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Core Selection by Wolf Packs in a Human-Dominated Landscape: A Case Study in the Mountains of Southern Poland

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CORE SELECTION BY WOLF PACKS IN A HUMAN-DOMINATED LANDSCAPE: A CASE STUDY IN THE MOUNTAINS OF SOUTHERN POLAND

By

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ABSTRACT

The wolf populations in Europe are mostly divided between the largely undeveloped countries of Eastern Europe, and the more developed Western European nations. Poland holds a special importance as a geographical link joining these populations into one contiguous population. The territories of two wolf packs in southwestern Poland were examined through the collection of scat data. Core areas were then defined using fixed-kernel density estimation techniques and 50% isopleths. Habitat variables were then compared between core plots and non-core plots. Scat marking of both packs resembled the Hot Spots pattern of marking proposed by Zub *et al*. (2003), rather than the Olfactory Bowl pattern suggested by Peters and Mech (1975). Core plots in both territories were found to be located significantly farther from primary roads than non-core plots, while core plots in one territory were also located significantly farther from human built-up areas than non-core plots. No significant differences were found in forest cover, elevation, or road density between core and non-core plots. These findings suggest that in a region with high human densities and increased levels of human penetration into the forest, wolves may more intensely utilize areas that minimize their exposure to frequent human disturbances, while adapting to occasional disturbances.

Acknowledgements

My pursuit of this degree has been a long and often trying journey, but I have received a lot of help and support along the way. When I started my intended project in Madagascar, I had the help and friendship of Gerard Stewart in Ifaty. Gerard helped me adapt to some very difficult conditions that I had not faced before, and introduced me to fieldwork in the developing world. Although I was unable to continue my initial project in Ifaty, I learned a great deal and am thankful for his guidance.

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This has been quite the journey, from my first day at UM, to the primitive living on the beaches of Madagascar, and finally to the long days of snowshoeing and hiking in the mountains of Poland. I have learned a lot throughout all this, been reminded of how truly lucky I am, and undoubtedly grown as a person. This has been a collection of experiences that I will never forget.

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INTRODUCTION AND RESEARCH OBJECTIVES

Carnivores hold a special place in the hearts of many people. None is a better example than the wolf, *Canis lupus*. The wolf is both loved and hated in the imaginations of many—regarded as a symbol of wilderness, an artifact of something special that has been nearly lost, and a sign of the return of wild nature; or, serving as a symbol of destruction, cost, and problems for others. Because of the polarizing effect of carnivores such as wolves, carnivore conservation has been highly controversial and riddled with challenges.

Research during the past few decades has illustrated the importance of large carnivores to many different ecosystems (McLaren & Peterson 1994; Wilcove *et al*. 1986; Post *et al*. 1999; Berger *et al*. 2000). Carnivores both directly (Terborgh 1988; Estes *et al.* 1998) and indirectly (Kotler *et al.* 1993; Brown *et al.* 1994) reduce numbers of prey, either by consuming the prey, or by acting as a motivation for prey animals to change their normal behaviors (favorite habitats, time of feeding, group size, etc.). These effects can be observed at several trophic levels. One classic example of this is the study conducted by McLaren and Peterson (1994) in which they found that predation by wolves in Isle Royale's boreal forests resulted in changes in both the numbers and behavior of moose (*Alces alces*), which in turn, also affected the recruitment and growth rates of balsam fir and other woody plants. After wolves disappeared from Yellowstone National Park, overstory recruitment of aspen stopped as the elk (*Cervus elaphus*) population grew and essentially browsed the aspen saplings to death (Ripple and Larson 2000). After wolf reintroduction to Yellowstone in 1995, researchers found that preferred habitat of the elk had shifted due to the presence of the wolf (Fortin *et al*. 2005), and as a result, aspen reestablished in many areas. Regarding an ever-increasing important topic, Wilmers and

Post (2006) found that wolves may help mitigate the effects of global warming in Yellowstone by ensuring that carrion always exists for scavenger species, despite mild winters.

Large carnivore conservation presents several challenges, including the large territories required for effective conservation (Pletscher *et al*. 1991; Blanchard & Knight 1991; Beier 1993; Craighead *et al*. 1982; Mattson *et al*. 1991). Due to the large migratory distances of species such as the wolf, it is difficult to set aside tracts of land that are large enough to contain all required habitats. In most cases, migratory corridors, or smaller sections of land that can be temporarily used by animals to move from one habitat to another, become extremely important (Beier and Noss 1998, Bennett 1990, Rabinowitz and Zeller 2010).

Another important challenge in achieving effective large carnivore conservation is the problem of human/wildlife conflict (Mishra 1997, Fredriksson 2005). Human beings are occupying areas that they had not previously inhabited, taking away valuable habitat from many species. As a result, humans are experiencing more encounters with wildlife, and when the species in question is a carnivore, such as a wolf or a grizzly bear, an element of danger also exists. Therefore, large carnivores have aroused strong feelings among people that live with them, as well as among those that live in other areas but dream of seeing them. As the human population continues to expand its reach into the remotest parts of the world, a pressing challenge is finding ways that people and carnivores can coexist.

Wolves were exterminated from most areas of northern and western Europe during the last two centuries, reaching their lowest numbers in the 1940's to the 1960's (Salvatori and Linnell 2005). Since the end of the 1960's, many populations have started to recover and reoccupy some of their former range, such as in northern Italy, France, Spain, Germany, and Switzerland (Salvatori and Linnell 2005). Throughout Europe, most areas suitable for wolves are located in mountainous regions where climatic and geomorphologic conditions render the areas less favorable to human development (Massolo and Meriggi 1998; Salvatori *et al.* 2002). The wolf is classified as a species of least concern in the 2010 Red List of the IUCN (Mech & Boitani, 2010), while CITES (Convention on International Trade in Endangered Species of the Wild Fauna and Flora) lists the wolf as a species of Lower Risk or Least Concern, except for the Mexican wolf population (Extinct in the Wild), the Iberian population (Lower risk: conservation dependent), the Italian population (Vulnerable), and populations in Bhutan, Pakistan, India, and Nepal, which are all listed in Appendix I, meaning that they are in danger of extinction (Salvatori and Linnell 2005).

Under the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats, 1979), wolves are listed in Appendix II as a strictly protected species, meaning that both the wolf and its habitats are fully protected. However, enforcement of this convention is a responsibility of the individual parties and individual countries may create specific exceptions. This has happened in Bulgaria, the Czech Republic, Finland, Latvia, Lithuania, Slovenia, Slovakia, Spain, and Turkey, who have all signed the Bern Convention, but where wolves continue to remain unprotected (Salvatori and Linnell 2005).

Canis lupus has been protected in Poland since April 1998. At the present, the wolf population in Poland is estimated to number 750 individuals (Nowak and Myslajek 2011). Wolf populations are found in the northeastern region of Poland, including the protected Bialowieza Primeval Forest, the southern region including the Polish

Carpathians (this wolf population is shared with Slovakia and Ukraine), and also in western Poland in a region bordering Germany.

The wolf population inhabiting the Beskidy Mountains of southern Poland is in the most danger. There, the population is limited to only a handful of packs. Greater densities of roads in southern Poland and more human-occupied areas have resulted in less suitable habitat than that in the northern part of the country (Jedrzejewski *et al.* 2005). In addition, many packs in this southern region inhabit border areas, where they are vulnerable to hunting during certain parts of the year.

Many studies have been conducted focusing on the presence of wolves in areas and several habitat suitability models have been constructed (Mladenoff *et al.* 1995; Massolo and Meriggi 1998; Glenz *et al.* 2001; Jedrzejewski *et al*. 2008). However, wolf presence in no way guarantees that a wolf population will survive or thrive in an area, as the population inhabiting the Beskidy Mountains in southern Poland demonstrates. In areas like the Beskidy Mountains, where human presence is a regular occurrence, optimal habitat does not exist. If wolf populations are to survive, those core habitats most important to wolves need to be identified and protected. Wolf-occupied areas have been identified, but a need exists for a finer-scale analysis of wolf territories in order to determine more subtle effects of habitat parameters and human influence on those areas wolves utilize most often.

Theuerkauf *et al.* (2003) studied the selection of den, rendezvous, and resting sites by wolves in the Bialowieza Forest in Poland. They found that habitat characteristics were less important in the selection of these sites than the spatial distribution of forest, public roads, and towns and villages. The Bialowieza Forest is a distinctly different study site than those in southern Poland. Approximately 100 km^2 of the Bialowieza Forest is protected as a national park, with half of that area strictly protected as a core area, where no motorized traffic is allowed and human entry is by permit only (Theuerkauf *et al.* 2003). The rest of the forest is used more intensely, yet human density is only approximately 7 inhabitants/km^2 in the forest itself, and 70 persons/km^2 in the areas surrounding the forest. In comparison, this study took place in southern Poland, where human density is much higher (average of 143 persons/km^2) and there are no restrictions on human entry (Jedrzejewski *et al.* 2005). How do wolves select these important habitats in an area in which it is nearly impossible to escape human disturbance? Would they choose thick forest cover and habitat quality over human avoidance, or would they seek to avoid people, even if that means inferior habitat?

This study seeks to aid in identifying those areas most valuable to wolves in this population through the analysis of scat locations within the territories of two wolf packs. Habitat variables, including physical, biological, and spatial attributes, will be recorded in areas heavily utilized by wolves and then compared to the same variables in areas utilized less intensely. In this way, variables that appear to most influence the value of an area to a wolf pack will be identified and used to predict areas of higher value for wolves in regions with high human presence. The information gathered from this study may be used to guide future conservation measures and increase the probability of their effectiveness.

The objectives of this paper are to:

1) Examine whether the patterns of wolf scat marking in two wolf pack territories could be classified as the olfactory bowl pattern proposed by Peters and Mech (1975); or the hotspots pattern proposed by Zub *et al*. (2003);
2) Identify any "core" areas within each wolf territory through kernel density estimation and map them using a GIS;

3) Compare any core areas to other areas within the territories by using a GIS to map and examine several habitat variables, including road densities, locations of built-up areas, forest cover, elevation, and distance to primary roads; and determine which variables appear to be the most important for core selection.

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STUDY AREA

The Beskidy Mountains of southern Poland include two mountain ranges: the Silesian Beskidy Mts. and the Zywiecki Beskidy Mts. (Figure 1). These two mountain ranges are part of the western-most range of the Polish Carpathian Mountains. The Carpathian Mts. contain the largest continuous wolf population in Central Europe, covering parts of Romania, Ukraine, Slovakia, and Poland (Salvatori *et al.* 2002). The study area covers approximately 745 km^2.

The elevation of the study area ranges from 300 to nearly 1600 meters above sea level (Nowak *et al*. 2005) and the forest community consists mostly of Norway spruce (*Picea abies*) and beech (*Fagus silvatica*), with spruce monocultures mostly dominating the higher elevations. The study area receives significant amounts of snow, with snow remaining in the valleys approximately 80 days per year and up to 160 days per year on the higher, north-facing slopes (Nowak *et al*. 2005).

The region is densely populated by humans (average of 150 people/km^2), particularly in villages located in the valleys and along the lower mountain slopes (Nowak & Myslajek 2004). In comparison, Poland as a whole has a mean population density of 124 people/ km^2 (Jedrzejewski *et al.* 2005). There are few nature reserves in the study region and most of the forest is exploited for logging, with logging roads penetrating nearly every area of forest. A large number of meadows and fields exist in the higher elevations as a result of past livestock grazing activities, and some of these areas are still used today. However, in general, livestock raising is now uncommon and exists on a much smaller scale, with only small flocks of sheep and herds of goats occasionally present. Numerous recreational hiking trails, a few ski areas, and several small vacation cabins and lodges bisect the forest. The region receives heavy human traffic, especially during the summer months. During the fall months (late September to November), large numbers of people travel into the forest to collect mushrooms. The mean density of public roads within the study area is 1.3 km/km^2 (Nowak *et al*. 2008).

Other large carnivores are also present in the region. Eurasian lynx (*Lynx lynx*) inhabit areas in eastern and southeastern Poland (Jedrzejewski *et al*. 2005; Niedzialkowski *et al*. 2006), while brown bears (*Ursus arctos*) occupy areas of the Carpathian Mountains in southeastern Poland (Jakubiec and Buchalczyk 1987). Both of these species, in addition to the wolf, are protected.

The Silesian Beskidy Mountains were naturally recolonized by wolves in 1996 (Nowak *et al*. 2008), while in the Zywiecki Beskid Mountains, small numbers of wolves existed prior to protection, mostly along the Polish-Slovakian border areas (Nowak *et al.* 2008). Nowak *et al.* (2008) found the number of wolves in the Zywiecki Beskid region to vary between 9 and 14 wolves over a 5- year period from 1998-2003. Within the same period, the wolf population in the Silesian Beskidy area fluctuated as the breeding pair of the Grapa pack repopulated the area in 1996, and then steadily grew when they successfully reproduced in 1998 and following years. In the spring of 2002, the pack split into two groups, with the original parents remaining in the area, while three individuals established a territory in an adjacent area (Nowak *et al.* 2008). Overall, the wolf population within the study area grew at a rate of approximately 8% per year, with the Silesian Beskidy population growing at a mean rate of 28% and the population of the Zywiecki Beskid region mostly remaining stable (Nowak *et al*. 2008).

This study will focus on the territories of two wolf packs, the Grapa pack and the Halny pack (Figure 2). Five wolf packs inhabit the region around the study area; however, due to problems associated with accessibility, border crossing logistics, and lack of data, only the territories of these two packs were examined for this study. The Grapa pack occupies a territory within the Landscape Park of the Silesian Beskid Mountains, while the Halny pack inhabits a territory that lies within the Zywiecki Landscape Park, bordering the Slovakian border.

FIGURE 1: MAP OF POLAND WITH STUDY AREA MARKED
(Modified from Google Earth, 2011)

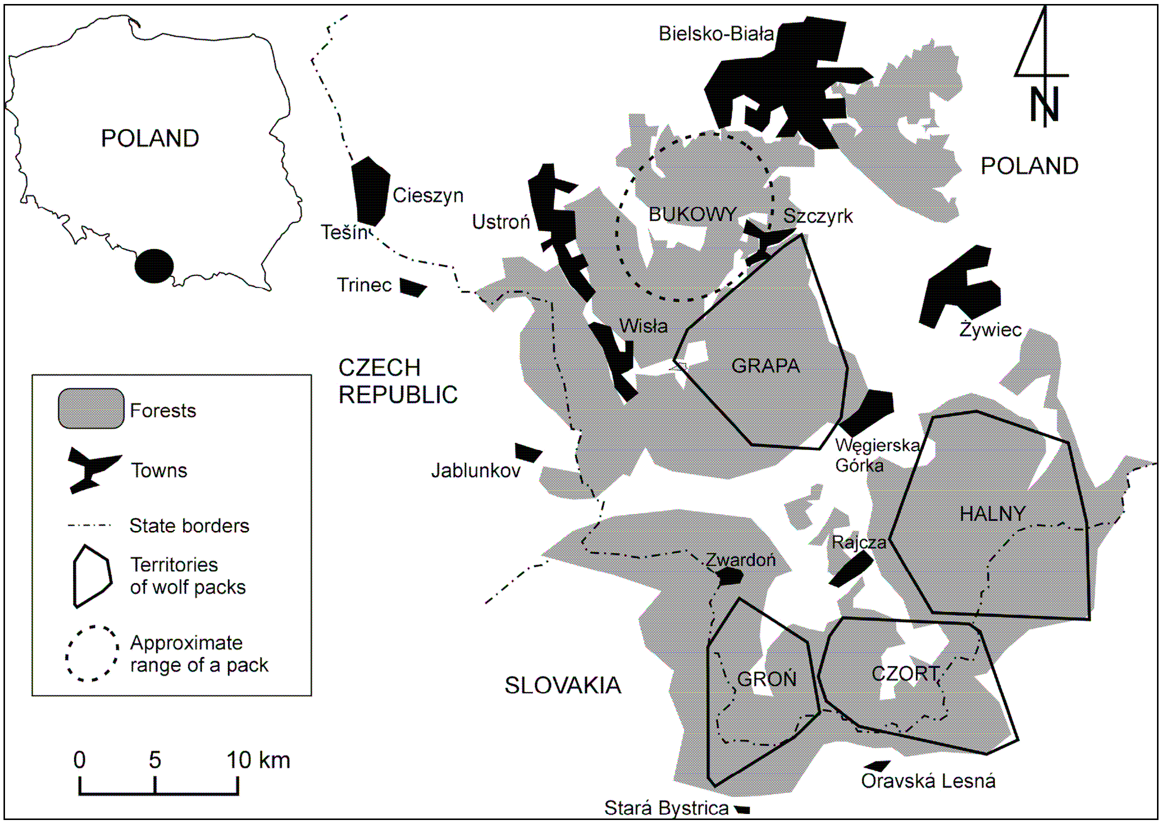

FIGURE 2: MAP OF PACK TERRITORIES (adapted from Nowak *et al.* 2008)

SOCIAL STRUCTURE AND REPRODUCTION

Wolves live in family-based social groups called packs, normally consisting of a male, female, newborn and older pups, and occasionally adults from other packs (Mech 1970). The breeding pair of wolves in the pack, also called the "alpha" wolves, generally guides the pack and takes responsibility for the division of labor within a pack (Mech 1970). The males usually act as the hunters and are responsible for providing food, while the females serve as caretakers for the pups in the pack (Mech 1999). The alpha pair breeds once per year, normally between the months of January and April (Mech 1970). Breeding begins at 2 to 3 years of age and the average litter size is 4-7 pups (Person and Russell 2009; Fuller 1989; Mech 1970; Okarma *et al.* 1998). Denning typically occurs in sandy soils where dens can be excavated, or under roots of fallen trees **(**Theuerkauf *et al.* 2003**,** Mech 1970, Fuller 1988). Rendezvous sites are also used as places where young wolves remain for several days, waiting for the adults of the pack to return from hunting excursions. These are mostly located in areas located far from roads and with at least some forest cover (Theuerkauf *et al.* 2003; Ballard and Dau 1983).

The number of individuals in a pack can vary greatly, both between packs and from year to year. This variation depends on a combination of factors, including successful reproduction, survival of pups, individual dispersal rates, and availability of prey (Mech 2007; Fuller 1989). It is common for wolves not belonging to the breeding pair of their pack to disperse during the spring months in an effort to form their own pack. This generally occurs when the dispersers reach two or three years of age (Fritts and Mech 1981, Fuller 1989). These dispersers often travel several hundred kilometers to find new territories and other dispersers of the opposite sex, resulting in the formation of a new pack (Gese and Mech 1991; Fuller 1989). Dispersion is extremely important in maintaining a wide gene pool between packs, lessening the chances for inbreeding.

Unlike many other large carnivores, wolves are extremely adaptable animals in many respects. This is partly due to their ability to quickly replace their numbers when given the chance. Wolves reach sexual maturity at an early age and are capable of producing large litters. They are able to modify pack structure in response to changing levels of mortality and regional prey abundance. Wolves accomplish this through altering fertility levels, the dispersion of individuals from one area to another, and changing their tolerance of other wolves in neighboring areas (Fritts and Mech 1981).

TERRITORY AND HABITAT

When it comes to habitat, wolves are very adaptable animals, basically able to occupy any habitat that can sustain their prey (Mech 1995). Some studies suggest that the main limiting factor for wolves, after human tolerance, is prey availability (Fuller *et al.* 1992, Carroll *et al.* 2000). In the northern Apennines in Italy, wolf presence was positively influenced by the availability of ungulate prey (Massolo and Meriggi 1998, Ciucci *et al.* 2003). In India, wolves were found to inhabit an alluvial plain and mosaic of croplands and grasslands in order to take advantage of large ungulate populations (Jethva and Jhala 2004).

Each wolf pack establishes a territory in which they hunt, raise pups, and defend from other packs. Mech (1970) found that two factors are mostly responsible for determining how large a pack territory is: the number of wolves in a pack, and the abundance of prey within a territory. In territories where prey is scattered and less abundant, territory size must be larger to ensure that there is enough prey to feed the pack (Ashenafi *et al*. 2005; Fuller 1989). In Poland, the average territory size of a wolf pack is

200 km^2 (Jedrzejewski *et al.* 2007), whereas territory size in winter in Minnesota ranged from 78-153 km^2 (Fuller 1989). Okarma *et al.* (1998) observed home ranges of 141-168 km^2 from May-September in the Bialowieza Primeval Forest in Poland, while winter home ranges in the same area varied from 99-271 km^2. Fritts and Mech (1981) found that wolf packs in northwestern Minnesota used the same territories during both summer and winter, averaging 344 km^2 in area. A review of home ranges of Eurasian wolves done by Okarma *et al.* (1998) found the largest home ranges in northern Scandinavia (415-500 km^2) and the smallest home ranges in areas of southern and central Europe (80-240 km^2). The researchers found that territories were largest in low-density colonizing populations, while packs living in established populations tended to have smaller home ranges.

Within each territory, wolves select a core area. This area is where a wolf pack spends the majority of its time, particularly during the denning and pup-rearing periods. Other areas within the core area are also selected for rendezvous sites, or areas in which young wolves wait for adult wolves to return from a hunt; and resting sites, where wolves rest for a short time, but do not return to. In a study done in the Bialowieza Primeval Forest, located on the Polish-Belarussian border, Okarma *et al*. (1998) found that core areas comprised 11-23 km^2 and made up 5-13% of the total home range. Also in the Bialowieza Forest, Jedrzejewski *et al*. (2007) found that the average core area comprised 17% of the average territory. Silva and Talamoni (2004) found that maned wolves in Brazil used a core area that equated to 3.8% of their total territory. Person and others (1996) reported that wolves in southeastern Alaska occupied territories of 280 km^2, and core areas of 124 km^2 (44.2% of the territory). In northwestern Minnesota, Fritts and Mech (1981) detected seasonal changes in the intensity of use of different parts of territories.

Wolves, like many large mammals, mark their territories using several different methods, including urine, scat, and ground scratching (Peters & Mech 1975, Mech and Boitani 2003, Barja *et al*. 2004). These marks are very important in olfactory communication. Wolves mark in order to assert dominance over other wolves, for marking territories to warn other wolves of their presence, for spatial orientation, and in the pair-bonding process (Peters & Mech 1975; Rothman & Mech 1979; Harrington 1981; Asa *et al*. 1984; Paquet & Fuller 1990; Vila *et al*. 1994). Intensity of marking can be affected by the presence of marks from other individuals, by the presence of specific landmarks (e.g. tree stumps), and by other stimuli (Peters & Mech 1975).

The different methods of marking have been studied frequently (Peters & Mech 1975; Paquet 1991; Asa *et al*. 1985), including the use of scat to mark territories (Zub *et al*. 2003). Two main theories concerning the pattern of territory marking by wolves with scat exist, the olfactory bowl pattern (Peters and Mech 1975), in which wolves equally distribute scats along the edges of their territory, and the hotspots pattern (Zub *et al*. 2003), in which wolves densely mark certain areas within their territories they deem the most valuable. Due to the energy required to mark locations with scats, it would make sense that those areas marked with wolf scats are considered to be the most valuable to them, whether they are territory boundaries or possible den sites. Barja *et al*. (2005) examined the patterns of wolf scat marking along roads within territories and found that Iberian wolves tended to leave scats on conspicuous objects in territory areas outside the den area. Asa *et al*. (1985) found that captive wolves deposited most of their feces near the gate to their enclosure, where their caretakers entered. Many studies have found that it is common for wolves to deposit scat at junctions (Barja *et al*. 2004; Vila *et al*. 1994). Several researchers (Barja *et al*. 2004; Vila *et al*. 1994) have proposed that wolves do this to maximize the chances of the scats being detected by other animals, including other wolves. This pattern of marking also reduces the number of scats needed to mark territories, thus minimizing the energetic costs of territory marking (Zub *et al*. 2003).

DIET

Wolves can be classified as opportunistic predators, as they prey on animals that take the least energy to kill. As a result, most wolf kills are the injured, young, or old individuals of prey populations (Mech 1970). In this way, wolves help keep prey populations healthy and improve the gene pool of prey species over time by preying on genetically inferior individuals. Depending on the habitat and prey species available, wolves may primarily prey on different ungulate species, such as moose, elk, deer, caribou (*Rangifer tarandus*), or in the unique example of the coastal wolves of Canada, they may even prey on salmon (Mech 1970, Fuller 1989**;** Darimont and Paquet 2002). In the Far East of Russia, wolves were found to mostly prey on red deer, while taking smaller percentages of wild boar and roe deer. Fuller (1989) found that beaver were an important secondary prey during the spring months.

In areas with low densities of prey populations, wolves may result to preying on livestock (Mech 1995; Meriggi and Lovari 1996). Wolf depredation on livestock has proven to be a very significant challenge to human tolerance of wolves, particularly in areas where high depredation rates occur. However, the perception of wolves as livestock killers is generally exaggerated (Bangs *et al.* 1995) and modified animal husbandry practices often help reduce depredation by wolves (Mech *et al.* 2000; Gula 2008).

