Influence of Linear Features and Snowmachine Activity on Resource Selection by Wolves

by

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Abstract

Snowmachines and the alterations made to the landscape from their activity can have profound impacts on the dynamics of wolves (*Canis lupus*) and their prey. Snowmachine activity can displace animals and disrupt their activity and movement patterns; conversely, the creation of trails can enable energy-efficient travel by wolves, thereby increasing the likelihood of encountering and successfully capturing prey. High hunting and trapping pressure could exacerbate these effects, particular during critical late-winter periods when animals are most stressed and anthropogenic activity is greatest. With its dense network of trails, the Nelchina Basin in south-central Alaska presented a unique opportunity to assess quantitatively the spatial and temporal relationships among wolves, human activity, prey resources, and snow characteristics. I monitored the movements of wolves telemetered with global positioning system (GPS) collars, quantified snowmachine activity using remote-sensing techniques and enumeration counters to delineate the timing and distribution of human use, defined relative moose (*Alces alces*) abundance using aerial surveys, and routinely measured snow depth and hardness to construct ecologically plausible resource selection models. The seasonal movements, distribution and use areas of wolves in the Nelchina Basin, Alaska, were not influenced consistently by snow or the distribution of prey. Nor did wolves exhibit a strong selection for or an avoidance of linear features (i.e., snowmachine trails, and seismic lines), potentially because responses were confounded by predator-management activities. Levels of recreational snowmachine activity were relatively low and followed predictable patterns by day, week, and season. Wolves appeared to respond to this pressure by using trails when snowmachine activity was least. Wolves travelled 3.7 times faster on trails than off trails, although the proportion of locations specifically on trails was low. Findings from this study suggest that for a heavily exploited wolf population, the cost of utilizing a network of linear features outweighed any potential energetic benefits associated with winter travel and prey capture.

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Chapter 1 : Introduction

Context

The ecological effects of linear disturbance on wildlife are increasingly a concern for resource managers and planners, yet little is understood about the implications for predators, particularly wolves (*Canis lupus*), and the dynamic role that human activity can have on predator-prey interactions (Baldwin and Stoddard 1973). As of 2003, there were 2.4 million snowmachines registered in North America, 34,000 of which were in Alaska (International Snowmachine Manufacturers Association 2010). This number rose to 55,249 by 2009 in Alaska. The production of light-weight, fuel-efficient snowmachines in the mid-1990s has allowed snowmachine activity to expand into areas where little or no activity previously existed. Because deep snow can impede the movements of wolves and ungulates by constraining energetics, food acquisition, behavior, and activity (Telfer and Kelsall 1984; Fuller 1991; Huggard 1993; Murray et al. 1995; Murray and Larivière 2002), the effects of snowmachine activity, including the resulting trails, have potential ecological consequences for wolves and the relationship with their primary winter prey, moose (*Alces alces*).

Winter Movements of Wolves

Opportunistic carnivores with broad habitat requirements such as wolves are well adapted to travel over widespread areas in search of abundant and vulnerable prey (Mech 1970; Mladenoff et al. 1995; Ciucci et al. 2003). Typical travel occurs at a lope maintaining sustained speeds of 8-9 km/h for many kilometers per day (Burkholder 1959; Mech 1966, 1970, 1994; Mech and Boitani 2003). In south-central Alaska, Burkholder (1959) observed a wolf pack in winter moving at 9.5 km/h (6 mi/h) and covering 72 km (45 mi) in less than 24 h; on Isle Royale, Michigan, wolves were observed traveling an average of 14.4 km (9 mi) per day (Mech 1970). Because winter-pack movements are related to hunting success and the relative abundance of prey (Peterson 1977; Alexander et al. 2005), Mech (1970) reported a more appropriate average of 2.4 km/h after considering numerous elements of winter movement patterns such as long-distance hunting forays, pursuit and capture, feeding, and local movements around the kill.

Wolves tend to follow easy travel routes in areas where they are most likely to encounter prey (Bergerud et al.1984; Mech and Boitani 2003; Alexander et al. 2005). Mech and Boitani (2003) summarized three characteristics of winter travel: long, linear routes (as opposed to meandering movement and search patterns), repeated use of travel routes, and a tendency to cover territories extensively rather than intensively. Linear features such as windswept areas, frozen waterways (e.g., lakes and rivers), trails established by animals and humans (e.g., secondary roads, seismic lines, utility corridors, and snowmachine trails), and areas devoid of vegetation have all been cited as landscape features used to facilitate travel efficiency by reducing travel time and increasing the amount of territory covered (Bergerud et al. 1984; Thurber et al. 1994; Singleton 1995; Paquet and Callaghan 1996; James and Stuart-Smith 2000; Kunkel and Pletscher 2001; Creel et al. 2002; Ciucci et al. 2003). Many travel routes connect or intersect land masses such as on Isle Royale, where wolves used a network of frozen lakes and bays adjacent to islands instead of a more difficult overland traverse (Mech 1966; Jordan et al. 1967; Peterson 1977). Ciucci et al. (2003) confirmed other's findings that the existence of a secondary road or trail network could influence the spatial organization and distribution of wolf packs (Thurber et al. 1994; Paquet and Callaghan 1996). In winter, when snow and winter severity become critical constraints on food acquisition and locomotion, the availability of these trails may have an even stronger influence on movement patterns.

Effects of Snow Morphology

The ecological importance of snow morphology can be described in terms of depth, density, hardness, and temperature (Klein et al. 1950; Coady 1974; Peek 1998). These characteristics change continually. Wind, gravity, and insolation settle and compact snow layers, while changes in temperature break down and consolidate snow crystals to increase their density (Kelsall and Prescott 1971; Peterson and Allen 1974). Snow density varies little among snow layers, but increases with increasing depth as winter progresses. Newly fallen snow typically has a density of 0.03 to 0.19 g/cm^3, whereas older snow and lower layers have densities of 0.23 to 0.50 g/cm^3 (Klein et al. 1950; Kelsall and Prescott 1971; Moen and Evans 1971). Hard layers or snow crusts result from the freezing and refreezing of snow surfaces and from wind compaction (wind crust) (Kelsall and Prescott 1971). Crusts are vertically and horizontally variable, and are facilitated by additional surface water or high relative humidity (Kelsall and Prescott 1971; Peterson and Allen 1974). Because density and hardness are inextricably linked, greatest hardness is also found in the lower layers where maturation has been the longest (Kelsall and Prescott 1971). These variations in snow morphology (i.e., increased depth, density, and hardness) can have profound ecological implications for wolves and their prey (Peterson and Allen 1974; Peterson 1977; Telfer and Kelsall 1984; Fuller 1991; Ciucci et al. 2003; Whiteman 2008).

Wolves generally travel in a single file though snow as shallow as 20-25 cm (Peterson 1977), creating a hard-packed network of trails and distributing locomotive expenditures throughout the pack (Mech 1970). As snow depth and density change, wolves alter their gaits or select travel routes with hard, compact snow to increase efficiency. Nasimovich (1955) observed that wolves sank to their chests with a snow density of <0.21 g/cm^3 and had difficulty chasing moose in 41 cm of snow, but could pursue prey in depths exceeding 50 - 60 cm.

With the exception of caribou (*Rangifer tarandus*), wolves have a lighter foot loading than their prey. Foot loading values for wolves range from 89 - 114 g/cm^2 (Nasimovich 1955), averaging 103 g/cm^2 (Foromozov 1946). Moose have foot loadings ranging from 420 to 1000 g/cm^2, depending on age and sex (Nasimovich 1955; Kelsall 1969; Kelsall and Prescott 1971). In exploring the adaptations of mammals for survival in snow, Telfer and Kelsall (1984) derived a morphological index of snow-coping ability for adult moose, caribou, and wolves with larger values representing an animal's greater ability to cope with snow. They considered the sexual dimorphism of chest height, body weight, and foot size in addition to foot loading values. Highest index values were calculated for caribou (154) and moose (140), followed by wolves (135). Although predator sample size was small, their results suggested that these relative indices between wolves and their ungulate prey, might account for the specific behavioral responses to threats by wolves (e.g., the similarity between wolves and moose may explain the tendency of moose to take defensive stances when attacked by wolves and the tendency of caribou to retreat from confrontations) (Mech 1966; Telfer and Kelsall 1984).

Prey Distribution and Relationships

In some multi-prey systems in Alaska where deer (*Odocoileus* spp.) and elk (*Cervus elaphus*) are absent, moose dominate the diet of wolves (Stephenson and Van Ballenberghe 1995). This is true in south-central Alaska during the winter when seasonal caribou usually are not available (Ballard et al. 1987; Dale et al. 1994; Golden 2005). Moose select winter habitats based on browse availability and quality, snow depth, and cover (thermal and defensive). Increasing snow depth and hardness reduce access to forage and impede mobility, making them more vulnerable to predation (Coady 1974). In response, moose migrate to lower elevations where snow depth is shallowest, and actively seek habitats where access to high-quality forage is greatest (Peek 1998). In the Nelchina Basin of Alaska, typically wolves do not follow moose across pack boundaries, but do follow these elevational movements, traveling though "prey-free" areas (i.e., higher elevations) to reach prey-abundant valleys (Ream et al. 1991; Singleton 1995; Kunkel and Pletscher 2001; Mech and Boitani 2003; T. Rinaldi, unpublished observations). As winter progresses or winter severity increases, moose reduce their activity and forage intake to reduce energy expenditures; aggregations of moose may develop. Similar to yarding by deer, extensive trail systems can develop in concentrated habitat to counteract impeding snow and predation pressure (Molvar and Bowyer 1994; Peek 1998).

Snow crust is rarely consistent enough to provide support for moose, particularly in Alaska (Coady 1974). The support capacity of snow is highly variable and is dependent on the presence and structure of snow layers. Numerous studies have indicated that partially supported travel may be more difficult and treacherous for moose because of increased resistance, loss of forward momentum, and abrasiveness of harder crusts (Murie 1944; Nasimovich 1955; Kelsall and Prescott 1971). Coady (1974) observed moose breaking though snow crusts 40 times stronger than their foot loading; yet in another instance in Alaska, Coady witnessed a cow and calf walking on a trail penetrating only 39 cm in 90-cm-deep snow when the hardness was 1000-2000 g/cm^2. The lighter foot loading of wolves allows supported travel across most crusts and potentially increases their successful capture of prey. Wolves have been observed sleeping throughout the day to take advantage of the snow crusting after temperatures drop at night (Mech and Peterson 2003). Others have documented increased rates of ungulate kills during the evening when crusts supported wolves but not their prey (Mech and Peterson 2003). These observations indicate that the complex effects of snow may in fact drive wolf-prey systems (Mech and Peterson 2003).

Effects of Anthropogenic Activity

The movement patterns of snowmachines and their impacts on the landscape are a result of diverse operator behaviors (e.g., values and type of experience sought), the type of snowmachines used, and numerous environmental variables (e.g., landscape, snow depth, and weather) (McCool 1978). In the Nelchina Basin of south-central Alaska, most snowmachiners are seeking an exploratory/touring experience that results in linear travel across moderately sloping terrain and valley bottoms. New trails are often created, but existing seismic lines, utility corridors, and all-terrain vehicle (ATV) trails are most frequently followed. A single pass by a snowmachine increases the rate of snow maturation by accelerating compaction and crusting; and increasing the surface temperature (Neumann and Merriam 1972). According to Whiteman (2008), over half of the compaction and increase in snow density that results from multiple snowmachine passes occurs with the initial pass. As a result, a network of compacted trails traversing the backcountry can potentially provide energy-conserving travel corridors for animals that are stressed such as during severe winters and in deep snow.

To understand the complexity of impacts caused by snowmachine activity on the winter ecology of wolves and their prey, it is important to examine the alterations made on the landscape (e.g., modification to habitat and snow morphology) and the animals' behavioral responses to both the stimulus (e.g., presence of snowmachines and resulting noise) and the landscape alterations. Although studies are few and many are contradictory, the presence of snowmachines and snowmachine noise elicits short-term physiological and behavioral responses such as elevated heart rates (Moen et al. 1982), increased glucocorticoid levels (Creel et al. 2002), and changes in daily activity and movement patterns (Soom et al. 1972; Bollinger and Rongstad 1973; Dorrance et al. 1975; Freddy et al. 1986; Colescott and Gillingham 1998).

Moose respond to snowmachine activity by increasing size of home ranges, movements, and distance to trails (Colescott and Gillingham 1998). Higher snowmachine activity also can result in lower numbers of ungulates immediately adjacent to trails, temporarily displacing animals to less optimal habitat (Dorrance et al. 1975; Colescott and Gillingham 1998). In deep snow and during critical periods of late winter, this increased physiological and energetic stress can lead to differential survival and reproduction, particularly if animals are displaced from important or preferred habitats (Ferguson and Keith 1982; Parker et al. 1984; Cassirer et al. 1992; Colescott and Gillingham 1998; Creel et al. 2002). The potential impacts may be further compounded if animals are subjected to intentional or unintentional harassment by snowmachines.

With continued exposure to constant and predictable levels of snowmachine activity, tolerance or habituation is possible (Dorrance et al. 1975; Richens and Lavigne 1978). Richens and Lavigne (1978) observed habituation by white-tailed deer (*Odocoileus virginianus*) within and between seasons as a decreased likelihood of fleeing from activity late in the winter and in subsequent years. Although ungulates use trails less than other habitats, trails can serve as easy travel routes to find patches of high-quality forage during periods when human activity is low (Dorrance et al. 1975; Richens and Lavigne 1978; James and Stuart-Smith 2000) and as escape corridors (Richens and Lavigne 1978).

Canids such as coyotes (*Canis latrans*) and foxes (*Vulpes vulpes*) may increase their activity on and around snowmachine trails, particularly during times of deep snow and minimal snowmachine activity (Neumann and Merriam 1972; Huff et al. 1972; McCool 1978; Murray and Boutin 1991; Crête and Larivière 2003). This behavior is most likely a response to counteract increasing sinking depths by increasing mobility and travel efficiency on hard, compact travel corridors that allow access to larger areas for increased hunting efficiency (Bergerud et al. 1984; Murray and Boutin 1991; James and Stuart-Smith 2000). Crête and Larivière (2003) estimated that coyotes traveling on hard surfaces rather than in soft snow conserved energetic expenditures by as much as 6%, which could result in differential survival and reproduction. Wolves are typically less abundant in areas with high road densities (Thiel 1985; Jensen et al. 1986; Mech et al. 1988; Fuller 1989; Person and Russell 2008) where increased human activity and potential for encounters can limit growth of local wolf populations though indirect and direct killing of wolves (Mech 1995; Mladenoff and Sickley 1998; Boitani 2003). If human traffic is minimal or predictable without negative consequences, however, wolves can also benefit from efficient travel on secondary roads, seismic lines, and snowmachine trails (e.g., Fritts and Mech 1981; Thurber et al. 1994; Singleton 1995; Paquet and Callaghan 1996; James and Stuart-Smith 2000; Kunkel and Pletscher 2001; Ciucci et al. 2003). In Alaska, there is anecdotal evidence that wolves commonly use and select roads and snowmachine trails for travel, based on the level of human use (Mech et al. 1988; Thurber et al. 1994; T. Rinaldi, unpublished observations), and wolves have been observed leaving trails to allow snowmachines to pass (Fritts et al. 2003; T. Rinaldi, unpublished observations). Kuzyk and Kuzyk (2002) observed smaller packs using trails more frequently than larger packs. The availability of roads and trails could influence the spatial and temporal distribution of packs (Thurber et al. 1994; Singleton 1995; Ciucci et al. 2003), increase hunting efficiency (Bergerud et al. 1984; Ciucci et al. 2003; Crête and Larivière 2003), and allow the occupation and utilization of sub-optimal habitats (Tremblay et al. 1998; Richer et al. 2002).

Snowmachines and the alterations made to the landscape from their activity can have profound impacts on the spatial and temporal ecology of wolves. The presence and noise from snowmachines potentially displace and disrupt daily activity and movement patterns (Soom et al. 1972; Bollinger and Rongstad 1973; Dorrance et al. 1975; Freddy et al. 1986; Colescott and Gillingham 1998); the creation of trails, however, may facilitate energy-efficient travel (James and Stuart-Smith 2000) and increase the likelihood of encountering and successfully capturing prey (Bergerud et al. 1984; Ciucci et al. 2003; Crête and Larivière 2003). High hunting and trapping pressure could exacerbate these effects, particularly during critical periods such as late winter when animals are most stressed and anthropogenic activity is greatest. The active predator management program in the Nelchina Basin of south-central Alaska, where wolf numbers were reduced through hunting and trapping, presented a unique opportunity to examine the above interactions and their effects. To address the consequences of snowmachine activity and linear disturbance on wolf spatial ecology, a quantitative assessment of the spatial and temporal relationships of wolves, anthropogenic disturbance, prey distribution, and snow characteristics was initiated.

Objectives

My overall goal was to define the movements and use areas of wolves in relation to linear disturbance, with two primary objectives and associated hypotheses:

1. **Quantify the spatial and temporal distribution of snowmachine-based human activity.**

   Although hunting and trapping from snowmachines exist throughout the winter in the Nelchina Study Area, recreational snowmachine activity is by far the dominant anthropogenic activity. The level of this activity depends on snow accumulation, temperature, and daylight. My objective was to quantify the spatial and temporal trends of snowmachine activity over the winter (15 November – 15 April).

   I hypothesized that: i) snowmachine activity would be highest during daylight hours and on weekends; and ii) activity and number of trails would increase with the progression of winter.

2. **Quantify movements by wolves in relation to the availability of linear features, prey, and snow characteristics.**

   Many studies have shown that during winter, both predator and prey are constrained by food limitations and the increased costs of locomotion in snow (Parker et al. 1984; Dumont et al. 2000; Ciucci et al. 2003). As snow depth and density change or winter severity increases, animals conserve energy by altering their gait or selecting runways with hard, compact, or shallow snow (Telfer and Kelsall 1984; Murray and Boutin 1991; Crête and Larivière 2003). Wolves use linear, windswept areas (e.g., lakes and rivers) and trails established by animals or humans (e.g., secondary roads, seismic lines, and snowmachine trails), particularly when snow is deep enough to impede their movements (Mech 1970; Fritts and Mech 1981; Thurber et al. 1994; Singleton 1995; Paquet and Callaghan 1996; Creel et al. 2002; Ciucci et al. 2003). The availability of linear features, trails and secondary roads provides wolves an opportunity to access extensive areas quickly and efficiently (James and Stuart-Smith 2000), further increasing the potential of encountering prey (Bergerud et al. 1984). If these linear features experience low levels of human activity, they can be one of the most influential variables on winter wolf movements (Thurber et al. 1994; Ciucci et al. 2003; Crête and Larivière 2003).

To assess the role of linear features, particularly snowmachine trails, on the temporal and spatial distribution of wolves, I quantified the movements of wolves in relation to the use of linear features, the relative distribution of moose, and the influence of snow morphology. I defined linear features as any anthropogenic trail created by ATVs or snowmachines, road, seismic line, or utility corridor.

I hypothesized that: i) home range size and movement rates of wolves would increase with density of linear features; ii) the use of linear features would increase as sinking depths in snow approached chest height; and iii) highest use of trails by wolves would occur when snowmachine activity was least.

Organization of Thesis

I organized this thesis as 2 independent chapters for submission to peer-reviewed publications following the Introduction (Chapter 1), with an additional chapter addressing application to management. Chapter 2 (*Seasonal Movements and Use Areas of Wolves in Relation to Linear Disturbance*) identifies seasonal movement rates, distribution, and home ranges of wolves, and relates these attributes to the level and distribution of snowmachine-based activity identified in the first objective. Chapter 3 (*Influence of Snow, Prey, and Anthropogenic Disturbance on Resource Selection by Wolves)*, which builds on Chapter 2, incorporates additional topographic and prey distribution parameters to identify the choices that wolves make on the landscape. Chapter 4 is a synthesis and application of important findings: *Wolves in Exploited Ecosystems: Implications for Management.*

Chapter 2 : Seasonal Movements and Use Areas of Wolves in Relation to Linear Disturbance

Introduction

The home range of an animal as originally defined by Burt (1943: 351) is "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young". The size of this range or 'use area' has been related generally to body size (McNab 1963; Harestad and Bunnell 1979) and to the availability of prey resources; however, many additional factors such as social organization (Damuth 1981), population (Fuller et al. 2003), exploitation (Mech and Boitani 2003), and habitat quality (McLoughlin et al. 2004; Milakovich 2008) play a role.

For wide-ranging, habitat generalists such as wolves (*Canis lupus*), the defended home range is their territory. Territoriality in a species occurs when resources such as prey have the potential to limit population growth (Brown 1969) and can be defined as the active defense of an area to the exclusion of other conspecifics (Milakovic 2008). Fuller et al. (2003: 172) hypothesized that "territoriality in wolves helps to stabilize population dynamics by tightening the feedback loop to local resources". The size of a wolf's territory and the density of a wolf population are directly related to prey abundance, prey type, and the mean rate of population change (Fuller 1989; Gasaway et al. 1992; Fuller and Murray 1998; Fuller et al. 2003). In areas where less vulnerable prey items such moose (*Alces alces*) are the primary prey, wolves need the greater available biomass found in larger territories to provide sufficient available prey (Fuller et al. 2003). This supposition is most evident at higher latitudes where the decreased primary and secondary productivity is inversely related to territory size (Okarma et al. 1998; Mech and Boitani 2003). Further, the high reproductive potential and dispersal by wolves leading to rapid growth in pack size encourages wolves to select for territories far larger than what they would need by themselves (Mech and Boitani 2003)

In addition to the relative distribution of neighboring wolf packs, topographic features (i.e., lakes, rivers, and islands) and anthropogenic features such as utility corridors, seismic lines, trails, roads, and human settlements can influence the structure and boundaries of wolf territories. The delineation of territories based on landscape features led Mech and Boitani (2003) to assert that wolves are aware of easily defended territorial boundaries and possibly of the extensiveness of their own territories. Because wolves seek energy-efficient travel routes to maximize prey encounters (Bergerud et al. 1984; Mech and Boitani 2003), many have concluded that the presence of secondary roads or a trail network could influence the spatial organization and distribution of wolf packs (Thurber et al. 1994; Paquet and Callaghan 1996; Ciucci et al. 2003; Whittington et al. 2004, 2005). The role of linear features may become more important in winter as they have the potential to facilitate expedient energy-minimizing travel to counteract the impediments of snow.

