rocky Mountains of the United States. Pages 107-125 in L.N. Carbyn, S.H. Fritts, D.R. Seip. Eds. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute Occasional Publication Number 35, University of Alberta, Edmonton.

Fuller, T. K. 1989. Population Dynamics of Wolves in North-Centeral Minnesota. *Wildlife Monographs*. 105:1-41.

Fuller, T.K., W.E. Berg, G.L. Radde, M.S. Lanarz, and G.B. Joselyn. 1992. A History and Current Estimate of Wolf Distribution and Numbers in Minnesota. *Wildlife Society Bulletin* 20:42-55.

Haight, R.G., D.J. Mladenoff, and A.P. Wydeven. 1998. Modeling Disjunct Gray Wolf Populations in Semi-Wild Landscapes. *Conservation Biology*.

Marston, R.A., J.E. Anderson. 1991. Watersheds and Vegetation of the Greater Yellowstone Ecosystem. *Conservation Biology*.5(3):338-346.

Maughan, Ralph. 1999. Ralph Maughan's Wildlife Report http://www.forwolves.org/ralph/

Mech, L. D. 1970. *The Wolf: the Ecology and Behavior of an Endangered Species*. Natural History Press, Garden City, New York.

Mech, L. D. 1989. Wolf Population Survival in an Area of High Road Density. *American Midland Naturalist* 121:387-389.

Mech, L. D. 1995. The Challenge and Opportunity of Recovering Wolf Populations. *Conservation Biology* 9(2):270-278.

Mech, L. D., S.H. Fritts, G.L. Radde, W.J. Paul. 1988. Wolf Distribution and road Density in Minnesota. *Wildlife Society Bulletin* 16(1).

Mech, L. D., L.G. Adams, T.J. Meier, J.W. Burch, B.W. Dale. 1998. *The Wolves of Denali*. University of Minnesota Press, Minneapolis.

Mladenoff, D.J., T.A. Sickley, R.G. Haight, A.P. Wydeven. 1995. A regional Landscape Analysis and Prediction of Favorable Gray Wolf Habitat in the Northern Great Lakes Region. *Conservation Biology*. 9(2):279-294.

Mladenoff, D.J., R.G. Haight, T.A. Sickley, and A.P. Wydeven. 1997. Causes and Implications of Species Restoration in Altered Ecosystems: A Spatial Landscape Projection of Wolf Population Recovery. *Bioscience*. 47:21-31.

Noss, R.F., H.B. quigley, M.G. Hornocker, T. Merill, and P.C. Paquet. 1996. Conservation Biology and Carnivore Conservation in the Rocky Mountains. *Conservation Biology* 10:949-963.

Ream R.R., M.W. Fairchild, D.K. Boyd, and A.J. Blakensley. 1989. First Wolf Den in United States in Recent History. *Northwest Naturalist*. 70:39-40.

Thiel, R.P. 1985. Relationship Between Road Density and Wolf Habitat Suitability in Wisconsin. *American Midland Naturalist* 113:404.

Thurber, J. M., R.O. Peterson, T.R. Drummer, S.A. Thomasma. 1994. Gray Wolf Response to Refuge Boundaries and Roads in Alaska. *Wildlife Society Bulletin*. 22:61-68.

U.S. Fish and Wildlife Service 2000. *Rocky Mountain Wolf Recovery 1999 Annual Report*.

Wiens , J.A.1989. Spatial Scaling in Ecology. *Functional Ecology*. 3:385-397.

5.0 Literature Cited (complete)

Allen, A.W., R. V. O'Neill, and T.W. Hoekstra. 1984. *Interlevel Relations in Ecological Research and Management: Some Working Principles from Hierarchy Theory*. USDA FS Rocky Mountain Forest an Range Experiment Station. Fort Collins CO. General Technical Report RM-110

Ballenberghe, V. V., A.W. Erickson, and D. Byman. 1975. Ecology of the Timber Wolf in Northeastern Minnesota. *Wildlife Monographs*. No 43.

Bangs, E.E. 1991. Return of a Predator: Wolf Recovery in Montana. *Western Wildlands* 17:7-13.