THE WOLF AS A TOP CARNIVORE

As a top predator within an ecosystem, the wolf has a significant impact on a variety of other species within the ecosystem, including the overall biodiversity of the system. As already mentioned, wolves help to regulate prey populations, particularly ungulates, by culling weaker individuals. In the absence of a top predator like the wolf, ungulate populations are able to explode. Because of the vast amounts of vegetation eaten by ungulates and other herbivores, certain species of vegetation can become depleted, causing the populations of smaller herbivores that normally feed on these species to collapse. The end result is a simplified food web and a loss of biodiversity (Terborgh *et al.* 1999).

In addition to the overpopulation of large herbivores as a result of the absence of a top carnivore like the wolf, meso-predators, such as the coyote, are also able to increase in numbers. As meso-predators tend to be more generalists in regard to diet, an explosion in their numbers can lead to a decline in the numbers of many species, thus also reducing biodiversity.

The presence of wolves not only helps deter the loss of biodiversity through the overpopulation of large herbivores and meso-predators, but can also help increase biodiversity. Wolves, as large carnivores, often leave behind carcasses for other scavengers to prey on (Wilmers *et al.* 2003). Omnivores, like grizzly bears, and other carnivores are likely to benefit from increased carrion availability (Murie 1944).

EFFECTS OF HUMAN ACTIVITIES ON WOLVES

Historically, the wolf has been greatly affected by human activity. In the early 1900s in the United States, wolves were exterminated throughout most of their historic range through the use of poisons, trapping, and organized wolf hunts, and large bounties were paid for each wolf pelt that was collected (Lopez 1978). Similar occurrences took place in Europe over the last two centuries, and most wolf populations in Western Europe collapsed, reaching a low in the 1940's to 1960's (Salvatori and Linnell 2005).

Recently, the indirect effects of humans have had the most significant detriment to wolves. Large carnivores often are considered good indicators of ecosystem integrity and health because of their sensitivity to landscape disturbances (Carroll *et al.* 2000; Landres *et al.* 1988). With increasing development occurring all over the world, forests are being destroyed and humans are starting to extend their reach into areas that had previously been mostly undisturbed. Habitat fragmentation, which is the subdivision of a large contiguous habitat into smaller fragments, is occurring at a faster pace now than at any other time in history. This is very harmful, in particular, to species like the wolf that require large tracts of land to survive (Noss 2001; Carroll *et al.* 2001). Habitat fragmentation results not only in habitat loss, but also a reduction in the existing habitat patch size and the isolation of the remaining habitat fragments. The end result is a collection of isolated, unviable animal populations because of a loss of genetic variability over time (Duke *et al.* 2001; Paquet *et al*. 2001; Pimm *et al.* 1988). In response to the threat of habitat fragmentation and isolation of animal populations, biologists have begun proposing the creation and protection of migratory corridors to facilitate genetic exchange between isolated populations (Maehr 1990; Paquet *et al.* 2001).

Several studies have shown that wolves tend to avoid developed areas and areas with high densities of roads (Jedrzejewski *et al.* 2004, Jedrzejewski *et al.* 2005, Mladenoff *et al.* 1995,Theuerkauf *et al.* 2003, Theil 1985). Fuller *et al.* (1992) found that nearly 90% of the wolves in Minnesota were located in townships with human densities less than 4 people per square kilometer. Jedrzejewski *et al.* (2004) found that the amount of forest cover, which is often associated with the extent of development in an area, was very important to wolf presence. From these studies, one can conclude that wolves tend to avoid humans when given the chance.

Humans are also responsible for direct mortality of wolves. In the western Carpathian Mts. in Poland and Slovakia, culls, including hunting mortality within the Slovakian regions and management actions taken by state forestry agencies, accounted for 83% of all recorded wolf deaths during an 8-year study (Nowak *et al.* 2008). When combined with collisions with motor vehicles (11%), humans were responsible for nearly all recorded deaths. Fritts and Mech (1981) also found that humans were directly responsible for the majority of wolf deaths in their study in Minnesota.

THE WOLF IN POLAND

Presently, Poland represents the western border of the contiguous geographic range of wolves in Europe (Boitani 2000; Jedrzejewski *et al.* 2004; Okarma 1993, Okarma 1997) (Figure 3). Situated between the largely undeveloped countries of Eastern Europe, where large populations of carnivores still exist, and the countries in Western Europe, where many populations of large carnivores have been eradicated or struggle to survive (Jedrzejewski *et al.* 2008), Poland can serve as a valuable link between these populations and habitats. The wolf has been protected throughout Poland since 1998, and current estimates put the wolf population at around 750 individuals (Nowak and Myslajek 2011). Viable wolf populations permanently inhabit the eastern part of the country, including Bialowieza Primeval Forest, near the Belarussian border (Theuerkauf *et al.* 2003). However, only a few packs and lone individuals inhabit western Poland, and many do not remain for more than a few years (Wolsan *et al.* 1992; Jedrzejewski *et al.* 2002). Southern Poland, including the Polish Carpathian Mountains, is also home to wolves

(Figure 4). On average, approximately 30 wolves inhabit the region each year (Nowak and Myslajek, pers. comm.). Average pack size in the southern mountains during the study period was approximately 4 wolves, with a maximum of 6 (Nowak and Myslajek pers. comm.).

In Poland, the majority of wolf populations inhabits managed forests (Jêdrzejewski *et al.* 2002), mostly consisting of coniferous plantations of pine, *Pinus silvestris,* in lowland areas and spruce, *Picea abies,* in mountains (Nowak *et al.* 2005). Roe deer, *Capreolus capreolus* comprises the majority of the ungulate community (>60%) in most of these exploited forests (Nowak *et al.* 2005, from Budna and Grzybowska 2000). In southern Poland, the wild ungulate community is made up of three species: roe deer, red deer (*Cervus elaphus)*, and wild boar (*Sus scrofa)*. Red deer was reported as being the most preferred prey in other regions in Poland, such as the Bialowieza Forest in eastern Poland (Jêdrzejewski *et al*. 1992, 2000, 2002) and the Bieszczady Mts, in the southeastern part of the country,(Śmietana and Klimek 1993), as well as in the study area (Nowak *et al.* 2005).

The average territory size of a wolf pack in Poland is approximately 200 km^2 (Jedrzejewski *et al.* 2007). In the western-most region of the Polish Carpathian Mountains, where the study site is located, Nowak *et al.* (2008) found the average wolf pack territory to cover approximately 158 km^2. In their 8-year study, Nowak *et al.* (2008) observed that in the Silesian Beskid Mountains, where no human hunting pressure occurred, the wolf population increased at an average rate of 28% per year. However, in the Żywiecki Beskid Mountains, where wolf territories overlapped with areas in Slovakia where hunting was allowed, no increase in population numbers was seen. Throughout the entire study area, mean population growth was 8% per year (Nowak *et al*. 2008).

The main threats to the future of the gray wolf in Poland are loss of habitat and planned development of transportation infrastructure. Wolves inhabiting the southern part of the country face significantly denser human settlements and transportation routes than those found in the north of Poland (Jedrzejewski *et al.* 2005). Wolves occupying the study area in southern Poland are also forced to contend with the threat of hunting, as the territories of many of these packs overlap areas in Slovakia, where wolf hunting is legal for two and a half months each year (Nowak *et al*. 2008). Compared with an average annual population growth rate of 28% in areas located completely within Poland, packs with territories extending into Slovakia failed to grow in numbers during the same 8-year period (Nowak *et al.* 2008). In fact, culling accounted for 83% of the recorded wolf mortalities in the region during this study period. Clearly, hunting within some wolf territories in southern Poland significantly impacts population numbers.

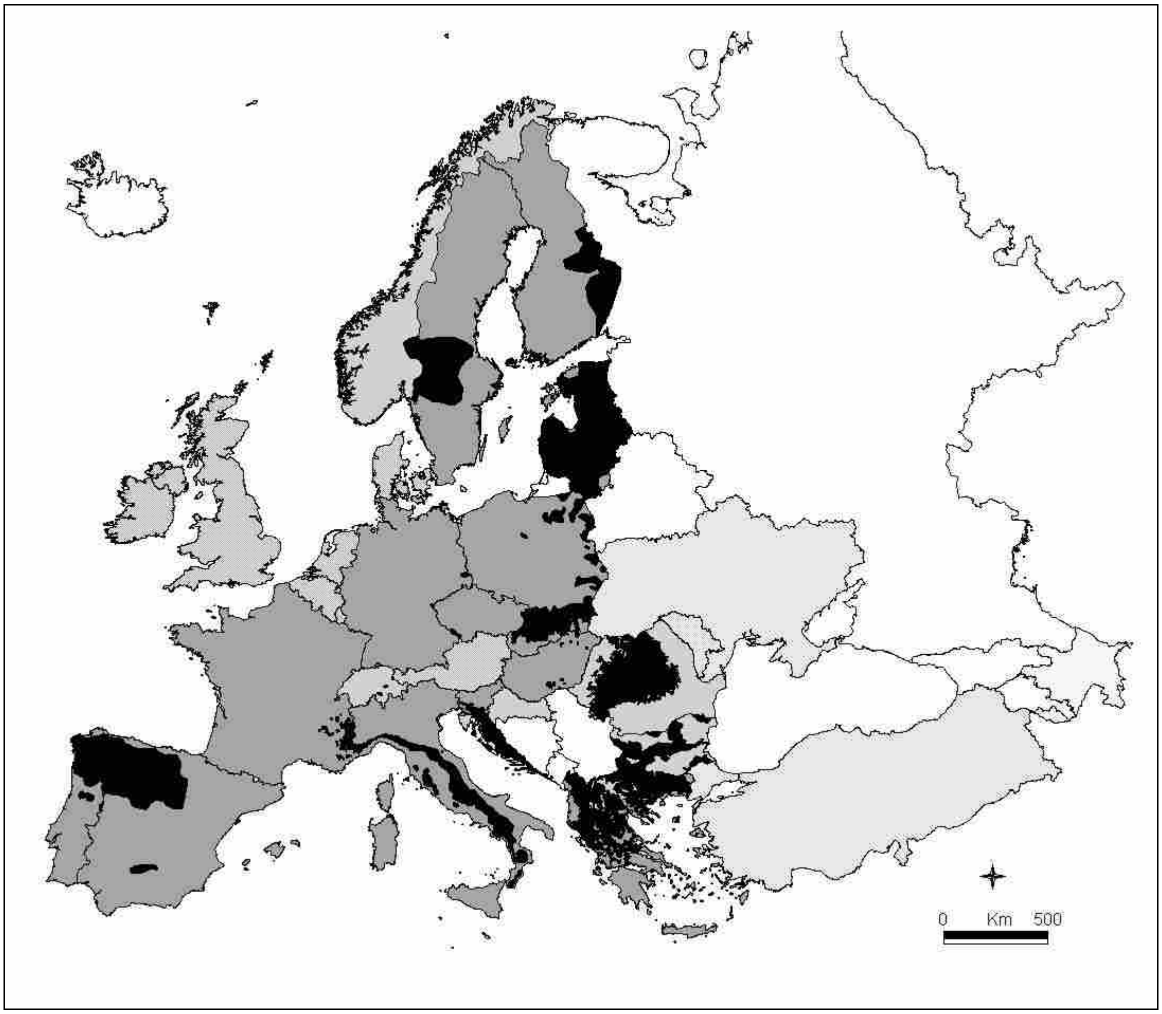

Figure 3: Wolf Distribution in Europe (adapted from Salvatori and Linnell 2005). Wolf occurrence is shown in black.

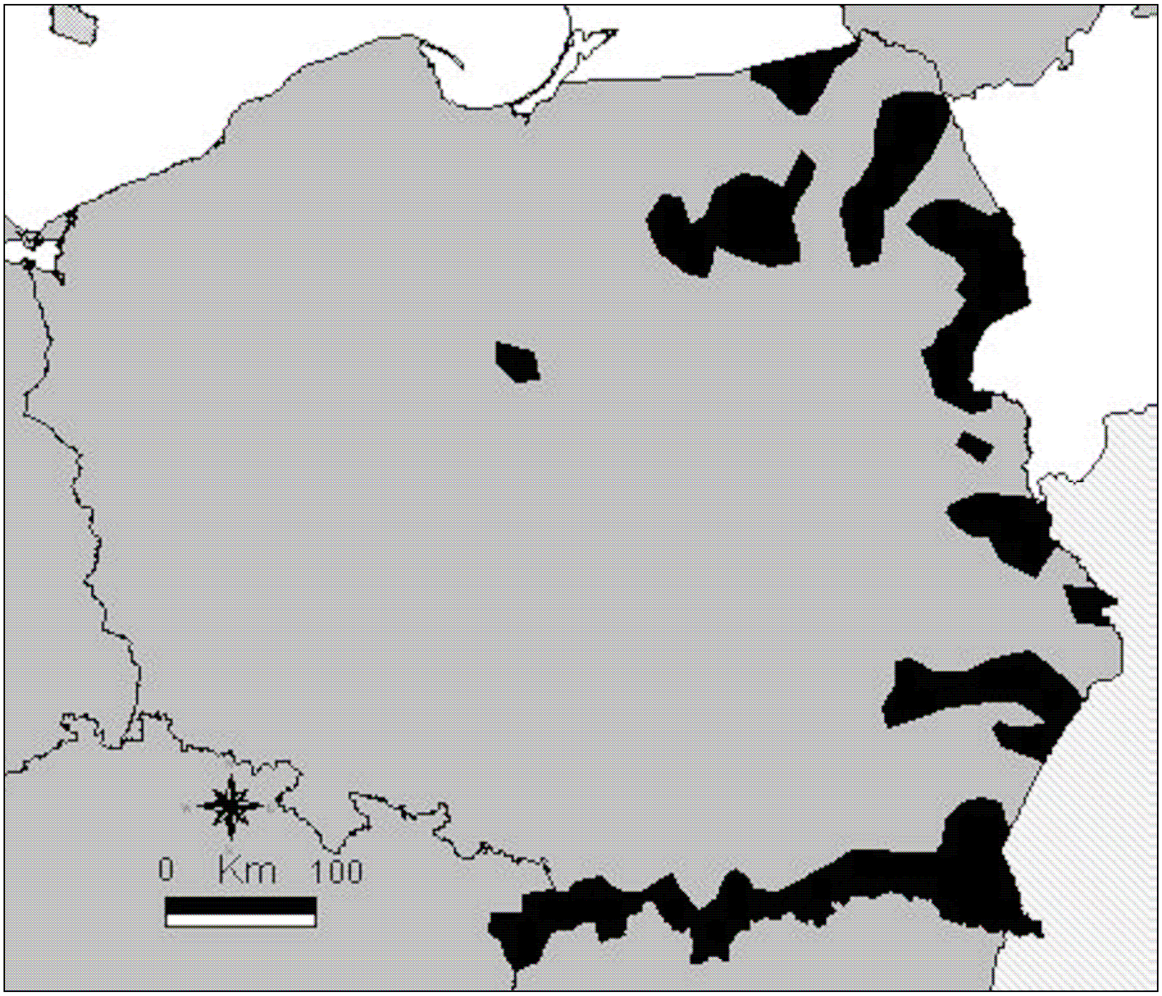

Figure 4: Wolf Presence in Poland (adapted from Salvatori and Linnell 2005)

DETERMINING WOLF TERRITORY AND CORE AREAS

The first step in identifying valuable areas for wolves is the determination of a territory or home range. This is basically the measure of how much space a wolf pack uses. The classic method of doing this involves creating Minimum Convex Polygons (MCPs) to encompass different percentages (i.e. 50%, 75%, 95%, etc.) of animal location data. Generally, the 95% or 100% level is used to define an animal's territory (the smallest polygon that encompasses either 95% or 100% of all animal locations). The advantage of MCPs is that they are easily compared between studies and are the most commonly used method for estimating territory or home range sizes (Harris *et al.* 1990).

Recently, advances in technology have enabled researchers to estimate territories and home ranges in new ways using contouring methods. These nonparametric methods are valuable in estimating complex probability density distributions and are capable of handling multiple centers of activity (Hemson *et al.* 2005). In short, these methods differ from MCPs by indicating centers of activity and how intensely different areas of an animal's range are used. The most commonly used and most reliable method is known as kernel density estimation, which describes the probability of finding an animal in a given place. This method consists of placing a kernel (a probability density) over each data point in the sample and then superimposing a rectangular grid over the data. A density estimate is obtained at each grid intersection by averaging the densities of all the kernels that overlap that point. Data records located near the point of evaluation will have a greater influence on the estimated density value than records located further away. Therefore, areas in which a large number of records exist will have a higher density estimate than those areas where there are only a few records. Home range estimates or core estimates are derived by drawing contour lines, or isopleths, based on the summed volumes of the kernels at grid intersections (Rodgers and Kie 2007). These isopleths define home ranges at different probability levels. A variety of kernel methods exist, including the standard bivariate normal curve, the Epanechnikov, the uniform, the triangular, the biweight, and the triweight kernels. However, they all give essentially the same results (Epanechnikov 1969; Worton 1989; Wand and Jones 1995).

An important consideration when performing kernel density estimations is the width of the kernels, often known as the bandwidth or smoothing parameter (*h*). The bandwidth basically is what tells the software how far to look from one data point for other data points. Narrow kernels result in nearby data records having the greatest influence on the density estimate, therefore illustrating fine detail of the internal structure of a home range (Seaman and Powell 1996). However, extremely small values of *h* tend to undersmooth in outer density isopleths, resulting in discontinuous "islands" (Hemson *et al.* 2005). Wide kernels give the general shape of the data distribution, but are not suitable to fine scale analysis. Since the size and shape of home ranges and core areas produced from using different values of *h* can differ so greatly, the selection of an appropriate *h* value is of great importance.

When performing fixed kernel estimation, where the bandwidth remains constant, a common method for selecting the appropriate bandwidth is the process of least squares cross- validation (LSCV). This process includes the inspection of several different bandwidths and then the selection of the bandwidth that yields the minimum squared distance between the fitted surface and the target surface (Hemson *et al.* 2005). This function is given by the equation:

$$h_{lscv} = \frac{1}{\pi h^2 n} + \frac{1}{4\pi h^2 n^2} \cdot \sum_{i=j}^{n} \sum_{j=l}^{n} \left(\exp\left[-\frac{d_{ij}^2}{4h^2} \right] - 4\exp\left[\frac{d_{ij}^2}{2h^2} \right] \right)$$

where d_{ij} is the distance between the *i*th and *j*th points and *h* is a value of the smoothing parameter examined.

Another common method for determining the appropriate smoothing parameter in kernel density estimation is the reference smoothing factor (h_{ref}). This function is given by the equation:

$$h_{ref} = \sigma n^{-1/6}$$

where *n* is the number of locations and σ is the standard deviation of the *x* coordinates, with *y* coordinates transformed throughout the calculations to have the same standard deviation (Worton 1989).

If a fixed bandwidth is unsatisfactory, adaptive kernel density estimation can be performed. This involves varying the bandwidth used to search for neighboring data points. Adaptive kernels are generally used when the use of a fixed bandwidth would result in undersmoothing in areas with sparse observations while oversmoothing in areas with many observations (Kerm 2003). In an adaptive kernel analysis, a density estimate is initially performed with a fixed bandwidth to obtain a general idea of the density at each observation point. After this initial calculation is performed, the bandwidth value is changed inversely with the density of observations (Kerm 2003). A larger *h* value is used over observations in areas of low density, while a smaller *h* value is used in areas with higher densities of observations. However, due to the increased complexity of performing an adaptive kernel density estimation, as compared to a fixed kernel estimation, and the scarcity of computational tools for performing such an analysis, fixed kernel methods are more frequently used (Davies *et al.* 2011).

METHODS

The study site was surveyed for the presence of wolf scats from 1 January 2005 through 31 December 2007 by the founders of The Association for Nature WOLF, Sabina Nowak and Robert Myslajek. I assisted in data collection from February 2006 to December of 2007. During this period, the territories of two wolf packs in the region (based on the findings of Nowak *et al.* 2008) were explored through hiking and snowshoeing on existing recreational hiking paths and logging roads in the area (Figures 5 and 6). The territories were delineated in a previous study by Nowak and Myslajek (pers. comm.) by creating 100% Minimum Convex Polygons encompassing all recorded evidence of wolf presence, including scat locations, urine marks, track locations, howling locations, and wolf kills. Topographic maps of the area, scaled to 1:50,000, were used to locate all possible hiking trails and logging roads within each wolf pack territory. Many studies have shown that wolves tend to utilize dirt roads and trails, particularly during winter, as they provide easier routes of travel (Mech 1970; Fritts and Mech 1981; Paquet *et al*. 1996; Ciucci *et al*. 2003).

Researchers attempted to find and record data on each wolf scat located on or near these paths and roads. When wolf tracks were found crossing these trails and roads, the tracks were followed to inspect whether any scats were located at a location along the tracks. Trails and roads were sampled in a non-systematic fashion, as weather and road conditions occasionally resulted in some areas being inaccessible. This resulted in areas with easier points of access having much higher survey intensity than other areas, although efforts were made to survey the entire territories (Figure 7) where possible (the location of nearly half the Halny territory within Slovakia prevented survey of this area). On occasion, surveys were also conducted in areas adjacent to but outside territory boundaries to observe whether wolves were utilizing these areas. Using GPS units, records were made on the location of each scat site. Each scat was removed from the trail after records were taken, so as to avoid pseudoreplication. GPS coordinates for each scat were then inputted into ArcGIS 9.3 (ESRI, Redlands, CA) and analyzed.