Understanding the distribution and level of anthropogenic activity associated with linear features is important in defining the consequences to wolves. The degree to which wolves tolerate human activity has much to do with their previous encounters. In general, wolves are less abundant in areas with higher road and human densities due to direct and indirect mortality (Mech 1970; Mech 1995; Mladenoff and Sickley 1998; Boitani 2003; Person and Russell 2008). Wolf populations subject to harvest should show a higher level of wariness to both human activity and linear features (McNay 2002). There is, however, much evidence suggesting tolerance and temporal adaptation by wolves (Boitani 1982, 2003; Vilá et. al 1995; Ciucci et al. 1997; Heilhecker et al. 2007; Merrill and Hebblewhite 2008). Such studies have identified the threshold of road densities for wolf colonization and persistence, as well as an increasing tolerance for higher human activity and road densities as recolonization progresses (Thiel 1985; Jensen et al.1986; Mech et al. 1988; Fuller 1989; Merrill 2000). A good example of the varying tolerances of wolves to anthropogenic disturbance is apparent in Lapland, where wolves in remote areas are reluctant to traverse ski tracks, versus in Finland, where more urban wolves have learned to move across roads, thus minimizing their probability of encountering humans (Pullainen 1993). In Alaska, wolves selected and avoided linear features on the Kenai Peninsula based on the level of human activity (Thurber et al. 1994) and frequently used roads in Denali National Park (Mech et al. 1998). Similar use of linear features by wolves also has been observed in Yukon, Alberta, and Ontario, Canada (James and Stuart Smith 2000; Whittington et al. 2004, 2005; MacKenzie 2008).

With the exception of the above-mentioned studies, there is little published work quantifying the direct use of linear features and the consequences of that use by wolves (i.e., rates of movement, energy conservation, encounters with prey, kill rates, distribution, and survival). Mills et al. (2006) noted that most of the previous empirical work relied on locations derived from very high frequency (VHF) telemetry and as a result, was troubled with inaccurate movement estimates (Musiani et al. 1998; Rooney et al. 1998; Kuahala and Tiilikainen 2002; Merrill and Mech 2003). Only recently have technological advances provided the ability to accurately quantify the consequences of linear disturbance. Global positioning system (GPS) transmitters enable animal locations at fine spatial and temporal scales (with accuracies within 15 m/fix) to define movement rates, movement distances, and home-range estimation (D'Eon et al. 2002). Readily available and affordable satellite imagery and remote-sensing techniques can now supplement time-consuming ground-based mapping efforts; and instruments designed to enumerate human activity on linear features can now reliably operate in extreme conditions over long periods of time.

My research objective was to apply these technologies to determine empirically how the presence of secondary roads and a trail system affected the seasonal movement, distribution, and use areas of wolves. For the 2 winter seasons I defined, I also enumerated snowmachine-based human activity and snow parameters across the trail system to gain insight into the temporal and spatial variation that may contribute to this dynamic. I hypothesized that the sizes of wolf home ranges (use areas) and movement rates should increase with the availability and higher densities of linear features. As winter progresses and snow conditions become more of a hindrance to movement, the use of linear features by wolves should increase, particularly during times when snowmachine activity is least.

Geographic and Ecological Background

This research was conducted in portions of Game Management Units (GMUs) 13 A, B, D, and E in the western Nelchina Study Area (NSA), south-central Alaska (Figure 2.1). The 17,000-km^2 study area extends from the eastern ridge of the Talkeetna Mountains (148^{o}00' W) east towards Glennallen (145^o 33' W), north to the Susitna River (62^o 45' N), and south to the Heavenly Hills (61^o 45' N). Elevations range from 450 m in the Lake Louise and Tyone Flats to 2100 m in the Talkeetna Mountains. A large portion of this area (31%) lies above 1220 m and is considered poor moose and wolf habitat (Ballard et al. 1987).

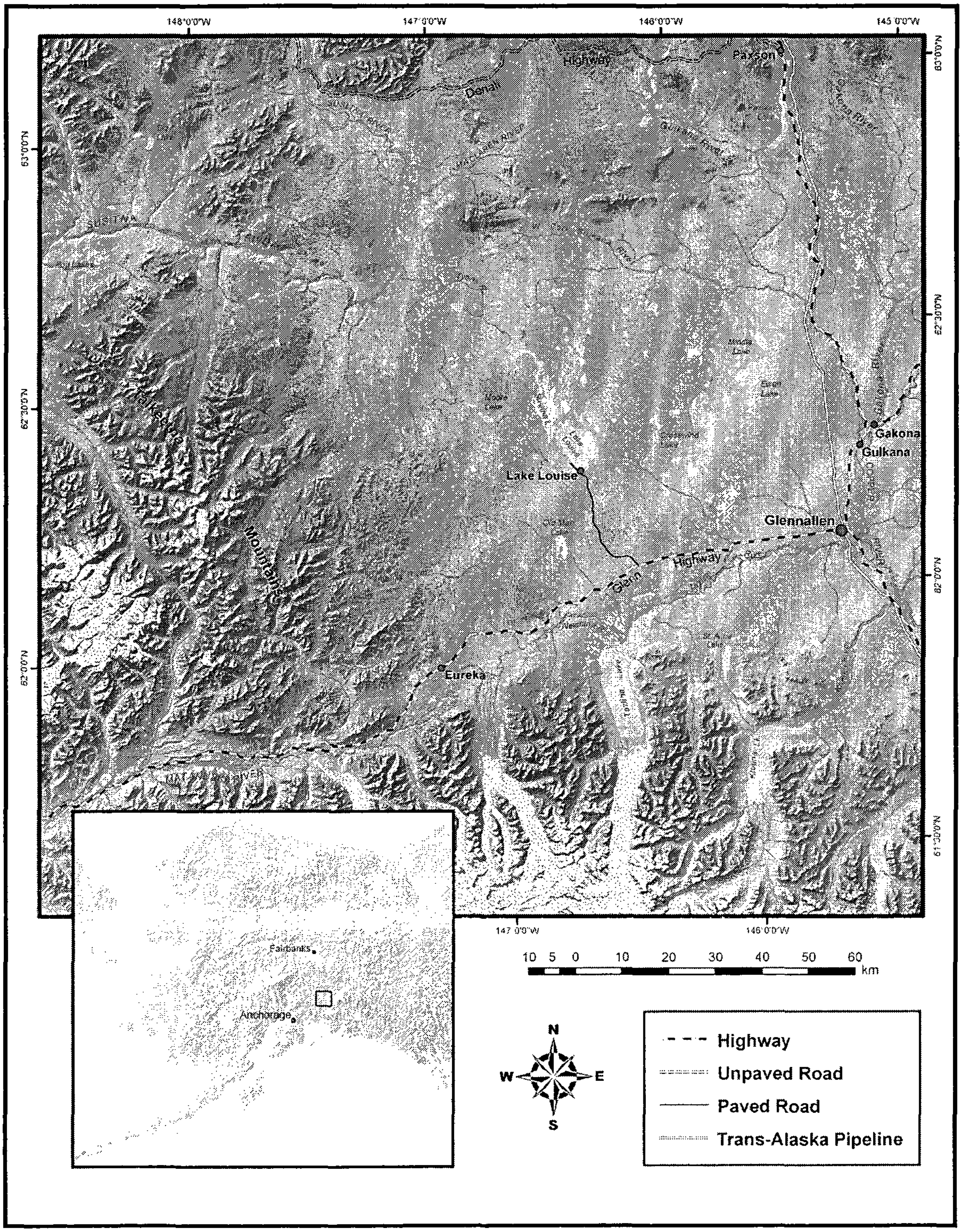


Figure 2.1. Location of the Nelchina Study Area in south-central Alaska, USA.

For the purpose of this study, I used the Glenn Highway to bisect the NSA into northern and southern units based on the distribution of human activity. Levels of human activity were relatively non-existent in the south compared to high recreational use in the northern portions.

Average daily temperatures in the NSA range from -14.6° C to -21.6° C in January and from 6.3° C to 15.7° C in July (Gardner 1985). Precipitation is also variable, averaging 24 cm annually. The 30-year average of monthly snow depths between November and April measured at 16 Natural Resources Conservation Service (NRCS) snow stations across the Nelchina Basin ranges from 30 to 89 cm.

Vegetation at elevations below 1000 m is dominated by spruce, deciduous, and mixed forests, including white spruce (*Picea gluaca*), black spruce (*Picea mariana*), paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), willow (*Salix* spp.), and alder (*Alnus* spp.) (Gardner 1985). Shrub and alpine communities dominate at higher elevations and consist of dwarf arctic and shrub birch (*Betula nana* and *B. glandulosa*), willow, alder, *Vaccinium* spp. and *Ledum* spp. Alpine zones include dwarf shrubs, *Dryas* spp., terrestrial lichens, mosses, forbs, and graminoids. Fire is the most profound natural disturbance in this ecosystem. Although no major fires have occurred in the last 40-50 years, the United States Bureau of Land Management completed several prescribed burns to restore vegetative diversity and improve winter moose habitat (U.S. Bureau of Land Management 2006).

A diversity of sympatric carnivores exist in the NSA. Wolverine (*Gulo gulo*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), and lynx (*Lynx canadensis*) are all subject to hunting and trapping, while grizzly bears (*Ursus arctos*) and black bears (*U. americanus*) are harvested more liberally under intensive management (i.e., high bag limits, extended harvest seasons, and liberal methods of take). Wolves are currently under active predator management to increase the number of harvestable moose and caribou (*Rangifer tarandus*) by reducing the number of non-human predators through hunting and trapping. This includes same-day-airborne (SDA) hunting implemented during the winter of 2002-2003. Same-day-airborne hunting allows citizen pilot/gunner teams via small fixed-wing aircraft to chase wolves into open areas where they can land to facilitate the shooting of wolves.

Mid-winter wolf densities at the beginning of the study averaged 7.4:1000 km^2 in the NSA (Golden 2005). The Alaska Department of Fish and Game reported that harvest increased from 59 wolves in 2003 to 228 wolves in 2004, followed by a decrease to 132 and 159 in 2005 and 2006, respectively. The primary prey species for wolves are moose and a seasonal influx of migratory caribou, although porcupines (*Erethizon dorsatum*), snowshoe hares (*Lepus americanus*), beavers (*Castor canadensis*), swans (*Cygnus* spp.), and numerous rodent species are also available.

Lake Louise and Glennallen are the only small human communities within the study area; however, the NSA experiences influxes of seasonal anthropogenic activity. The Glenn Highway provides easy access to a network of all-terrain vehicle (ATV) and seismic trails north of the highway for recreational users primarily from the Matanuska Valley, Anchorage, and Glennallen. The Richardson Highway bounds the NSA on the extreme eastern side and provides additional, albeit limited, access into the Nelchina Basin.

The density of these trails is highest near the Glenn Highway west of Glennallen. A few cabins, seasonal hunting camps, and small seasonal gold mines are linked by a trail network and can be accessed easily with ATVs, snowmachines, and small fixed-wing aircraft (Ballard et al. 1987). The seasonal influx of human activity begins in August with sport and subsistence hunting for moose and caribou via all-terrain vehicles (ATV) and horse. Recreational snowmachine use follows with the first substantial snowfalls in November and has been estimated to number in the thousands of users annually. Furbearer trapping also begins in October and extends until April, representing the majority of winter human activity in the northern portions of the study area.

Methodology

Wolf Captures and Location Data

Twelve wolves in 5 packs were captured via aerial darting and fitted with downloadable GPS collars (Followit AB, Lindesberg, Sweden) during the winters of 2004 and 2005. Twelve of the collars were Tellus I collars (<800 g) with 15-min fix intervals and were placed on alpha individuals. Two Simplex C collars were used on subordinate pack members to readily locate and identify the packs through the VHF transmitters (GPS data acquired by the Simplex models were not used in analyses because of their differences in fix schedules). I recaptured 5 wolves over the course of the study to replace collars. Two of the 5 packs were south of the Glenn Highway (southern NSA) to serve as a control, free from significant snowmachine trails and predator management activity.

Wolf packs were located using fixed-wing aircraft (Piper Super Cub) and a light-turbine MD-500 helicopter (MD Helicopters, Mesa, AZ, USA). A two-person capture crew based aboard the helicopter anesthetized wolves with 500 mg of Telazol (Fort Dodge Animal Health, Overland Park, KS, USA) delivered from a cartridge-fired Pneu-Dart rifle. Induction time ranged from 3-8 min regardless of pursuit time. During animal processing, I collected morphometric data from all captured animals. I also determined age, sex, and reproductive status. I defined age based on tooth wear as described by Gipson et al. (2000) and body condition subjectively based on tooth wear, physical abnormalities, pelage condition, and body palpations. To ensure the safety of all study animals, I adhered to all ADF&G Animal Care and Use Committee protocols.

Every 2 weeks I attempted to download GPS data via fix-winged aircraft to identify possible kill sites. Weather constraints prevented these flights on a consistent basis and I abandoned this effort in mid-winter 2005. All GPS data for each wolf were stored on board the collar and subsequently downloaded when the collar was recovered. GPS data acquired during the first 8 h after the capture crew departed were eliminated from analyses to minimize the influence of the capture operations and the effects of Telazol on movements. After removing errant GPS fixes (locations beyond reasonable biological movements) with a filter code developed by ADF&G (Elizabeth Solomon, ADF&G, 2006), I screened the remaining locations to delete values with high Percent Dilution of Precision (PDOP), a measure of the geometrical strength of the GPS satellite configuration, (2D fixes $\geq$ 10 and 3D fixes $\geq$ 25) (D'Eon and Delparte 2005). I defined 3 seasons for wolves based on periods of snowfall and human activity: early winter (15 November - 14 February, low snow depth and low human activity), late winter (15 February - 15 April, peak snow depth and higher human activity), and summer (16 April - 14 November, snow-free and nominal human activity).

Quantification of Snow Characteristics

I measured snow depth, density, and hardness at 16 existing NRCS snow stations and 13 snowmachine enumeration sites (see below). Along with scheduled surveys, I visited

NRCS sites monthly via fixed-wing aircraft and snowmachine as weather allowed. To examine the snow conditions that animals experienced on and adjacent to trails, I quantified snow characteristics of both at the snowmachine enumeration sites every 2 weeks to coincide with the maintenance and data downloads for radio-beam counters.

I used a federal snow sampler (Carpenter Machine Works, Seattle, WA, USA) under NRCS guidelines (United States Department of Agriculture - Soil Conservation Service 1984) to measure snow depth and snow water equivalent (SWE) and calculated the density of snow from those measurements. I used a Ramsonde penetrometer to assess the hardness of snow on snowmachine trails and a smaller Alta Ramsonde penetrometer or powder ram (Snowmetrics, Fort Collins, CO, USA) to quantify the hardness of snow off trails. Because I was interested in the hardness of the entire snow column, I found it most appropriate to calculate an integrated ram-hardness number (R_I), as defined by Coady (1974). The integrated ram hardness is calculated from each depth increment (i) (cm) multiplied by its ram hardness number (R) (kg), and then by summing these values from the surface to the ground.

Index of Snowmachine Activity on Trails

I placed radio-beam counters (12-RBX2003, Chambers Electronics, Inverness, Scotland) across trails at 13 sites throughout the NSA to enumerate snowmachine activity in hourly intervals. Radio-beam counters emit a radio frequency across the trail that, when altered by an object moving through the beam, records that change in frequency as a 'pass' on the trail to a downloadable data logger (Gemini Data Loggers, West Sussex, United Kingdom). The main advantage of using radio-beam counters is their ability to operate at temperatures $\leq$-30^{o} C through snow, and across trails $\leq$25 m wide. I adjusted the internal potentiometer to eliminate noise and to reduce the potential of recording non-anthropogenic activity. This setting was identified before deployment after numerous controlled trials with snowmachines, during which time I determined that the counters were accurate 95% of the time.

I selected snowmachine enumeration sites based on *a priori* knowledge of snowmachine activity in an attempt to sample adequately all types and levels of trail activity, and I relocated counters as necessary to fulfill this goal. I downloaded the data loggers to a laptop biweekly, coinciding with snow measurements.

Because different sections of the same linear feature experienced different levels of snowmachine activity, I summarized the hourly snowmachine data by trail section and classified similar sections based on median weekly passes. Linear features with ≤20 passes/week were classified as having low-level activity (L); 20.1 – 60.0 passes were designated as medium level (M); and trails that exceeded 60.1 median passes/week were classified as high (H). Additionally, I generated a simple index of human activity from the product of the total number of snowmachine passes divided by the total numbers of radio-beam counters deployed in the study area at that time. This index helped to correct for sampling effort and assign a level of snowmachine activity to the entire trail system at any given point in time.

Mapping/Remote Sensing

Snowmachine activity begins with the first substantial snowfalls in mid - late November. Trails develop from the road system initially following the existing linear features (i.e., ATV and seismic trails), and as winter progresses, snowmachine trails continue to diverge into the alpine and trail-less drainages. Many primary trails do not experience any activity until January because of topographic patterns of snowfall. To generate a spatially and temporally accurate map of trails, I used a survey grade GPS (Leica GS-20, Leica Geosystems, St. Gallen, Switzerland) with a phase antenna (AT501: Survey grade L1 C/A code) mounted on a snowmachine. While mapping linear features, I categorized trails by: 1) feature width (single: $\leq$2.0 m, double: $\geq$ 2.1 to 4.0 m, seismic line: 4.1 - 7.0 m, or highway: $\geq$7.1 m); 2) substrate type (trail, lake, river, seismic line, or road); and 3) condition (groomed, broken by snowmachine, or overgrown). In subsequent analyses, I used only feature width and substrate type. I processed all raw GPS trail data using GIS DataPro for Windows (Leica Geosystems, St. Gallen, Switzerland). The software uses Scripps orbit and permanent array center (SOPAC) reference stations in Palmer, Valdez, and Glennallen, Alaska to calculate sub-meter resolution.

To supplement ground-based linear feature mapping, I acquired a full scene 2.5-m panchromatic SPOT 5 satellite image (SPOT Image Corporation, Toulouse, France), detailing the late-season expansion or 'peak' period trail network in March 2006 (Figure 2.2). I geocorrected the image using the sub-meter linear feature layer for reference and mapped ground control points. I evaluated accuracy using Root Mean Square Error (RMSE), the quality of the georeferencing process in final map units, around 11 ground control points and obtained a value of 0.761 which is well below the accuracy threshold for panchromatic SPOT imagery of 1.5 (Jensen 2004).

To augment information on linear features outside the SPOT 5 area of the NSA, I acquired 2 georeferenced aerial photographs. After all images were mosaiced together in Leica Photogrammetry Suite Ver.9.0 (Leica Geosystems, Heerbrugg, Canton St. Gall,

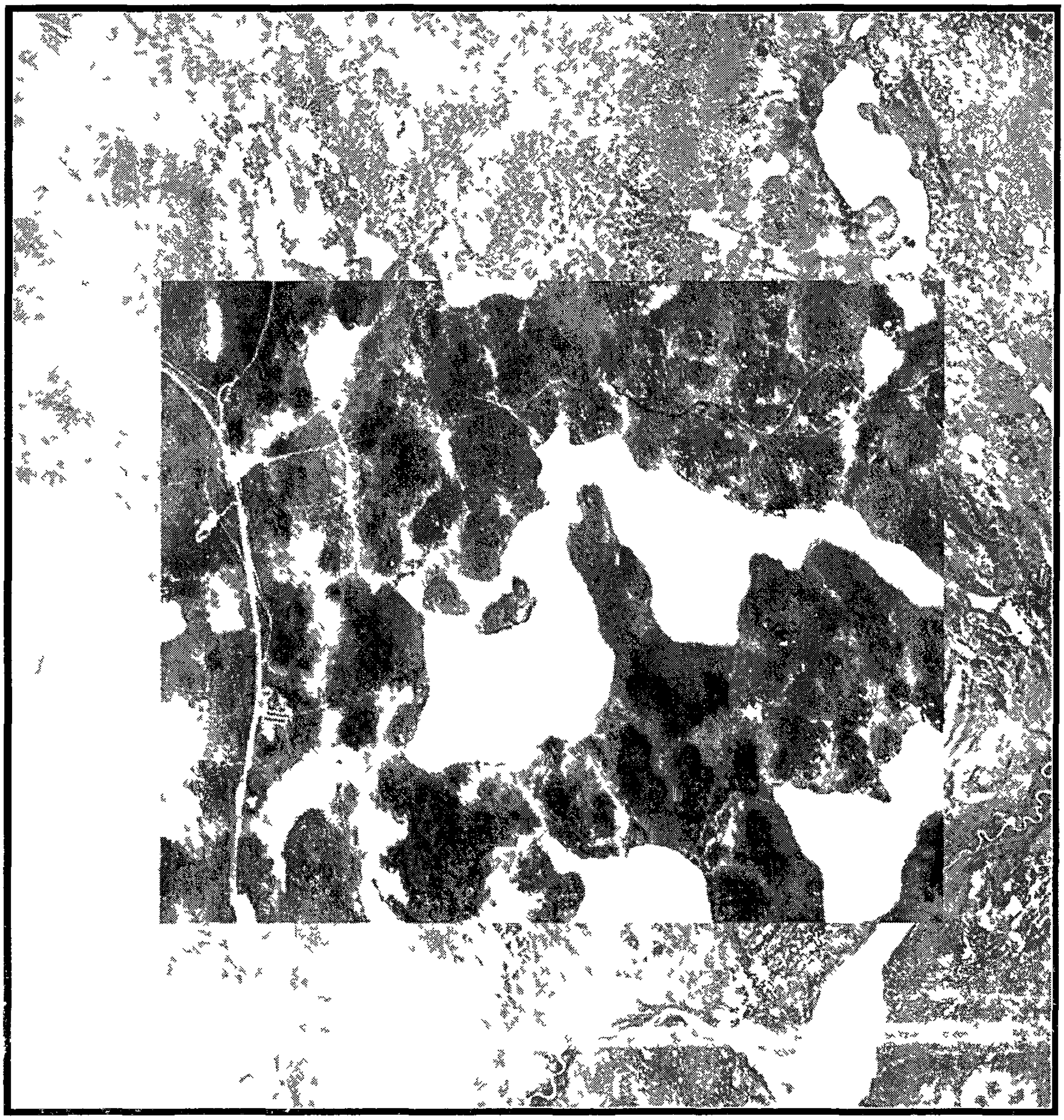


Figure 2.2. Sample of the spatial resolution achieved via SPOT-5 pan-chromatic imagery to extract all linear features in the core of the Nelchina Study Area, south-central Alaska Linear features included trail-type, river-type, lake-type, road-type, and seismic line-type trails Inset is 6 km^2

Switzerland), I used ArcMap 9.1 for Windows (ESRI, Redlands, CA, USA) to digitally extract ephemeral trails, roads, and seismic lines that I was unable to detect via snowmachine. I buffered all linear features by 30 m beyond their actual widths (15 m on each side) to account for potential GPS collar error, and classified all linear features by their widths and substrate.