Bangs, E.E., S.H. Fritts. 1996. Reintroducing the Gray Wolf to Central Idaho and Yellowstone National Park. *Wildlife Society Bulletin*. 24(3):402-413

Bangs, E.E., S.H. Fritts, D.R. Harms, J.A. Fontaine, M.D. Jimenez, W.G. Brewster, and C.C. Niemeyer. 1995. Control of Endangered Gray Wolves in Montana. Pages 127-134 in L.N.Carbyn, S.H. Fritts, D.R. Seip. eds. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute.. Occasional Publication Number 35, Univ. Alberta, Edmonton.

Bass, R. 1992. *The Ninemile Wolves*. Ballantine Books, New York.

Boitani, L., F. Corsi, and E. Dupre. 1997. *Large Scale Approach to Distribution Mapping: The Wolf in the Italian Peninsula*. Oral Presentation, 1997 Annual Meeting for the Society for Conservation Biology, Victoria, Canada.

Boyce, M.S. 1995. Anticipating consequences of Wolves in Yellowstone: Model Validation. Pages 199-210 in L.N. Carbyn, S.H. Fritts, and R.R, Seip, eds. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute, University of Alberta, Edmonton Alberta.

Boyd-Hedger, D.K. 1997. *Dispersal, Genetic Relationships, and Landscape Use by Colonizing Wolves in the Central Rocky Mountains*. Ph.D. Thesis. University of Montana, Missoula, Mt. 184 pp.

Carroll, C., P. Paquet, R. Noss, and J. Strittholt. (Draft 1998) *Modeling Carnivore Habitat in the Rocky Mountain Region: A Literature Review and Suggested Strategy*.

Corsi, F., E. Dupre, and L. Boitani. 1999. A Large-Scale Model of Wolf Distribution in Italy for Conservation Planning. *Conservation Biology* 13:1, 150-159

Cowan, I. M. 1947. The Timber Wolf in the Rocky Mountain National Parks of Canada. *Canadian Journal of Research*. 25:139-174

Donovan, L. M, D.L. Rabe et al. 1987. Use of Geographic Information systems to Develop Habitat Suitability Models. *Wildlife Society Bulletin* 15:574-579.

Fritts, S.H., and L.D. Mech. 1981. Dynamics, Movements, and Feeding Ecology of a Newly Protected Wolf Population in Northwestern Minnesota. *Wildlife Monographs* 80.79p.

Fritts, S.H., L.N. Carbyn. 1995. Population viability, Nature Reserves, and the Outlook for Gray Wolf Conservation in North America. *Restoration Ecology* 3:26-38.

Fritts, S.H., E.E. Bangs, J.A. Fontaine, W.G. Brewster, J.F. Gore. 1995. Restoring the Wolf to the Northern Rocky Mountains of the United States. Pages 107-125 in L.N. Carbyn, S.H. Fritts, D.R. Seip. Eds. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute. Occasional Publication Number 35, University of Alberta, Edmonton.

Fuller, T. K. 1989. Population Dynamics of Wolves in North-Centeral Minnesota. *Wildlife Monographs*. 105:1-41.

Fuller, T.K., W.E. Berg, G.L. Radde, M.S. Lanarz, and G.B. Joselyn. 1992. A History and Current Estimate of Wolf Distribution and Numbers in Minnesota. *Wildlife Society Bulletin* 20:42-55

Greig-Smith. 1979. Pattern in Vegetation. *Journal of Ecology*. 67, 755-779.

Haight, R.G., D.J. Mladenoff, and A.P. Wydeven. 1998. Modeling Disjunct Gray Wolf Populations in Semi-Wild Landscapes. *Conservation Biology* 12:(4) 879-888.

Hayes, R.D., and J.R. Gunson. 1995. Status and Management of Wolves in Canada. Pages 21-33 in L.N. Carbyn, S.H. Fritts, and D.R. Seip, Eds. *Ecology and Conservation of Wolves in a Changing World*. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta.

Marston, R.A., J.E. Anderson. 1991. Watersheds and Vegetation of the Greater Yellowstone Ecosystem. *Conservation Biology*. 5(3):338-346.