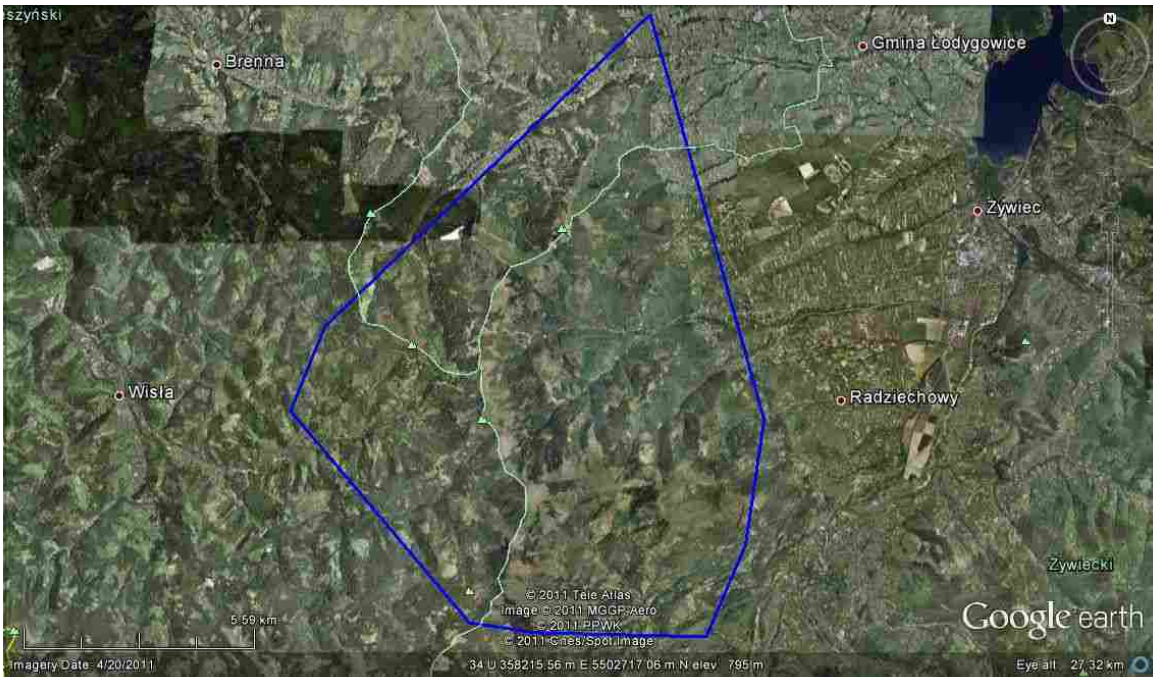

Figure 5: Grapa Territory

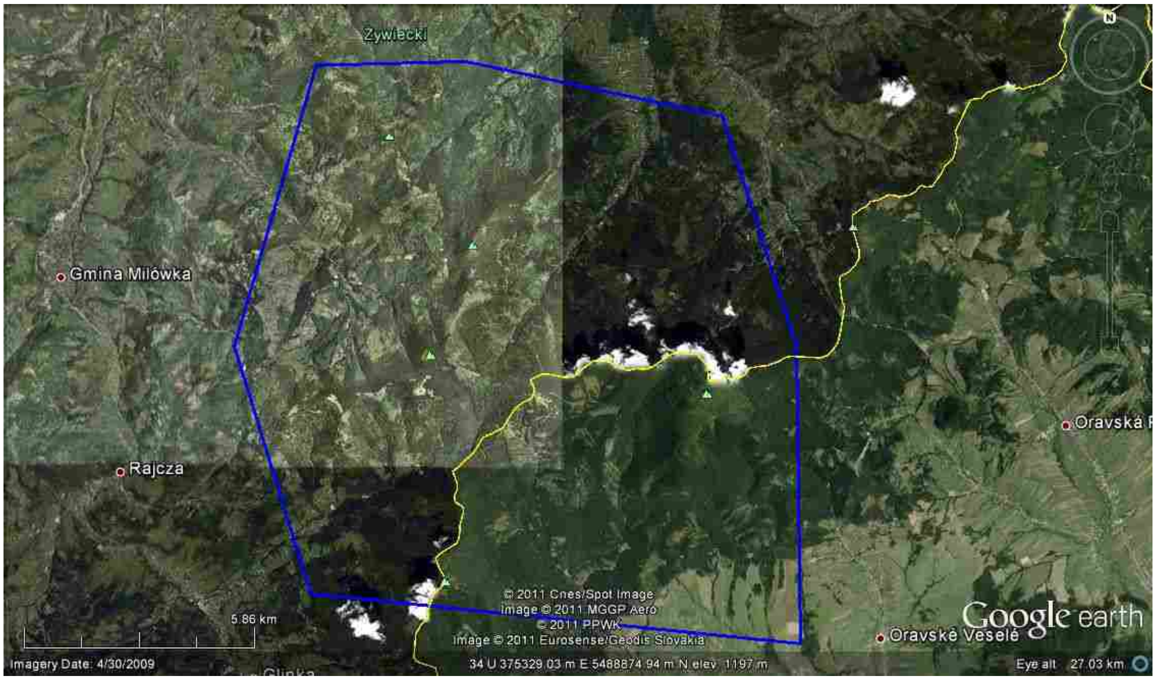

Figure 6: Halny Territory

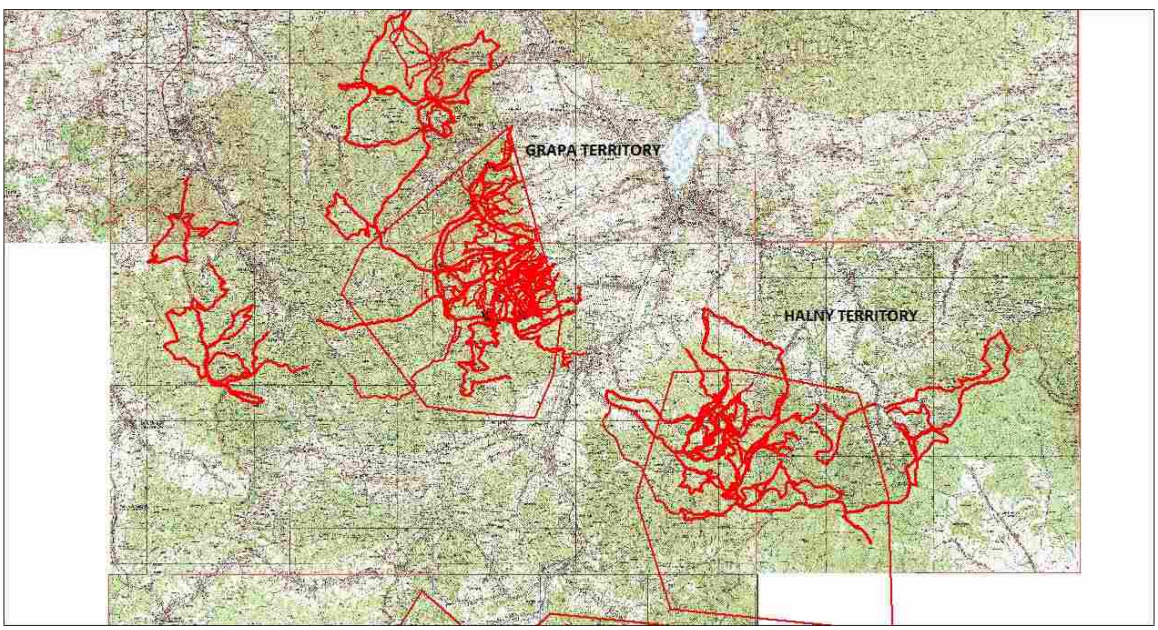

Figure 7: Tracking surveys conducted within study area, 2005-2007.

OBJECTIVE 1: OLFACTORY BOWL VS. HOT SPOTS PATTERN OF MARKING

ArcGIS 9.3 (ESRI, Redlands, CA) was used to examine the locations of wolf scats in relation to one another. In total, 177 scats were recorded during the three-year study period: 125 within the territory of the Grapa pack, and 52 within that of the Halny pack (see Tables 13 and 14, Appendix). Single fixed- kernel density estimation was used to analyze scat locations in each wolf pack territory. This analysis was performed using the Home Range Tools extension developed for ArcGIS 9.3 by Rodgers *et al.* (2007).

For the kernel analysis, I chose to use a fixed bandwidth equal to h_{ref}, or the reference bandwidth (Worton 1995) I decided against the use of an adaptive kernel because researchers have shown that in simulation studies, adaptive kernels tend to produce contours with more bias than did fixed kernels (Worton 1995, Seaman and Powell 1996). The method of calculating the bandwidth through the process of Least Squares Cross Validation (LSCV) was not chosen because when this *h* value was used, only small islands of areas with higher densities of scats were created and no core area was detected (Figures 6 and 7). Steiniger *et al.* (2010) also observed that h_{LSCV} was unacceptable when examining home ranges of grizzly bears in Alberta, Canada. Hemson *et al.* (2005) found that h_{LSCV} failed more than half the time when examining data sets consisting of more than 100 points, while also failing when examining intensively-used areas, such as core areas.

Based on the findings of Peters and Mech (1975), we would expect to see scats mostly concentrated around the perimeters of the territories of each pack, as these areas are the most vulnerable and most likely to be penetrated by wolves from other packs (Olfactory Bowl Pattern). However, Zub *et al*. (2003) found that wolves only marked certain areas within their territories that seemed to be more valuable to them, producing a hot spots pattern of marking.

Because scat locations were recorded over a period of three years, I had hoped to do separate analyses for each year, in addition to analyzing the data set as a whole, in order to detect whether any annual changes existed. However, due to an insufficient number of scat records, this proved to be impossible. In the case of the hot spots pattern found by Zub *et al.* (2003), those sites heavily marked would correspond to den sites, pup-rearing sites, and rendezvous sites, all comprising a core area where the wolves spent most of their time.

If areas with significantly higher densities of scats than surrounding areas were found, then these areas would be considered "hotspots," suggesting that these packs scat mark core areas more than territory boundaries.

OBJECTIVE 2: IDENTIFICATION OF CORE AREAS

After a single fixed- kernel density estimation was performed using the Home Range Tools extension (Rodgers *et al.* 2007) to ArcGIS 9.3, core areas were identified as areas contained within 50% probability isopleths, meaning the smallest area that yielded a 50% probability of finding a wolf scat in the area. Okarma *et al.* (1998) used 50% MCPs when looking at radiolocations to determine core areas. Person and others (1996) used MCPs including 75% of radiolocations to find core areas of wolves in southeastern Alaska. When studying Canada lynx, Burdett *et al*. (2007) found that core areas corresponded to 60% isopleths of radiolocations. I chose to use 50% isopleths to determine core areas because I wanted to be certain the area I was analyzing was located in a core area. Jedrzejewski *et al.* (2007) also used 50% MCPs to define core areas in their study of wolves in the Bialowieza Forest, Poland. Area values were calculated for each core using ArcGIS 9.3.

OBJECTIVE 3: COMPARISON OF HABITAT PARAMETERS ASSOCIATED WITH HUMAN PRESENCE BETWEEN CORE AREAS AND NON-CORE AREAS

Satellite imagery and land cover data for southern Poland was obtained from CORINE land cover data (European Environment Agency 2006) at a resolution of 100 meters. Using ArcGIS 9.3, 17 random circular plots within each wolf pack territory were generated, with 5 of those occurring within the territory's defined core area, and the remaining 12 located within the territory but outside the core area. Plot area was chosen based on the maximum area that would allow 5 plots of a given area to fit within the defined core area. This would likely differ between territories as I was expecting to find core areas of different sizes in each territory. Each randomly selected plot was examined in relation to 6 habitat parameters: 1) habitat type, 2) percent forest cover, 3) mean elevation, 4) density of roads (both public-use and special-use roads, such as logging roads and other roads closed to the public) and high-use trails, 5) distance to nearest primary road or highway, and 6) straight-line distance to nearest built-up area (defined as any area consisting of more than 5 human-inhabited dwellings).

These particular parameters were chosen because they are good approximates of human presence in these areas. Jedrzejewski *et al.* (2005) found that wolves in southern Poland selected habitats with more forest cover (mean 50.5%) and smaller densities of villages, railways, and roads. Road density has also been shown to negatively influence the presence of wolves (Mech 1989; Mech 1995; Maldenoff *et al.* 1995; Theil 1985) in several other areas. The density of roads and trails was examined, rather than the distance to the nearest road or trail, because of the small size of the study area and because numerous roads and trails bisect the area. It is extremely difficult to find an area of any significant size within the study area that is void of any roads or trails. Therefore, if the presence of roads and trails was a factor in core area selection, it would more likely be that the wolves were choosing to utilize areas with fewer roads and trails rather than areas distant from any. In areas where few roads and trails exist, the distance to any road or trail would seem more appropriate. However, the distance to the nearest primary highway was chosen because primary highways are good indicators of frequent human-use, whereas smaller roads in the mountains may only indicate seasonal or occasional use. Similar studies of wolf habitat suitability have also analyzed the distance to the nearest water source (Kusak *et al.* 2005), as this is important for wolf survival. However, many of these studies were conducted in areas where water sources were scarce. The area for this study is very mountainous, with numerous streams flowing down to the valleys in nearly every area. Therefore, this parameter was not believed to be a limiting factor in core area suitability, and was not analyzed during this study.

All forest cover data were obtained from CORINE land cover data (European Environment Agency 2006). These data were classified into 44 different habitat types (see Table 17, Appendix). In addition, data for broadleaf forest, coniferous forest, and mixed forest cover were combined to obtain forest cover values for each plot. All other habitat types were classified as non-forest cover. Mean elevation for each sample plot was calculated using ArcGIS 9.3 to analyze a raster produced from a digital elevation model of the study area obtained from the National Imagery and Mapping Agency. The raster was converted into polygons and the areas and elevations of all polygons located within each random plot were then calculated and a weighted average was obtained. Road densities (km/km^2) were calculated by digitizing aerial photos of the study area obtained from Google Earth (Google Earth Inc., Mountain View, CA). Shapefiles of the random plots generated in ArcGIS 9.3 were imported into Google Earth, and then all distinguishable roads and trails within each plot were digitized and measured. Densities were calculated in km/km^2. Distance to the nearest built-up area was also calculated in Google Earth. This distance was measured from the center of each random plot to the nearest area containing at least five human-built structures. I decided not to use the Corine land cover data for this analysis because of its scale of 100m x 100m, and I was unsure if a small group of houses or structures would be detected at that scale. A primary highway layer was obtained from CloudMade data, derived from OpenStreetMap, (available, at mapcruzin.com) and using ArcGIS 9.3, the distance from the center of each random plot to the nearest primary highway was measured.

Habitat parameters found within core plots and those found in plots located outside core areas were statistically compared using the Mann-Whitney U-test. This test was chosen because it does not assume a normal distribution of the data, can compare unequal sample sizes, and because it compares medians rather than means. I felt this was important as it was difficult determining exact distance measurements from plot centers to the nearest built-up areas, and a statistical test examining how medians compare rather than means would be less sensitive to small discrepancies in measurement.

RESULTS

OLFACTORY BOWL VS. HOT SPOT MARKING PATTERN

In total, 177 scats were analyzed within both wolf pack territories: 125 within the territory of the Grapa pack , and 52 within that of the Halny pack. Initially, in addition to testing whether the olfactory bowl or hot spots pattern prevailed, I had also hoped to test whether there was an annual change in this pattern within each territory. However, due to the small sample sizes and the inconsistencies in survey intensity between packs and also between years, this was not possible. Yearly totals can be found in Table 1.

	2005	2006	2007	TOTALS
GRAPA	78	12	35	125
HALNY	35	5	12	52
TOTALS	**113**	**17**	**47**	**177**

Table 1: Numbers of scats found within each wolf pack territory, by year, over the 3-year study period

The small number of scats found within all territories during 2006 was a result of very low sampling intensity. This was mostly due to the lack of volunteers and personnel available for tracking surveys. Recorded scat numbers increased during 2007 as survey intensity increased. Scat numbers were greatest for the Grapa pack (71% of total, n= 125), as the territory of this pack was the most accessible, allowing for increased survey intensity. Fewer scats were consistently found in the Halny territory due to difficulty of access and its location in the Slovakian border region.

One area in particular seemed to be very important for the Grapa pack, an area referred to as Hala Radziechowska. This area consists of a high ridgeline running through a large, open meadow. A major hiking trail bisects this area and 40 scats (32%) were found along or within 150 m of a 1.3 km stretch of this hiking trail. An area of only 0.4 km^2, comprising only 0.3% of the total territory area, contained nearly 1/3 the total number of scats found within the territory. Single scat locations and small groups of 2-4 scats were occasionally recorded outside this area, but there were no discernible groupings any larger than this (Figure 8).

Fixed-kernel density estimations were performed on scat locations of each pack, in order to detect any areas with significantly higher scat densities than surrounding areas. Reference bandwidths were used in all analyses.

The Grapa pack pattern of scat marking showed high densities of scats in a single area (Figure 9). This result suggests that the wolves of the Grapa pack were scat marking in hot spots, rather than in a uniform fashion around the territory periphery, as would have been observed if the olfactory bowl marking pattern was present.

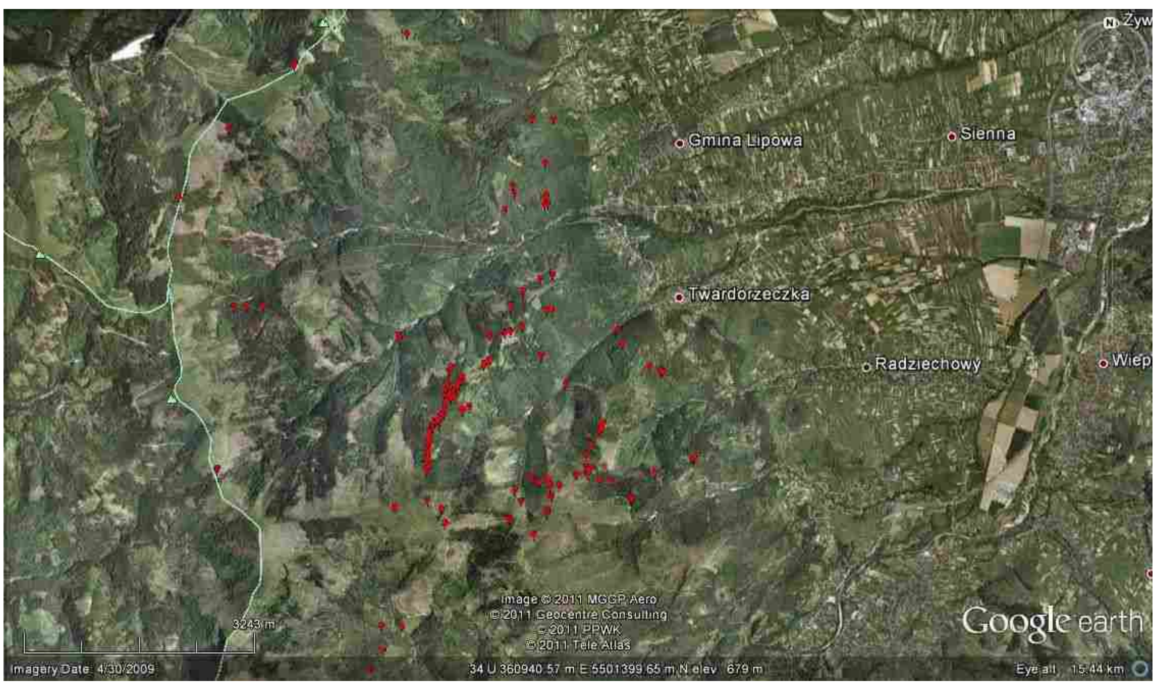

Figure 8: Grapa scat locations **(Modified from Google Earth, 2011)**

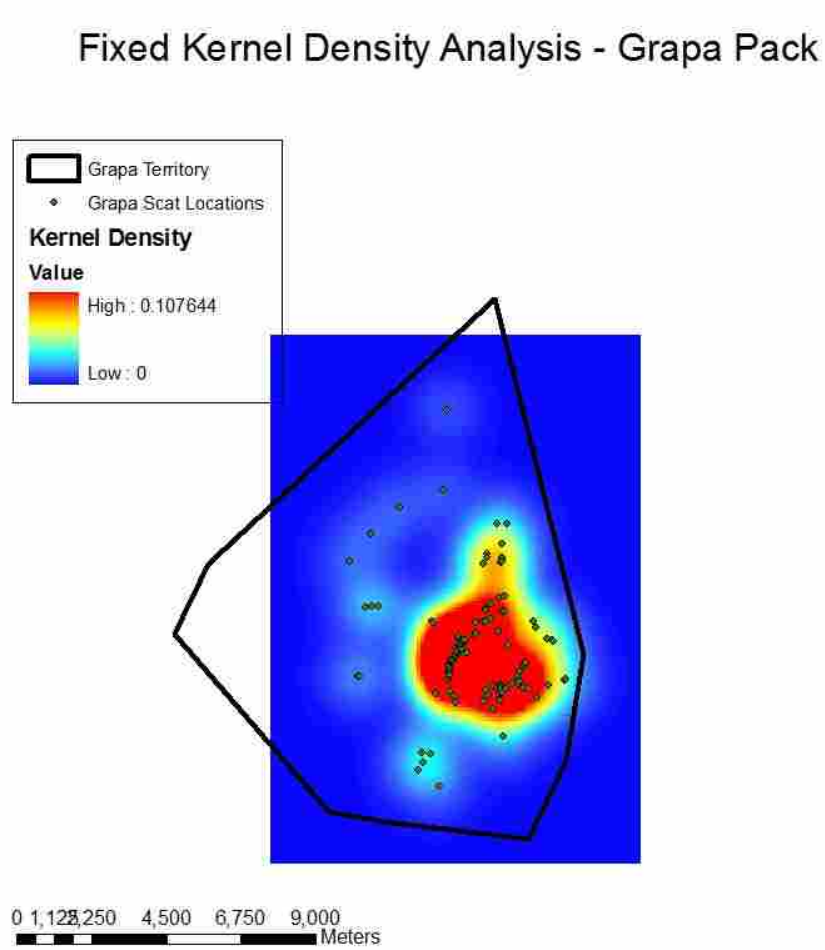

Figure 9: Fixed Kernel Density Analysis – Grapa Pack. Bandwidth of h_{ref} = 540.313m was used.

Like the Grapa wolves, the Halny wolves also seemed to scat mark most heavily in a single area (Figure 10). Two groups of scats were observed in this area. The first group was along a hiking path for approximately 700 meters, where 12 scats were deposited (23% of the total). The second group was along another hiking trail, for a distance of approximately 660 meters, where 11 scats (21%) were recorded. These two hiking paths were separated by a distance of only 575 meters. Therefore, 44% of the total number of scats was found in an area of roughly 0.49 km^2, or approximately 0.3% of the total territory size (Figure 10), which is very similar to the pattern of scat marking by the Grapa pack. No scats were found along the southwestern border of the Halny territory, which was the only border adjacent to another territory. This would seem to refute the Olfactory Bowl pattern, and support the Hot Spots pattern. However, we need to be careful with these data because only a small section of the adjacent territory borders was surveyed, as much of the area is located in Slovakia, where tracking was prohibited.

Fixed kernel density analysis showed the presence of one hot spot where scat density was much higher than surrounding areas (Figure 11). This area encompassed both trails mentioned above along which several scats were found. Therefore, we can only conclude that from the limited data collected, the Hot Spots pattern seems to be more prevalent.

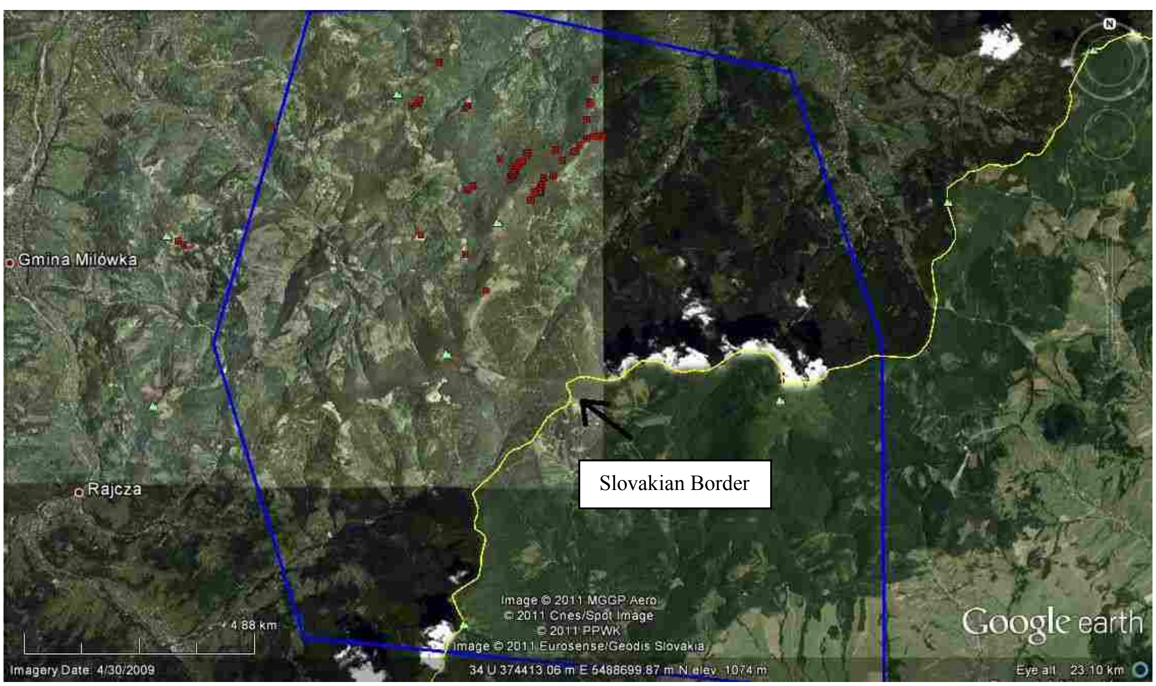

Figure 10: Halny scat locations (Modified from Google Earth, 2011)

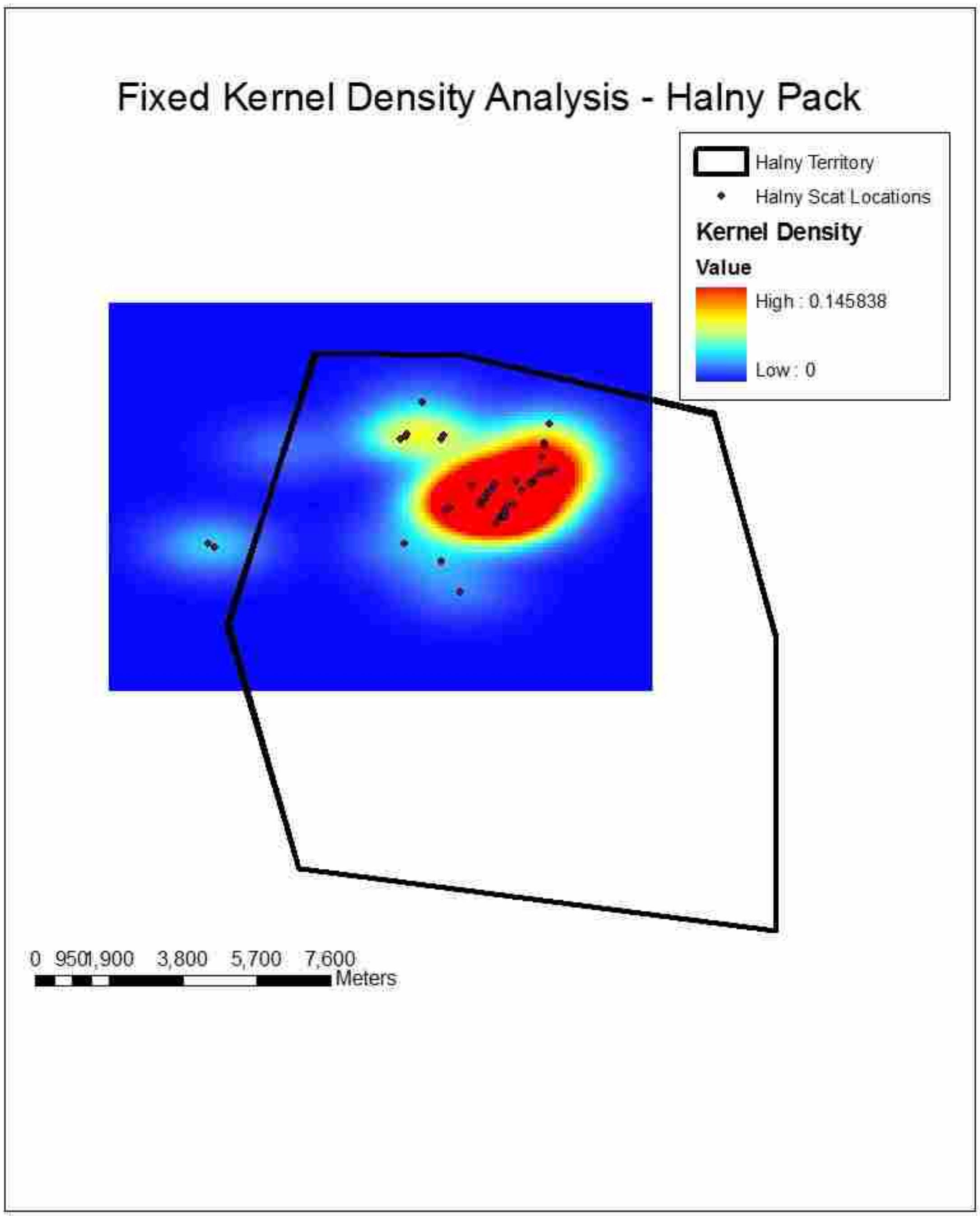

Figure 11: Fixed Kernel Density Analysis – Halny Pack. The Home Range Tools extension (Rodgers *et al.* 2007) for ArcGIS was used to transform the x and y coordinates to obtain similar variances. After transformation, the h_{ref} bandwidth of 0.517m was used.