The linear-feature layer was input into ArcGIS Spatial Analyst 9.1(ESRI, Redlands, CA, USA) to calculate the density of all linear features (based on the length of features) across the NSA. I rasterized human activity with each section of linear feature, weighted by its corresponding human activity classification, to create a spatial surface of human activity.

Home Range and Movement Analysis

To estimate seasonal and annual use areas of wolf packs, I created 95% minimum convex polygons (MCP) for comparability with previous studies and to reduce any bias related to extra-territorial movements (Mohr 1947). For these estimates, I used HRT: Home Range Tools ver. 1.1 (Rodgers et al. 2007) and ArcMap 9.1. Within each wolf pack's seasonal MCPs as well as across the study area, I used ArcMap 9.1 to extract all linear features to compute the total length and density of these features.

I calculated movement rates by pack and season both on and off linear features using 2 comparisons: average directed movement rate (15-min consecutive fixes with a directed movement ≥100 m to eliminate localized wanderings) and average activity movement rate (all consecutive 15-min fixes). Both distances were transformed to km/h.

I compared home ranges and movement rates, tested for differences between on-trail and off-trail wolf locations and movement rates, with pack and season as treatments, using one-way ANOVA except when data could not be transformed to normality, in which case I used Kruskal-Wallis one-way ANOVA on ranks. Additionally, I used a chi-squared (χ^2) contingency table to evaluate differences in trail use between weekdays and weekends across seasons, and χ^2 tests to evaluate whether trail use was proportional to days of the week (4 of 7 days) and weekends (3 of 7 days) within each season. I applied Pearson Product Moment Correlation (r) to measure the linear relationships between snow characteristics, linear features, and human activity. I tested for differences between snow hardness on and off trail using a t-test. For all data, means are presented as mean ± 1 SE unless otherwise noted. All statistical analyses were completed in STATA 9.2 (STATACORP, College Station, TX, USA).

Results

There was high turnover in the wolf population in the Nelchina Study Area between February 2005 and April 2006 primarily because of increasing wolf harvest due to predator management activities (such as trapping and same-day-airborne hunting) during study years. I collected 188,773 GPS locations from 16 Tellus collars on 10 wolves, representing an effective fix rate of 90.51% ± 2.9% (range 60 - 99%) across seasons and packs. I removed 14,776 errant fixes (7.8%), and 2,746 2D locations with PDOP ≥10 (1.57% of the data set), which is within the acceptable range of <10% described by D'Eon and Delparte (2005) for removing outliers and not introducing systematic bias (Figure 2.3).

Home Ranges

Home-range sizes of wolf packs in the Nelchina Study Area were highly variable with no effect of season ($F_{2,9} = 1.45$, $P = 0.284$) or pack ($F_{3,8} = 1.40$, $P = .312$). There was

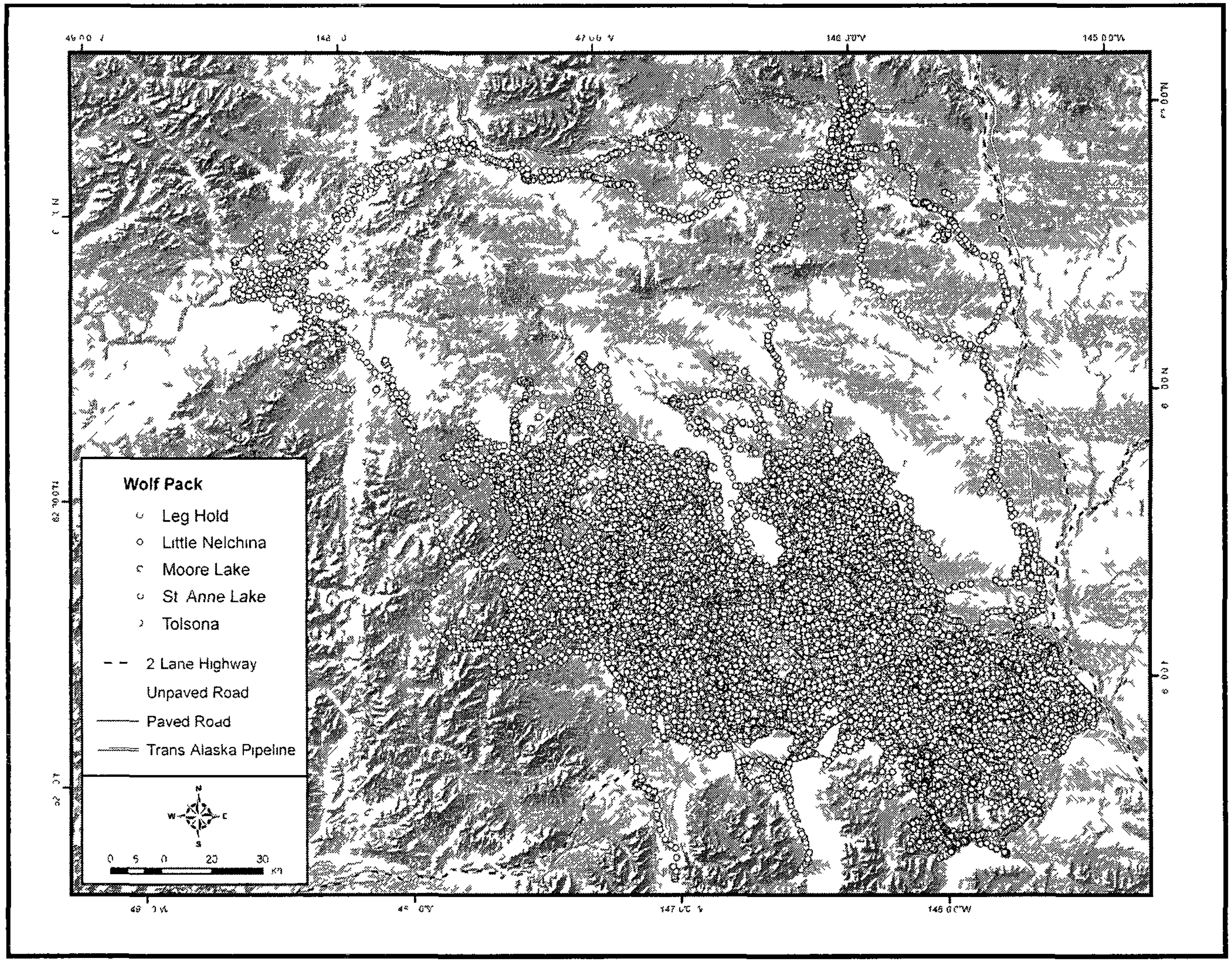


Figure 2.3. Locations of wolves by pack from February 2005 to April 2006 in the Nelchina Study Area, south-central Alaska

considerable overlap in use areas (Figure 2.4). Annually, wolves ranged over 1434 – 13,799 km^2 (Table 2.1). Although the largest pack (St. Anne Lake) ranged the furthest when the pack dispersed and made a 2-month exploratory foray following culling by same-day-airborne hunters, across packs there was no relationship between pack size and home range size ($r = 0.796$, $P = 0.204$).

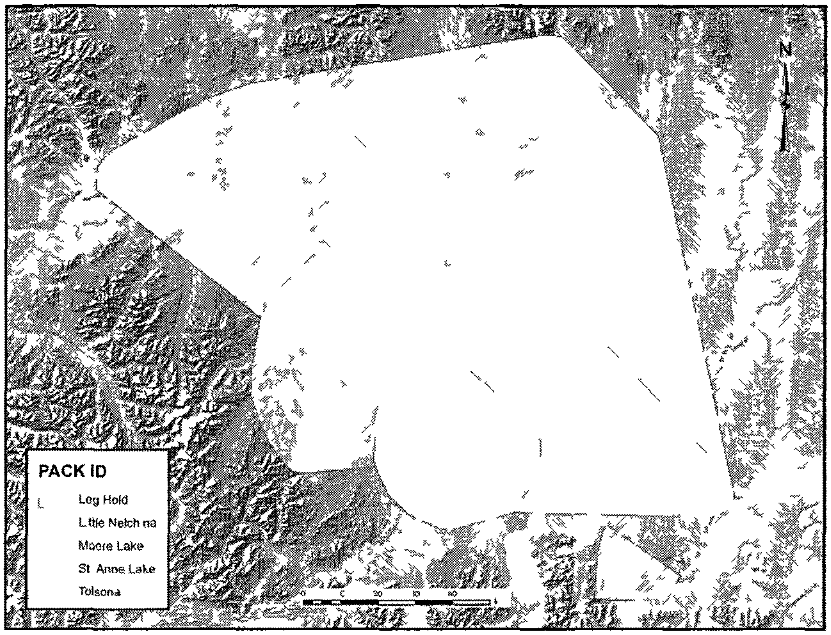
Movement Rates

Directed seasonal movement rates across packs ranged from 1.8 km/h in late winter to 3.3 km/h in summer (Table 2.1). These rates varied significantly by season (Kruskal-Wallis: $\chi^2 = 1967.04$, $df = 2$, $P < 0.001$), and by pack ($\chi^2 = 618.73$, $df = 4$, $P < 0.001$). Annual directed movement rates by packs did not increase significantly with the density of linear features within seasonal home ranges ($r = 0.612$, $n = 4$, $P = 0.272$) (Table 2.1). The average within that average movement rate was 0.93 km/h (n= 159,310 consecutive locations across seasons) also varied significantly by pack ($\chi^2 = 668.88$, $df = 4$, $P < 0.001$) and season ($\chi^2 = 3869.22$, $df = 2$, $P < 0.001$), peaking during the summer. All packs travelled slowest in late winter, which also was the season with greatest snow depths.

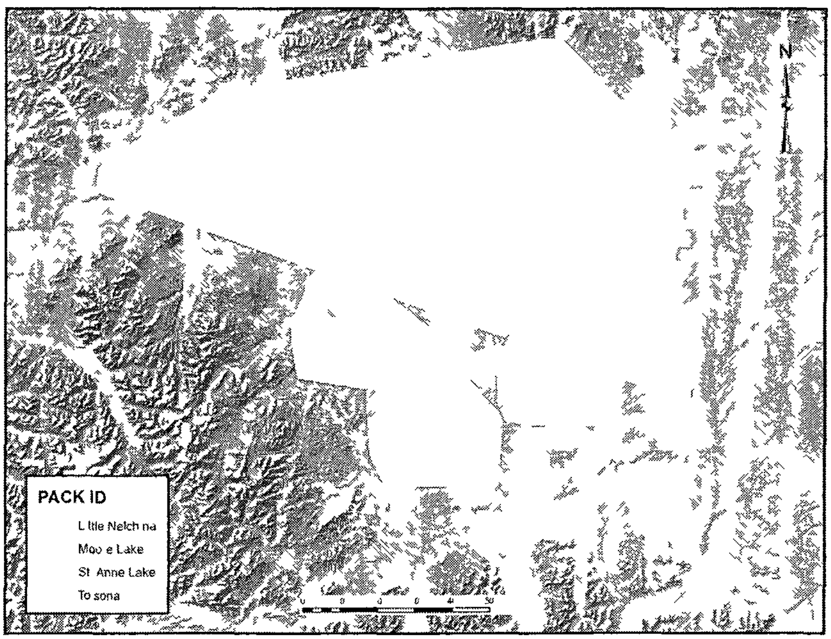
When moving directionally (>100 m), wolves travelled on anthropogenic trails at an average of 4.2 ± 0.05 km/h across seasons, which was significantly faster than when traveling off trails (2.7 ± 0.01 km/h) (all $\chi^2 > 232.318$, $df = 1$, all $P < 0.001$; Figure 2.5). For average activity without directed movement, the differences in rates of movement were even more profound for wolves traveling on trails (3.1 ± 0.05 km/h) compared to travel off trails (0.83 ± 0.003 km/h) (all $\chi^2 > 105.211$, $df = 1$, all $P < 0.001$). Although the maximum distance travelled off trails in a 15-min period by wolves for all seasons was 1.33 times farther than distances travelled on trail (6695 m vs. 5017 m), the mean distance travelled

Wolf Home Ranges, 2004 – 2006

A) Annual

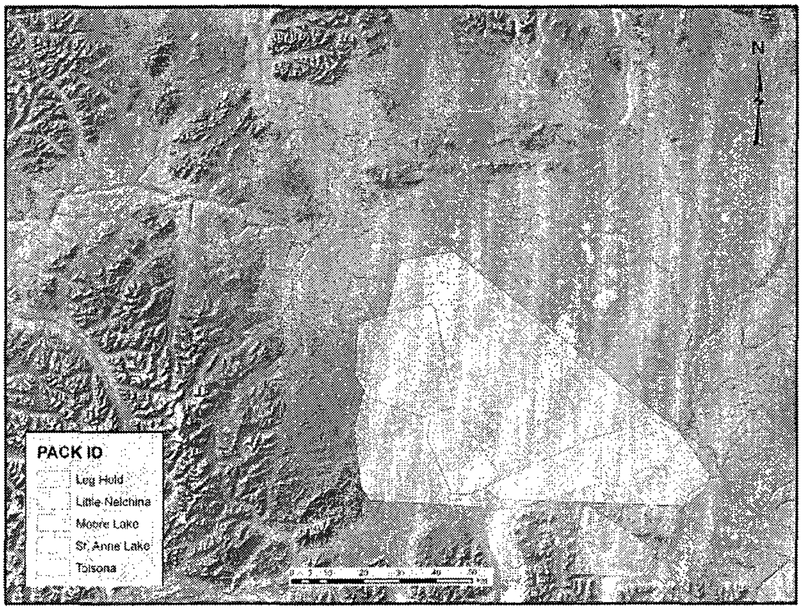


B) Early Wınter



Wolf Home Ranges, 2004 – 2006

C) Late Winter



D) Summer

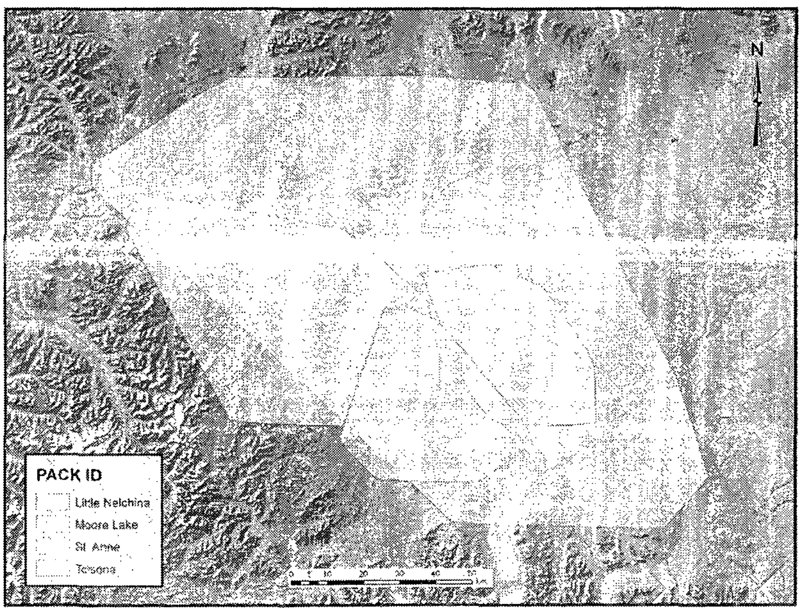


Figure 2.4. Locations and sizes of annual (A) and seasonal (B-D) ranges, as determined by 95% minimum convex polygons (MCP) for wolf packs in the Nelchina Study Area in south-central Alaska, 2004-2006. The St. Anne Lake pack dispersed in 2005 with pack members joining the Tolsona and Little Nelchina packs and forming the Leg Hold pack.

Table 2.1. Attributes of the areas used by 5 wolf packs in relation to density of linear features in the Nelchina Study Area in south-central Alaska, 2004-2006. The St. Anne Lake pack dispersed in 2005 with pack members joining the Tolsona and Little Nelchina packs and forming the Leg Hold pack. Reported pack sizes are the maximum numbers of individuals observed at any one time. Sizes of annual and seasonal ranges are 95% minimum convex polygons. Mean movement rates (± SE) are based on consecutive GPS fixes (directed for travel >100 m and average for all 15-min consecutive locations).

Attribute by season	Wolf Pack				
	Little Nelchina	Moore Lake	St. Anne Lake	Tolsona	Leg Hold
GPS locations (n)	43,565	26,276	42,287	49,323	9730
Maximum pack size	5	2	8	2	3
Range size (km^2)					
Annual	1434	2710	13799	3387	
Early Winter	1231	949	8890	740	
Late Winter	280	638	920	4151	303
Summer	1708	3912	13,514	1475	
Directed movement rate (km/h)					
Annual	2.8 (0.02)	2.6 (0.02)	2.7 (0.02)	2.8 (0.01)	
Early Winter	2.3 (0.03)	2.2 (0.05)	2.8 (0.05)	2.7 (0.04)	
Late Winter	1.8 (0.03)	1.8 (0.04)	2.2 (0.04)	2.5 (0.05)	1.8(0.03)
Summer	3.3 (0.02)	2.8 (0.02)	2.8 (0.02)	2.9 (0.02)	
Average movement rate (km/h)					
Annual	0.4 (0.01)	0.9 (0.01)	0.8 (0.01)	0.8 (0.01)	
Early Winter	0.6 (0.01)	0.7 (0.02)	1.0 (0.03)	0.8 (0.02)	
Late Winter	0.5 (0.01)	0.5 (0.01)	0.7 (0.02)	0.7 (0.02)	0.5 (0.01)
Summer	1.2 (0.01)	1.0 (0.01)	1.0 (0.01)	1.2 (0.01)	
Linear feature density (km/km^2)					
Annual	0.56	0.07	0.17	0.46	
Early Winter	0.50	0.07	0.01	0.43	
Late Winter	2.31	0.11	0.23	0.48	
Summer	0.50	0.03	0.18	0.52	
Proportion of all locations on linear features	0.015	0.002	0.007	0.029	
Proportion of directed movements on linear features	0.032	0.005	0.019	0.068	

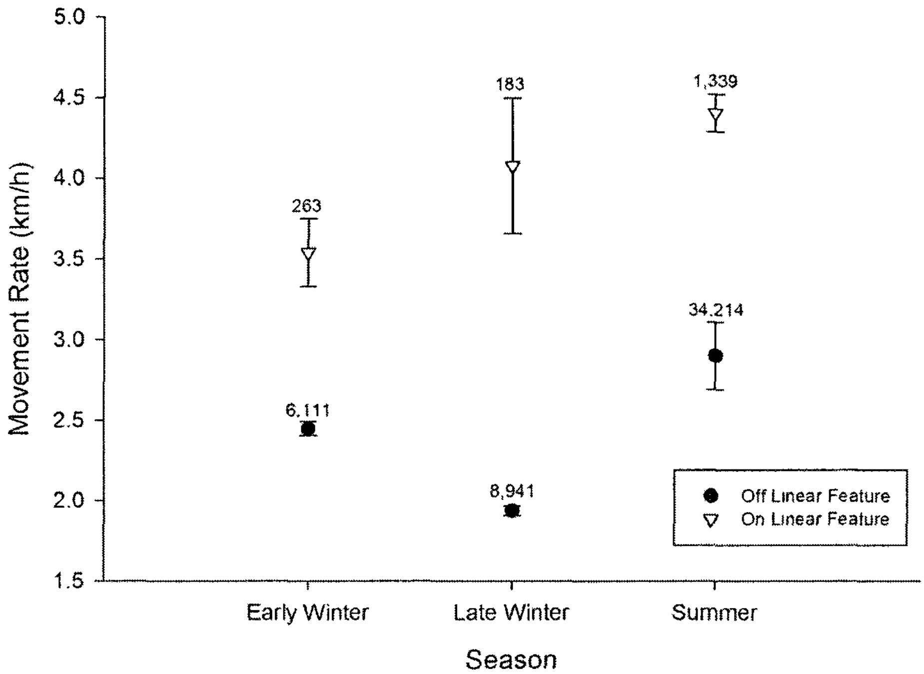


Figure 2.5. Rate (mean ± SE) of directed movement within season by wolves on and off linear features in the Nelchina Study Area, south-central Alaska from 2004 to 2006. The number of observations (n) for each season is provided above standard error bars.

on anthropogenic trails was 1.6 times higher.

Seasonally, packs moved on linear features directionally at 3.5 ± 0.1 km/h in early winter, 4.1 ± 0.2 km/h in late winter, and 4.4 ± 0.1 km/h in summer (Figure 2.5). Although the movement rates on trails in early winter and late winter did not differ between the two winter seasons, wolves moved significantly faster in summer ($\chi^2 = 39.206$, df = 2, $P < 0.001$). Activity movements on trails were 2.5 ± 0.1 km/h in early winter, 2.9 ± 0.2 km/h in late winter, and 3.2 ± 0.1 km/h in summer. These rates differed only between the winter seasons and summer when wolves moved significantly faster ($\chi^2 = 45.493$, df = 2, P < 0.001). All off trail movements (directed and activity) differed significantly by season (all $\chi^2 > 1873.971$, df = 2, all $P < 0.001$). Lowest movement rates were observed for wolves off trail in late winter (directed = 1.9 km/h ± 0.01; activity = 0.52 km/h ± 0.01).

Linear Feature Analysis and Trail Use by Wolves

There were 2409 km of anthropogenic trails (including snowmachine/ATV types, and those on rivers, lakes, and seismic lines) and an additional 815 km of roads in the NSA during this study in winter (Table 2.2; Figure 2.6). Because many of these trails were ephemeral and available only in winter, there were fewer kilometers available in summer. Areas with the highest density of linear features occurred along the Glenn Highway and centered around Lake Louise with 2.13 km/km^2, compared to an average of 0.11 ± 0.25 km/km^2 across the study area (Figure 2.7). The density of linear features within the areas used by wolf packs in the NSA was highly variable among packs and across seasons. There was no significant relationship between sizes of annual and seasonal home ranges and the density of linear features within their home ranges (r = 0.853, $P = 0.0658$) (Table 2.1).