Maughan, R. 1999. *Ralph Maughan's Wildlife Reports*. http://www.forwolves.org/ralph/

Mech, L. D. 1970. *The Wolf: The Ecology and Behavior of an Endangered Species*. Natural History Press, Garden City, New York

Mech, L. D. 1989. Wolf Population Survival in an Area of High Road Density. *American Midland Naturalist*. 121:387-389.

Mech, L. D. 1995. The Challenge and Opportunity of Recovering Wolf Populations. *Conservation Biology* 9(2):270-278.

Mech, L. D., S.H. Fritts, G.L. Radde, W.J. Paul. 1988. Wolf Distribution and Road Density in Minnesota. *Wildlife Society Bulletin* 16(1)

Mech, L. D., L.G. Adams, T.J. Meier, J.W. Burch, B.W. Dale. 1998. *The Wolves of Denali*. University of Minnesota Press, Minneapolis.

Mladenoff, D.J., T.A. Sickley, R.G. Haight, A.P. Wydeven. 1995. A regional Landscape Analysis and Prediction of Favorable Gray Wolf Habitat in the Northern Great Lakes Region. *Conservation Biology*. 9(2):279-294.

Mladenoff, D.J., R.G. Haight, T.A. Sickley, and A.P. Wydeven. 1997. Causes and Implications of Species Restoration in Altered Ecosystems: A Spatial Landscape Projection of Wolf Population Recovery. *Bioscience*. 47:21-31.

Mladenoff, D.J., 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):1-10pp

Morrison, M.L., B.G. Marcot, R.W. Mannan. 1998. *Wildlife Habitat Relationships: Concepts and Applications*. University of Wisconsin Press.

Noss, R.F., H.B. Quigley, M.G. Hornocker, T. Merill, and P.C. Paquet. 1996. Conservation Biology and Carnivore Conservation in the Rocky Mountains. *Conservation Biology* 10:949-963.

Nowak, R.M. 1983. A Perspective on the Taxonomy of Wolves in North America. Pages 10-19 in *Wolves in Canada and Alaska: their status biology and management*. L.N. Carbyn. editors. Canadian Wildlife Service. Rep. Ser. No. 45, Ottawa.

Paquet, P.C., J. Wierzchowski, and C. Callaghan. 1997. *Assessing Reserve Designs Using a Predictive Habitat Suitability and Movement Model*. Oral Presentation, 1997 Annual Meeting of the Society for Conservation Biology, Victoria, Canada.

Peterson, R O. 1998. *Ecological Studies of Wolves on Isle Royal, Annual Report* 1997-1998. School of Forestry and Wood Products, Michigan Technological University.

Peterson, R.O., J.D. Woolington, T.N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs*. 88:52p.

Pimlot, D.H. 1967. Wolf Predation and Ungulate Populations. *American Zoology* 7:267-278

Ream R.R., M.W. Fairchild, D.K. Boyd, and A.J. Blakensley. 1989. First Wolf Den in United States in Recent History. *Northwest Naturalist*. 70:39-40.

Smits, L. 1963. King of the Wild. *Michigan Conservation* 32(1) :45.

Thiel, R.P. 1985. Relationship Between Road Density and Wolf Habitat Suitability in Wisconsin. *American Midland. Naturalist*. 113:404.

Thompson, D.Q. 1952. Travel, Range, and Food Habits of Timber Wolves in Wisconsin. *Journal of Mammalogy* 33:429-442.

Thurber, J. M., R.O. Peterson, T.R. Drummer, S.A. Thomasma. 1994. Gray Wolf Response to Refuge Boundaries and Roads in Alaska. *Wildlife Society Bulletin*. 22:61-68.

U.S. Fish and Wildlife Service. 1987. *Northern Rocky Mountain Wolf Recovery Plan*. U.S. Fish and Wildlife Service, Denver, Co. 119pp.

U.S. Fish and Wildlife Service 2000. *Rocky Mountain Wolf Recovery 1999 Annual Report.*

Ville, N. De La, S. H. Cousins, C. Bird. 1998. Habitat Suitability Analysis Using Logistic Regression to Outline Potential Areas for Conservation of the Gray Wolf. *Innovations in GIS: Selected Papers from the Fifth National Conference on GIS Research in UK* . Steve Carter editor. Taylor and Francis Group.

Wiens , J.A.1989. Spatial Scaling in Ecology. *Functional Ecology*. 3:385-397.