IDENTIFICATION OF CORE AREAS

Kernel density analysis performed on scat locations of each wolf pack yielded areas of higher density than surrounding areas. Isopleths were produced at the 50%, 90%, and 95% levels. Based on previous studies, isopleths at the 50% level were considered to delineate core areas.

The 50% isopleth produced from the kernel density analysis of the Grapa scat locations covered an area of 8.29 km^2 (Figure 12). This constituted 6.8% of the whole territory area (122 km^2).

The 50% isopleth produced with the Halny scat data covered an area of 5.68 km^2 (Figure 13), which comprised only 3.2% of their territory (175 km^2). Table 2 shows the areas of the isopleths generated during fixed-kernel density estimations of both pack's scat locations.

Areas of Isopleths (km^2)		
Isopleth	Grapa Pack	Halny Pack
50%	8.29	5.68
90%	36.13	26.78
95%	53.64	36.69

Table 2: Areas of Isopleths Generated By Fixed-Kernel Density Analysis Using A Reference Bandwidth

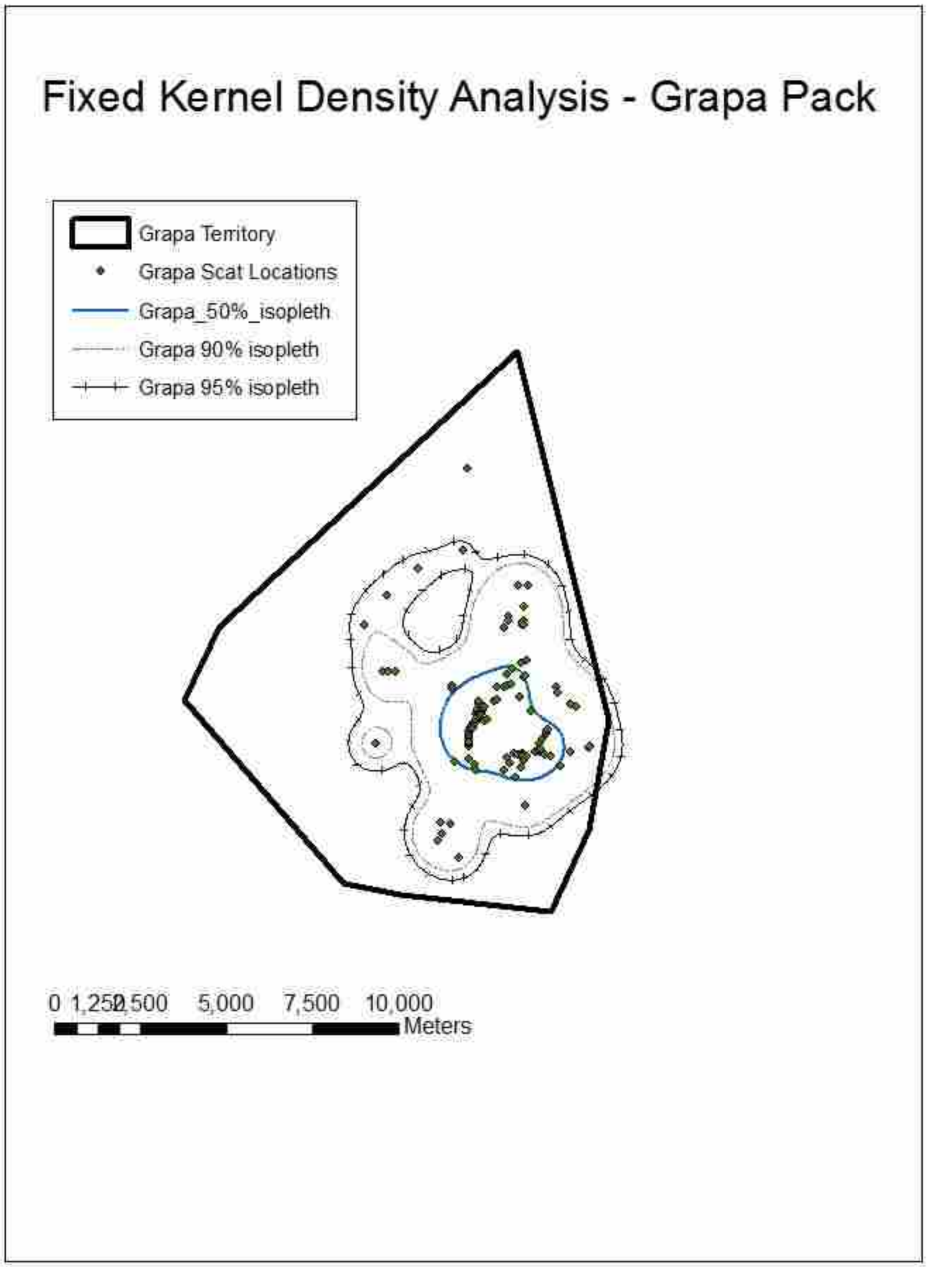

Figure 12: Isopleths Produced from Fixed-Kernel Density Estimation, Grapa Pack.

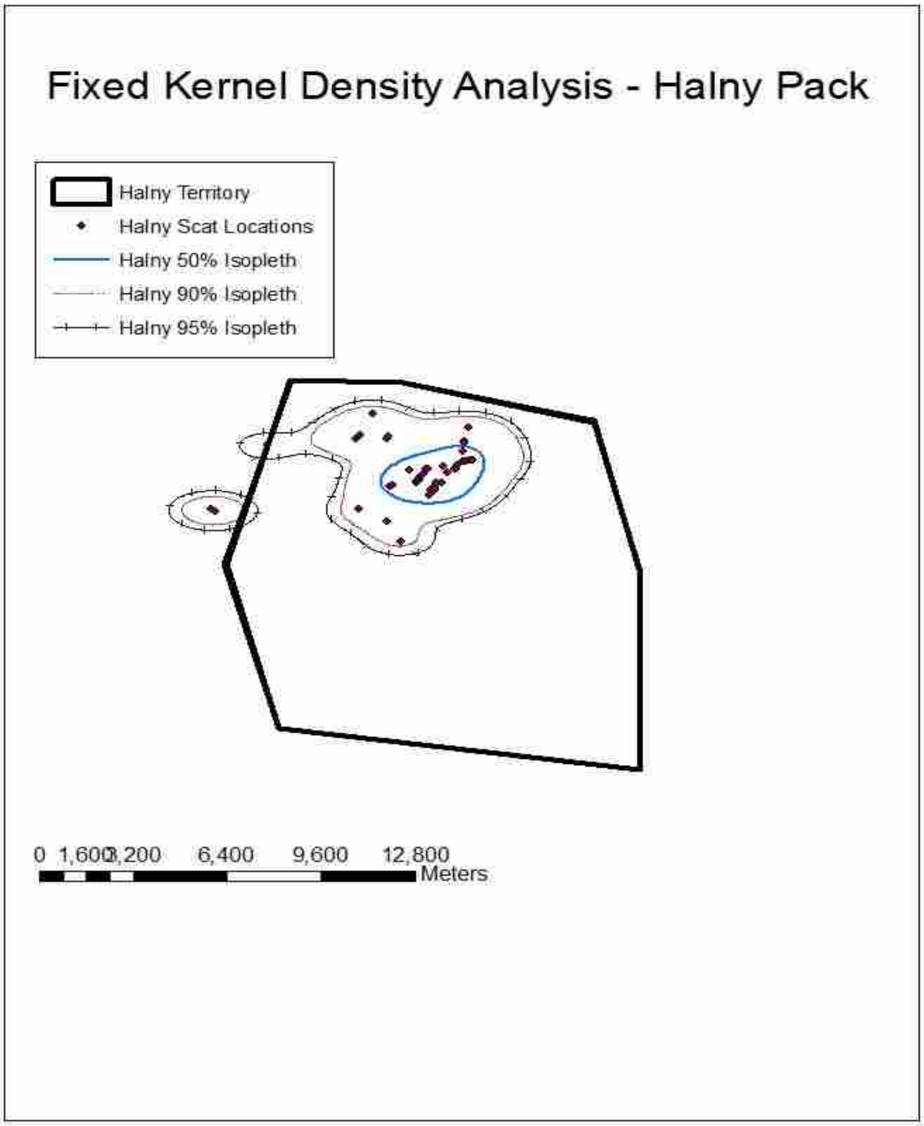

Figure 13: Isopleths Produced from Fixed-Kernel Density Estimation, Halny Pack.

COMPARISON OF HABITAT PARAMETERS TO DETERMINE RELATIONSHIP BETWEEN SCAT LOCATIONS AND EXTENT OF HUMAN PRESENCE

Fixed-kernel density analysis produced core areas of 8.29 km^2 and 5.68 km^2 for the Grapa and Halny packs, respectively. Based on these areas, I chose to generate circular random plots of size 0.785 km^2 (radius = 0.500 km) for the Grapa territory and 0.502 km^2 (radius = 0.548 km) for the Halny territory. These sizes were chosen to enable the generation of five random circular plots within each core area, and 12 outside the core areas in each territory (Figures 14 and 15), to allow for subsequent habitat analysis.

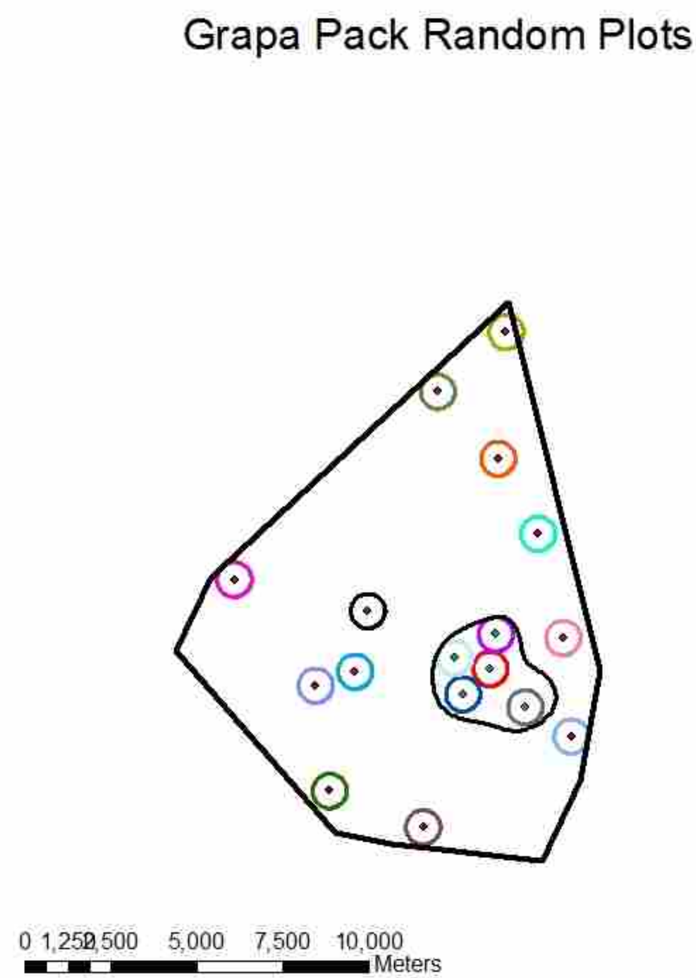

Figure 14: Random points and plots generated in Grapa territory. 5 random points were generated within core area, and 12 outside. Then circular plots with radius of 0.500 km were created around these points.

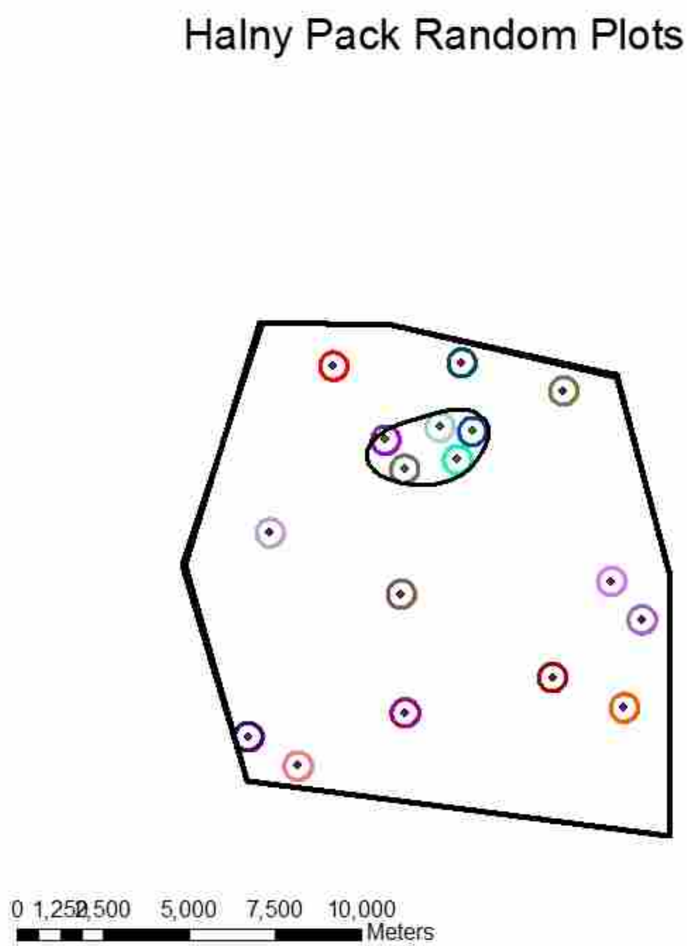

Figure 15: Random points and plots generated in Halny territory. 5 random points were generated within core area, and 12 outside. Then circular plots with radius of 0.500 km were created around these points.

LAND COVER

GRAPA PACK

Table 3 shows that coniferous forest comprised the majority of area within both core plots (mean = 54.7%) and non-core plots (mean = 63.5%). Core plots, on average, included more area of broad-leaved forest (19.9%) than did non-core plots (1.9%), and a Mann-Whitney U-test (see Table 18, Appendix) showed this result to be significant ($z = 2.0028$, $p > 0.0226$). Core plots also tended to have more mixed forest cover (mean = 18.6%) than non-core plots (6.9%), although this wasn't significant at the 95% level ($z = 1.3472$, $p > .089$). Both core and non-core plots showed similar areas of transitional woodland-shrub (core mean = 6.8%; non-core mean = 8.0%). Areas of discontinuous urban fabric, non-irrigated arable land, and agricultural area were rare in both core and non-core plots, with only a few plots containing any. Both core (mean = 93.2%) and non-core plots (mean = 72.3%) were characterized by high percentages of forest cover.

Grapa Pack

Land Cover	Core Plots Mean (%)	Core Plots Min-max	Non-Core Plots Mean (%)	Non-Core Plots Min-max
Broad-leaved forest	19.9	0 - 60.8	1.9	0 - 16.5
Coniferous forest	54.7	33.4 - 91.1	63.5	0 - 100
Mixed forest	18.6	0 - 36.3	6.9	0 - 60.1
Transitional woodland-shrub	6.8	0 -25.1	8.0	0 - 33.6
Natural grasslands	0	0 - 0	0	0 - 0
Complex cultivation patterns	0	0 - 0	5.5	0 - 23.4
Discontinuous urban fabric	0	0 - 0	5	0 - 51.9
Land principally occupied by agriculture, with significant areas of natural vegetation	0	0 - 0	2.4	0 - 28.3
Non-irrigated arable land	0	0 - 0	6.8	0 - 52.5
Forest Cover	93.2	74.9 - 100	72.3	0 - 100
Non-Forest Cover	6.8	0 - 25.1	27.7	0 - 100

Table 3: Land Cover for Random Plots, Grapa Territory. Forest cover values include broad-leaved forest, coniferous forest, and mixed forest cover. Non-forest cover includes all other types of land cover.

HALNY PACK

Both core and non-core plots within the Halny territory mostly consisted of coniferous forest (Table 4). Mean percentage of coniferous forest cover in core plots was 71.5%, while only slightly lower in non-core plots (58.8%). Core plots consistently contained more area of mixed forest cover (mean = 25.0%) than non-core plots (mean = 6.6%), but this difference was not shown to be significant ($z = 1.792$, $p > 0.0366$). Both core and non-core plots had very little broad-leaf forest cover (core mean = 0.5%; non-core mean = 4.7%). Non-core plots consisted of more transitional woodland-shrub (mean = 19.9%) than did plots within the core area (mean = 3.0%), although this difference did not prove to be significant ($z = 1.2649$, $p > 0.103$). Two non-core plots had large areas of land categorized as complex cultivation patterns, while this land cover was not found in any other non-core plot or core plot. Small areas of non-irrigated arable land and agricultural land were found in a small percentage of the non-core plots, but were not found within core plots. Both core (mean = 97.0%) and non-core (mean = 70.0%) plots were characterized by large percentages of forest cover. This difference (see Table 19, Appendix) proved to be significant at the 94% level ($z = 1.8974$, $p> .0289$).

Halny Pack

Land Cover	Core Plots Mean (%)	Core Plots Min-max	Non-Core Plots Mean (%)	Non-Core Plots Min-max
Broad-leaved forest	0.5	0 - 2.6	4.7	0 - 56.6
Coniferous forest	71.5	53.7 - 86.8	58.8	7.9 - 100
Mixed forest	25.0	0 - 44.7	6.6	0 - 56.6
Transitional woodland-shrub	3.0	0 - 15.0	19.9	0 - 83.6
Natural grasslands	0	0 - 0	7.6	0 -63.7
Complex cultivation patterns	0	0 - 0	0	0 - 0
Discontinuous urban fabric	0	0 - 0	2.0	0 - 23.8
Land principally occupied by agriculture, with significant areas of natural vegetation	0	0 - 0	0.4	0 - 4.7
Non-irrigated arable land	0	0 - 0	6.8	0 - 52.5
Forest Cover	97.0	85 - 100	70.0	16.1 - 100
Non-Forest Cover	3.0	0 - 15.0	30.0	0 - 83.9

Table 4: Land Cover for Random Plots, Halny Territory. Forest cover values include broad-leaved forest, coniferous forest, and mixed forest cover. Non-forest cover includes all other types of land cover.

ELEVATION

GRAPA PACK

Elevations within core plots were more uniform compared to those within non-core plots. Mean elevation of core plots ranged from 823m - 974m, while the range of non-core plots was 493m - 1135m (see Table 5). Most of the core area included mountainous areas, with few areas of valley bottoms (Figure 16). Non-core plots included more valley bottoms, but also a few of the higher peaks not located within the core area. Mean elevation of core plots (909m) was slightly higher than that of non-core plots (830m). Mann-Whitney U-tests (Table 20, Appendix) showed no significant difference ($z = 0.8433$, $p > 0.1995$) between the two groups.

GRAPA PACK					
Core Plots		Non-core Plots			
Plot	Elevation (m)	Plot	Elevation (m)	Plot	Elevation (m)
Core1	887	Terr1	693	Terr7	633
Core2	823	Terr2	632	Terr8	1014
Core3	974	Terr3	736	Terr9	493
Core4	928	Terr4	790	Terr10	959
Core5	934	Terr5	1135	Terr11	926
		Terr6	1093	Terr12	854

Table 5: Mean elevations for random plots within the Grapa territory.

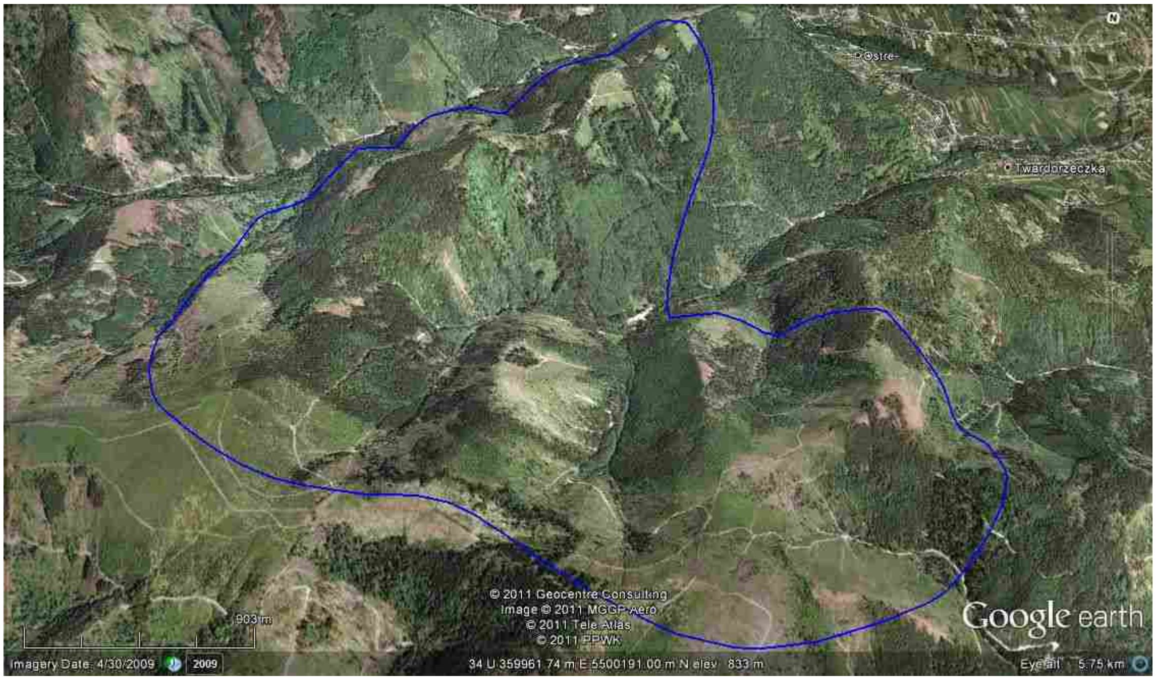

Figure 16: Topography of the Grapa Core Area. Core is delineated in blue.
(Modified from Google Earth, 2011)

HALNY PACK

Similar to those of the Grapa pack, the Halny core plots seemed to be more consistent in elevation, with a range of 861 m – 1191 m (Table 6), than non-core plots (670 m – 1345 m). Core plots were concentrated around the higher elevations of the mountains and did not include valley bottoms (Figure 17), yielding a higher mean elevation (1072 m) than non-core plots (976 m). However, a Mann-Whitney test (Table 21, Appendix) showed no significant difference ($z = 0.5270$, $p > 0.2991$).

HALNY PACK					
Core Plots		Non-core Plots			
Plot	Elevation (m)	Plot	Elevation (m)	Plot	Elevation (m)
Core1	1191	Terr1	1345	Terr7	670
Core2	1066	Terr2	932	Terr8	1241
Core3	861	Terr3	1267	Terr9	1141
Core4	1101	Terr4	785	Terr10	836
Core5	1141	Terr5	862	Terr11	676
		Terr6	1191	Terr12	762

Table 6: Mean elevations for random plots within the Halny territory.