Table 2.2. Total length of linear features mapped remotely and via snowmachine during the winters of 2004-2005 and 2005-2006 in the Nelchina Study Area, south-central Alaska.

Linear Feature	Length (km)
Trail Type	1171.55
Seismic Type	1032.34
River Type	66.33
Lake Type	139.48
Roads	815.14

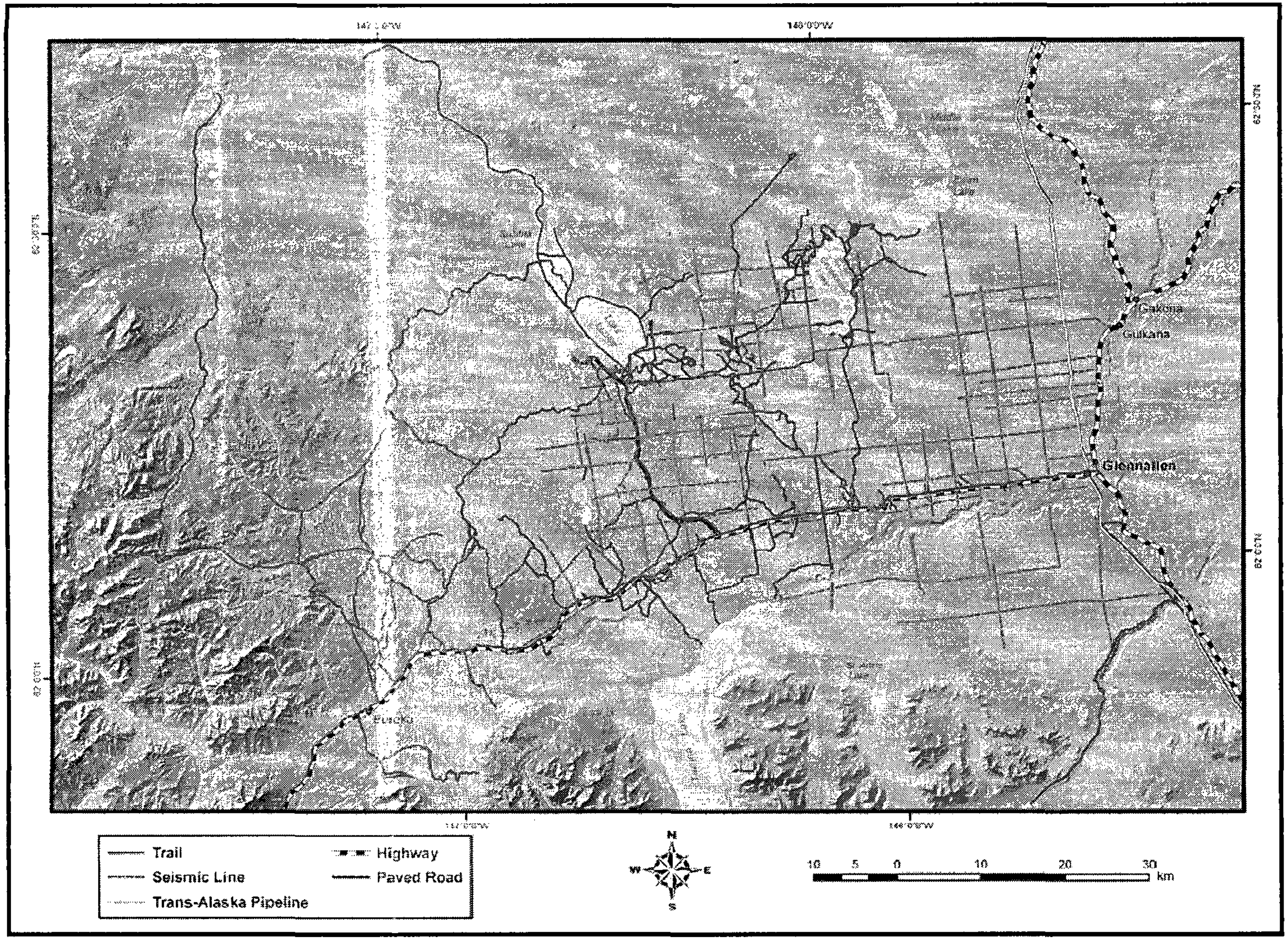


Figure 2.6. Distribution of linear features in winter throughout the Nelchina Study Area, south-central Alaska, 2004-2006.

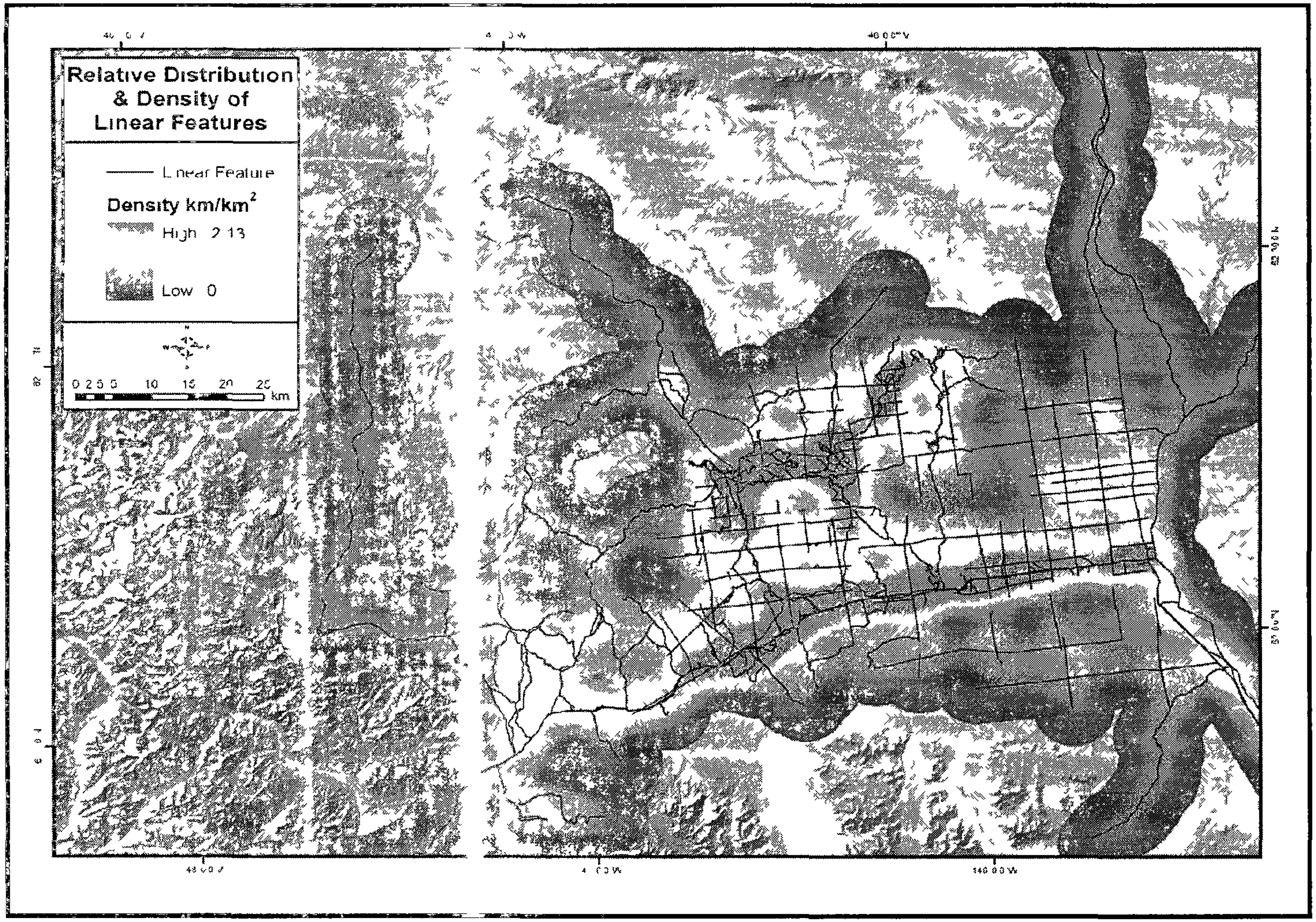


Figure 2.7. Distribution of all linear features at peak period of winter activity (March-April) centered around Lake Louise, in the Nelchina Study Area, south-central Alaska, during the winters of 2004-2005 and 2005-2006. Shades of warmer colors (i e , red) indicate areas with higher densities of linear features

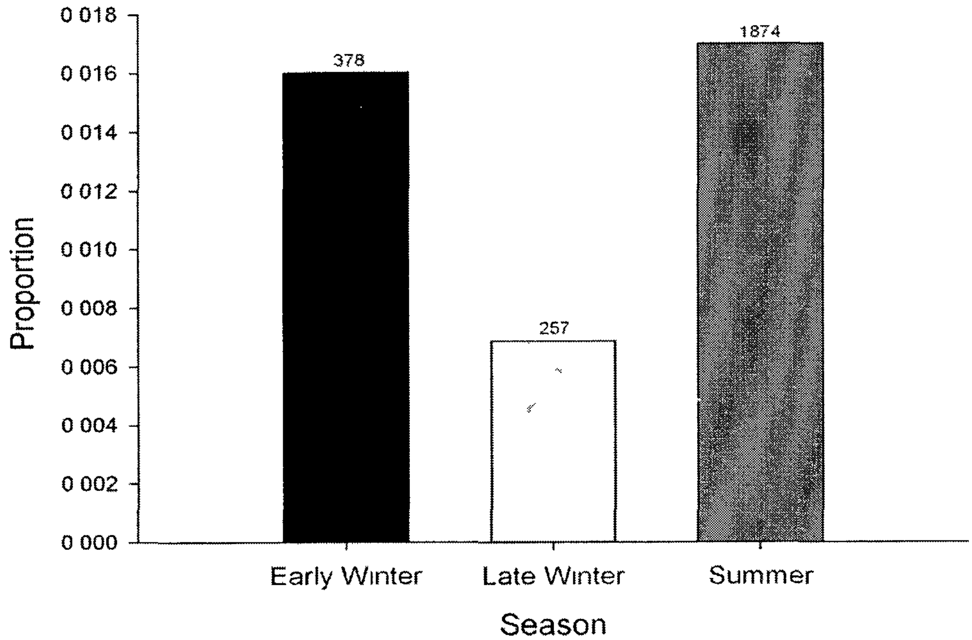
Areas used by the Tolsona and Little Nelchina packs consistently had relatively higher densities of linear features even though sizes of seasonal ranges varied markedly, which coincided with relatively consistent movement rates (Table 2.1). Additionally, the Little Nelchina and Tolsona packs' territories appeared to be bounded to the west and east, respectively, by the Lake Louise Road and the Glenn Highway to the south. With little exception, the St. Anne pack did not cross the Trans-Alaska Pipeline corridor (Figure 2.3).

The proportion of wolf locations observed on linear features, however, was highest for the packs that had the highest density of linear features available in their home ranges (Table 2.1). The proportion of use on linear features was on average 2.1 times greater when wolves exhibited directed travel (consecutive locations with travel $\geq$100 m) and varied among packs (Table 2.1).

Wolves used linear features more in the early winter and in the summer than they did in late winter (Figure 2.8A) when snow depth and snow hardness were greatest. In winter, use tended to be greater on trails on weekdays compared to weekends (Figure 2.8B), but was significantly different only during early winter (χ^2= 6.6369, df = 1, $P < 0.010$; late winter: χ^2= 0.1471, df = 1, $P > 0.701$).

Although trail use as a proportion of locations was generally low across seasons, wolves did follow a subtle crepuscular trail-use pattern. The proportion of locations on linear Features was greatest during no-daylight hours in winter. Trail use by wolves peaked in the evening in early winter and around midnight in late winter, and was least in the afternoon during summer (Figure 2.9).

A)



B)

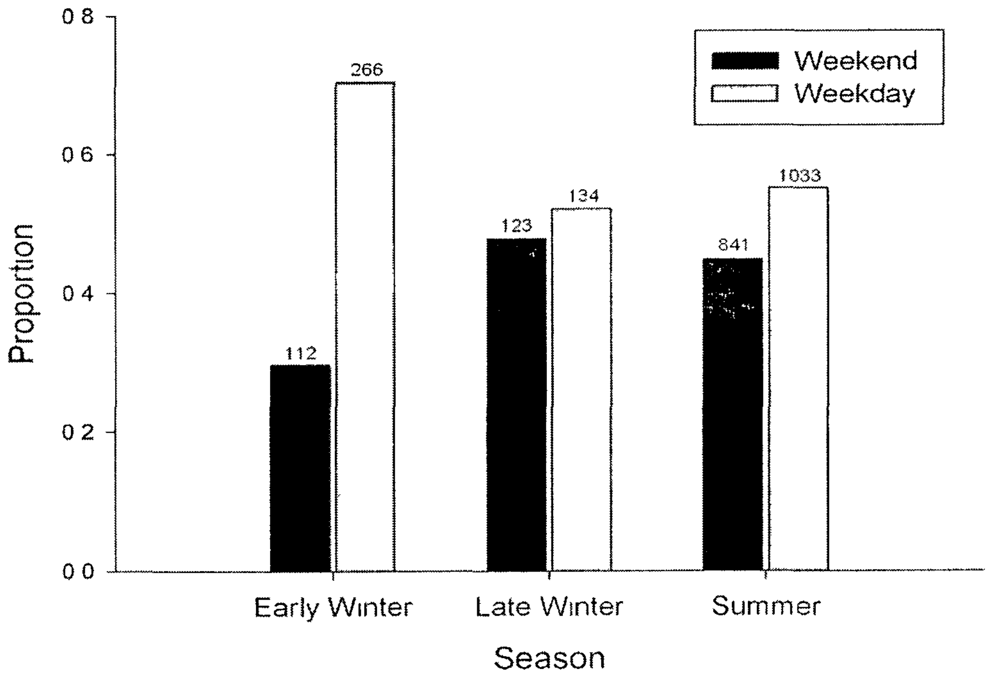
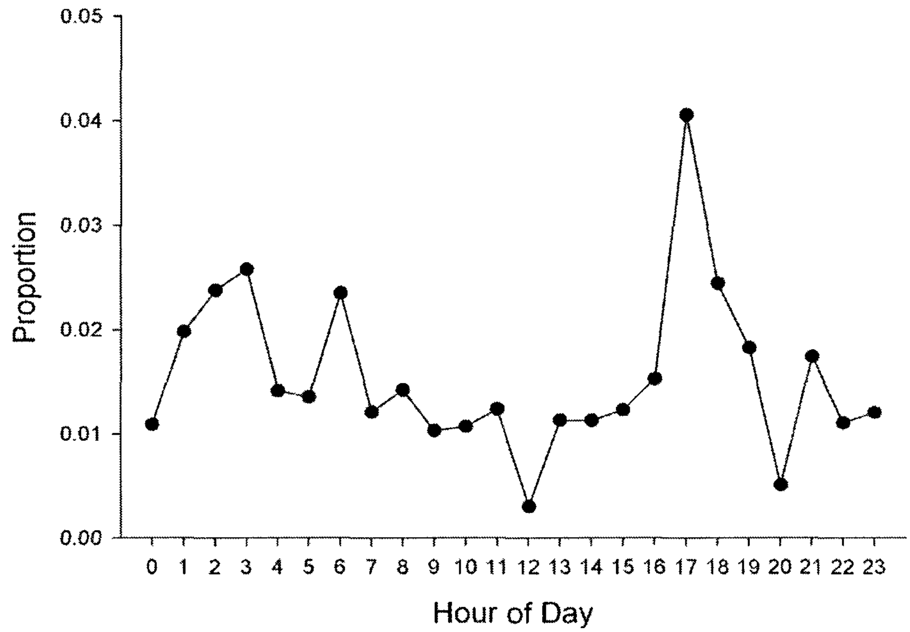
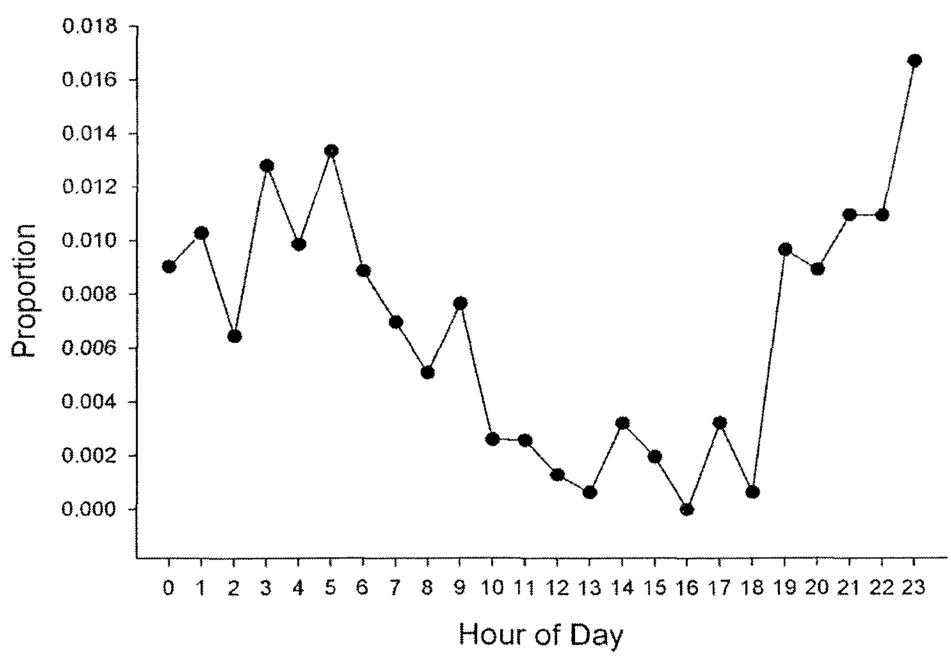


Figure 2.8. Proportion of wolf locations (n = 2509) on linear features by season (A) and relative to day of the week within season (B) in the Nelchina Study Area, south-central Alaska, 2004-2006. Numbers above bars indicate number of occurrences of wolf locations on linear features.

A) Early Winter



B) Late Winter



C) Summer

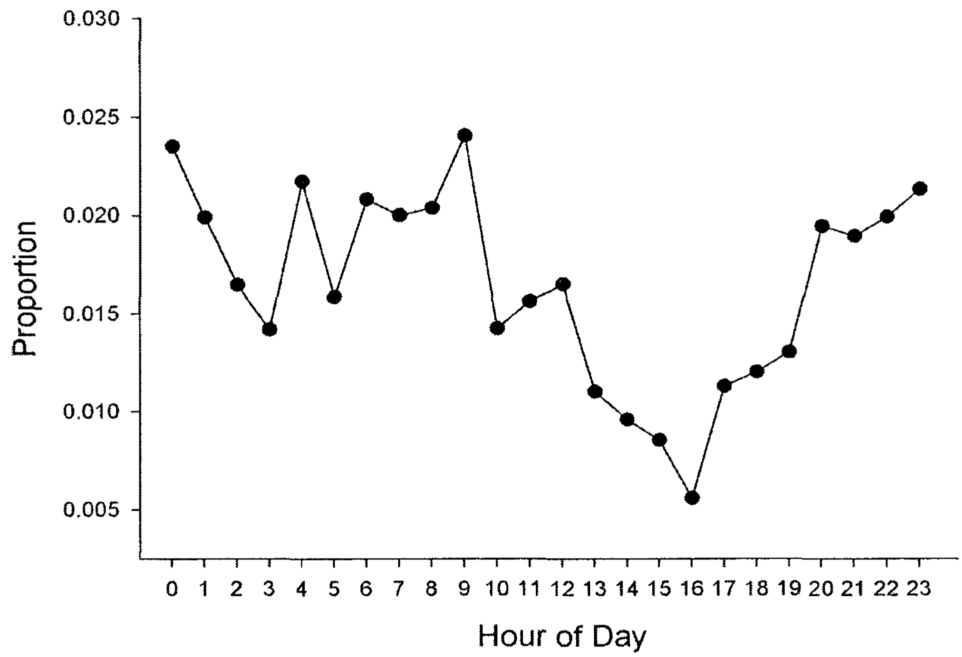


Figure 2.9. Proportion of wolf locations (n = 2509) on linear features by hour for early winter (A), late winter (B), and summer (C) in the Nelchina Basin, south-central Alaska, 2005-2006.

When using linear features across seasons, 60% of use locations by wolves were on trail-type trails (trails made by ATVs and snowmachines), followed by seismic-type trails (trails on seismic lines) at 36% (Figure 2.10A). The proportion of locations on lake-, river-, and road-type trails was low in all seasons. Within seasons, use of trail-type trails was greatest during early winter; use of seismic lines was least in early winter (Figure 2.10B).

Human Activity

Over the course of 1.5 winters, 17,398 snowmachine passes were recorded by radio-beam counters, with a mean hourly activity index (passes per radio-beam counter) of 0.079 ± 0.002. Of the 545 linear feature trail sections, 72.1% were categorized as having ≤20 snowmachine passes per week (low activity level). Trail sections with medium (>20.1 – 60 passes) and high activity levels (≥60.1 passes) accounted for only 24% and 3.9% of linear features, respectively.

Snowmachine activity in the Nelchina Study Area was concentrated most along the road system and radiated from areas of human settlement (Figure 2.11). Seasonally, snowmachine activity increased as the winter progressed from an early winter activity index of 0.062 ± 0.004 to a late winter mean of 0.090 ± 0.003 (Figure 2.12A). It also followed diurnal patterns, peaking on the weekends and during holidays (Figure 2.12B).

Diurnal snowmachine activity climbed steadily with increasing daylight. Most activity occurred during mid-day hours for both winter seasons (Figure 2.13). The highest recorded snowmachine traffic on the trail system in a 1-h period was 181 passes during a late winter snowmachine club gathering. This event also represented the most snowmachines on the trail system at one time with an activity index of 17.37. Times of lowest snowmachine activity corresponded to highest trail use by wolves (Figure 2.13).

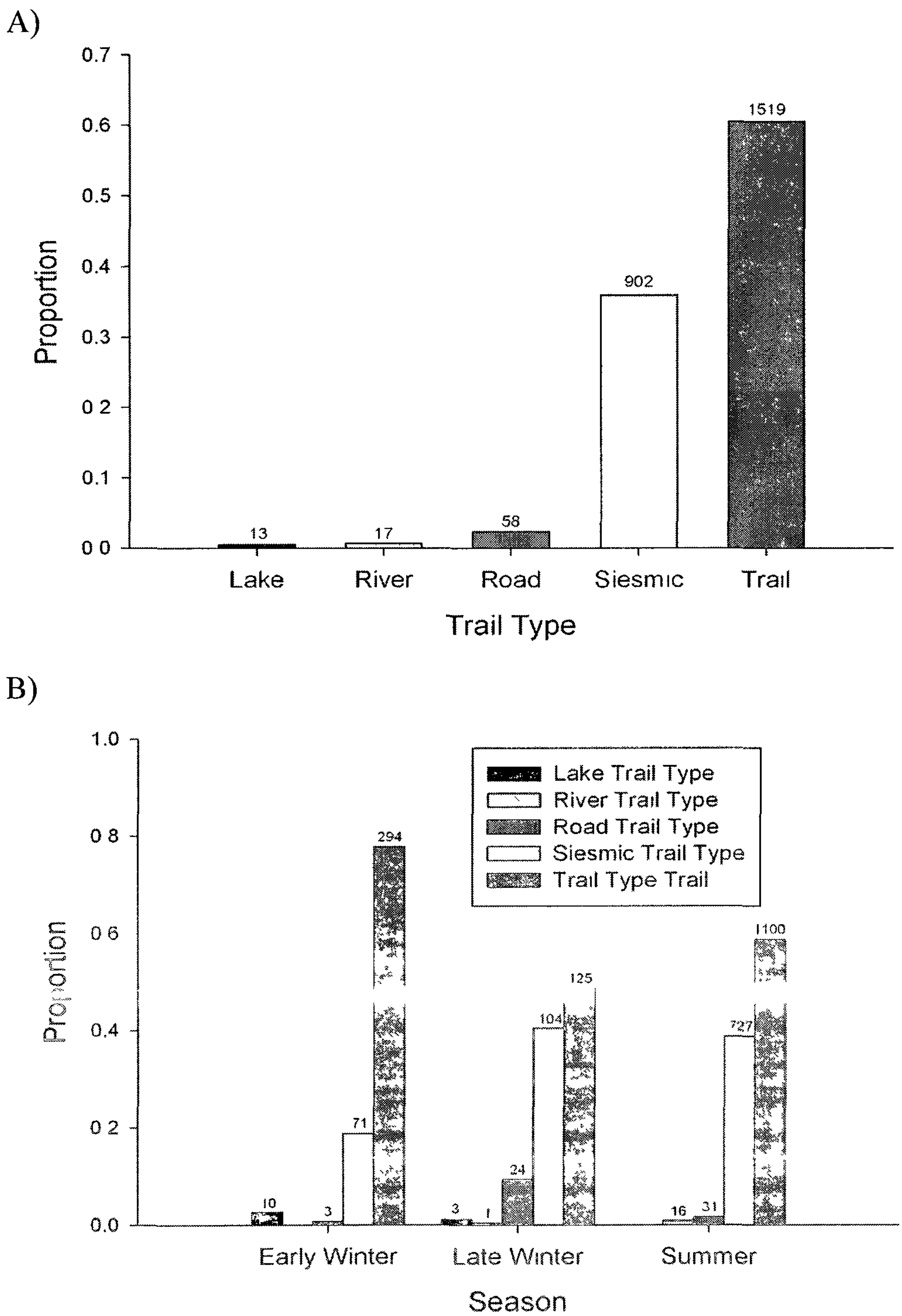


Figure 2.10. Proportion of wolf locations (n = 2509) on linear features by classified trail types across seasons (A) and within seasons (B) in the Nelchina Study Area, south-central Alaska, 2004-2006. Numbers above bars indicate the number of occurrences of wolf locations on linear features. Lake-type trail was available only in winter when frozen.

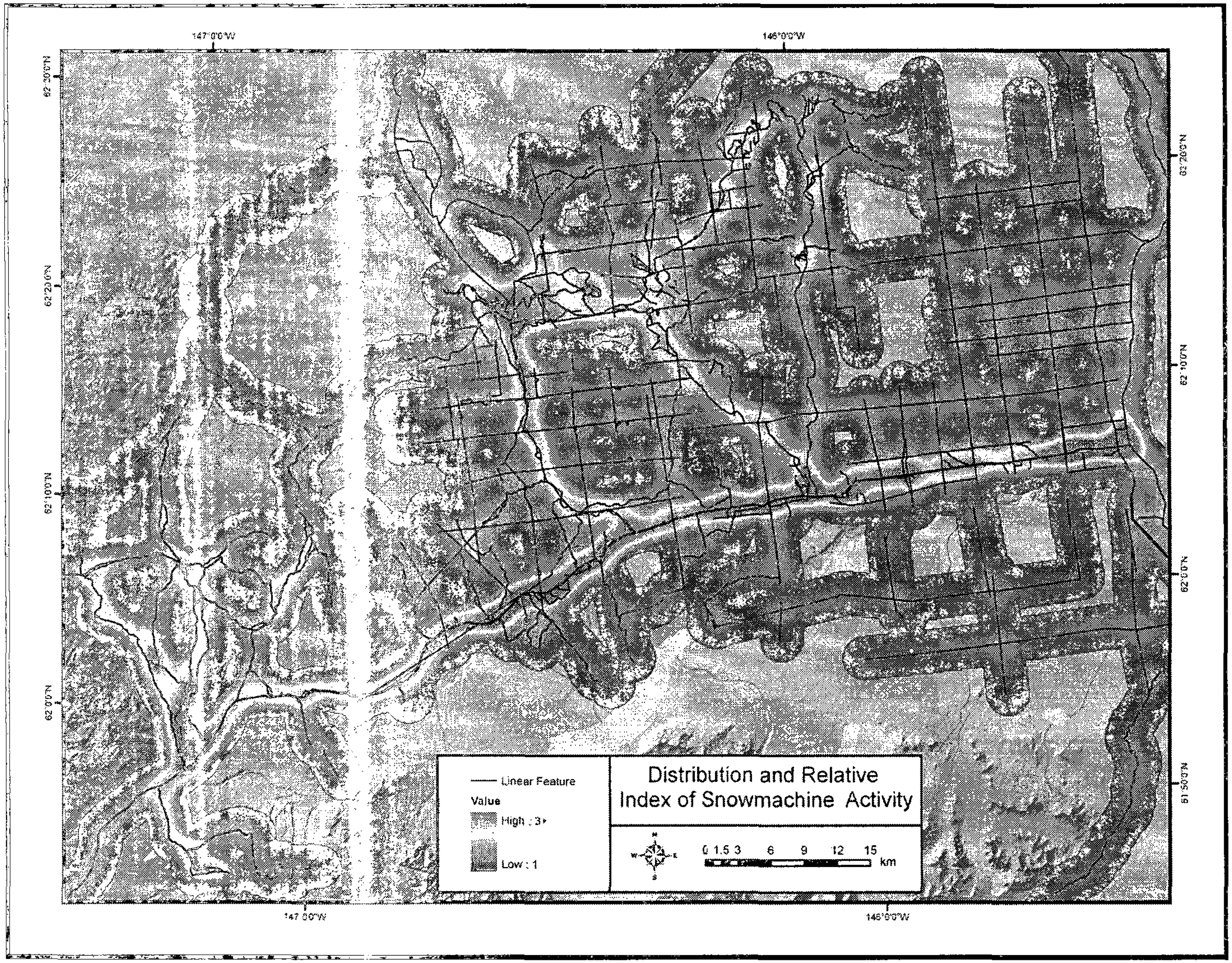
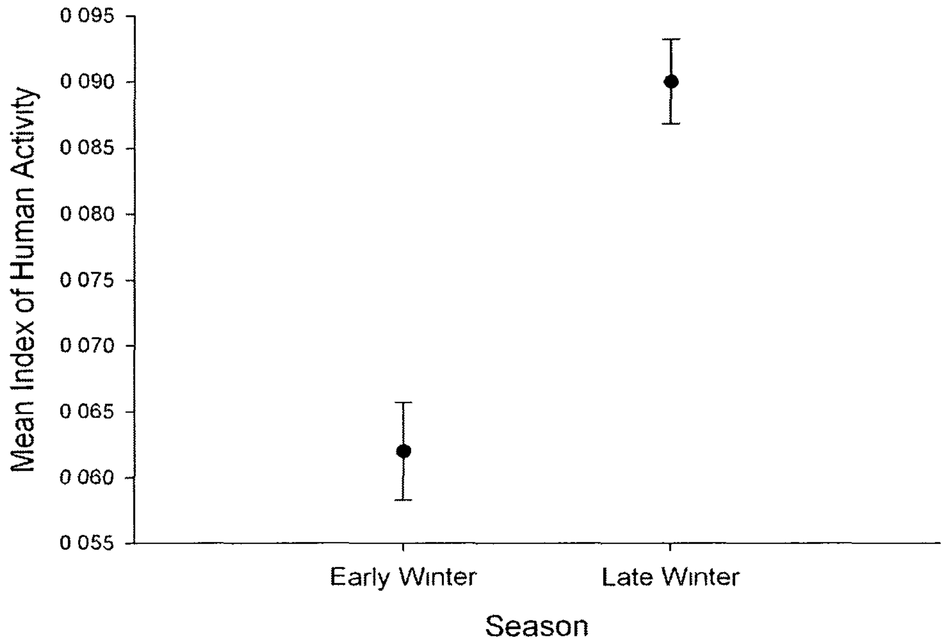


Figure 2.11. Levels of snowmachine activity in the Nelchina Study Area in south-central Alaska, concentrated around primary roads and human settlements, 2005-2006.

A)



B)

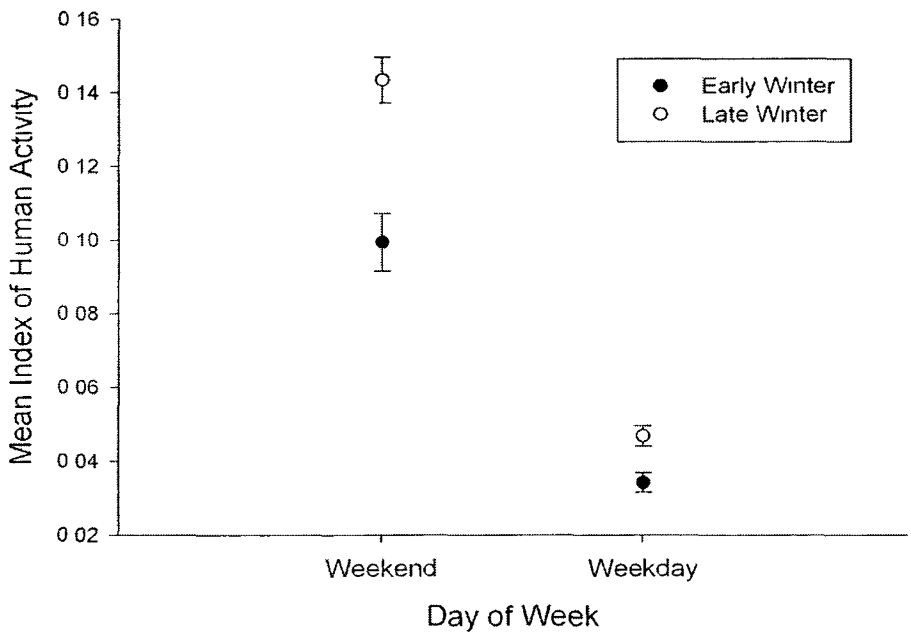


Figure 2.12. Index (mean ± SE) of human activity on snowmachine trails by season (A) and on weekends (Friday, Saturday and Sunday) and weekdays (B) during winter in the Nelchina Study Area, south-central Alaska, 2005-2006. The index of human activity was derived from the total number of snowmachine passes recorded divided by the total number of radio-beam counters deployed at a given time.

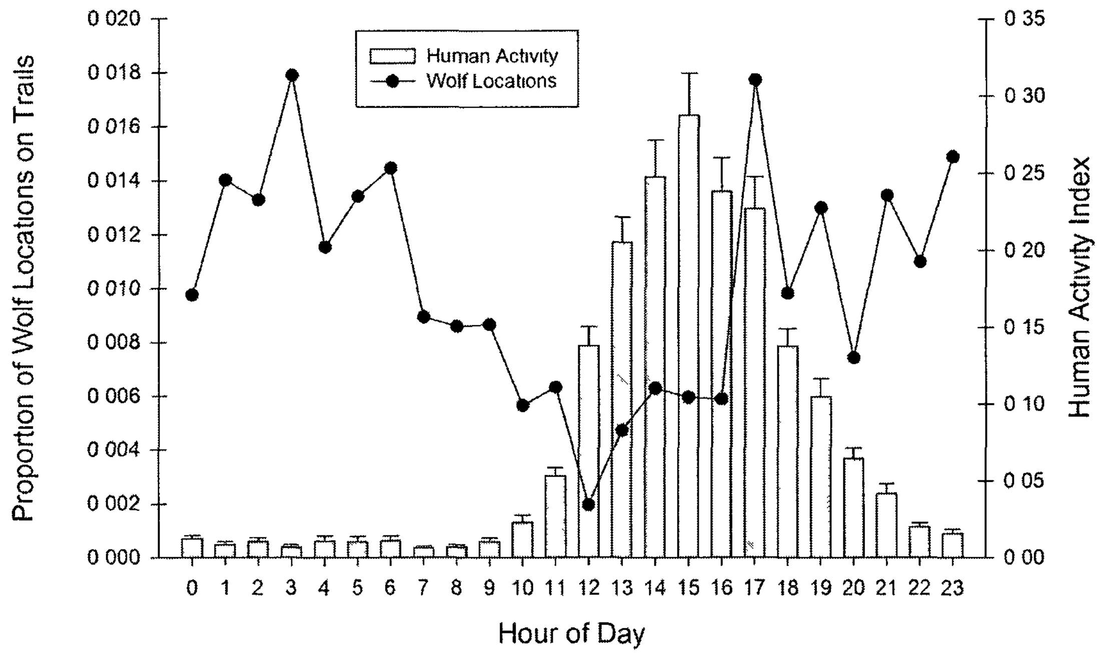


Figure 2.13. Proportion of wolf locations (n = 635) on linear features in winter (2 seasons combined) in relation to an index of human activity (mean ± SE) by hour in the Nelchina Study Area, south-central Alaska, 2004-2006. The index of human activity was derived from the total number of snowmachine passes divided by the total number of radio-beam counters deployed at a given time.

Snow Morphology

Snowfall patterns and first dates of snowfall were variable across the Nelchina Study Area. Annual mean snow depth over the 2 winters of study was 57 cm ± 1.26 (n = 207) between December 2004 and April 2006, which was consistent with NRCS historical data (http://www.ak.nrcs.usda.gov) (Appendix A: Tables A.1, A.2, A.3, A.4). Snow depth increased as the winters progressed from a mean depth of 49.6 ± 0.43 cm in early winter to 63.1 ± 0.97 cm in late winter. A maximum snow depth of 137 cm was recorded in the western NSA in early March 2006.

There was very little variability in the density of snow across the Nelchina Study Area, with an annual mean of 0.17 ± 0.11 g/cm^3. Snow density increased as winter progressed from a mean density of 0.16 ± 0.01 g/cm^3 in early winter to 0.18 ± 0.01 g/cm^3 in late winter.

The hardness of snow was sensitive to the time of day when measurements were recorded, particularly in late winter when temperatures could vary 10° C from early morning to late afternoon. In an attempt to compensate for this variation, I tried to measure hardness only in the morning. Snow hardness increased over the progression of winter from 49.04 ± 7.62 kg/cm^2 in early winter to 62.82 ± 4.82 kg/cm^2 in late winter. On trails, snow hardness was 23.7 times greater and significantly different than areas off trails (t = -14.672, df = 34, P <0.001), with integrated ram hardness (R_I) values ranging from a mean of 1128.71 ± 72.44 kg/cm^2 in early winter to 1404.43 ± 94.78 kg/cm^2 in late winter.

Discussion

Annual and Seasonal Use Areas

Mean annual home ranges of wolves in the Nelchina Study Area, as defined by 95% MCP (4326 km^2), were larger and more variable than ranges documented for many other populations of wolves at similar latitudes (638 – 1868 km^2, Stephenson and James 1982; Peterson et al. 1984; Ballard et al. 1987; Hayes 1995; Mech et al. 1998). The estimates for packs from this study in the Nelchina Study Area, however, are comparable to some previous estimates calculated in the Nelchina Basin where Burkholder (1959) observed a wolf pack using 6272 km^2 over a 6-week period and in Denali National Park where a pack of 10 wolves occupied an area of 4335 km^2 (Mech et al. 1998). When data from the St. Anne Lake pack were removed from the calculation because of a 2-month dispersal from their normal range, annual home ranges for other wolves in the Nelchina Study Area averaged 1958 km^2. This average is more consistent with wolf studies by Ballard et al. (1987), who observed some packs in the Nelchina Study Area with average home range sizes of 2308 km^2.

Variability in average territory size of wolves depends on the dynamics of the wolf population and the distribution and density of available prey types (Fuller et al. 2003). In North America, 33% of the variation in mean territory size and 35% of the variation in mean area per wolf are explained by the variation in prey density (Fuller et al. 2003). In areas such as the Nelchina where wolves prey primarily on moose, territory size and area per wolf are approximately 3-4 times greater than where wolves prey primarily on deer (*Odocoileus* spp., Fuller et al. 2003).

Estimation of home-range size varies with the estimator used and the number of locations relative to the collection period (Bekoff and Mech 1984; Ballard et al. 1997; Mech and Boitani 2003). As sample size increases, mean home-range size increases asymptotically and variability decreases (Arthur and Schwartz 1998; Powell 2000; Girard et al. 2002). I used a 95% MCP to calculate all home ranges, which tended to overestimate the areas actually used during annual and seasonal time frames. The fine-scale GPS fix rate of 15-min and an effective fix rate >90% clearly identified areas used and not used by wolves. The MCP estimator, therefore, may not accommodate fine-scale data sets well, and the changing use areas of an exploited and dynamic wolf population. Decreasing the percentage of locations used in defining the MCP or implementing more robust techniques such as parametric and nonparametric kernel density estimators (Getz and Wilmers 2004; Getz et al. 2007) may decrease biases and more accurately represent actual use areas. This issue warrants further investigation (Burgman and Fox 2003). An advantage of using the MCP estimator, however, is to enable comparisons of overall home range size with most other wolf studies.

Active predator reduction in the form of liberal hunting and trapping regulations, and same-day-airborne hunting at the onset of my research made it difficult to maintain continuity of individual study animals. Although the influence of these management activities would be difficult to quantify, it is clear the program had an effect on population size and structure. Several wolf packs were eliminated or reduced to single individuals during the winter of 2003-2004 (e.g., Moore Lake and Tolsona). Wolf harvest, although not as intense, continued through the study years. Spring wolf densities in the study area ranged from 7.4 ± 1.10 wolves/1000 km^2 in 2002 to 3.9 wolves/1000 km^2 in 2006 (Golden 2005; ADF&G, unpublished data). Despite this reduction in the wolf population, I was able to construct a large data pool that far exceeded suggested minimum sample sizes for location and movement studies (Seaman et al. 1999; Girard et al. 2002).

There was no significant relationship between pack size and home range size although the largest pack, the St. Anne Lake pack, roamed the farthest. Habitat quantity and quality likely are the primary drivers for the differences among territories of individual packs (Ballard et al. 1998). The St. Anne Lake pack occupied a low-elevation open spruce forest and bog mosaic, characteristic of low-density moose populations and the western portion of the NSA. Ballard (1987) concluded that wolves did not cross territories to follow migratory moose and caribou, but the St. Anne Lake pack dispersed and expanded north into the predator management area. The linear distance travelled during the late summer and early winter foray by the St. Anne Lake pack exceeded 660 km roundtrip and occurred in late October after the alpha male was killed. This was a linear departure of ≥170 km from their home range during a 2-month period. Based on the timing, these wolves may have moved northward to follow migrating caribou; however, their movement may also have been an exploratory response to an open or poorly defended territory because of the high level of wolf exploitation in the predator management area. By January, the St. Anne Lake pack returned to a more southern use area within the range of their earlier defined territory.

Recolonization of wolf territories and general pack distribution after the elimination of packs or reduction in size during wolf control efforts was rapid and consistent with historical territory establishment (Ballard et al. 1987; ADF&G, unpublished data). Despite using a 95% MCP to avoid inflation by extra-territorial movements, I observed considerable territorial overlap across seasons, although not at the annual scale. The high level of exploitation made it difficult to ascertain if this overlap was due solely to bias associated with MCP analysis or to the more fluid territorial boundaries associated with the dynamics of a recolonizing wolf population.

The loss of stricter boundaries in early and late winter may be consistent with the shifting associated with the typical peak dispersal periods in autumn and early winter. The additive effects of exploitation from trapping, which peaked in early winter, and same-day-airborne hunting, which peaked in late winter when snow was deepest, likely affected pack structure, thereby opening territories and creating boundaries that were more fluid. New animals from areas outside the same-day-airborne hunting zone could utilize these unstable areas and establish themselves in poorly defended territories.

Movement Rates

Sizes of seasonal ranges used by wolves in the NSA generally corresponded with respective movement rates during early winter, late winter, and summer, which has been identified in previous studies (Milakovic 2008). Movements during summer were greatest and probably a reflection of poorly defended territorial boundaries during recolonization after winter predator management activities and the seasonal influx of migratory caribou and moose calves. Others have reported an increase in movement rates during denning and pup-rearing periods due to pack members emanating from the den or rendezvous sites to hunt and return (Mech et al. 1988; Fuller et al. 2003; Mech and Boitani 2003). The Little Nelchina Pack was the only pack to den and coincidentally had the highest movement rates in relation to all other packs during the denning period of 2005.

The size of home ranges and rates of movement in winter declined among NSA packs as the season progressed and suggest a response to changing snow characteristics and the energy-minimizing and extensive linear travel strategy exhibited by wolves in winter (Mech and Boitani 2003). Additionally, wolves may have altered their movements in response to predator management activities. On repeated occasions, I observed previously captured wolves responding immediately to the sound of aircraft by altering their rate and direction of travel.