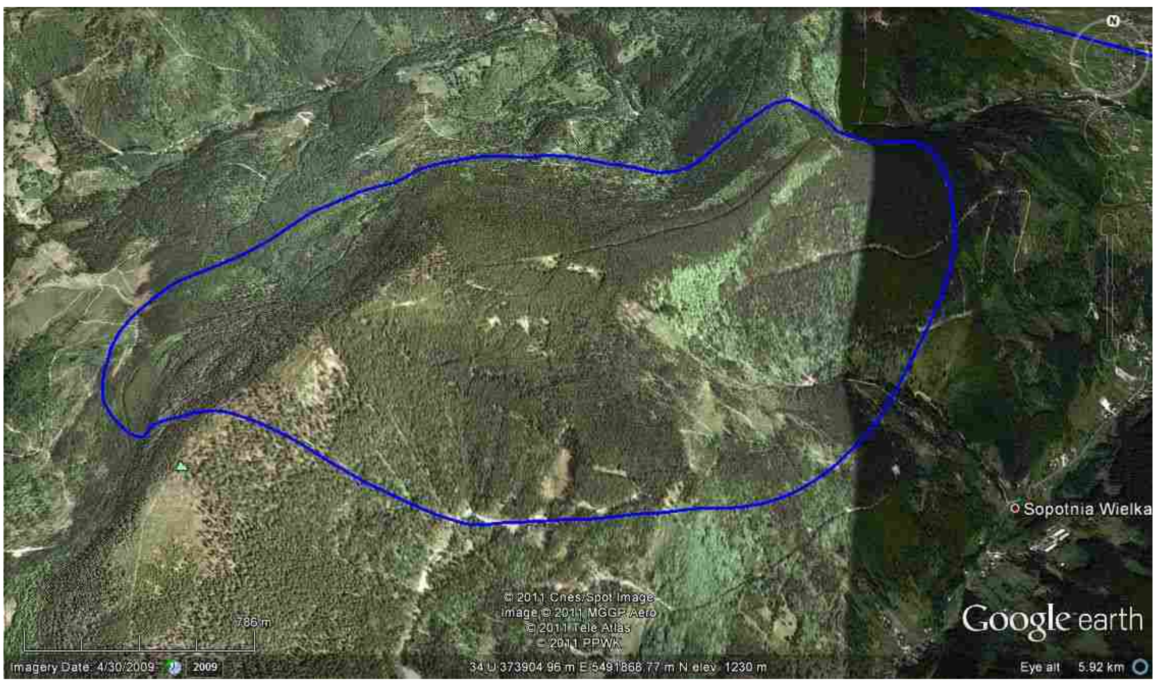

Figure 17: Topography of the Halny Core Area. Core is delineated in blue.
(Modified from Google Earth, 2011)

STRAIGHT-LINE DISTANCE TO BUILT-UP AREAS

GRAPA PACK

Core plots were located anywhere from 2136 m to 3729 m away from the nearest built-up area (any area consisting of 5 constructed buildings or more). One non-core plot actually contained a built-up area (Figure 18). The plot located the greatest distance from a built-up area was found in the core, at a distance of 3.7 km (Table 7). Core plots were located an average of nearly 3 km from built-up areas, while non-core plots were located closer to built-up areas, at an average of 1.1 km. A Mann-Whitney test (Table 20, Appendix) indicated that this difference was significant ($z = 2.6056$, $p > 0.0046$).

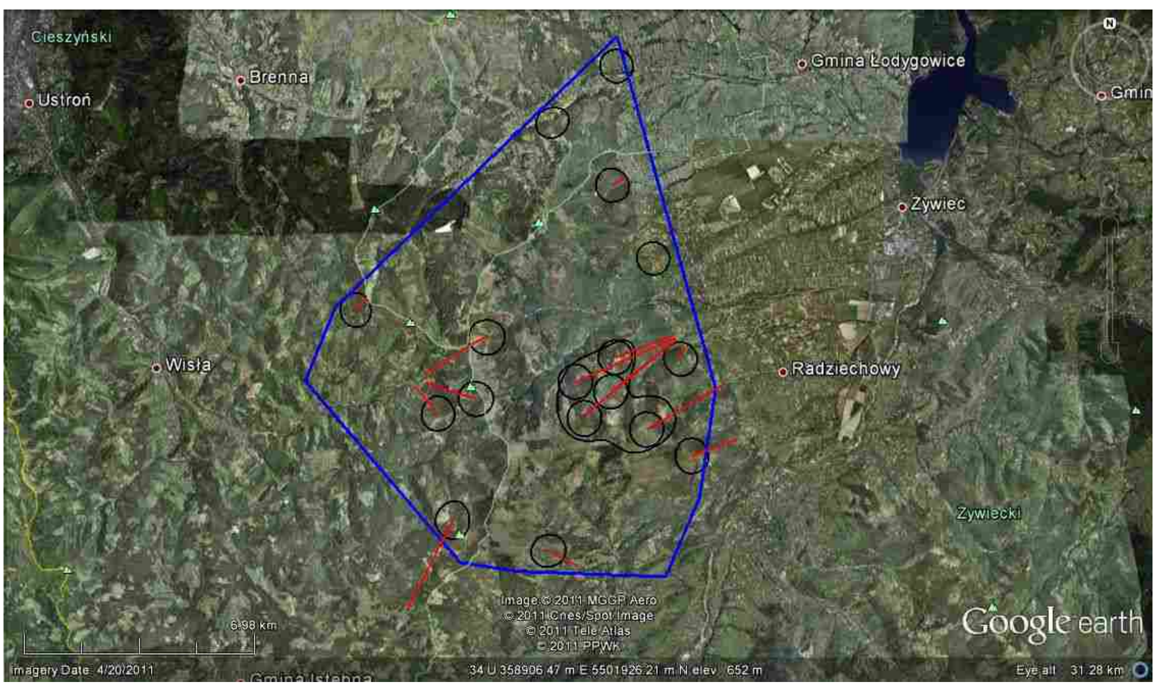

Figure 18: Distance to nearest built-up area from each random plot, Grapa Territory. Red lines indicate the nearest straight-line distance from the center of each circular plot. If no red line is shown for a plot, the center of that plot is located in a built-up area. (Modified from Google Earth, 2011)

GRAPA PACK					
	Distance (m)		Distance (m)		Distance (m)
Core 1	2136	Terr 1	494	Terr 7	108
Core 2	3338	Terr 2	252	Terr 8	2316
Core 3	3729	Terr 3	572	Terr 9	0
Core 4	3008	Terr 4	1641	Terr 10	1264
Core 5	2609	Terr 5	3209	Terr 11	1214
		Terr 6	1853	Terr 12	582
Mean	**2964**				**1125**

Table 7: Straight-line distances to human built-up areas from core plots and non-core (territory) plots, Grapa territory.

HALNY PACK

The nearest core plot to a built-up area was located at a distance of approximately 1.17 km, while the nearest non-core plot was approximately 0.24 km away (Table 8). Core plots ranged from 1.17 – 3.0 km away from the nearest built-up areas, while non-core plots had a larger range of 0.24 – 3.7 km (Figure 19). Core plots were located a mean distance of 2.1 km from the nearest built-up area, while non-core plots were a mean of 1.8 km away. Mann-Whitney tests (Table 21, Appendix) showed no significant difference ($z = 0.5270$, $p > 0.2991$).

HALNY PACK					
	Distance (m)		Distance (m)		Distance (m)
Core 1	2589	Terr 1	3158	Terr 7	238
Core 2	1168	Terr 2	2150	Terr 8	3714
Core 3	3031	Terr 3	3380	Terr 9	2066
Core 4	2240	Terr 4	638	Terr 10	1992
Core 5	1700	Terr 5	1088	Terr 11	323
		Terr 6	2840	Terr 12	562
Mean	**2146**				**1846**

Table 8: Straight-line distances to human built-up areas from core plots and non-core (territory) plots, Halny territory.

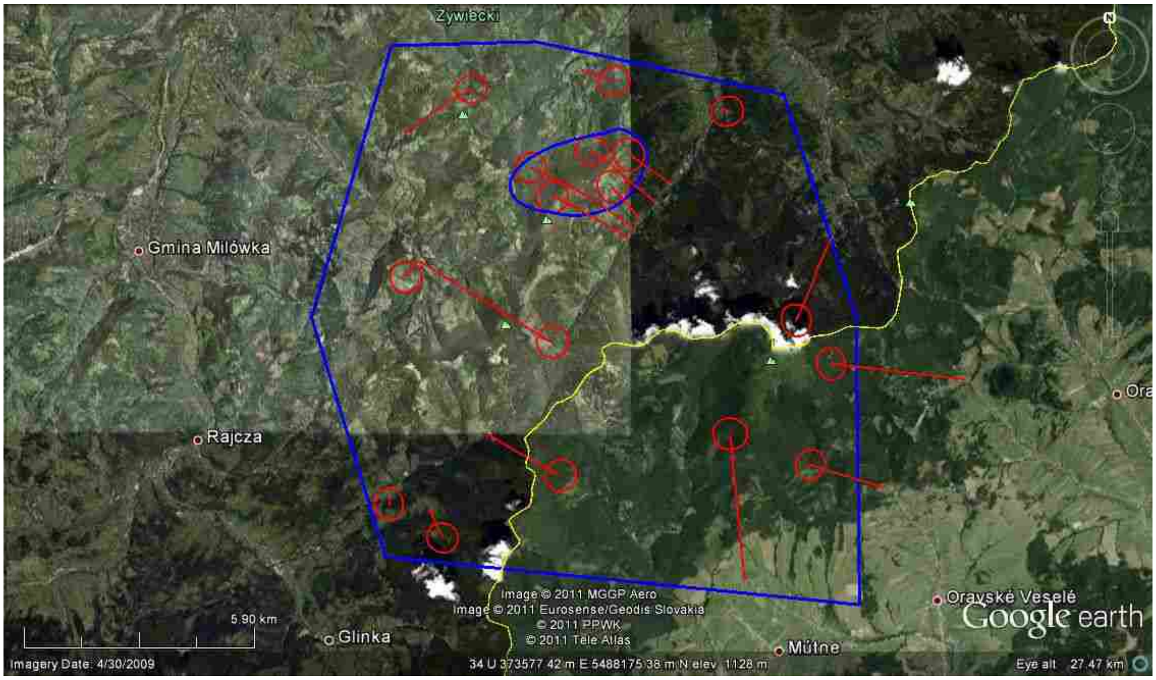

Figure 19: Distance to nearest built-up area from each random plot, Halny Pack. Red lines indicate the nearest straight-line distance from the center of each circular plot.
(Modified from Google Earth, 2011)

ROAD DENSITY

GRAPA PACK

The extent of roads within plots varied greatly, from just over 1 km to nearly 9.5 km. Both the plot characterized by the lowest density of roads and the plot with the highest density of roads were non-core plots (Table 9). Mean road density was found to be higher within non-core plots (5.40 km/km^2), although a Mann-Whitney test revealed that the difference was not significant ($z = 1.2649$, $p > 0.1030$) (see Table 20, Appendix).

GRAPA PACK					
	Road Density (km/km^2)		Road Density (km/km^2)		Road Density (km/km^2)
Core 1	3.45	Terr 1	1.38	Terr 7	10.06
Core 2	2.32	Terr 2	5.22	Terr 8	3.25
Core 3	5.30	Terr 3	2.36	Terr 9	12.01
Core 4	3.99	Terr 4	5.03	Terr 10	4.61
Core 5	1.89	Terr 5	3.97	Terr 11	6.99
		Terr 6	3.94	Terr 12	5.96
Mean	**3.39**				**5.40**

Table 9: Road densities within core plots and non-core (territory) plots, Grapa territory.

HALNY PACK

Much lower road densities were found within plots located in the Halny territory (Table 10). No roads were located within four of the plots, including two within the core area, and two outside the core. The highest road density was found within a non-core plot (6.61 km/km^2), as were the next three highest road densities. The majority of plots were characterized by road densities of 1.0 - 3.0 km/km^2. Differences in road densities between core and non-core plots were not significant (Mann Whitney U-test, $z = 0.8960$, $p > 0.1851$) (see Table 21, Appendix).

HALNY PACK					
	Road Density (km/km^2)		Road Density (km/km^2)		Road Density (km/km^2)
Core 1	0.00	Terr 1	0.00	Terr 7	1.51
Core 2	3.40	Terr 2	2.47	Terr 8	0.00
Core 3	0.30	Terr 3	0.00	Terr 9	5.41
Core 4	1.49	Terr 4	2.61	Terr 10	6.61
Core 5	2.37	Terr 5	3.78	Terr 11	1.47
		Terr 6	2.95	Terr 12	4.96
Mean	**0.97**				**1.69**

Table 10: Road densities within core plots and non-core (territory) plots, Halny territory.

DISTANCE TO NEAREST PRIMARY ROAD

GRAPA PACK

Random plots were located anywhere from approximately 0.10 - 5.2 km away from the nearest primary road (Table 11). Four non-core plots were located less than a kilometer from the nearest primary road, while the closest core plot to a primary road was located at a distance of approximately 3.7 km. All core plots were located greater than 3.5 km away from any primary road, while only two non-core plots were located at that distance. Core plots were located an average distance of 4.6 km from the nearest primary road, while non-core plots averaged a distance of only 1.9 km. A Mann-Whitney U-test (Table 20, Appendix) indicated that core plots were located significantly farther from primary roads than non-core plots ($z = 2.9515$, $p > 0.0016$).

Grapa Pack							
	Distance (km)			**Distance (km)**			**Distance (km)**
Core 1	4.31		Terr 1	2.08		Terr 7	0.50
Core 2	5.06		Terr 2	0.31		Terr 8	3.28
Core 3	4.92		Terr 3	4.30		Terr 9	0.13
Core 4	3.78		Terr 4	2.27		Terr 10	1.48
Core 5	5.20		Terr 5	1.88		Terr 11	4.02
			Terr 6	2.43		Terr 12	0.24
Mean Core Distance (km)		**4.65**					
Mean Territory Distance (km)		**1.91**					

Table 11: Core and Non-core plot distances from nearest primary road, Grapa Territory.

HALNY PACK

Only two plots within the Halny territory were located closer than 1 km from the nearest primary road, and both were non-core plots (Table 12). Non-core plots ranged in distance from 0.2 – 6.0 km to the nearest primary road, with an average of nearly 3.7 km. Core plots, in contrast, were generally located much farther from primary roads, ranging from 5.3 – 7.8 km, with an average of 6.4 km. A Mann-Whitney U-test (Table 21, Appendix) showed this difference to be significant ($z = 2.5298$, $p > 0.0057$).

Halny Pack							
	Distance (km)			**Distance (km)**			**Distance (km)**
Core 1	7.28		Terr 1	2.92		Terr 7	0.39
Core 2	5.74		Terr 2	3.14		Terr 8	5.90
Core 3	7.81		Terr 3	2.79		Terr 9	5.35
Core 4	6.21		Terr 4	0.21		Terr 10	6.05
Core 5	5.31		Terr 5	4.50		Terr 11	2.35
			Terr 6	5.68		Terr 12	5.01
Mean Core Distance (km)		**6.47**					
Mean Territory Distance (km)		**3.69**					

Table 12: Core and Non-core plot distances from nearest primary road, Halny Pack.

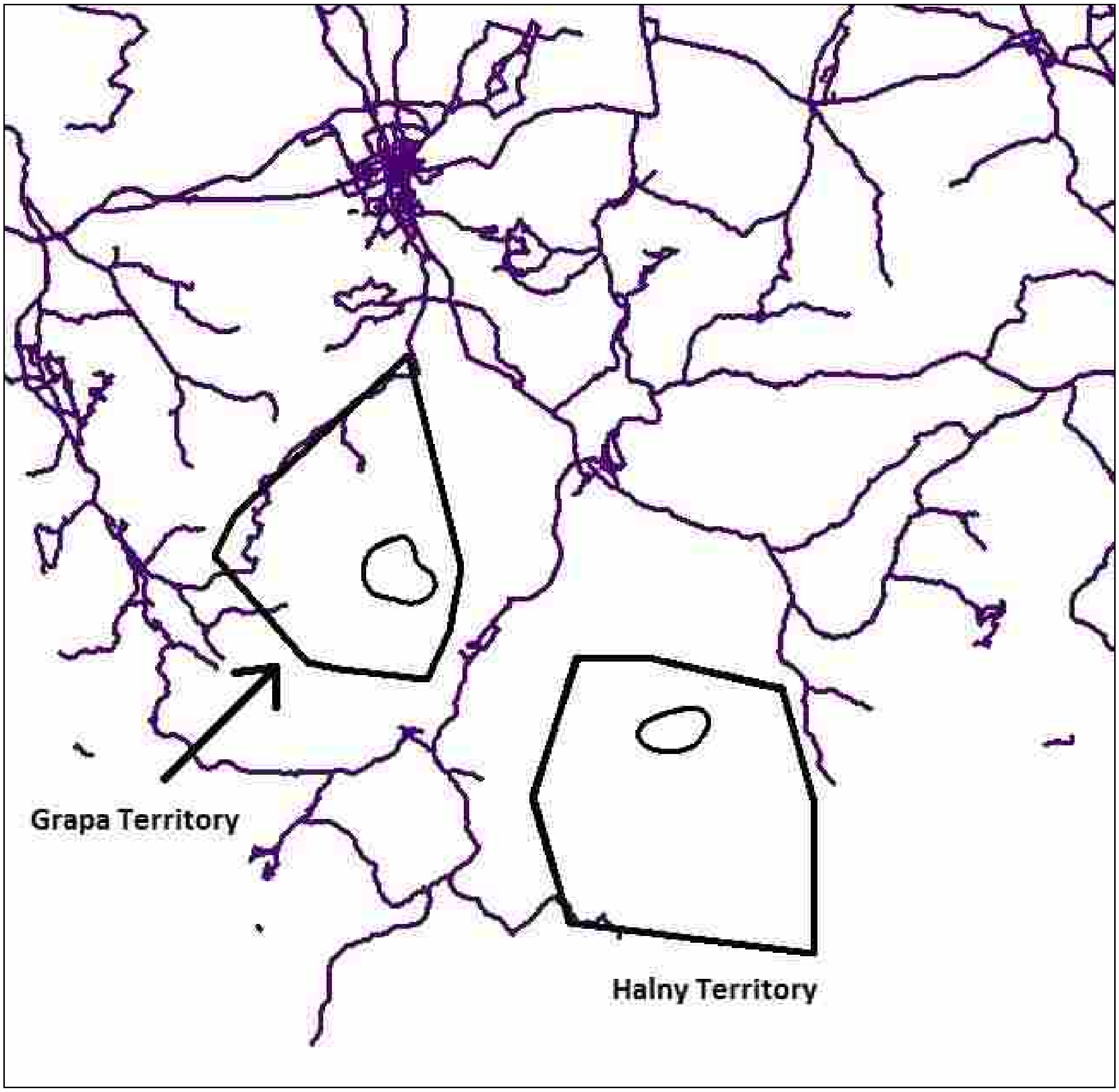

Figure 20: Territories and Core Areas of the Grapa Pack and Halny Pack, in relation to primary roads (shown in purple).

DISCUSSION

OLFACTORY BOWL VERSUS HOT SPOTS MARKING PATTERNS:

GRAPA PACK

I found that the hot spots pattern of territory marking, suggested by Zub *et al.* (2003), more accurately described the marking patterns of both the Grapa and Halny wolf packs within the study area than did the olfactory bowl pattern proposed by Peters and Mech (1975). This hot spots pattern was most obvious in the Grapa territory, since the majority of scats were recorded there. This was most likely a function of increased survey intensity, as this was the most accessible territory and the closest to any significant town. The Grapa territory was also the most easily surveyed because of its location completely within Polish borders, making thorough sampling possible.

The Grapa territory is bordered to the north by the territory of the Bukowy pack (see Figure 2, page 13), and if the Olfactory Bowl pattern existed, I would have expected to see more marking along this territory boundary line. There are two possible explanations for the Grapa's marking in hot spots: The first is that the majority of Grapa scats found were found along two different sections of trails, both located within a short distance of one another. Not only are these two sections in proximity to one another, but they are also two of the more popular hiking trails in the area and located close to a junction where several hiking trails converge. Many researchers have observed that wolves tend to heavily mark junction areas (Vila *et al.* 1994; Barja *et al.* 2004; Zub *et al.* 2003). This could be one possible explanation for a high density of scats in the area, as this would maximize the probability that any wolves from other packs traveling in the area and using hiking trails as travel paths would find them. However, the other possible explanation is that more scats were found in this area because of the fact that it is an area where many hiking trails converge, and therefore, sampling intensity was likely higher in this area. As most scats were deposited in the winter months (Table 13, Appendix), any wolf movement on or near the trail system or roads within the territory should have been detectable and tracks could have been followed to determine any other existing scats located away from trails and roads.

There are also two explanations for the lack of scats found in the periphery regions of the Grapa territory. The first explanation is the proximity of the Grapa territory to heavily-occupied human areas all along the eastern territory boundary. This likely results in the Grapa wolves not utilizing this area nearly as much as some of the other areas within their territory. Zub *et al.* (2003) found that wolf scat deposition rates were similar in areas with similar utilization rates, based on radiolocations. This would suggest that we wouldn't find as many scats within this periphery area due to the likelihood that this area is under-utilized by the Grapa wolves.

The second explanation for the lack of scats observed near the territory boundaries of the Grapa pack is that there are no bordering wolf pack territories immediately adjacent to the Grapa territory (Figure 2, page 13). The nearest wolf pack territory is the Bukowy territory. However, there is a bustling town separating the Grapa and Halny territories, and therefore, similar to the heavily-occupied areas adjacent to the eastern Grapa territory boundaries, these areas are likely under-utilized by the Grapa wolves. The Grapa wolves would probably not need to worry about scat marking this location, as the probability that the Bukowy wolves would cross through the town of Szczyrk and enter the Grapa territory is low.

The most logical explanation for the Grapa wolves' pattern of hot spot scat marking is that the area most heavily marked corresponded to a core area. This area likely would have been an area where a den was located or where the majority of pup raising occurred. According to Zub *et al*. (2003), this would have been the most important area for the Grapa wolves, and therefore, the most heavily marked with scats. In fact, when looking at separate data provided by Nowak and Myslajek (pers. comm.) on den locations and pup-rearing sites for the Grapa pack during the study period, it is clear that the majority of scats found within the Grapa territory were concentrated around one of two pup-rearing areas (Figure 21). This correlation provides further evidence of the hot spots marking pattern.

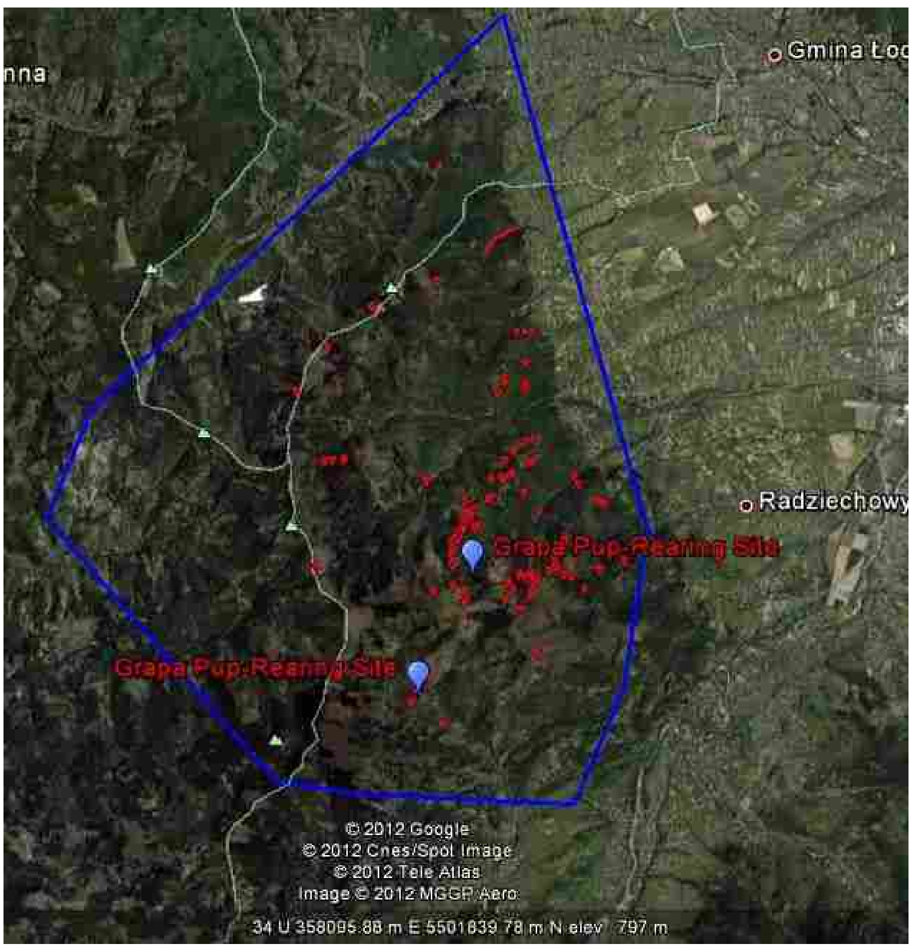

Figure 21: Grapa scat locations (shown in red) in relation to den locations and pup-rearing areas, 2005-2007.