'Directed' travel rate based on consecutive fixes ≥100 m was calculated to understand the effect that available linear features had on wolves when they were moving. When moving directionally on trails, wolves among all packs travelled 1.6 times faster than when off trails (4.2 km/h vs. 2.7 km/h). This difference was 3.7 times greater when considering all non-directed movements (3.1 km/h vs. 0.83 km/h) and clearly identifies how compacted trails facilitate expedient travel. Even though wolves have a lighter foot loading than moose, the benefits of expedient and potentially more efficient travel on trails could be more profound in late winter when the effects of snow are the most restrictive to movements. Wolves have been observed sinking to their chests in snow densities of <0.21 g/cm^3 (Nasimovich 1955), and the snow densities derived from snow water equivalent in the NSA did not exceed that value in early winter (0.16 ± 0.01 g/cm^3) or late winter (0.18 ± 0.01g/cm^3) within either study year. Further, linear features in the NSA had a compacted substrate of snow 23.6 times harder on average than adjacent uncompacted areas.

Influence of Linear Features

The winter trail system in the NSA originates from an existing trail network comprised of ATV trails and seismic lines. As snow accumulates during winter, secondary and ephemeral trails become accessible, and cross-country travel is possible. In some winters, access to many trails could be delayed as late as January, although they may remain navigable into mid-April. During this study, levels of snowmachine activity progressed with increasing temperature and daylight until activity peaked in late March. At this point in the winter season, the NSA experiences over 12 h of potential light and the daytime high temperatures have risen from a mean of -17° C in January to -1° C in March. On a daily basis, snowmachine activity also was highest during peak daylight hours and on weekends, consistent with the academic calendar. The trail system and study area are extensive and, although the highest level of activity occurred near the trailheads and around Lake Louise, overall levels of snowmachine activity in proportion to the length and density of trails was relatively low.

My hypotheses drew on the conclusions of many authors who suggested that the presence of secondary roads or a trail network could strongly influence the spatial and temporal distribution of packs (Thurber et al. 1994; Singleton 1995; Ciucci et al. 2003), leading to increases in hunting efficiency (Bergerud et al. 1984; Ciucci et al. 2003; Crête and Larivière 2003; Whittington et al. 2004, 2005) by providing access to larger areas and allowing the occupation of sub-optimal habitats (Bergerud et al. 1984; Tremblay et al. 1998; Murray and Boutin 1991; James and Stuart-Smith 2000; Richer et al. 2002). I assumed that if human activity was minimal or predictable on these compacted and vegetation-free corridors, wolves could maximize travel efficiency and become more effective predators by using these features to counteract the increasing sinking depth of snow. This would imply that the size of a wolf pack's home range would increase with the availability or density of linear features. The average density of linear features across the Nelchina Study Area (0.11 ± 0.25 km/km^2) was low compared with other study areas (e.g., Fritts et al. 2003). In addition, most existing studies have focused more on road densities rather than the network of snowmachine trails as my work did. Whittington et al. (2005) reported that wolves selected lower road and trail densities when thresholds began to exceed 1.0 km/km^2, but wolves continued to travel through areas at densities greater than 1.0 km/km^2. Further, only 10% of those wolf locations were in areas with trail densities that exceeded 2.9 km/km^2. I did not detect relationships among use of trails, size of home ranges, and density or availability of linear features, but the densities of trails in the NSA did not exceed those thresholds.

Whittington et al. (2005) observed that wolves using linear features responded more to the level of human activity than to the density of roads and trails, avoiding humans only at high levels. The approach to model human activity in wolf studies varies from the use of human densities (Heilhecker et al. 2007) and human-use digital atlases (Merrill and Hebblewhite 2008) to functions of road densities (Ciucci et al. 2003). Shepard and Whittington (2006) enumerated human activity on a trail system using trail cameras, but failed to publish any values to facilitate comparisons. Although all wolves in the experimental area (north of the Glenn Highway) in the NSA had access to linear features, and the level of human activity associated with them was very low and predictable, wolves used linear features only 1.5% of the time. By day of the week and even by hour, trail use was low. That small percentage of use by wolves occurred when human activity was least, similar to the spatio-temporal avoidance of humans during daylight in Banff National Park and in Europe (Boitani 1982; Vilá et. al 1995; Ciucci et al. 1997; Boitani 2003; Merrill and Hebblewhite 2008). In late winter when trail use was expected to be highest due to the constraints of snow, wolves were on linear features <1% of the time. I expected that if linear features facilitated advantageous travel and increased prey encounter rates, that the proportion of locations on trails would be considerably higher, particularly in winter. The difference between snow hardness values on linear features versus adjacent areas was profound and exemplifies the supportive structure of snowmachine trails. Overall, snow was relatively shallow and rarely exceeded the chest height of wolves. As a result, it appears that snow did not inhibit wolf movement to the degree that the use of trails added significant benefit or outweighed the potential for human encounters, such as when human activity and human-induced mortality were highest in late winter.

Wolf packs with the highest proportion of trail use occupied areas with the highest density of linear features (Table 2.1). Previous work reported the selection of natural linear features such as frozen rivers and lakes as travel corridors, but wolves in the NSA selected for river-type and lake-type trails the least. It has been suggested that wolves are more susceptible to mortality in areas of Alaska where hunters and trappers can access frozen lakes and streams in winter (Person and Russell 2008). Based on availability and the proportion of wolf locations on linear features, wolves generally did not appear to show fidelity to linear features (see Chapter 3). Given that all linear features were buffered to compensate for GPS error, this lack of propensity for trails is probably not underestimated. Therefore, the meager use of compacted and vegetation-free linear features may be associated more with cautious opportunism as opposed to any form of selection or preference. One overlying explanation for this wariness or clear avoidance of linear features by wolves is likely due to the high level of exploitation by humans. Most observed populations of wolves that have some degree of fidelity to linear features are not subject to hunting, trapping, or active predator management activities. Models developed by Person and Russell (2008) for a network of logging roads on Prince of Wales Island in southeast Alaska, however, predicted that a road density of >0.9

km/km^2 would yield a harvest of 1.2 wolves/1000 km^2. Densities of linear features in the Nelchina Study Area exceeded those thresholds near the Glenn Highway.

Further, as others have noted, the prey items of wolves, in this case moose and caribou, could be distancing themselves from linear features (Dorrance et al. 1975; Colescott and Gillingham 1998; Johnson 2000; Rowland et al. 2000; Dyer et al. 2001; Papouchis et al. 2001; James and Stuart-Smith 2000; Whittington et al. 2005). The largely dispersed ungulate population observed in the NSA could further compound the lack of fidelity to linear features by wolves (see Chapter 3)

Summary

The seasonal movement, distribution, and use areas of wolves in the Nelchina Study Area were affected minimally by the presence and distribution of linear features; however, it is difficult to discern if the responses were confounded by predator management activities. The seasonal and annual home ranges of wolves exhibited overlap and showed some of the dynamism often associated with recolonizing populations and human-dominated landscapes. Although the territorial boundaries for packs closest to roads appeared to be shaped by the locations of such features (i.e., Little Nelchina, Tolsona, and St. Anne packs), there was no evidence that the size of home ranges were dictated by the distribution or density of linear features.

Trails can expedite travel on occasions when they are used, but wolves in the NSA did not use linear features extensively. The lack of wolf locations on linear features could suggest an overall avoidance, but the establishment and persistence of packs in areas of highest densities of linear features, and the number of locations in proximity to linear features, refutes complete avoidance. My results suggest that the response by wolves to factors such as the presence of linear features and the associated snowmachine activity were likely affected by the high level of anthropogenic harassment and harvest. Wolves subject to heavy hunting pressure are short-lived and either discreetly move across their home ranges avoiding human encounters or suffer direct mortality. Without a mechanism to separate out the effects of exploitation, determining the underlying factors that define movement and distribution is difficult. For resource managers seeking to understand the complex relationship of wolves, linear features, and recreational human activity (i.e., snowmachining), this research provides an example of the adaptability and variability in wolf-human relationships. It also suggests that harvest strategies in areas with a network of linear features should consider the increased risk of mortality to wolves.

Chapter 3 : The Influence of Snow, Prey, and Anthropogenic Disturbance on Resource Selection by Wolves

Introduction

As human activity increases and expands into the backcountry through recreation, exploration, and development, linear features including roads, trails, and seismic lines become permanent artifacts on the landscape. In recent years there has been conflicting evidence describing how these linear features can affect spatial and temporal distribution, movements, and population dynamics of wildlife (Mech 1989; Thurber et al. 1994; James and Stuart-Smith 2000; Whittington et al. 2005; Merrill and Hebblewhite 2008). Although most activities associated with linear features have negative consequences for wildlife (i.e., loss of habitat and degradation of habitat, displacement from areas, disruption of daily activity and movement patterns, and mortality), some may facilitate energy-efficient travel, increase access into high-quality habitats (Dorrance et al. 1975; James and Stuart-Smith 2000), maximize encounters with prey (Ciucci et al. 2003), and provide escape corridors (Richens and Lavigne 1978).

For habitat generalists such as wolves that follow easy travel routes in areas where they can maximize encounters with prey (Bergerud et al. 1984; Mech and Boitani 2003) and minimize encounters with humans (Fritts et al. 2003; Ciucci et al. 2003), secondary roads or trail networks can influence the spatial organization and distribution of packs (Thurber et al. 1994; Singleton 1995; Paquet and Callaghan 1996; Ciucci et al. 2003). Typically wolves are less abundant in areas with high road densities because of direct or indirect mortality (Mech 1995; Mladenoff and Sickley 1998; Boitani 2003); however, if human traffic is minimal or predictable, wolves can benefit greatly from efficient travel on linear features through increased hunting efficiency (Bergerud et al. 1984; Ciucci et al. 2003; Crête and Larivière 2003) and the occupation of sub-optimal habitats (Tremblay et al. 1998; Crête and Larivière 2003; Richer et al. 2002). Many studies suggest that use of trails by wolves is influenced more by the level of human activity in an area than by the density of linear features (Thurber et al. 1994; James and Stuart-Smith 2000; Jaeger et al. 2005; Whittington et al. 2005). In winter, when snow and winter severity become critical constraints on food acquisition and locomotion, the availability of these hard, compact travel corridors that counteract increasing sinking depths in snow may have an even stronger influence on movement patterns. Merrill and Hebblewhite (2008) recently determined that responses of wolves to human disturbance were correlated with social structure, and were strongest in winter and weakest in summer.

In the Nelchina Basin of Alaska, moose dominate the diet of wolves during winter after the seasonal caribou have migrated north (Ballard et al. 1987; Dale et al. 1994; personal observation). In response to predation risk and the impediments associated with increasing snow depth and hardness, moose migrate to lower elevations seeking areas with easier access to high-quality forage (Ballard et al. 1997; Peek 1998). To lower energy expenditures, moose reduce their activity and forage intake as winter progresses or winter severity increases. As a result, aggregations of moose can develop in concentrated habitats (Molvar and Bowyer 1994; Peek 1998). Wolves in the Nelchina Basin follow these elevational movements within their territories to seek out prey-abundant areas (Ballard et al. 1987; Singleton 1995; Kunkel and Pletscher 2001; Mech and Boitani 2003). The highly variable support capacity of snow is rarely hard enough to provide support for moose, thereby restricting their movements. In contrast, wolves with their lighter foot loading are often able to travel across snow surfaces, increasing the likelihood of capturing prey (Kelsall and Prescott 1971; Coady 1974). Many have observed wolves altering their behaviors to utilize the supportive snow crusts when temperatures drop at night and early in the day (Mech and Peterson 2003). These complex interactions add to the premise that snow drives wolf-prey systems (Mech and Peterson 2003).

The primary forms of human activity in the Nelchina Basin of south-central Alaska include hunting, trapping, and exploratory snowmachining. The state's continual increase in the human population and the production of light-weight, fuel-efficient snowmachines in the 1990's has enabled the expansion of snowmachine activity into areas where little or no activity previously existed. Consistent with other recreational areas, snowmachines in the Nelchina Basin typically follow existing all-terrain vehicle (ATV) trails and seismic lines across moderately sloping terrain and valley bottoms (Noss et al. 1996; Whittington et al. 2005), although new trails are frequently created. The creation of snowmachine trails accelerates the rate of snow maturation by increasing surface temperature, compaction, and crusting (Neumann and Merriam 1972). According to Whiteman (2008), over half of the compaction and increase in snow density that results from multiple snowmachine passes occurs with the initial pass. Thus, even a single pass by a snowmachine creates a compacted trail that can facilitate expeditious energy-minimizing travel.

Resource selection functions (RSFs) have recently been applied to examine human-wildlife interactions (Mladenoff et al. 1995; Ciarniello et al. 2007; Merrill and Hebblewhite 2008; Jedrzejewski et al. 2008). Models define selection of resources in relation to their availability (McDonald and Boyce 1999; Manly et al. 2002; Johnson et al. 2005). I used logistic regression-based resource selection functions to model winter selection by wolves in an ecosystem exploited by humans. In addition to describing how the presence of linear features, specifically snowmachine trails, defined the spatial and temporal distribution of wolves during winter (Chapter 2), I used remote sensing, geographic information systems (GIS), and high-resolution global positioning systems (GPS) to identify factors that may encourage the use or avoidance of various categories of trails by wolves. Fine temporal and spatial scales of the data layers provided the opportunity to look at actual trail use in addition to trail proximity without making large assumptions or using categorical proximity classes (Whittington et al. 2005; MacKenzie 2008).

Study Area

The 17,000-km^2 Nelchina Study Area (NSA) in south-central Alaska is a portion of the Nelchina Basin that extends from the eastern ridge of the Talkeetna Mountains (148°00' W) east towards Glennallen (145° 33' W), north to the Susitna River (62° 45'N), and south to the Heavenly Hills (61° 45' N) (Fig 3.1). Elevations range from 450 m in the Lake Louise and Tyone Flats to 2100 m in the Talkeetna Mountains. Thirty-one percent of the Nelchina Study Area is higher than 1220 m in elevation and is considered poor moose and wolf habitat (Ballard et al. 1987). The NSA encompasses portions of Game Management Units (GMUs) 13 A, B, D, and E. A detailed description of the NSA is given in Chapter 2.

Methodology

Wolf Captures and Location Data

Twelve wolves in 5 packs (Leg Hold, Moore Lake, Little Nelchina, St. Anne Lake, and Tolsona) were captured via aerial darting and fit with downloadable GPS collars (Televilt AB, Lindesberg, Sweden) during the winters of 2005 and 2006. I opportunistically

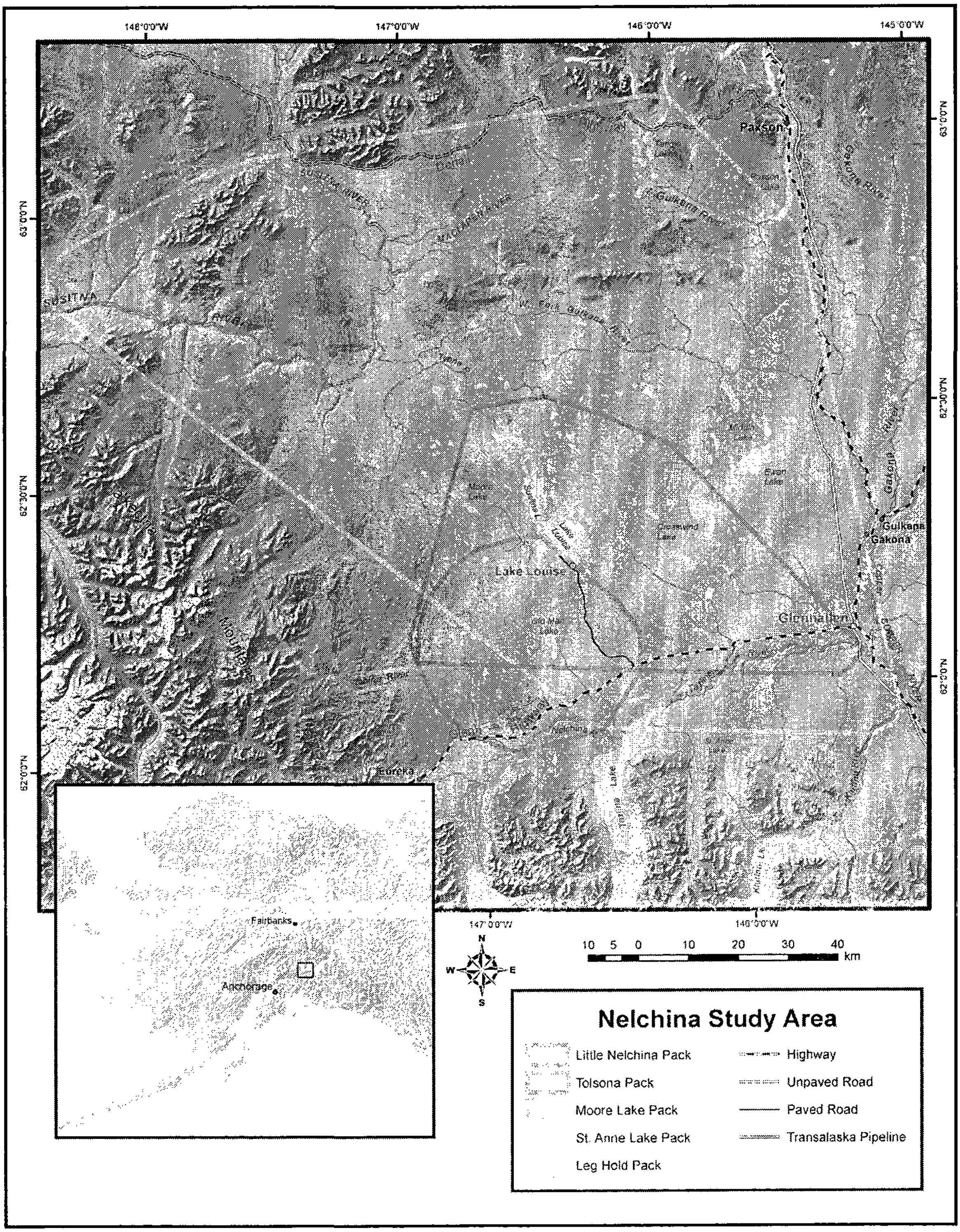


Figure 3.1. The location of the Nelchina Study Area in south-central Alaska and the annual home ranges (95% MCP) for the 5 wolf packs that resided there between February 2005 and April 2006.

fit 10 Tellus I collars on alpha individuals with 15-min fix intervals and 2 Simplex C collars with 1-h fix intervals on subordinate pack members. I used the VHF transmitters in the Simplex collars only to maintain pack identification. Data acquired from the Simplex models were not used in analyses because of limited temporal resolution and lack of independence from alpha individuals. I recaptured 5 wolves to replace Tellus collars during the study. Two of the 5 packs were initially collared south of the Glenn Highway (southern NSA) to serve as a control – free from significant snowmachine trails and predator management activity. In response to predator control activities that reduced pack sizes and opened territories in 2005, the St. Anne Lake pack shifted north into the eastern edge of the NSA.

Location data were recovered by collar retrieval via animal recapture or through collar drop-off mechanisms. Data used in analyses began 8 h after the capture crew departed to minimize the influence of capture operations and immobilization on animal movement. After removing errant fixes (points beyond reasonable biological movements), I also removed values with high percent dilution of precision (PDOP), a measure of the geometrical strength of the GPS satellite configuration (2D fixes $\geq$ 10 and 3D fixes $\geq$ 25), according to D'Eon and Delparte's (2005) recommendation. Fix rate was defined as the number of fixes acquired divided by the total number of potential fixes from the time of deployment until recovery given the criteria mentioned above.

Resource selection by wolves was analyzed for 3 seasons: early winter (15 November – 14 February, low snow depth and human activity), late winter (15 February – 15 April, peak snow depth and human activity), and summer (16 April – 14 November, snow free and nominal human activity). I analyzed summer data because 64.4% ($n = 110{,}155$) of total GPS data collected occurred between winter seasons. The area available for resource selection by wolves was based on movement potential. This movement potential (potential distance available for movement between fixes) was defined by a circular buffer around each GPS location (used point) with a radius equal to the 99^{th} percentile longest movement by individual wolves in the 15-min intervals (1500 m). I then randomly generated 1 availability point within the buffer for each observed GPS location using a Visual Basic script (M.P. Gillingham, University of Northern British Columbia, unpublished) in Excel 2003 (Microsoft Inc, Redmond, WA, USA). Because of the very fine temporal resolution of my data set, I used only locations that fell on the hour (i.e., minute = 0) to reduce issues of spatial and temporal dependence, and verified that there was no overlap between used and available points (Manly et al. 2002).

Inputs for Resource Selection Models

Topography

Topographical covariates in resource selection model sets including slope, aspect, and elevation were derived from a 25-m raster digital elevation model (DEM) acquired from the Alaska Department of Fish and Game (ADF&G). To minimize issues of perfect separation between used and available points, I defined aspect as 2 continuous variables: northness (i.e., cosine (aspect)) and eastness (i.e., sine (aspect)) (Palmer 1993). For northness, north and south aspects are indicated by the values of 1.00 and -1.00, respectively, whereas east and west aspects are suggested by values near 0.00. Eastness values of 1.00 and -1.00 indicate east and west exposures; northern and southern exposures are suggested by values near 0.00 (Palmer 1993).

Snow

I measured snow depth, density and hardness at 16 existing Natural Resources Conservation Service (NRCS) snow stations and at 13 snowmachine enumeration sites usually every 2 weeks over the course of 2 winters to quantify the snow conditions that wolves experienced both on and adjacent to linear features. Not all of the sites were sampled during every sampling period because of weather and logistical constraints. To define the hardness of the entire snow column, I calculated an integrated ram-hardness number (R_i), as defined by Coady (1974). The density of snow was derived by dividing the snow water equivalent (SWE) by the total depth of snow (cm^3) (see Chapter 2). Using these snow variables as predictors, I applied a backwards stepwise regression to develop coefficients for the 16 biweekly periods from 1 December 2004 to 11 April 2006. From this, I linearly interpolated the snow values between the closest two biweekly periods for the date on which the used and available points were taken to create snow values for the dates of every used and random wolf location. If for any biweekly period the individual coefficients were not statistically significant, I used the intercept which contained the average values across all of the snow survey sites for that particular period.

Moose Distribution

To assess prey availability in the Nelchina Study Area, I flew two, 3-day moose surveys using 3 Piper Super Cubs in early winter (December 2005) and late winter (March 2006). I designed the survey quadrats based on the standard sample unit for the Geospatial Population Estimator of 2 min of latitude and 5 min of longitude (Kellie and DeLong 2006). This created 470 16-km^2 quadrats with a survey area of 7520 km^2 and represented approximately 80% of the core area used by wolves and 44% of the study area. I flew these units with a search intensity of 7 min/quadrat or 2.28 km^2/min. All quadrats were subsequently classified as having relative high prey value (H $\geq$3 moose/quadrat) or low prey value (L $\leq$2 moose/quadrat) based on the natural breaks in the plotted values from the surveys. From these data, I generated an early season and a late season GIS polygon layer of prey value in ArcMap 9.1 for Windows (ESRI, Redlands, CA, USA). Caribou were not a significant factor during prey surveys because of their migration out of the NSA during study winters.

Anthropogenic Disturbance

Linear features were defined by their substrate, width, and human use as they were mapped on the ground via snowmachine or digitally extracted from satellite and aerial photographic images using ArcMap 9.1. I classified 5 trail types (trail, river, lake, seismic line, and road), assigning a categorical width as single ($\leq$2.0 m), double ($\geq$2.1 - 4.0 m), seismic line (4.1-7.0 m), or highway ($\geq$7.1 m), and I recorded whether the features were broken by snowmachine, groomed, or overgrown. Spatial data for linear features were mosaiced and rasterized to create density variables for all trails and for all linear features (trails plus all linear features not used as trails such as roads and utility corridors).

I defined snowmachine activity at different scales using 4 variable sets: activity feature, human activity period, activity level linear, and activity level trail. After categorizing each trail (i.e., linear features used exclusively as snowmachine routes) and linear feature (i.e., all seismic lines, roads, and trails), I assigned categories for activity feature to the linear features based on the median number of weekly snowmachine passes: high ($\geq$60.1 passes/week), medium (20.1 - 60 passes/week), or low ($\leq$20 passes/week) (Figure 3.2). The human activity period variable was the total number of snowmachines divided by the number of counters deployed on the trail

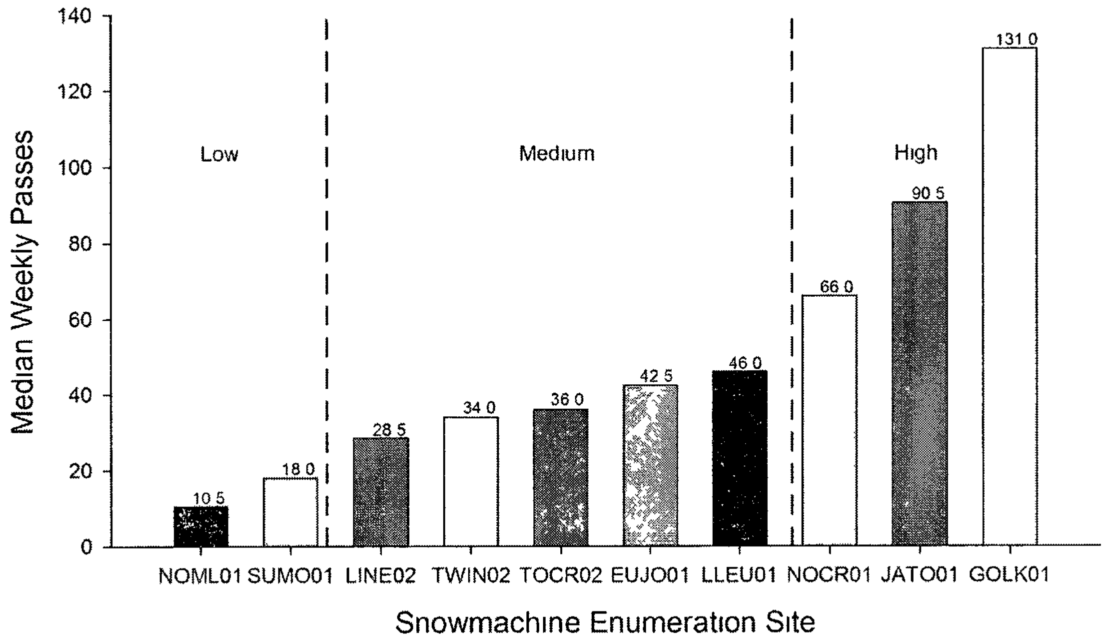


Figure 3.2. The median of weekly snowmachine passes (n = 17,398) at 10 snowmachine enumeration sites across the Nelchina Study Area during the winters of 2005-2006

system at any particular hour at that given time (see Chapter 2). I used two interaction variables to further enumerate human activity: activity level linear (distance (m) to linear feature x human activity period) and activity level trail (distance (m) to trails x human activity period).

Proximity to Input Attributes

To more accurately define the relationship between linear features and trail use by wolves, I buffered all linear features by 30 m (15 m on each side) beyond their actual measured widths. This was to compensate for GPS error in measurements that exceeded the radius of linear features (McLoughlin et al. 2004). All wolf locations within this buffer were defined as 'on' linear features. Additional input variables from hydrologic layers (i.e., river, lake, and a combination of all water features), anthropogenic feature layers (linear feature type, feature width, activity feature), and seasonal prey layers were queried as 'distance to' features using Model Builder in ArcMap 9.1 for all used and random points. I also input the quadratic of these covariates to determine if their probability of use or relationship to wolves was non-linear.

Resource Selection Model Evaluation

I used the information-theoretic approach to evaluate ecologically plausible models constructed across years for individual wolves and all wolves (global models) by season (Burnham and Anderson 2002). I assessed collinearity among all variables using a tolerance threshold of <0.20 to avoid inflation of selection coefficients and error terms (Menard 2002). The same suite of models was used for individual wolves and for all wolves by season, although not all models were run for all seasons (i.e., no snow or human activity variables in summer were incorporated; there were no data for some animals in particular seasons; and some variables were dropped due to collinearity; Table 3.1). Individual and global seasonal models were ranked using Akaike's Information Criterion (AIC_c) corrected for small sample

Table 3.1. Ecologically plausible models developed *a priori* for all animals (pooled) and individuals to describe resource selection by wolves in the Nelchina Study Area of south-central Alaska. Areas of relative moose density (prey), human activity, and snow parameters (depth and hardness) were not included in summer models because data were not available.

Model	Early Winter	Late Winter	Summer
Density + Water[a] + Linear Features[a]			√
Depth + Density + Rivers[a] + Lakes[a]		√	
Depth + Density + Rivers[a] + Lakes[a] + High Activity Feature[a]	√		
Depth + Density + Rivers[a] + Lakes[a] + Low Activity Feature[a]	√	√	
Depth + Hardness + Density + Linear Features[a]	√	√	
Depth + Hardness + Density + Rivers[a] + Lakes[a] + High Activity Feature[a]	√	√	
Depth + Hardness + Density + Rivers[a] + Lakes[a]		√	
Depth + Hardness + Density + Rivers[a] + Lakes[a] + Low Activity Feature[a]	√	√	
Depth + Hardness + Activity Period + Activity Level (Linear) + Linear Feature[a] + Density + Rivers[a]	√	√	
Depth + Hardness + Activity Period + Activity Level (Trail) + Trails[a] + Density + Rivers[a]	√	√	
Depth + Hardness + Prey + Density	√	√	
Depth + Hardness + Prey + Density + Rivers[a] + Lakes[a]	√	√	
Depth + Hardness + Prey + Activity Period + Activity Level (Linear) + Linear Features[a] + Density + Rivers[a]	√	√	
Depth + Hardness + Prey + Activity Period + Activity Level (Trail) + Trails[a] + Density + Rivers[a]	√	√	
Depth + Hardness + Prey + Linear Feature[a]	√	√	
Depth + Hardness + Prey + Trails[a]	√	√	
Depth + Hardness + Prey + Water[a]	√	√	
Depth + Activity Period + Activity Level (Linear) + Linear Features[a] + Density + Rivers[a] + Lakes[a]	√	√	
Depth + Activity Period + Activity Level (Trail) + Trails[a] + Density + Rivers[a] + Lakes[a]	√	√	
Depth + Prey + Density	√	√	
Depth + Prey + Density + Rivers[a] + Lakes[a]		√	
Depth + Prey + Density + Rivers[a] + Lakes[a] + High Activity Feature[a]	√		
Depth + Prey + Density + Rivers[a] + Lakes[a] + Low Activity Feature[a]	√	√	

Table 3.1. Continued.

Model	Early Winter	Late Winter	Summer
Depth + Prey + Activity Period + Activity Level (Linear) + Linear Features[a] + Density + Lakes[a]		√	
Depth + Prey + Activity Period + Activity Level (Linear) + Linear Features[a] + Linear Density + Rivers[a] + Lakes[a]	√	√	
Depth + Prey + Activity Period + Activity Level (Trail) + Density + Rivers[a]		√	
Depth + Prey + Activity Period +Activity Level (Trail) + Trails[a] + Linear Density + Rivers[a]+ Lakes[a]	√	√	
Depth + Prey + Linear Features[a]	√		
Depth + Prey + Trails[a]	√		
Depth + Prey + Water[a]	√		
Elevation + Density + Water[a] + Linear Features[a]			√
Elevation + Slope + Aspect	√	√	√
Elevation + Slope + Aspect + Rivers[a] + Lakes[a]	√	√	
Elevation + Slope + Aspect + Trails[a]	√	√	√
Elevation + Slope + Aspect + Water[a]			√
Elevation + Water[a] + Trail[a]			√
Elevation + Water[a] + Linear Features[a]			√
Prey + Density + Rivers[a] + Lakes[a]+ High Activity Feature[a]	√	√	
Prey + Density + Rivers[a] + Lakes[a]+ Low Activity Feature[a]	√	√	
Prey + Density + Rivers[a] + Lakes[a]		√	
Prey + Activity Period + Activity Level (Linear) + Density + Rivers[a] + Lakes[a]	√	√	
Prey + Activity Period + Activity Level (Trail) + Density + Rivers[a] + Lakes[a]		√	

[a] Variable is defined as a 'distance to' feature

sizes (n/K < 40; Burnham and Anderson 2002). The strength of evidence that any particular model was the best within the model set was determined using Akaike weights (w_i). Single models with $w_i \geq 0.95$ were selected as the top model; however, if there were cases for which there was not a single model with $w_i \geq 0.95$, the w_i from the best competing models were summed until $w_i \geq 0.95$ (unless competing models were subsets of the top models) (Burnham and Anderson 2002). For these competing model sets, selection coefficients were then averaged based on their relative w_i weights (Burnham and Anderson 2002; Arnold 2010). K-fold cross-validation procedures (Boyce et al. 2002) were used to determine the predictive ability of the final models and select the most parsimonious models. Each k-fold resulted in an averaged Spearman's rank correlation coefficient (r_s) with a threshold $r_s \geq 0.648$ for $n = 5$ and $\alpha = 0.05$ (Zar 1999). For all data, means are presented as mean ± 1 SE unless otherwise noted. All statistical analyses were performed in STATA 9.2 (STATACORP, College Station, TX, USA).

Results

I retrieved 188,703 GPS locations from 16 Tellus collars on 10 alpha wolves between February 2005 and April 2006, for an average of 6290 locations per season per wolf. Fix rates averaged 90.51% ± 2.9% (range 60 - 99%) across seasons. None of the collars failed in the field; however, because of predator control activities, 2 collars were never recovered and no individual wolf was collared for the entire study period. I removed 17,522 (9.3% of the total fixes) errant locations and fixes with poor geometry. This resulted in 171,181 locations for analysis. Data for analyses were for 2 wolves from the Leg Hold pack (NW051 and NW052), 2 wolves from the Little Nelchina pack (NW043 and NW044), 2 wolves from the Moore Lake pack (NW040 and NW049), 2 wolves from the St. Anne Lake pack (NW041 and NW045), and 2 wolves from the Tolsona pack (NW042 and NW047) (Table 3.2).

Snow depth, snow density, and snow hardness were variable and tended to increase with the progression of winter (Figure 3.3; Figure 3.4; Figure 3.5). Mean snow depth over both study years increased from an early winter depth of 49.6 ± 3.7 cm in December to 64.1 ± 2.57 cm in April. During study years, the depth of snow exceeded 65 cm only in a few locations in late winter. There was very little water content in the snowpack as evidenced by the low density of snow. Mean snow density was 0.17 ± 0.01 g/cm^3 across study years and generally increased from an average of 0.158 ± 0.005 g/cm^3 in early winter to 0.175 ± 0.014 g/cm^3 in late winter. The continuing snowfall and rising ambient temperatures as winter progressed affected the hardness of snow through insolation and compaction. Overall, snow hardness averaged 23.6 times greater on compacted linear features than in adjacent areas in early winter (1179.29 ± 87.96 kg/cm^2 vs. 42.22 ± 6.06 kg/cm^2) and in late winter (1326.19 ± 82.59 kg/cm^2 vs. 59.67 ± 4.37 kg/cm^2) when there were paired measures on and off trail.

During the course of the 2 moose surveys in early and late winter I recorded 944 moose. In early winter, the total moose observed was 562, with the highest density quadrat having a minimum of 16 moose. There were 91 quadrats classified as having high prey value (H $\geq$ 3 moose/unit) and 379 quadrats with low prey value (L $\leq$ 2 moose/unit) (Figure 3.6). In late winter, moose were less aggregated and only 310 individuals were observed. Only 1 quadrat exceeded 9 moose during the survey. There were 43 quadrats classified as high prey value and 427 as low prey value in late winter (Figure 3.7).

During the winters of this study, the Nelchina Study Area was traversed by a minimum of 2409 km of trails and an additional 815 km of roads. On average, wolf packs

Table 3.2. Capture and survival data (age, sex, capture date, recovery date, number of total locations acquired, fate, and mortality date) by pack and animal (ID) for wolves in the Nelchina Study Area in south-central Alaska, 2005-2006.

Pack	Animal ID	Sex	Age	Deployment Date (mo/day/yr)	End Date (mo/day/yr)	# of GPS Locations	Fate	Mortality Date
Leg Hold	NW051	M	4-5	2/23/2006	4/17/2006	4,901	Released	
	NW052	M	1-2	2/23/2006	4/17/2006	4,829	Released	
Little Nelchina	NW043	M	3-4	2/17/2005	7/10/2005	13,070	Trapped	3/2007
	NW044	F	3	2/17/2005	2/9/2006	30,495	Trapped	2/16/2006
	NW048	M	1+	10/26/2005	2/21/2006		SDA*	2/21/2006
	NW050	M	1+	10/29/2005	2/21/2006		SDA	2/21/2006
Moore Lake	NW040	M	3	2/19/2005		20,815	Unknown	
	NW049	F	2-3	10/26/2005	12/28/2005	5,461	Trapped	Unknown
St. Anne Lake	NW041	M	5-6	2/17/2005	9/9/2005	19,612	SDA	10/2005
	NW045	F	2-3	4/5/2005	1/7/2006	22,675	SDA	1/8/2006
Tolsona	NW042	F	2	2/17/2005	12/8/2005	22,986	Trapped	12/2005
	NW047	M	5	4/5/2005	3/18/2006	26,337	Trapped	12/2006

* Harvested through same-day-airborne hunting (SDA)

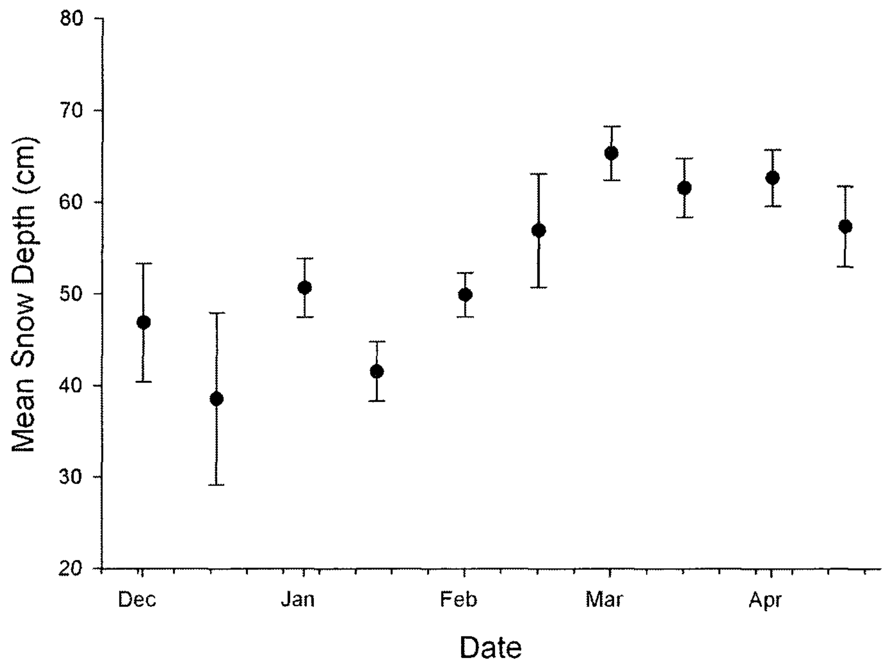


Figure 3.3. Snow depth (mean ± SE) measured every 2 weeks at 16 Natural Resources Conservation Service (NRCS) snow stations and near 13 snowmachine enumeration sites (off trail) in the Nelchina Study Area, south-central Alaska, 2005-2006.

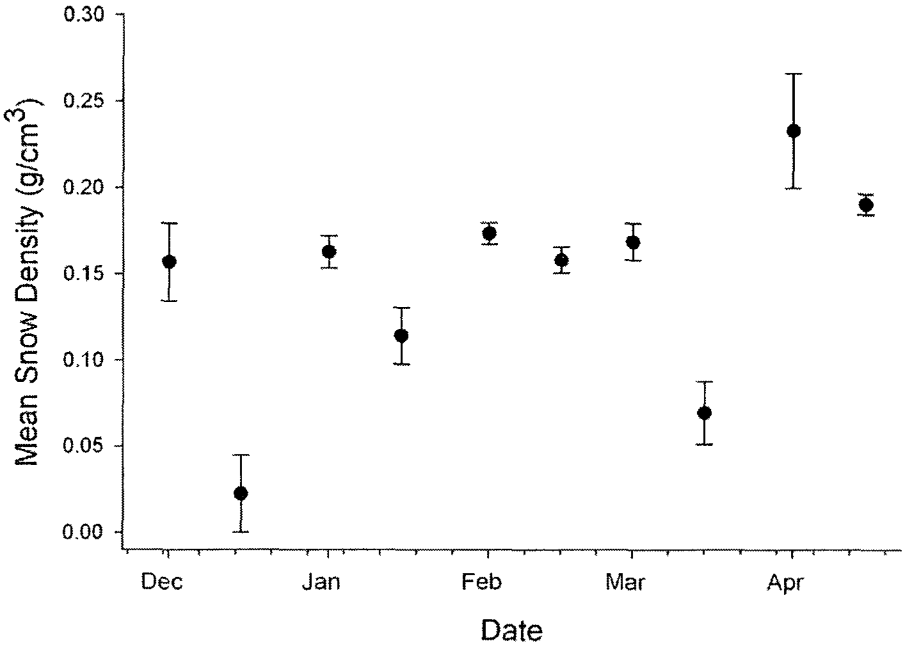


Figure 3.4. Snow density (mean ± SE) calculated from snow water equivalent (SWE) at 16 Natural Resources Conservation Service (NRCS) snow stations and near 13 snowmachine enumeration sites (off trail) in the Nelchina Study Area, south-central Alaska, 2005-2006.

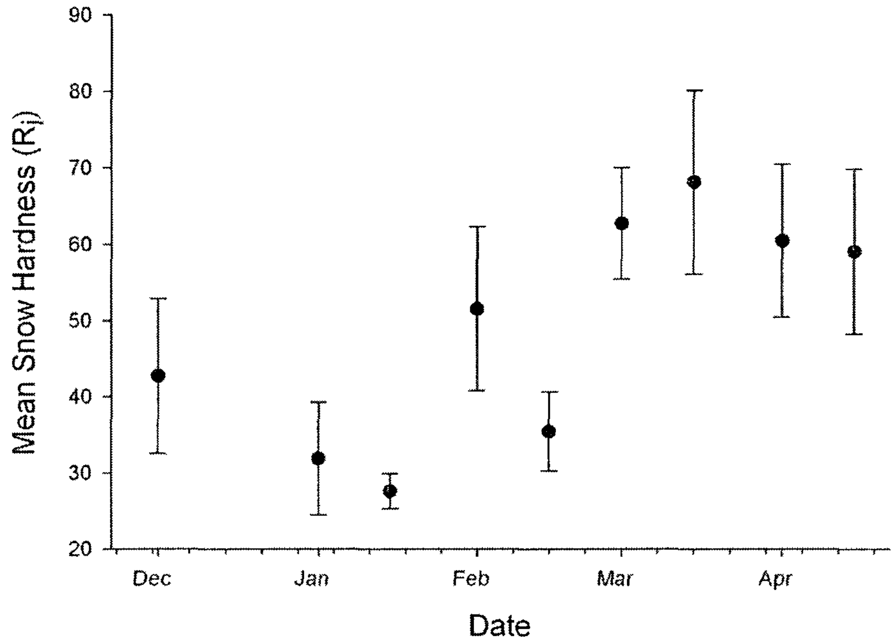


Figure 3.5. Snow hardness measured with an Alta Ramsonde Penetrometer (R_i, mean ± SE) at 16 Natural Resources Conservation Service (NRCS) snow stations and near 13 snowmachine enumeration sites (off trail) in the Nelchina Study Area, south-central Alaska, 2005-2006.