HALNY PACK

The hot spots pattern of scat marking also seemed to dominate the territory marking of the Halny pack. From Figure 10 (page 40), we can see that the Halny wolves seemed to scat mark most heavily in a single area, but in two separate groups. These groups were both along hiking paths and were only separated by a distance of 575 meters. No scats were found along the southwestern border of the Halny territory, which was the only border adjacent to another territory (the Czort Pack; refer to Figure 2, page 13). This would seem to refute the Olfactory Bowl pattern, and support the hot spots pattern. However, I have less confidence in this conclusion than that concerning the Grapa wolves. Only a small section of the adjacent territory borders was surveyed, as much of the area is located in Slovakia, where tracking was prohibited. Therefore, the survey intensity was much higher in areas located in Poland, and as a result, we were much more likely to find scat locations within the interior of the territory, rather than the periphery regions.

The most accessible, and therefore, the most heavily surveyed region of the Halny territory was the northwestern portion of the territory. The territory borders in this region were all in closer proximity to towns and villages than most of the other boundary regions. As the probability of rival wolves entering this area was very small, there would be no reason for the Halny wolves to mark this area. Peters and Mech (1975) mostly examined two wolf pack territories that were surrounded by other territories when they proposed their Olfactory Bowl marking pattern. Since the Halny territory only borders one other pack territory, this would be the only periphery where we would expect to see a significant number of scats, and not territory boundaries that border human-occupied areas.

As with the Grapa pack, data on den locations and pup-rearing areas (Nowak and Myslajek, pers. comm.) showed that these areas corresponded to the areas most heavily scat marked (Figure 22). The single pup-rearing area found, like the scat locations, was possibly a result of the increased survey intensity within the Polish section of the Halny territory. However, these findings are in agreement with the explanation of Zub *et al*. (2003) that wolves tend to concentrate scat marks in areas most valuable to them.

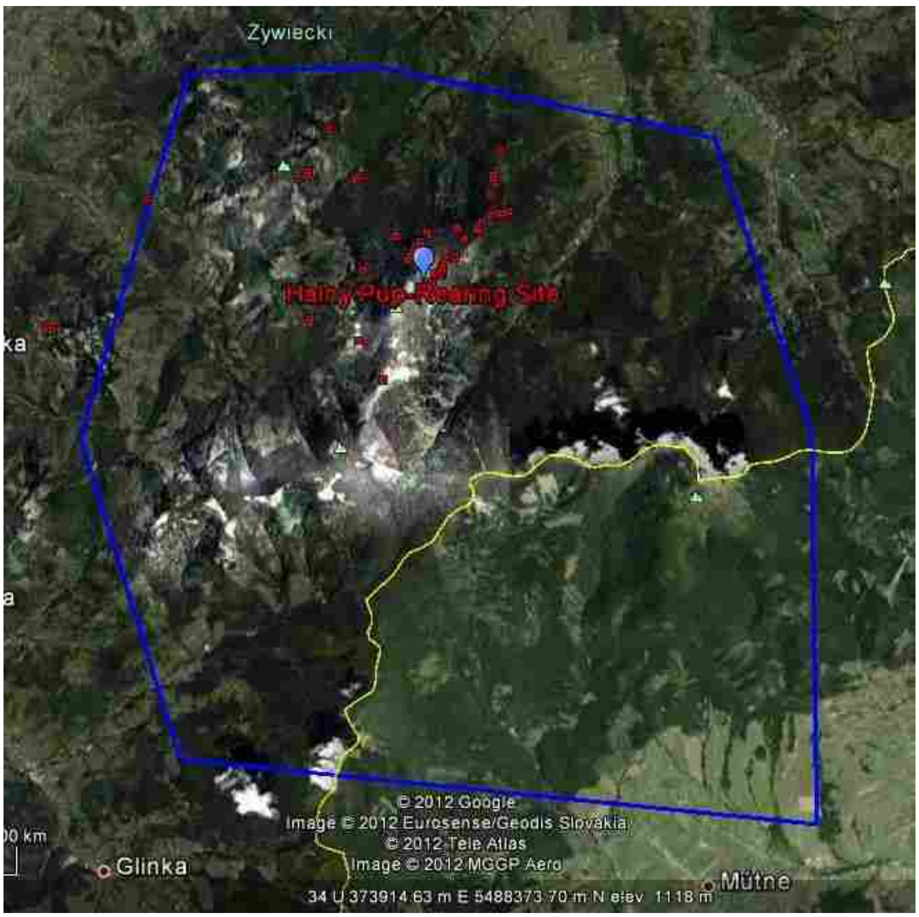

Figure 22: Halny scat locations (shown in red) in relation to den locations and pup-rearing areas, 2005-2007.

IDENTIFICATION OF CORE AREAS:

GRAPA PACK

Fixed-kernel density estimation was performed using the reference bandwidth of 540.3 meters. The resulting 50% isopleth yielded an area of 8.29 km^2. Based on the findings of Zub *et al.* (2003), this would also correspond to the area where 50% of radiolocations would be if radio-tracking would have been conducted. Okarma *et al.* (1998) considered the core area of wolf packs in the Bialowieza Primeval Forest in Poland to be the area containing 50% of radio locations. Therefore, this same area, determined through fixed-kernel density of scat locations, was considered to be the core area. At 8.29 km^2, this area constitutes only 6.8% of the total territory size of the Grapa pack. However, this is similar to the findings of Okarma *et al.* (1998). They found core areas made up 5-13% of the total territory area in the Bialowieza Forest. Jedrzejewski at al. (2007) found that the average core area comprised 17% of the average territory in another study, while Silva and Talamoni (2004) found that maned wolves in Brazil used a core area that equated to 3.8% of their total territory. Person and others (1996) reported that wolves in southeastern Alaska occupied territories of 280 km^2, and core areas of 124 km^2 (44.2% of the territory). The size of the Grapa core area in relation to total territory size is on the lower end of the range found by other researchers likely because of the different landscapes in which the studies were conducted. Approximately 100 km^2 of the Bialowieza Forest is protected as a national park, with half of that area strictly protected as a core area, where no motorized traffic is allowed and human entry is by permit only (Theuerkauf *et al.* 2003). The national park area is nearly the size of the entire Grapa territory (100 km^2 versus 122 km^2) and the strictly protected core is nearly half the size. The areas surrounding the Grapa territory are populated with twice the density of people

(143 persons/km^2) (Jedrzejewski *et al.* 2005) than the areas surrounding the Bialowieza Forest (70 persons/km^2) (Theuerkauf *et al.* 2003) and there are no restrictions on human entry. In Southeastern Alaska, Person (1996) found core areas that were larger than the entire Grapa territory. Human intrusion was obviously much lower there than in the Grapa territory. In contrast, the Grapa pack, inhabiting the accessible mountains of southern Poland, where forestry operations, hikers, and even vehicles penetrate the forest, have a much smaller area to find solitude and protection.

In their study of maned wolves in Brazil living within a private nature reserve surrounded by ecotourism development, Silva and Talamoni (2004) found smaller core areas (equal to only 3.8% of total territory size) than the Grapa core area. This is likely a more accurate comparison, based solely on the extent of human activity within the study areas.

In examining how the calculated core area of the Grapa pack compares to the den locations and pup-rearing areas found by Nowak and Myslajek (pers. comm.), we can see that the core area contains one of the pup-rearing areas (Figure 23). This also provides confidence that the core area found through the fixed-kernel density analysis is accurate.

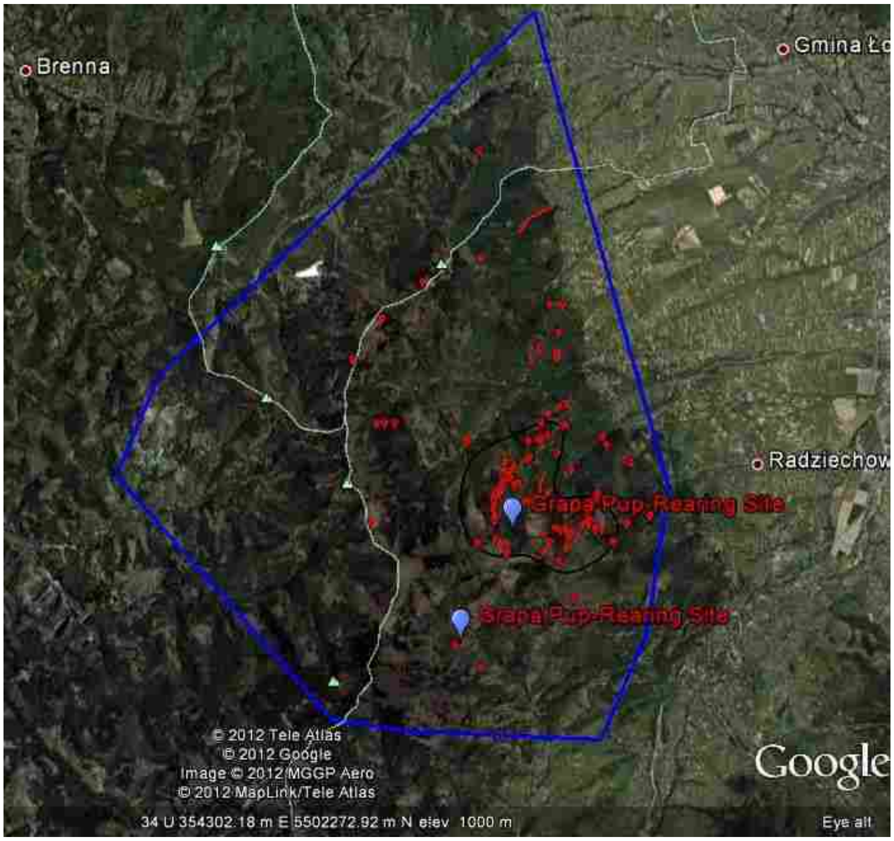

Figure 23: Grapa scat locations (shown in red), den locations, and pup-rearing areas in relation to the core area (delineated in black).

HALNY PACK

Fixed-kernel density estimation using the reference bandwidth of 0.517 m, transformed to produce *x* and *y* coordinates with similar variances, yielded a 50% isopleth encompassing an area of 5.68 km^2. This represented an area equal to 3.2% of the total size of the Halny territory. Although the 90% isopleth contained an area of nearly 5 times as large as the 50% isopleth (26.78 km^2) (Table 2, page 42), it only contained a little more than a handful of additional scat locations than the 50% isopleth. Therefore, the 50% isopleth was considered as delineating the Halny core area.

Due to the remoteness and difficulty in access of the Halny territory when compared to the Grapa territory, I had expected to see a Halny core area comprising a larger percentage of the total territory than the Grapa core. As mentioned before, studies examining wolf core areas generally found that core area size was inversely related to the extent of human activity within the territory and surrounding areas (i.e. the more human activity within an area, the more a wolf pack tended to concentrate their core within a smaller area). The Halny core area may have been smaller in relation to the total territory size than that of the Grapa core area as a result of sampling bias. The region in which most of the Halny scats were found was the region that was surveyed most intensely, due to the ease of accessibility in comparison to other regions. Areas near the border, besides being difficult to access due to long distances, were also sparsely surveyed because of border crossing issues. Therefore, possibly another area with dense collections of scats existed within the portion of the territory located in Slovakia, and through further study, this area could possibly be determined to be the core.

Figure 24 (page 71) yields support that the core area found through fixed-kernel density analysis represents a true core area. The pup-rearing area for the Halny pack during the study period was located within the determined core area. This is reasonable in that the area most densely scat marked, and the area where most pup-raising occurred, would be part of the most valuable area to the Halny wolves.

Assuming that the core determined in this study through fixed-kernel analysis is the actual core area of the Halny pack, the most probable explanation for the small size of the core in relation to the rest of the territory is that the Halny wolves were trying to avoid Slovakian hunters near the border regions. In Slovakia, wolves can be hunted for two and a half months each year (Nowak *et al.* 2008). Because they are protected in

Poland year-round, the Halny wolves may have chosen to locate their core area within Poland, basically cutting the territory size in half (Figure 24). When this is considered, the Halny core area is roughly the same size in relation to the size of the territory as the Grapa core in relation to the Grapa territory.

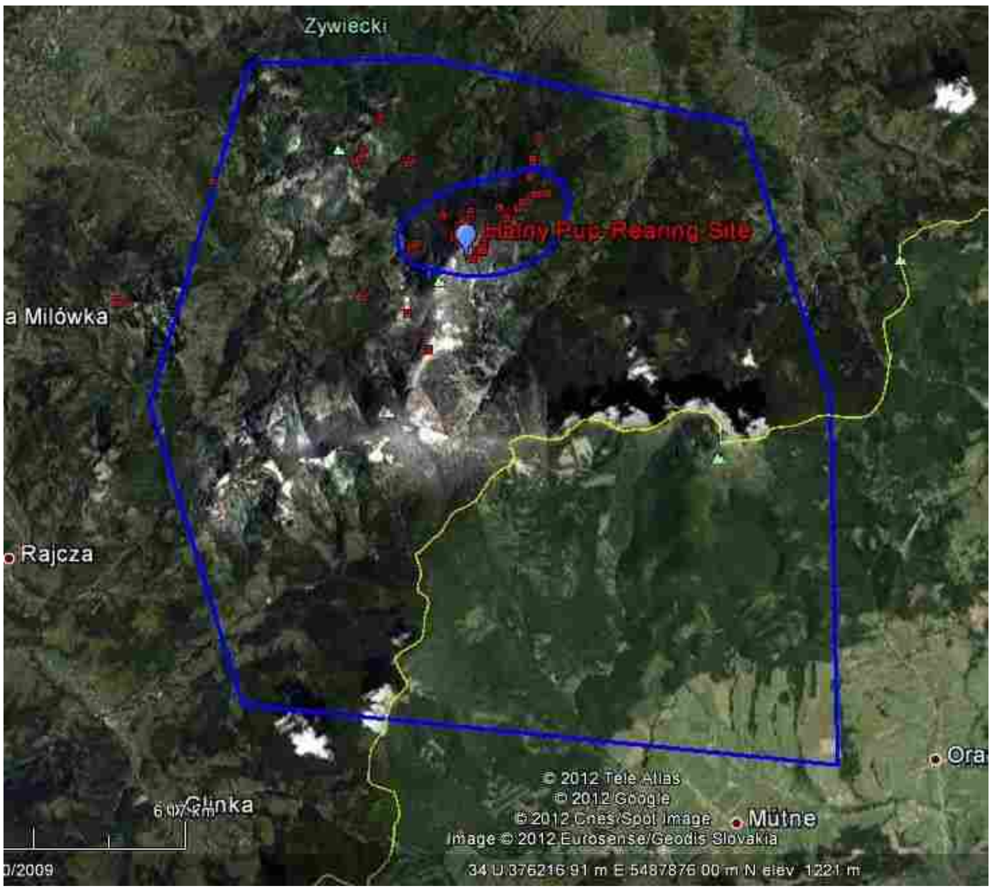

Figure 24: Halny scat locations (shown in red), den locations, and pup-rearing areas in relation to the core area (delineated in blue). The Polish-Slovakian border is shown in yellow.

HABITAT PARAMETERS OF CORE AREAS IN RELATION TO HUMAN PRESENCE

LAND COVER

GRAPA PACK

The only significant difference found between core and non-core plots regarding land cover involved the amount of broad-leaved forest cover. Core plots had significantly higher percentages of broad-leaved forest cover than non-core plots ($z = 2.0028$, $p > 0.0226$). However, non-core plots contained slightly more coniferous cover than core plots, and there was no significant difference in overall forest cover between core and non-core plots. This would suggest that there is something attractive about broad-leaved forest. However, among the five core plots, only 2 had any significant amount of broad-leaved forest cover (Table 17, Appendix), and in only one of those did broad-leaved forest constitute the majority of land cover. Therefore, broad-leaved forest cover was not distributed throughout the core area, but rather concentrated in a small area. What, if anything, would lead the Grapa wolves to select a core area with a larger percentage of broad-leaved forest cover?

Perhaps this choice had to do with preferences for den selection. Because most of the scats recorded in this study were found in the winter months (October – May), the delineated core area probably was associated with denning sites. However, wolves have been found to dig burrows to den, as well as use fallen trees (Nowak *et al.* 2008). Therefore, it does not seem likely that this would explain the large percentage of broad-leaved forest cover within two of the core plots.

Perhaps the Grapa wolves were only following their main prey species, red deer (*Cervus elephus*) and roe deer (*Capreolus capreolus*), down into the broad-leaved forests, where the deer were feeding. It has been documented that wolves will utilize valley bottoms and lower areas during the winter more than other times of the year because that is where many of their prey species tend to congregate during the winter in order to more easily find food. However, Barancekova *et al.* (2010) found that in the Czech Republic and Germany, coniferous trees made up a slightly larger portion of the roe deer diet than broad-leaved trees. This would seem to suggest that roe deer would not select these patches of broad-leaved forest in order to feed on the trees, but rather avoid the valley bottoms where they are more likely to encounter humans. They could find conifers to feed on at the higher elevations. However, studies by Cransac *et al.* (2001) and Latham *et al.* (1999) on roe deer diet preferences found that the deer heavily fed on heather and brambles, which both grow in sunny, open habitats. Sherlock and Fairley (1993) found that heather was also an important food source for red deer in the winter. Broad-leaved trees such as beech and oak often start growing in these areas, and their young shoots are a favorite food for roe deer in the spring (Cransac *et al.* 2001). This proximity to favorite prey species would be particularly beneficial to the Grapa wolves in the late spring when pups are born. The Grapa pack only consisted of 2 or 3 wolves during this study, and therefore, the pack could not afford having to cover large distances in order to obtain food. Therefore, the combination of young broad-leaved tree shoots and the presence of brambles and heather in these sunny, open areas may attract roe deer, and in turn, attract the Grapa wolves as well.

HALNY PACK

No significant differences in land cover between core plots and non-core plots were found. When compared to the Grapa territory plots, there was much less available broad-leaved forest cover, which may explain why the Halny wolves didn't select a core containing significantly more cover of this type than surrounding areas – they didn't have that option. Forest cover between core and non-core plots differed quite a lot, although this didn't quite prove to be significant at the chosen level of certainty. However, this suggests that the Halny wolves may have located their core area in a region with thick forest cover, as this area was available to them on the Polish side of the border, where hunting pressure on wolves is significantly less than on the Slovakian side.

ELEVATION

GRAPA PACK

Mann-Whitney U-tests showed no significant difference in elevation between core and non-core plots. I was expecting to find that core plots were located at higher elevations than non-core plots in the wolves' attempts to avoid human disturbances. However, this is not what I found. Higher elevations are much harsher environments during the winter months, where significant amounts of snow can accumulate. In addition, the highest point within the Grapa territory is a peak named Skrzyczne, at an elevation of 1257 m. Skrzyczne is also one of the highest peaks in the Polish part of the Silesian Beskidy Mountains. This would seem like a good place for a wolf pack to locate a core area, particularly if they are trying to avoid people. However, Skrzyczne is different – on the top of the peak is a huge lodge, and the mountain receives heavy use during the winter because it has been converted into one of the largest ski resorts in

Poland, with a funicular railway servicing the top. This would be the last place a wolf pack would want to be during winter. The resort is also a popular hiking destination in the summer, and therefore, any wolves in the area would likely avoid using the area for any significant amount of time in any season.

In addition to the popularity of Skrzyczne, the highest parts of the Grapa territory are joined together by a popular trail network that receives heavy human traffic during the summer (Figure 25). This trail network includes the trails to/from the top of Skrzyczne, where hikers are able to take a chairlift up from the town of Szczyrke during the summer to gain easy access to the high country trails. The accessibility of the high mountains within the Grapa territory, both in the summer and the winter, most likely forces the Grapa pack down into intermediate areas where they can avoid people, yet still have relatively easy access to prey.

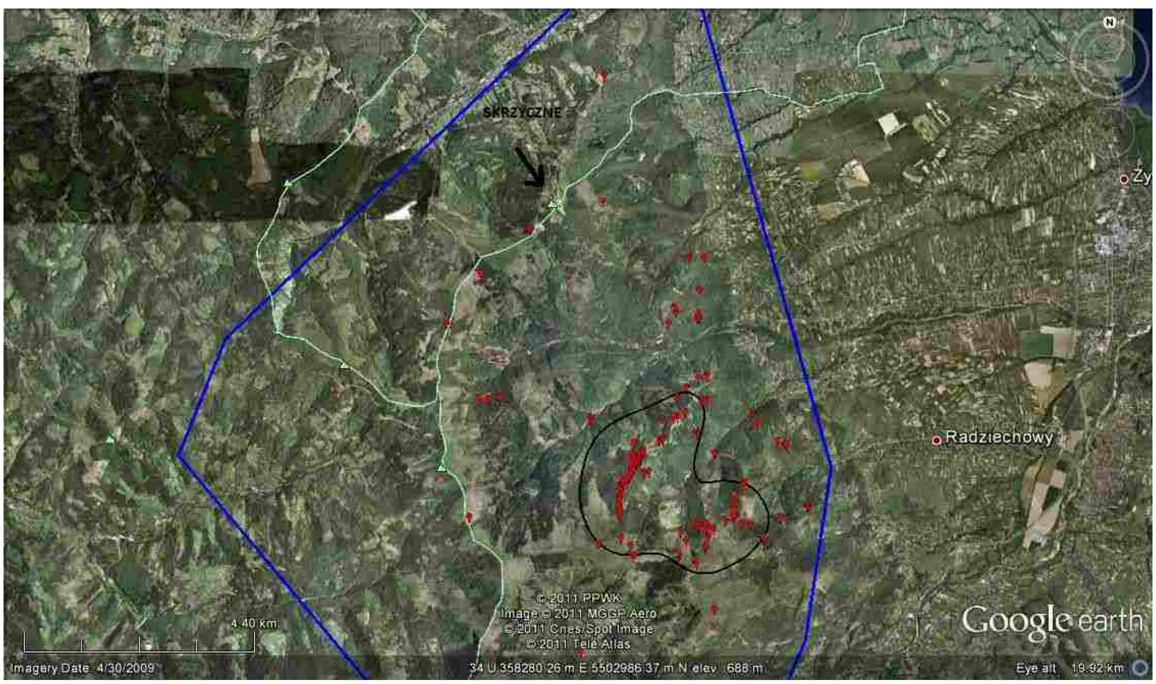

Figure 25: Grapa territory (delineated in blue), scat locations (red), core area (black), and the high mountains within the area. The green lines indicate major hiking trails. Note that the trails run along the spine of the highest mountains in the region, including the highest point, Skrzyczne, located near the top of the territory. (Modified from Google Earth, 2011)

HALNY PACK

The territory of the Halny pack was on average approximately 150 m higher than that of the Grapa pack. No significant difference was found in elevation between core plots and non-core plots. This would lead us to believe that elevation played no part in the Halny wolves' selection of this area. However, a closer examination suggests that this might not necessarily be accurate. The highest points in the territory are all in the Slovakian part, or within a 1-kilometer distance of the border. This is where Pilsko (1429 m) is found. Once again, Slovakian regions are open to hunting for 2.5 months each year, so it is more likely that given a choice, the Halny wolves would locate a core area within Poland, where they wouldn't have to worry about encountering hunters. These high elevations bring very difficult conditions during the winter as well. Prey species move down lower where they are able to find food, and the Halny wolves may follow them, as other researchers have found (Paquet *et al.* 1996).

Excluding the Slovakian part of the territory, there are two other main areas of higher elevations within the territory. A hiking lodge exists in one of these areas (Figure 26). This hiking lodge (Rysianka Schronisko) is located in the second highest part of the territory within Poland. This lodge receives significant use during the summer, as it is an overnight shelter. The lodge is closed during winter. The traffic that surrounds this lodge, and on the trails leading up to it, would probably discourage the Halny wolves from using this area as a core area.

The highest part of the territory within Poland is near Romanka (1366 m). Although much less accessible than Skrzyczne in the Grapa territory, Romanka also has four major hiking trails leading to its peak, including one from the hiking lodge mentioned above. The core area of the Halny pack is located just below the top of

Romanka. This is possibly the highest the Halny wolves could go before encountering more people.

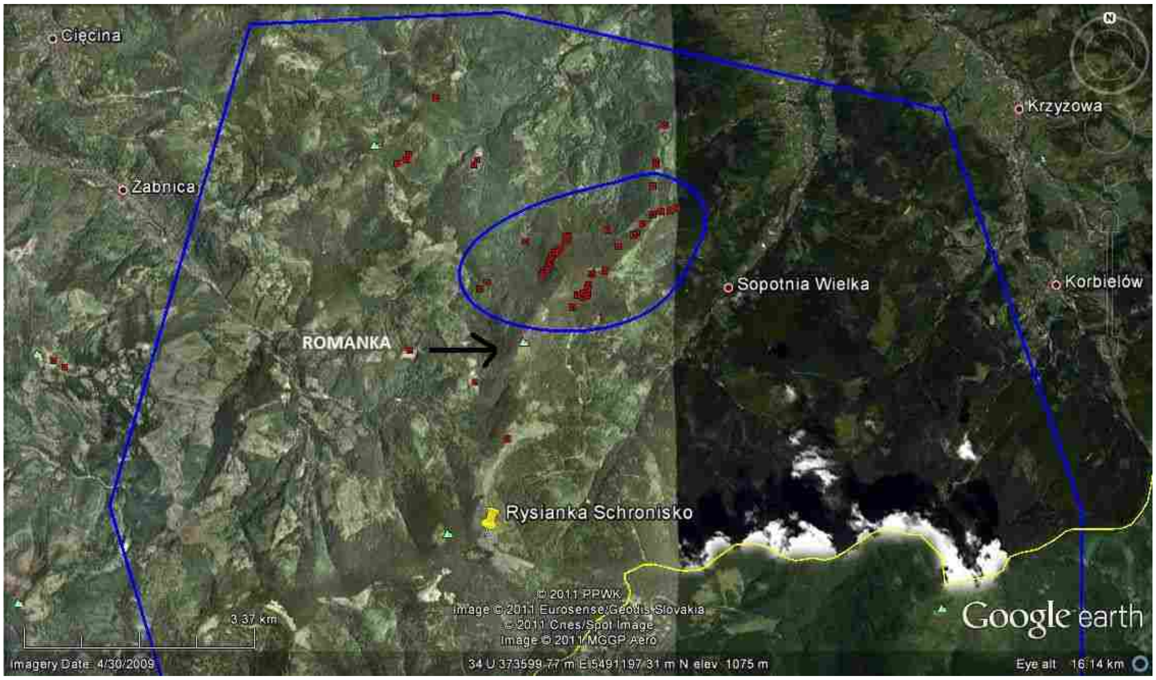

Figure 26: Halny Territory. The highest point, Pilsko, is located in the Slovakian part of the territory (yellow line shows the national border). Rysianka Schronisko, an overnight hiker shelter, is located in the middle of the territory on the Polish side The core area is located below Romanka, the highest point within the Polish part of the territory. (Modified from Google Earth, 2011)

STRAIGHT-LINE DISTANCE TO THE NEAREST BUILT-UP AREA

GRAPA PACK

In comparison to non-core plots, core plots were located significantly farther from the nearest built-up areas. Several of the non-core plots were within 500 meters of the nearest built-up area, probably as a result of the Grapa wolves following roe and red deer down into agricultural areas during the winter months. In contrast, core areas likely contain den sites, which wolves would want to locate as far from people as possible. This is a challenge in a landscape such as this, in which human areas basically surround a wolf territory. While utilizing other areas of the territory at night, as found in other studies (Theuerkauf *et al.* 2003), for hunting and traveling, the core area is nearly always located in areas where human presence is minimal. The location of the core area probably gave the Grapa wolves the best compromise between close proximity to a food source and avoidance of people.

HALNY PACK

Mann-Whitney U-tests showed no significant difference in straight-line distance to the nearest built-up area between core and non-core plots in the Halny territory. Within the Polish part of the territory, there were no other areas that were significantly farther from a built-up area than the core area. However, there were areas on the Slovakian side that were located a greater distance from the nearest built-up area. These sites were not surveyed due to border crossing issues. The constant traffic of hikers in the area of the Rysianka schronisko would discourage a core area in that part of the territory, and along with the two towns of Zabnica and Sopotnia Wielka, would limit the areas available to wolves away from people. The border areas, based solely on the fact that they are located farther away from built-up areas than any other areas in the territory, would seem like a good place for a core area. In considering this, it seems that there must be another reason why the core area is not located in the border region. One possible reason is that the presence of hunters in the fall months causes the Halny wolves to avoid the area. There is also the possibility that there is a core area located in the border region, but due to decreased sampling intensity, we were not able to detect it.

ROAD DENSITY

GRAPA PACK

Within the territory of the Grapa wolves, core plots tended to have lower densities of roads as compared to non-core plots, although this difference was not shown to be significant through Mann-Whitney U-tests. Both core plot road densities (mean = 3.39 km/km^2) and those of non-core plots (mean = 5.40 km/km^2) were much higher than road densities found in other wolf pack territories in other studies. In his study in north-central Minnesota, Fuller (1989) found that no wolf territories had road densities larger than 0.72 km/km^2. Mladenoff and others (1995) found that wolf packs in Wisconsin inhabited territories with an average road density of only 0.23 km/km^2. These data illustrate how much of the forest in the Silesian Beskidy Mountains is penetrated by humans. There are no areas within the Grapa territory of any size with similar road densities to those found in the studies mentioned above. Both Mladenoff and Fuller only examined roads open to the public and maintained roads, and therefore, these values are likely to be lower than those found in this study, where all roads and trails, regardless of use, were examined. However, this study illustrates that the Grapa pack's options for choosing areas of low road density are incredibly limited.

HALNY PACK

As with the Grapa plots, no significant difference in road densities was found between core plots and non-core plots. Road densities throughout the Halny core and the territory as a whole were approximately 1/3 of those found in the Grapa territory. This is probably due to the higher elevations found in the Halny territory. The steeper slopes of the region also create complications in road construction. In addition, the fact that the territory is in a border region likely results in fewer roads, as roads are not permitted to cross the border. Despite much lower road densities than the Grapa territory, these densities were still high compared to those found in other studies. Even the core area had higher road densities than the highest densities found in any wolf territory in the Fuller (1989) study. These data, along with those of the Grapa pack, suggest that the wolves living in this mountainous region of southwestern Poland have learned to adapt to higher road densities than most studied packs within the U.S. solely out of necessity. It is nearly impossible for them to find areas that aren't penetrated by roads. Although not statistically significant, the packs did seem to locate core areas in places where roads were not so extensive.

DISTANCE TO NEAREST PRIMARY ROAD

GRAPA PACK

Mann-Whitney U-tests revealed that core plots were located significantly farther from any primary roads than non-core plots. This would suggest that the Grapa wolves have grown accustomed to secondary roads within their territory, as the road density analysis revealed that it was nearly impossible for them to find any areas with low road density. However, they are still wary of primary roads where there is a fairly consistent amount of traffic. The secondary roads within the territory are mostly logging roads, and are used only occasionally. There are very few All-Terrain Vehicles (ATVs) used in the area, so most motorized activity within the forest is from temporary and localized logging operations.

Distances to primary roads were greater than distances to nearest built-up areas, also suggesting that the Grapa wolves have grown used to certain levels of disturbance, but this does not include heavy traffic.

Paquet *et al.* (1999) used 1-km buffer areas around roads to delineate core security areas for a wolf reintroduction feasibility study in Adirondack Park. They stated that previous findings (Chapman 1977; Paquet *et al.* 1996) suggested that this distance reflected the distance at which human activities are known to disturb wolves. Therefore, when looking at the results of this study, we can either assume that these core areas just coincidentally occur in the middle of the territories, where the distance to the nearest primary road is more likely to be greater, or that there was a specific avoidance of the roads themselves. Looking at Figure 20 (page 61), one can clearly see that the Grapa core is not located directly in the center of their territory. If it were, the distances to the nearest primary roads would be considerably smaller. Therefore, I conclude that there was a specific avoidance of primary roads by the Grapa pack.

HALNY PACK

More support for a specific avoidance of primary roads is provided by the location of the Halny core area. In the Halny territory, core plots were also found to be located significantly farther from primary roads than non-core plots. Distances were nearly 50% longer when compared to those of the Grapa plots. This is partly due to the larger territory size of the Halny pack (175 km^2) compared to the Grapa territory (122 km^2), as pack territories rarely contain primary roads. Even the Grapa territory, located in an area where secondary road density is nearly 6 times the highest density found within Minnesota wolf pack territories, only contains a few small sections of primary roads (Figure 20, page 61). Like the Grapa core plots, plots within the Halny core area were located farther from primary roads than from built-up areas. This lends more support for the argument that both the Halny wolves and the Grapa wolves have developed a certain tolerance and resilience to human disturbance because that is what they have been forced to do in a human-dominated landscape.

UNCERTAINTIES AND ASSUMPTIONS

While this study provides a more detailed picture as to why the Grapa and Halny packs locate their core areas in the places they do, we need to be careful because of many uncertainties associated with this study. The first uncertainty concerns the territory boundaries themselves. The boundaries were taken from a study by Nowak *et al.* (2008), in which the researchers used 100% MCPs to delineate the territories. While this is a common practice, there is also the possibility that an individual wolf from each pack had made a single exploratory trip to an area outside the pack's actual territory, for some reason or another. Because 100% MPCs were used, this would result in a larger territory size than the actual territory size. This would result in the possibility that some of the random plots analyzed in this study, most notably the plots located around the territory edges, were actually not part of the territory at all, and therefore, the comparisons between core and non-core plots would not be completely accurate. However, I believe that the general findings would not be significantly different than those found in this study. The location of the core areas would not be affected, and would still be located in the interior of the territories, away from primary roads and built-up areas. Only the non-core plot locations would possibly be affected, and this is really no different than the generation of random plots within the territory. There is an equal chance of random plot generation producing other non-core plots farther from primary roads and built-up areas.

Another point of uncertainty concerns the inconsistency of survey intensity within and between pack territories. The Grapa territory was surveyed more intensely than the Halny territory due to its proximity to the base of operations. It was much more accessible, particularly in bad weather, because of its lower elevation, and also could be surveyed more thoroughly because of its location completely within Polish borders. This is the reason most scats recorded in this study came from the Grapa territory. In addition to differences in survey intensity between territories, there was also inconsistency within the territories themselves. Most sampling was carried out by hiking along a logging road or hiking trail and attempting to find scats, or if scats weren't present, tracks that could be followed and hopefully lead to scats in another area of the forest. Some hiking trails were easier to access than others, particularly in the winter when most of the sampling occurred. Because most sampling occurred by following hiking trails, the areas where a number of hiking trails converged were probably sampled the most. This could have resulted in more scats being found in these areas due to increased surveying intensity. In fact, most scats recorded in the Grapa territory were found in an area where three hiking trails converged. This may have simply been a result of sampling bias.

Roads and trails nearer to villages were sampled more heavily, and therefore, we were much more likely to find scats in these areas than in areas located farther from villages. Obviously this could skew the results of scat locations, and therefore, affect the determination of core areas. However, because the areas located nearer to villages were sampled more intensely, any scats located further within the territories that were missed would only contribute to core areas located further from built-up areas. In this way, I would expect the differences between core and non-core plots to only be more significant. This is particularly true in the case of the Halny pack, whose territory straddles the Polish/Slovakia border. Because of the legal issues involved in crossing over to Slovakia to sample, and also the remoteness of the border itself, both the border region and the Slovakian portion of the territory were not sampled thoroughly. Other studies have found that wolves tend to locate cores along border areas because of decreased human activity (Findo and Chovancova 2004). In fact, in a study conducted over a period of 8 years, Nowak *et al.* (2008) found that the core area of the Halny pack was located near the border area. They used the distribution of scat locations, track locations, prey remains, den locations, resting places, and howling surveys to determine this core area. This was clearly a more thorough study. However, Nowak's study concluded 4 years before the commencement of this study, so there is the possibility that the core area of the Halny pack changed during this time period. This could be due to some disturbance in the border area, a change in the distribution of red or roe deer, or perhaps some other reason.

Core areas were determined through fixed-kernel density analysis, and one important aspect of this analysis is the bandwidth that is chosen. In this study, I chose to use the reference bandwidth, h_{ref}. Both Worton (1995) and Seaman and Powell (1996) argued that analyses using the reference bandwidth overestimate home range sizes, and they argued for the application of the bandwidth produced from least squares cross-validation (LSCV). However, when the LSCV bandwidth was applied, no core areas were apparent, only small islands around each scat location. Steiniger *et al.* (2010) also found that h_{LSCV} was unacceptable when examining home ranges of grizzly bears in Alberta, Canada. Hemson *et al.* (2005) found that h_{LSCV} failed more than half the time when examining data sets consisting of more than 100 points, while also failing when examining intensively-used areas, such as core areas. Core areas produced from fixed-kernel analysis using the reference bandwidth produced core areas equal to 6.8% and 3.2% for the Grapa and Halny packs, respectively. Both values represent the smaller end of the spectrum when compared to other studies, so likely represent at least a portion of the true core areas, if not the entire core areas. I would be a little more cautious about the chosen bandwidth if the kernel analysis produced significantly larger core areas in relation to territory sizes (i.e. 20% or greater).

The Halny pack faces one significant challenge that the Grapa pack does not have to deal with, and that is the danger posed by Slovakian hunters. The effects of hunting activities on the Halny wolves are uncertain. Nowak *et al.* (2008) found that hunting accounted for the deaths of 15 wolves in this area within a 4-year period, accounting for 83% of all wolf mortality. Hunting numbers and mortality estimates were not obtained for the period of this study, but with such a high toll taken on the Halny wolves by hunting, it would not be unreasonable to assume that a core area would be located away from the border in order to minimize chance encounters with hunters. The effects on core selection of the Halny pack remain uncertain, but further studies looking at the areas most visited by Slovakian hunters and numbers of wolf kills in the area have the potential to shed some light on this.

Within both territories, the effects of logging activities on core selection are also unknown. Because of the high densities of roads within both territories, but particularly the Grapa territory, logging occurs throughout the territories. Logging activities, locations, and times were all difficult to document, and therefore, their effects on core area selection are difficult to determine. Depending on the extent of logging in different locations within the territories, core areas may have been altered during the study period. Due to the relatively small sample sizes over the course of the 3-year period, these changes would have been hard to detect, as it was necessary to group all scat locations from one pack together to get an overall picture. In order to detect any change in the location of core areas, more intensive sampling would have been required each year to record sufficient scat samples for that year.

In addition to the possibility of a change in core area location from year to year, there is also the possibility that the size of the core area changed, not just on an annual basis, but on even a seasonal basis. Person *et al.* (1996) found that home ranges of wolves in southeastern Alaska were 50% smaller in the months of April through August, when denning and pup-rearing occurred, than in winter. Since many studies determine the size and location of core areas through MCPs and kernel density isopleths, at either the 50% or 75% probability levels, this would also result in a decrease in the size of the core area. Therefore, it is safe to assume that the size of core areas also changes as wolves utilize different areas more heavily during different seasons. Because of the small numbers of scats found during each season, the detection of any change in size to the core area would not be observed.

Another variable not examined in this study is ungulate numbers. Therefore, we are unsure as to the effects of ungulate numbers and behavior on core selection and territory utilization by both the Grapa and Halny packs. Other studies have found that wolves tend to follow prey species to lower elevations during the winter (Paquet *et al.* 1996). As mentioned earlier, this would help explain why pack core areas, determined through scat concentrations, were located in intermediate elevations and not at the highest elevations within the territories.

Some uncertainty also existed in the measurement of road distances and densities. These measurements were obtained by digitizing aerial images from Google Earth (Mountain View, California). Because some regions of the territories were more densely forested than others, it was at times difficult to determine whether roads existed in these areas with thick canopy cover. It is possible that small sections of roads were not recorded due to not being able to be detected through aerial imagery. This would result in slightly modified road density values, with more heavily-forested plots possibly having higher road densities than what was recorded. However, the overall findings would likely remain unchanged, as this most likely limited to small sections of roads in only a few plots, if any.

Because roads and trails were found using aerial images, no distinctions were made concerning the amount of use any one road or trail received. Therefore, roads and trails that are used frequently were grouped with those that rarely receive any use. The result is that only the actual presence of a road or trail was examined, rather than whether the road or trail received actual use. This could have a large effect on habitat utilization by wolves in both packs, and not be accounted for in this study.

This study was conducted in an area with low densities of both wolves and wolf packs. There were few areas where the territory of one wolf pack directly bordered that of another pack. This may have contributed to the findings of a hot spots pattern of marking rather than the Olfactory Bowl pattern. In their study, Peters and Mech (1975) examined a region with many different bordering wolf pack territories. In this case, the wolves of one pack may have felt that it was important to mark the peripheries of their territory as a warning to wolves from other packs. In this study, neither the Grapa wolves nor the Halny wolves had to be concerned with neighboring wolf packs, and therefore, might have not felt the need to mark their territory borders.

The final uncertainty is associated with weather conditions during the study period. Weather conditions, and in particular, snowfall amounts, can have important effects on habitat utilization by wolves. Fuller (1991) found mobility of wolves in Minnesota tended to decrease with winter severity. Paquet *et al.* (1996) also suggested that wolves may have difficulty traveling in snow depths greater than 50 cm due to their low chest heights. Weather conditions would also be a major determinant of habitat use by ungulate species during the winter, which would significantly affect where wolves spend their time. Severe winters would congregate ungulates in the lowlands, while mild winters may allow ungulates to remain up higher and still find enough food. Snow cover data (National Climatic Data Center) for southwestern Poland for the study period indicate that the winter of 2005 was an abnormally harsh winter, with daily snow cover at an elevation of 857 m in February recorded at an average of nearly 55 cm, compared to only 29 cm in the same month in 2004. Most scats analyzed in this study were recorded in 2005, and therefore, if Grapa or Halny wolves chose different core areas that year because of the harsh weather, the kernel-density analysis would have been biased toward this location. However, Figure 27 (Appendix) shows that the scat locations recorded from January-March 2005 for the Grapa wolves were found in the same area as those scats found in 2006 and 2007, and therefore, I believe that the kernel density analysis revealed an accurate core area for the Grapa pack, and not just a core area used in the winter of 2005.

CONCLUSION

The findings of this study suggest that human activity is having an effect on the behavior of both the Grapa pack and the Halny pack. The Grapa pack selected a core area that was significantly farther from human built-up areas than other random plots within their territory. No similar significant difference was found in the Halny territory, but within the Polish part of their territory, there were no other areas located farther from built-up areas that could have been chosen. A core area could have been located in the Slovakian part of the territory, where the distance to the nearest built-up areas would have been even greater, but border issues made sampling there difficult.

The only significant difference between core plots and non-core plots found in both territories was the distance to the nearest primary road. In both the Grapa and Halny territories, core plots were found to be significantly farther from primary roads than non-core plots. These distances were frequently smaller than those to the nearest built-up areas, suggesting that the avoidance of primary roads is more of a factor in core selection than proximity to people.

More research should be conducted in order to provide a clearer picture of the behaviors and preferences of the Grapa and Halny wolves. Probably the most valuable information would be obtained through use of radio or GPS collars. Daily movements could be observed and core areas, based on time spent in certain areas, could be more accurately defined. Such data collected from the Halny wolves could also tell us how hunting within the Slovakian part of their territory affects their movement, particularly in the fall months. This would also provide valuable data concerning their use of the Slovakian part of their territory, as compared to the Polish part, which we were not able to be survey in this study, but remains a large question.

The viability of the wolves in both the Grapa and Halny packs remains uncertain. If hunting within Slovakia continues to account for 83% of mortality in the Zywiecki Landscape Park (Nowak *et al.* 2008), where the Halny territory is located, then the likelihood of population growth in that region is minimal. The Zywiecki Landscape Park contains the territories of three wolf packs, all straddling the Polish-Slovakian border. Therefore, a certain extent of connectivity exists between these territories, helping to provide some level of resilience against a sudden population collapse.

No such connectivity exists within the Silesian Beskidy Range, where the Grapa territory is located. The Bukowy pack is the only other pack to inhabit the area, and their connection to the Grapa pack is uncertain due to the location of a resort town between the territories. Although situated completely within the Polish borders, and therefore, not as prone to hunting mortality as the Halny wolves, the Grapa pack has limited room to roam, and the opportunity for individual wolves to disperse into new areas is minimal due to the multiple centers of urban activity surrounding the area.

In the few years since this study concluded, the bark beetle has devastated huge stands of spruce in the Silesian Beskidy Mountains, the location of the Grapa territory. This has led to increased fragmentation in the landscape and decreased cover in many forest patches, limiting areas suitable for wolf utilization. Although not examined in this study, this could have a significant effect on the behavior of the Grapa wolves.

It seems that the Grapa pack and Halny pack have both learned to adapt to a certain level of human activity within and around their territories. In many cases, this has been forced upon them. While it is nearly impossible for them to completely avoid people, both packs seem to have selected core areas that minimize high levels of frequent disturbance, like those associated with primary roads, and in the case of the Grapa pack, also human built-up areas. Because of the limited connectivity of the Grapa wolves to other wolf packs, and the vulnerability of the Halny wolves to Slovakian hunters, it seems imperative that the existing habitat be protected from any excessive development and that there is a need for more cooperation between Poland and Slovakia in the area of wolf management. The density of roads in southern Poland is already much higher than in the north of Poland, and extensive road development is being planned for the near future within the region (Nowak and Myslajek, pers. comm.). This could be a disaster for the wolves within the study region, as both packs clearly avoided primary roads. Highway traffic in Poland has more than doubled in the last decade (Niedzialkowski *et al.* 2006), and this is a worrying trend. Connections to other populations are also a concern, particularly for the Grapa pack. A great deal of research should be conducted on the planned road development in order to minimize impacts in areas that could be valuable to wolves and other carnivores within the region. Research on structures such as wildlife over/underpasses should also be reviewed in order to provide these structures in the most beneficial areas to promote carnivore migration and movement. This is particularly important in the case of the wolf populations in Poland, which help link larger populations in the countries of Eastern Europe, with smaller populations found scattered throughout the more developed countries of Western Europe. If these measures are not taken, the Grapa pack and Halny pack might be seeing their last years in the region. If these measures are taken, and further research is conducted in protecting areas large enough for the wolves to fulfill all their biological needs and maintain connections with other Polish and Slovakian populations, then the Grapa and Halny packs may survive. They have already shown that they are capable of adapting to a great deal.

APPENDIX

Date	Longitude (E)	Latitude (N)	Date	Longitude (E)	Latitude (N)	Date	Longitude (E)	Latitude (N)
1/17/2005	19.0036	49.6651	5/11/2005	19.0506	49.6422	4/16/2007	19.0699	49.6189
1/17/2005	19.0089	49.6340	5/11/2005	19.0508	49.6428	4/17/2007	19.0700	49.6318
1/18/2005	19.0090	49.6341	5/11/2005	19.0508	49.6428	4/17/2007	19.0710	49.6436
1/18/2005	19.0111	49.6528	5/11/2005	19.0512	49.6432	4/17/2007	19.0730	49.6330
2/4/2005	19.0121	49.6728	5/11/2005	19.0513	49.6424	4/23/2007	19.0748	49.6353
2/5/2005	19.0134	49.6529	5/11/2005	19.0517	49.6437	4/23/2007	19.0749	49.6339
2/5/2005	19.0165	49.6530	5/11/2005	19.0519	49.6439	4/23/2007	19.0751	49.6332
2/7/2005	19.0242	49.6799	5/11/2005	19.0524	49.6443	4/23/2007	19.0751	49.6332
2/7/2005	19.0348	49.6092	5/11/2005	19.0524	49.6445	4/23/2007	19.0757	49.6339
2/8/2005	19.0362	49.6140	5/13/2005	19.0525	49.6408	4/24/2007	19.0757	49.6365
2/8/2005	19.0367	49.6111	7/7/2005	19.0537	49.6411	4/25/2007	19.0774	49.6323
2/8/2005	19.0390	49.6496	8/6/2005	19.0563	49.6461	5/7/2007	19.0775	49.6380
2/8/2005	19.0393	49.6491	8/6/2005	19.0570	49.6495	5/9/2007	19.0777	49.6385
2/8/2005	19.0399	49.6137	10/2/2005	19.0571	49.6464	5/9/2007	19.0780	49.6391
2/17/2005	19.0410	49.6298	10/2/2005	19.0571	49.6463	5/22/2007	19.0796	49.6320
2/17/2005	19.0422	49.6850	10/2/2005	19.0594	49.6652	5/22/2007	19.0810	49.6502
2/17/2005	19.0428	49.7066	11/9/2005	19.0594	49.6652	5/22/2007	19.0818	49.6486
2/17/2005	19.0438	49.6050	11/9/2005	19.0600	49.6497	5/25/2007	19.0834	49.6296
2/17/2005	19.0462	49.6356	11/9/2005	19.0609	49.6530	5/25/2007	19.0834	49.6296
2/17/2005	19.0462	49.6362	11/9/2005	19.0609	49.6530	5/25/2007	19.0869	49.6457
2/18/2005	19.0464	49.6340	11/9/2005	19.0609	49.6680	5/25/2007	19.0876	49.6331
2/18/2005	19.0464	49.6366	11/9/2005	19.0609	49.6281	6/5/2007	19.0890	49.6452
2/18/2005	19.0465	49.6371	11/23/2005	19.0610	49.6499	8/2/2007	19.0894	49.6451
2/18/2005	19.0465	49.6382	11/24/2005	19.0612	49.6671	8/8/2007	19.0948	49.6346
2/22/2005	19.0465	49.6346	11/24/2005	19.0617	49.6312	10/21/2007	19.0951	49.6347
2/22/2005	19.0465	49.6352	12/8/2005	19.0630	49.6299			
2/22/2005	19.0465	49.6369	12/8/2005	19.0631	49.6506			
2/22/2005	19.0465	49.6350	12/8/2005	19.0632	49.6547			
2/22/2005	19.0465	49.6380	5/11/2006	19.0646	49.6763			
2/22/2005	19.0466	49.6306	5/14/2006	19.0648	49.6325			
2/23/2005	19.0466	49.6378	8/4/2006	19.0654	49.6264			
2/23/2005	19.0468	49.6384	8/4/2006	19.0663	49.6321			
2/23/2005	19.0470	49.6388	8/4/2006	19.0664	49.6562			
2/23/2005	19.0471	49.6389	8/9/2006	19.0665	49.6471			
2/23/2005	19.0472	49.6391	8/9/2006	19.0669	49.6660			
2/23/2005	19.0474	49.6395	8/17/2006	19.0670	49.6668			
2/24/2005	19.0481	49.6390	9/24/2006	19.0671	49.6708			
4/24/2005	19.0485	49.6399	9/30/2006	19.0672	49.6670			
4/24/2005	19.0489	49.6293	12/13/2006	19.0675	49.6660			
4/24/2005	19.0489	49.6402	12/16/2006	19.0676	49.6526			
4/24/2005	19.0492	49.6427	2/3/2007	19.0678	49.6290			
5/2/2005	19.0492	49.6404	4/11/2007	19.0678	49.6288			
5/11/2005	19.0493	49.6410	4/11/2007	19.0679	49.6326			
5/11/2005	19.0495	49.6417	4/11/2007	19.0681	49.6323			
5/11/2005	19.0497	49.6277	4/12/2007	19.0683	49.6319			
5/11/2005	19.0497	49.6436	4/12/2007	19.0686	49.6526			
5/11/2005	19.0500	49.6457	4/12/2007	19.0686	49.6306			
5/11/2005	19.0500	49.6453	4/12/2007	19.0687	49.6567			
5/11/2005	19.0503	49.6425	4/12/2007	19.0687	49.6763			
5/11/2005	19.0505	49.6422	4/14/2007	19.0699	49.6189			

Table 13: Grapa Pack Scat Data

Date	Longitude (E)	Latitude (N)		Date	Longitude (E)	Latitude (N)
2/9/2005	19.21593	49.583224		10/12/2005	19.24874	49.571588
2/9/2005	19.21779	49.583719		10/12/2005	19.24973	49.573139
2/9/2005	19.21834	49.584429		10/12/2005	19.24985	49.572621
2/9/2005	19.23086	49.583481		10/12/2005	19.25016	49.573258
2/9/2005	19.23152	49.584120		10/12/2005	19.25356	49.565692
3/27/2005	19.26448	49.574837		10/12/2005	19.25382	49.566136
3/27/2005	19.26655	49.575897		10/12/2005	19.25383	49.566581
3/27/2005	19.26819	49.576285		10/12/2005	19.25409	49.567081
3/27/2005	19.26983	49.576394		10/12/2005	19.25780	49.574082
3/27/2005	19.27138	49.576726		7/16/2006	19.25383	49.565800
3/31/2005	19.23283	49.566762		7/16/2006	19.26341	49.573610
3/31/2005	19.23429	49.567586		8/15/2006	19.25714	49.568805
3/31/2005	19.24176	49.572767		8/15/2006	19.26669	49.579695
3/31/2005	19.25198	49.565779		10/1/2006	19.21849	49.558975
3/31/2005	19.25307	49.565541		5/12/2007	19.14869	49.557790
3/31/2005	19.25316	49.566013		5/12/2007	19.15094	49.556970
3/31/2005	19.25982	49.571903		5/13/2007	19.17491	49.580060
10/12/2005	19.23860	49.548090		5/14/2007	19.22377	49.591670
10/12/2005	19.24511	49.568290		5/14/2007	19.25470	49.568420
10/12/2005	19.24548	49.568767		5/14/2007	19.26288	49.573430
10/12/2005	19.24610	49.568965		5/14/2007	19.26739	49.583010
10/12/2005	19.24653	49.569402		5/14/2007	19.26740	49.582970
10/12/2005	19.24677	49.569999		5/14/2007	19.26744	49.582420
10/12/2005	19.24708	49.570676		7/24/2007	19.23190	49.554988
10/12/2005	19.24764	49.571112		8/15/2007	19.25107	49.564290
10/12/2005	19.24819	49.571350		8/15/2007	19.26924	49.587560

Table 14: Halny Pack Scat Data

	Core1	Core2	Core3	Core4	Core5	**MEAN**
Broad-leaved forest	5.2%	31.0%	2.3%	0.0%	60.8%	**19.9%**
Coniferous forest	33.4%	39.9%	70.1%	91.1%	39.1%	**54.7%**
Mixed forest	36.3%	29.1%	27.5%	0.0%	0.0%	**18.6%**
Transitional woodland-shrub	25.1%	0.0%	0.1%	8.9%	0.1%	**6.8%**
Natural grasslands	0.0%	0.0%	0.0%	0.0%	0.0%	**0.0%**
Complex cultivation patterns	0.0%	0.0%	0.0%	0.0%	0.0%	**0.0%**
Discontinuous urban fabric	0.0%	0.0%	0.0%	0.0%	0.0%	**0.0%**
Land principally occupied by agriculture, with significant areas of natural vegetation	0.0%	0.0%	0.0%	0.0%	0.0%	**0.0%**
Non-irrigated arable land	0.0%	0.0%	0.0%	0.0%	0.0%	**0.0%**

	NC1	NC2	NC3	NC4	NC5	NC6	NC7	NC8	NC9	NC10	NC11	NC12	**MEAN**
Broad-leaved forest	0.0%	1.2%	16.5%	0.0%	0.0%	0.0%	0.0%	4.8%	0.0%	0.0%	0.0%	0.6%	**1.9%**
Coniferous forest	99.6%	29.6%	31.5%	66.4%	97.0%	51.9%	58.5%	88.8%	0.0%	39.9%	100.0%	98.6%	**63.5%**
Mixed forest	0.0%	0.0%	0.0%	0.0%	0.0%	16.0%	0.0%	6.4%	0.0%	60.1%	0.0%	0.0%	**6.9%**
Transitional woodland-shrub	0.0%	0.0%	17.4%	33.6%	3.0%	32.1%	10.5%	0.0%	0.0%	0.0%	0.0%	0.0%	**8.0%**
Natural grasslands	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	**0.0%**
Complex cultivation patterns	0.3%	16.7%	6.3%	0.0%	0.0%	0.0%	23.4%	0.0%	18.9%	0.0%	0.0%	0.8%	**5.5%**
Discontinuous urban fabric	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	7.6%	0.0%	51.9%	0.0%	0.0%	0.0%	**5.0%**
Land principally occupied by agriculture, with significant areas of natural vegetation	0.0%	0.0%	28.3%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	**2.4%**
Non-irrigated arable land	0.1%	52.5%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	29.3%	0.0%	0.0%	0.0%	**6.8%**

Table 15: Land Cover Composition of Core and Non-core Plots, Grapa Territory

	Core1	Core2	Core3	Core4	Core5	**MEAN**
Broad-leaved forest	0.0%	2.6%	0.0%	0.0%	0.0%	**0.5%**
Coniferous forest	85.0%	53.7%	55.3%	86.8%	76.7%	**71.5%**
Mixed forest	0.0%	43.7%	44.7%	13.2%	23.3%	**25.0%**
Transitional woodland-shrub	15.0%	0.0%	0.0%	0.0%	0.0%	**3.0%**
Natural grasslands	0.0%	0.0%	0.0%	0.0%	0.0%	**0.0%**
Complex cultivation patterns	0.0%	0.0%	0.0%	0.0%	0.0%	**0.0%**
Discontinuous urban fabric	0.0%	0.0%	0.0%	0.0%	0.0%	**0.0%**
Land principally occupied by agriculture, with significant areas of natural vegetation	0.0%	0.0%	0.0%	0.0%	0.0%	**0.0%**
Non-irrigated arable land						

	NC1	NC2	NC3	NC4	NC5	NC6	NC7	NC8	NC9	NC10	NC11	NC12	**MEAN**
Broad-leaved forest	0.0%	0.0%	0.0%	56.6%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	**4.7%**
Coniferous forest	100.0%	79.6%	76.4%	43.4%	27.9%	19.6%	31.5%	100.0%	72.2%	94.8%	51.8%	7.9%	**58.8%**
Mixed forest	0.0%	0.5%	8.1%	0.0%	0.0%	56.6%	0.0%	0.0%	0.0%	5.2%	0.2%	8.3%	**6.6%**
Transitional woodland-shrub	0.0%	19.9%	15.3%	0.0%	72.1%	0.0%	0.0%	0.0%	27.8%	0.0%	20.4%	83.6%	**19.9%**
Natural grasslands	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	63.7%	0.0%	0.0%	0.0%	27.6%	0.0%	**7.6%**
Complex cultivation patterns	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	**0.0%**
Discontinuous urban fabric	0.0%	0.0%	0.0%	0.0%	0.0%	23.8%	0.1%	0.0%	0.0%	0.0%	0.0%	0.2%	**2.0%**
Land principally occupied by agriculture, with significant areas of natural vegetation	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	4.7%	0.0%	0.0%	0.0%	0.0%	0.0%	**0.4%**
Non-irrigated arable land	0.1%	52.5%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	29.3%	0.0%	0.0%	0.0%	**6.8%**

Table 16: Land Cover Composition of Core and Non-core Plots, Halny Territory

Continuous urban fabric	Agro-forestry areas
Discontinuous urban fabric	Broad-leaved forest
Industrial or commercial units	Coniferous forest
Road and rail networks and associated land	Mixed forest
Port areas	Natural grasslands
Airports	Moors and heathland
Mineral extraction sites	Sclerophyllous vegetation
Dump sites	Transitional woodland-shrub
Construction sites	Beaches, dunes, sands
Green urban areas	Bare rocks
Sport and leisure facilities	Sparsely vegetated areas
Non-irrigated arable land	Burnt areas
Permanently irrigated land	Glaciers and perpetual snow
Rice fields	Inland marshes
Vineyards	Peat bogs
Fruit trees and berry plantations	Salt marshes
Olive groves	Salines
Pastures	Intertidal flats
Annual crops associated with permanent crops	Water courses
Complex cultivation patterns	Water bodies
Land principally occupied by agriculture, with significant areas of natural vegetation	Coastal lagoons
UNCLASSIFIED LAND SURFACE	Estuaries
UNCLASSIFIED WATER BODIES	Sea and ocean
NO DATA	

Table 17: Corine Land Cover Classifications

	Sum of Ranks				
	Core (%)	Non-Core (%)	Mann-Whitney U Statistic	z Statistic (corrected for ties)	Probability > z
Broadleaf Forest	64	89	49.0000	2.0028**	0.0226
Coniferous Forest	39.5	113.5	24.5000	0.5798	0.281
Mixed Forest	51	69	36.0000	1.3472	0.089
Transitional Woodland Shrub	50.5	102.5	35.5000	0.5798	0.281
Complex Cultivation Patterns	30	123	15.0000	1.5811	0.0569
Discontinuous Urban Fabric	40	13	25.0000	0.527	0.2991
Land Principally Occupied by Agriculture	42.5	110.5	27.5000	0.2635	0.3961
Non-irrigated Arable Land	37.5	115.5	22.5000	0.7906	0.2146
Forest Cover	53	89	32.0000	0.5664	0.2856
Non-Forest Cover	34.5	18.5	19.5000	1.1068	0.1342

Table 18: Land Cover Statistics, Grapa Pack
** indicates significance at the 95% level

	Sum of Ranks				
	Core (%)	Non-Core (%)	Mann-Whitney U Statistic	z Statistic (corrected for ties)	Probability > z
Broadleaf Forest	48	105	33.0000	0.3162	0.3759
Coniferous Forest	53	100	38.0000	0.8433	0.1995
Mixed Forest	62	91	47.0000	1.792	0.0366
Transitional Woodland Shrub	33	120	18.0000	1.2649	0.103
Complex Cultivation Patterns	40	113	25.0000	0.527	0.2991
Land Principally Occupied by Agriculture	37.5	115.5	22.5000	0.7906	0.2146
Non-irrigated Arable Land	42.5	110.5	27.5000	0.2635	0.3961
Forest Cover	63	90	48.0000	1.8974	0.0289
Non-Forest Cover	29	124	14.0000	1.6865	0.0458

Table 19: Land Cover Statistics, Halny Pack

	Sum of Ranks				
	Core (%)	Non-Core (%)	Mann- Whitney U Statistic	z Statistic (corrected for ties)	Probability > z
Elevation	53	100	38.0000	0.8433	0.1995
Straight-line Distance to Nearest Built-up Area	65	71	50.0000	2.6056**	0.0046
Road Density	33	120	18.0000	1.2649	0.103
Distance to Nearest Primary Road	73	80	58.0000	2.9515**	0.0016

Table 20: Results of Mann-Whitney U-tests of Habitat Parameters, Grapa Pack
** indicates significance at the 95% level

	Sum of Ranks				
	Core (%)	Non-Core (%)	Mann- Whitney U Statistic	z Statistic (corrected for ties)	Probability > z
Elevation	50	103	35.0000	0.527	0.2991
Straight-line Distance to Nearest Built-up Area	50	103	35.0000	0.527	0.2991
Road Density	36.5	116.5	21.5000	0.896	0.1851
Distance to Nearest Primary Road	69	84	54.0000	2.5298**	0.0057

Table 21: Results of Mann-Whitney U-tests of Habitat Parameters, Halny Pack
** indicates significance at the 95% level

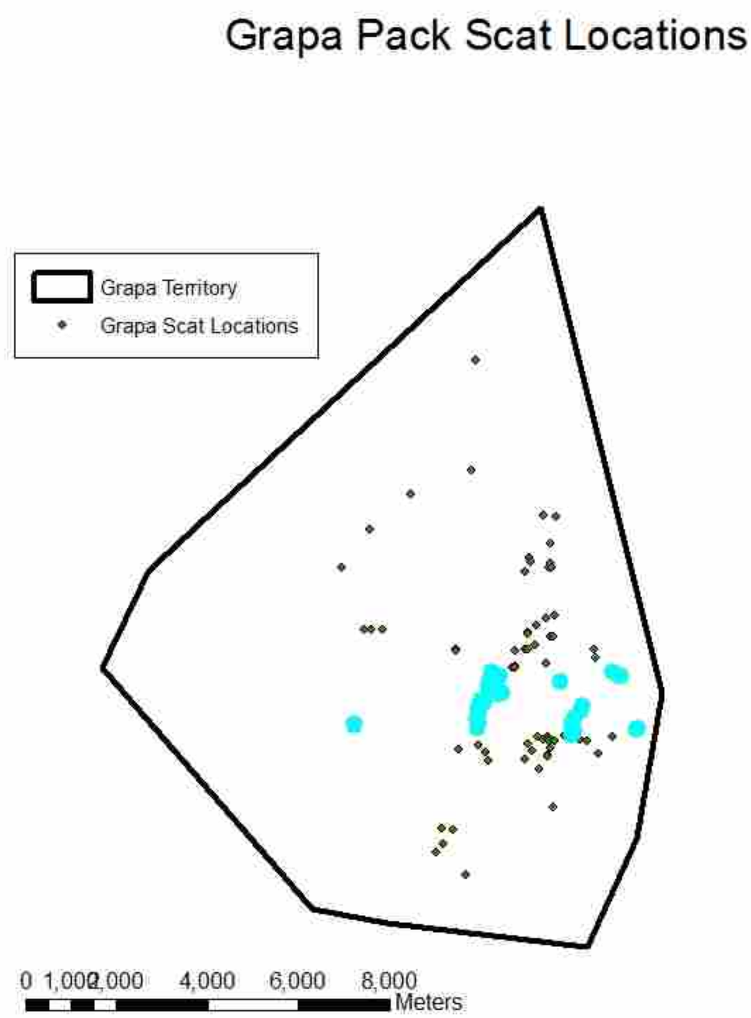

Figure 27: Scat locations recorded within the Grapa territory. Those scats found between January 2005 and March 2005 are highlighted, showing similar locations to other scats found in subsequent years.

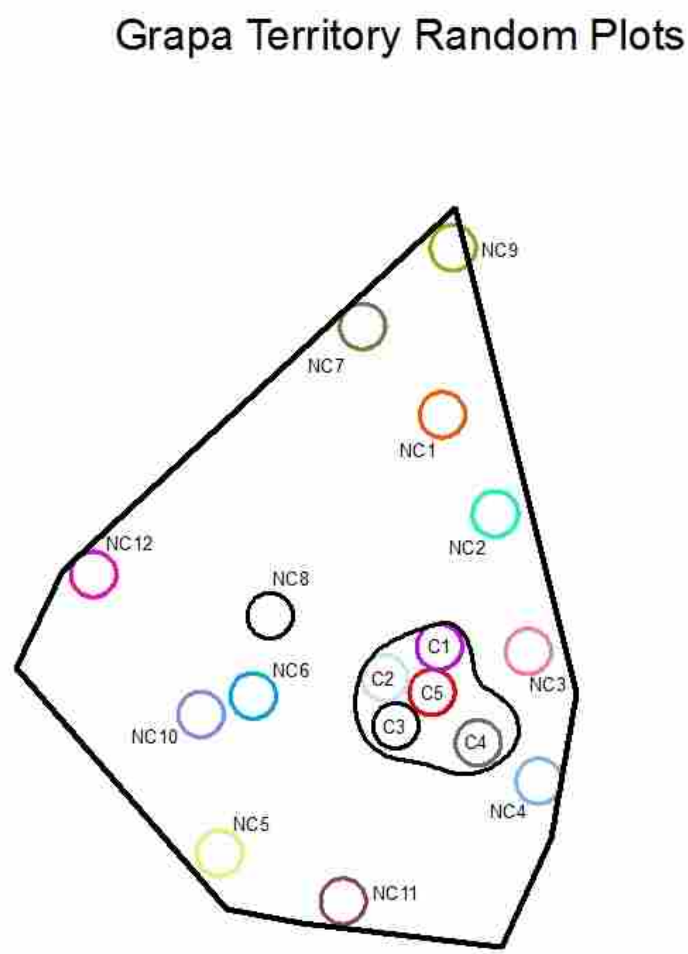

Figure 28: Random plots within the Grapa Territory.
NC = Non-core, C = Core.

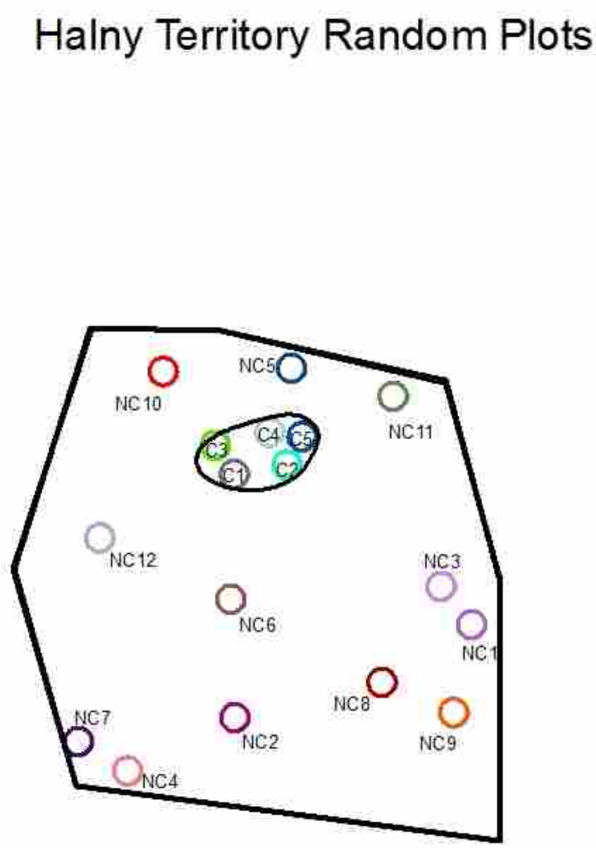

Figure 29: Random plots within the Halny Territory.
NC = Non-core, C = Core.

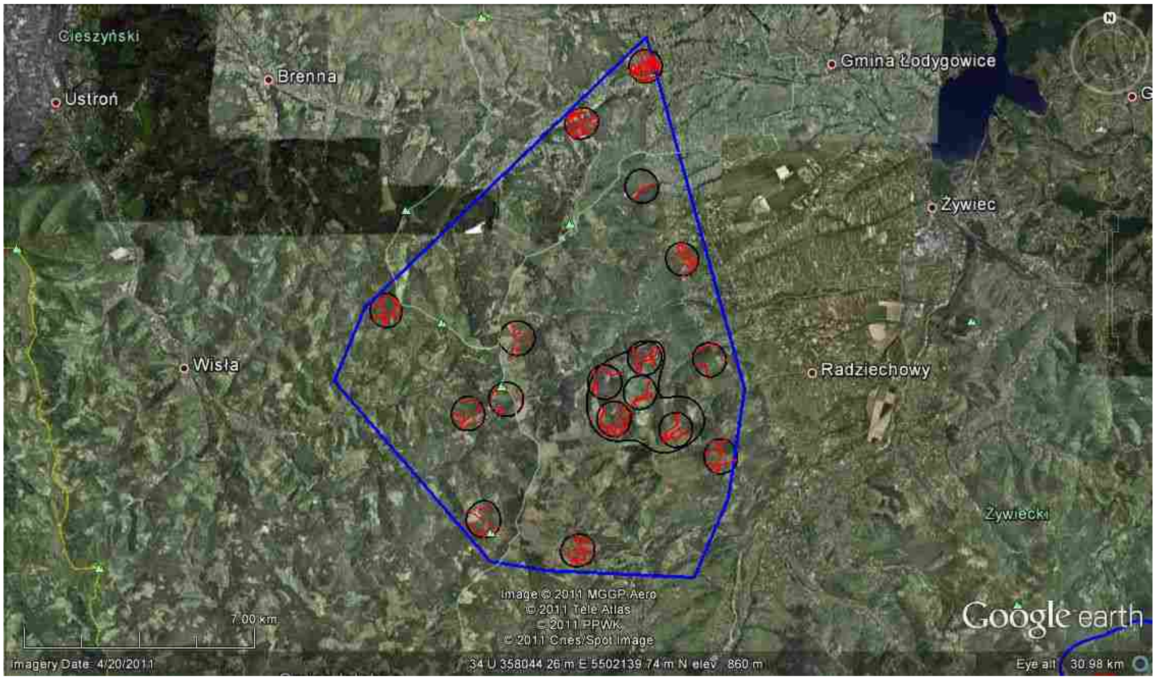

Figure 30: Random plots within the Grapa territory, with red lines marking road locations.

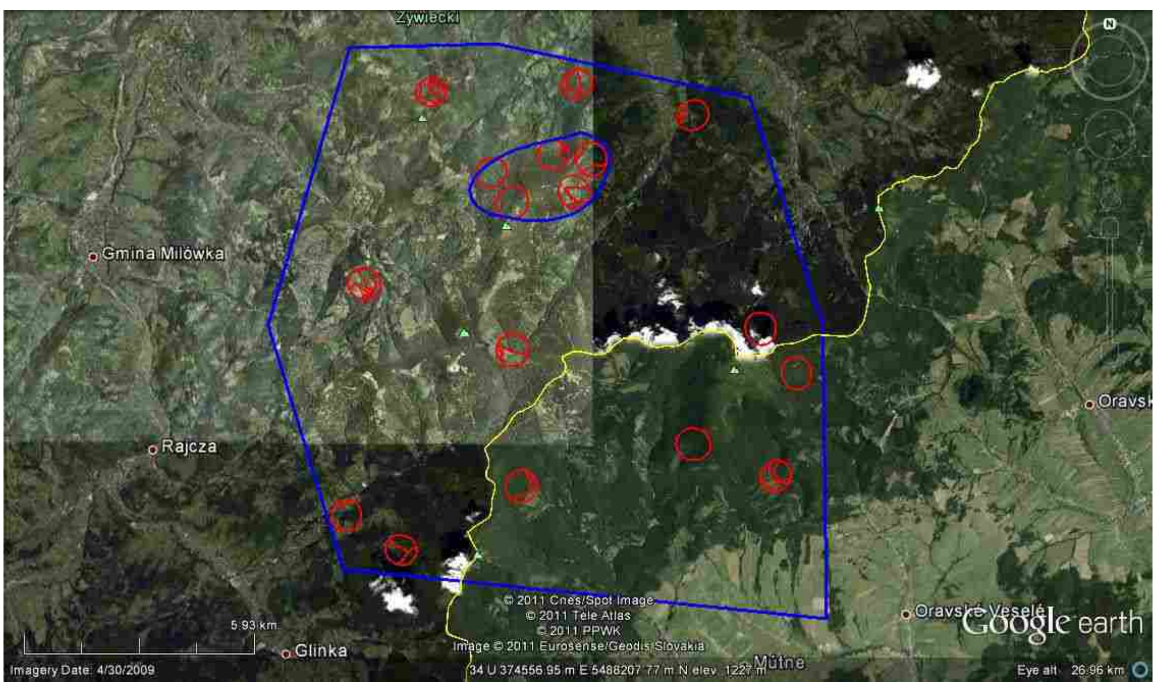

Figure 31: Random plots within the Halny territory, with red lines marking road locations.

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