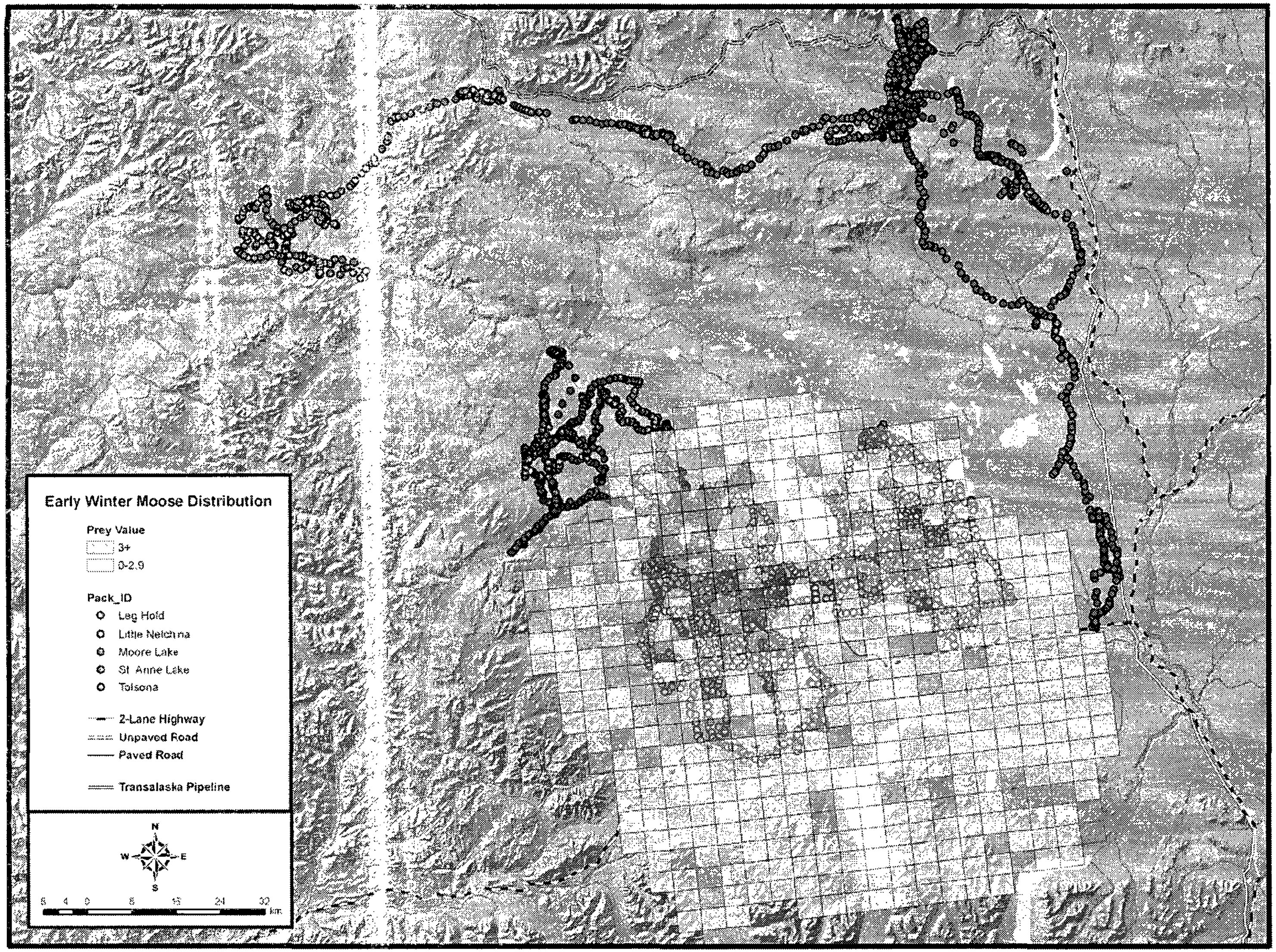


Figure 3.6. Location of the early winter (December 2005) moose survey area in relation to the early winter (15 November – 14 February) movements of wolves in the Nelchina Study Area in south-central, Alaska.

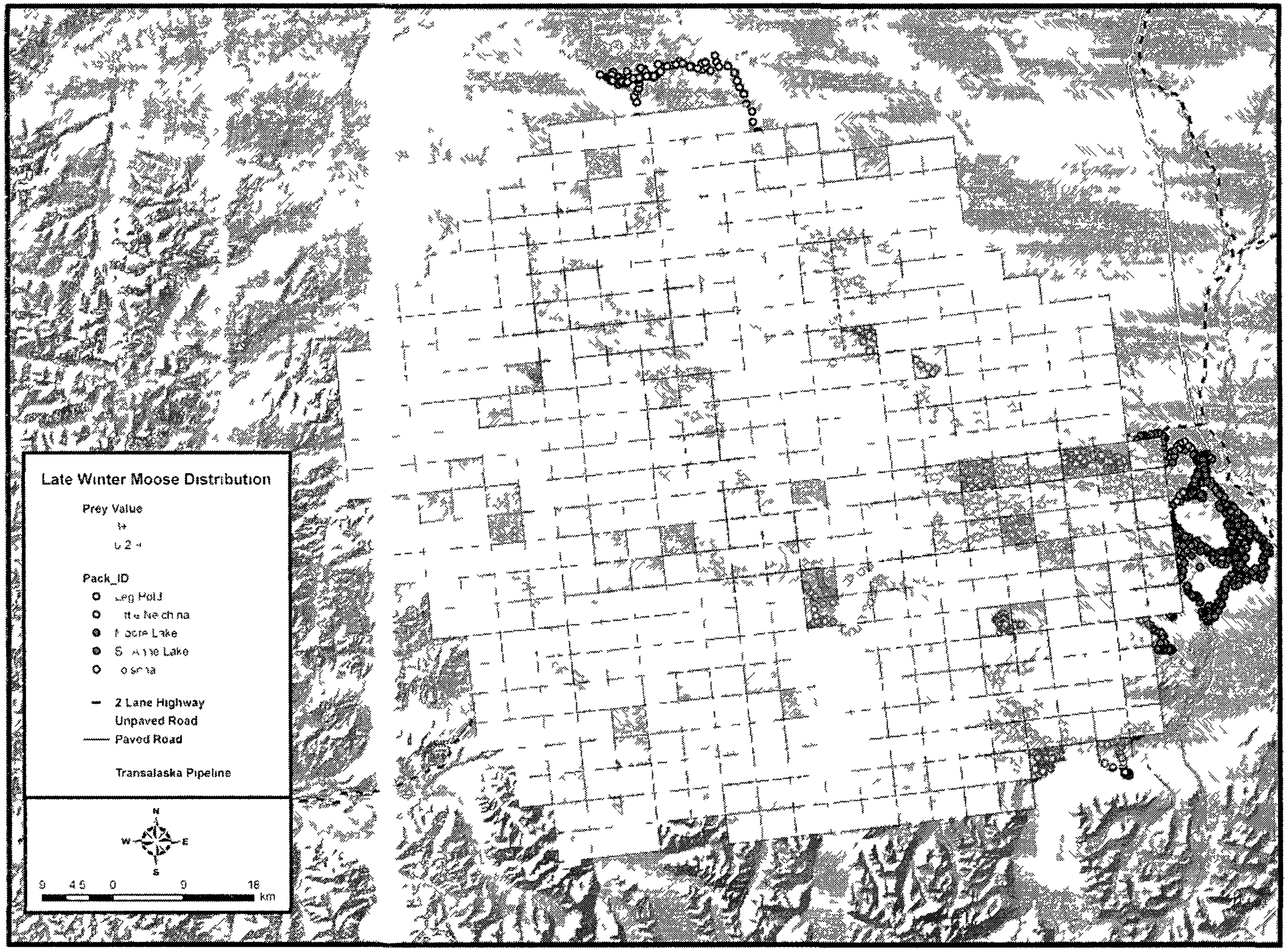


Figure 3.7. Location of the late winter (March 2006) moose survey area in relation to the late winter (15 February – 15 April) movements of wolves in the Nelchina Study Area in south-central, Alaska.

north of the Glenn Highway had 0.31 km^2 of linear features within their annual home range, and the spatial distribution of roads appeared to define the distribution of packs along the Glenn Highway (a 2-lane paved road). The Tolsona and Little Nelchina Packs were separated from each other with little overlap by the Lake Louise road and by the highway boundary to the south (see Chapter 2).

Resource selection by wolves in early winter was best explained by distance to water, snow and hardness, and distance to high prey areas (Table 3.3). This global model performed well ($r_s = 0.948$). In late winter, wolves appeared to select areas based on distance to rivers and lakes, elevation, slope, and aspect, although model validation was not as high ($r_s = 0.648$).

Not all resource selection models for all wolves were validated using k-fold cross validation and so there were no models for some individuals in some seasons (Table 3.3). For those models that did cross-validate, average r_s for individual wolves ranged from 0.851 to 0.942 for 4 models in early winter, 0.807 to 0.928 for 8 models in late winter, and 0.778 to 0.883 for 7 models in summer. The significant attributes in the global models corresponded with many of the individual models and there were no significant parameters in global models that were not selected or avoided by individual wolves. Variation in selection, however, was high for individuals within seasons. Some animals selected for and others against the same attribute (Table 3.4).

Early Winter

Across wolves, there was strong selection for proximity to all water features ($\beta = -2.742 \pm 0.197$, $P < 0.01$; Table 3.4; Figure 3.8) in early winter. The global model for resource selection

Table 3.3. Final resource selection models across all wolves (global) and for individuals by season for 9 wolves in the Nelchina Study Area, south-central Alaska, 2004-2006. Included statistics are: sample size (n), number of parameters (K), log-likelihood (LL), Akaike's Information Criterion corrected for small sample size (AICc), Akaike weights (w_i), evidence ratios (E_r), and average Spearman's correlation coefficient r_s from the k-fold cross validation (n = 5). All *P* values for $r_s \leq 0.05$.

Season	Animal ID	Model	n	K	LL	AIC_c	w_i^a	E_r^a	r_s^b
Early Winter	**GLOBAL**	Depth + Hardness + Distance to High Prey (km) + Distance to Water (km)[c]	11794	5	-8046 880	16105 750	1 000	1 00	0 941
	NW042[c]	Elevation (m) + Slope + Aspect + Distance to Rivers (km)[c] + Distance to Lakes (km)[c]	1158	9	-783 800	1585 725	0 629	1 00	0 519
		Elevation (m)+ Slope + Aspect + Distance to Trails (km)[c]	1158	7	-786 384	1586 841	0 360	1 75	0 427
	NW044	Depth + Hardness + Distance to High Prey (km) + Distance to Water (km)[c]	4208	6	-2833 229	5678 472	1 00	1 00	0 942
	NW045[d]	Elevation (m)+ Slope + Aspect	2172	5	-1495 703	3001 424	0 84	1 00	0 517
		Elevation (m) + Slope + Aspect + Distance to Trails (km)[c]	2172	7	-1495 644	3005 327	0 12	7 04	0 573
	NW047	Depth + Hardness + Distance to High Prey (km) + Distance to Water (km)[c]	2432	6	-1596 980	3205 985	1 00	1 00	0 851
	NW049[c]	Depth + Hardness + Distance to High Prey (km) + Linear Feature Density (km/km^2) + Distance to Rivers (km)[c] + Distance to Lakes (km)[c]	1824	9	-1243 869	2505 817	0 03	28 04	0 706
		Distance to High Prey(km) + Linear Feature Density (km/km^2) + Distance to Rivers (km)[e] + Distance Lakes (km)[c] + Low Activity Features (km)[c]	1824	9	-1242 863	2503 804	0 08	10 25	0 529
		Distance to High Prey(km) + Linear Feature Density (km/km^2) + Distance to Rivers (km)[c] + Distance to Lakes (km)[i] + Distance to High Activity Features (km)[c]	1824	9	-1244 050	2506 178	0 02	33 58	0 677
		Depth + Hardness + Linear Feature Density (km/km^2) + Distance to Rivers (km)[c] + Distance to Lakes (km)[c] + Distance to Low Activity Features (km)[c]	1824	10	-1242 652	2505 404	0 03	22 80	0 627
		Elevation(m)+ Slope + Aspect + Distance to Rivers (km)[c] + Distance to Lakes (km)[c]	1824	9	-1240 536	2499 150	0 79	1 00	0 682
	NW051	Elevation (m) + Slope + Aspect + Distance to Rivers (km)[c] + Distance to Lakes (km)[e]	2424	9	-1478 485	2975 031	1 00	1 00	0 928
	NW052	Elevation (m) + Slope + Aspect + Distance to Rivers (km)[e] + Distance to Lakes (km)[c]	2464	9	-1534 507	3087 073	1 00	1 00	0 915

80

Table 3.3. Continued.

Season	Animal ID	Model	n	K	LL	AIC_c	w_i^a	E_r^a	r_s^b
Late Winter	**GLOBAL**	Elevation (m) + Slope + Aspect + Distance to Rivers (km)[c] + Distance to Lakes (km)[c]	18742	9	12753 680	25525 367	0 999	1 00	0 68
	NW040[c]	Distance to High Prey (km) + Linear Feature Density (km/km^2) + Distance to Rivers (km)[e]+ Distance to Lakes (km)[c] + Distance to Low Activity Features (km)[e]	2526	9	-1612 500	3243 056	0 78	1 00	0 832
		Elevation (m) + Slope + Aspect + Distance to Rivers (km)[c] + Distance to Lakes (km)[c]	2526	9	-1614 554	3247 166	0 10	7 81	0 689
		Elevation (m) + Slope + Aspect + Distance to Rivers (km)[c] + Distance to Lakes (km)[e]	2580	9	-1737 636	3493 328	1 00	1 00	0 589
	NW041[d]	Elevation (m) + Slope + Aspect + Distance to Trails (km)[c]	1744	7	-1185 033	2384 115	0 58	1 00	0 427
	NW042[d]	Elevation (m) + Slope + Aspect + Distance to Rivers (km)[c] + Distance to Lakes(km)[c]	1744	9	-1183 434	2384 952	0 38	1 52	0 520
	NW043	Elevation (m) + Slope + Aspect + Distance to Rivers (km)[c] + Distance to Lakes (km)[c]	2590	9	-1718 574	3455 205	1 00	1 00	0 858
	NW044	Elevation (m) + Slope + Aspect + Distance to Rivers (km)[c] + Distance to Lakes (km)[c]	2540	9	-1698 555	3415 167	1 00	1 00	0 807
	NW047	Depth + Hardness + Distance to High Prey(km) + Distance to Water (km)[c]	1456	6	-983 018	1978 076	0 97	1 00	0 842
	NW051	Elevation (m) + Slope + Aspect + Distance to Rivers (km)[c] + Distance to Lakes (km)[c]	2424	9	-1478 485	2975 031	1 00	1 00	0 928
	NW052	Elevation (m) + Slope + Aspect + Distance to Rivers (km)[e] + Distance to Lakes (km)[e]	2464	9	-1534 507	3087 073	1 00	1 00	0 915

Table 3.3. Continued.

Season	Animal ID	Model	n	K	LL	AIC_c	w_i[a]	E_r[a]	r_s[b]
Summer	GLOBAL	Elevation (m) + Slope + Aspect + Distance to Water (km)[e]	55230	7	-38167 387	76348 773	1 00	1 00	0 58
	NW040	Elevation (m) + Slope + Aspect + Distance to Water (km)[e]	7864	7	-5411 165	10885 120	1 00	1 00	0 778
	NW041	Elevation (m) + Slope + Aspect + Distance to Water (km)[e]	7276	7	-4961 131	9936 273	1 00	1 00	0 791
	NW042[c]	Elevation (m) + Distance to Water (km)[e] + Distance to Trails (km)[e]	8632	6	-5942 265	11896 5371	0 085	7 83	0 762
		Elevation (m) + Distance to Water (km)[e] + Distance to Linear Features (km)[e]	8632	6	-5942 315	11896 6367	0 081	8 24	0 771
		Elevation (m) + Linear Feature Density (km/km^2) + Distance to Water (km)[e] + Distance to Linear Feature (km)[e]	8632	7	-5941 020	11896 0498	0 11	6 14	0 807
		Linear Feature Density (km/km^2) + Distance to Water (km)[e] + Distance to Linear Feature (km)[e]	8632	6	-5942 700	11897 4072	0 055	12 11	0 815
		Elevation (m) + Slope + Aspect + Distance to Water (km)[e]	8632	7	-5939 205	11892 4199	0 669	1 00	0 758
	NW043[c]	Elevation (m) + Slope + Aspect + Distance to Water (km)[e]	3948	7	-2355 773	4769 512	0 95	1 00	0 914
		Elevation (m) + Linear Feature Density (km/km^2) + Distance to Water (km)[e] + Distance to Linear Feature (km)[e]	3948	7	-2359 527	4777 020	0 02	42 68	0 840
	NW044	Elevation (m) + Slope + Aspect + Distance to Water (km)[e]	8528	7	-5725 880	11515 110	1 00	1 00	0 781
	NW045	Elevation (m) + Slope + Aspect	8728	7	-5908 710	11880 940	1 00	1 00	0 883
	NW047	Elevation (m) + Slope + Aspect + Distance to Water (km)[e]	9348	7	-6394 070	12852 140	1 00	1 00	0 820
	NW049	Elevation (m) + Slope + Aspect + Distance to Water (km)[e]	906	7	-595 250	1238 162	1 00	1 00	0 654

[a] Burnham and Anderson (2002)
[b] Boyce et al. (2002)
[c] These models were averaged as in Burnham and Anderson (2002. 150, 162)
[d] These models were dropped due to poor performance
[e] Modeled as a quadratic with both a linear and a squared term

Table 3.4. Comparison of significant selection coefficients (β, $P \leq 0.05$) by season for 9 individual wolves and across all wolves (global) in the Nelchina Study Area, south-central Alaska. + indicates the number of wolves that significantly selected for a particular parameter; – refers to the number of wolves that significantly avoided that feature. For global models, significant β values are in bold.

Parameter	Early Winter			Late Winter			Summer		
	+	-	All	+	-	All	+	-	All
Elevation (m)		2		1		**-0.001**	3	1	**0.001**
Slope	2			4	1	**0.015**	1	7	**-0.015**
Eastness				1	2	**-0.073**	1	2	0.002
Northness	1				4	**-0.188**	2	6	-0.061
Depth (cm)			-0.001		1				
Hardness (r_i)			0.003	1					
Distance to Prey (km)			0.001	1					
Distance to Trails (km)		1						1	
Distance to Trails(km^2)	1						1		
Density (km/km^2)					1		1	1	
Distance to Linear Features (km)								1	
Distance to Linear Features (km^2)							1		
Distance to Rivers (km)		1			5	**-0.716**			
Distance to Rivers (km^2)	1			5		**0.189**			
Distance to Lakes (km)		2		3	2	**-0.180**			
Distance to Lakes (km^2)	1			2	3	0.017			
Distance to Water (km)		2	**-2.742**		1			7	**-0.219**
Distance to Water (km^2)	2		**2.023**	1			8		**0.087**
Distance to Low Activity Features (km)		1			1				
Distance to High Activity Features (km)	1			1					

83

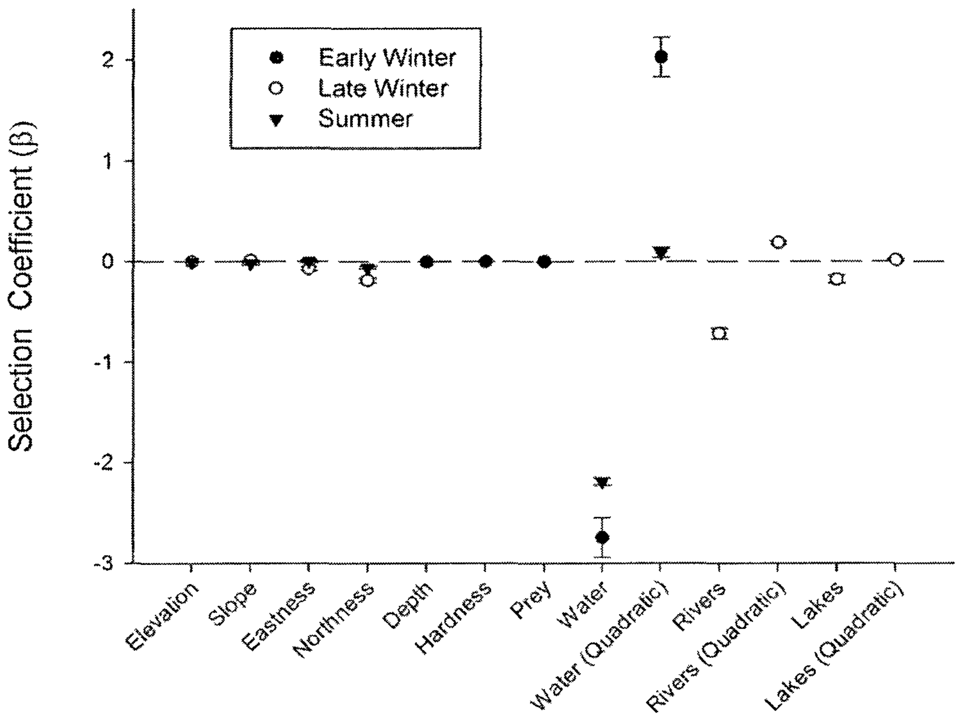


Figure 3.8. Comparison of all selection parameters identified in the global resource selection models for wolves by season in the Nelchina Study Area of south-central Alaska. Error bars represent 1 SE. The summer model did not meet the minimum k-fold cross-validation threshold and is provided anecdotally.

also included avoidance of areas with higher prey and deeper snow, and selection for snow hardness, but these attributes were not significant.

Factors affecting resource selection varied among individual wolves. Further, some wolves selected for factors that other wolves avoided. Hydrologic features were the most important parameter in early winter for 4 of the individual wolves with validated models (Appendix B: Table B.1). Some animals selected for areas close to water (n = 2; NW044, NW047). Others selected specifically for or against the distance to lakes and rivers (n = 2; NW042, NW049). As an example, NW049 avoided lakes, but simultaneously showed a strong selection for proximity to rivers.

The importance of topography and snow characteristics also varied among animals. Two of the wolves showed significant selection for lower elevations with some degree of slope being important (all $P < 0.01$). Snow depth, snow hardness, and distance to areas of high prey were important (although not significantly; all $P > 0.147$)in the cross-validated models describing resource selection by 3 animals.

Anthropogenic parameters were identified as important, but were not significant variables in any of the final models. Only wolf NW042 with access to trails selected against areas with high trail density (β= -0.287 ± 0.060, $P < 0.001$). Wolf NW049 selected for both low-activity features (β -0.011 ± 0.004, $P < 0.01$) and high-activity features (although not significantly) while simultaneously avoiding areas with a high density of linear features (β = -0.031 ± 0.020).

Late Winter

In late winter, wolves generally selected for lower elevations with some slope and southwest exposures (Table 3.4). Wolves also selected for close proximity to rivers and lakes ($P < 0.01$; Figure 3.8). Snow morphology and anthropogenic variables were not parameters in the late-winter global model.

There were 6 models for individual wolves that validated in the model set for late winter (Appendix B: Table B.2). Slope was important in selection models for 5 of 6 wolves. Aspect was also important for these animals, but was significant in only 3 of the models (slope $P < 0.05$, aspect $P < 0.01$). With the exception of wolf NW040, southwest exposures with some topography were selected. Elevation also was included in each of these models, but was either not significant or with a coefficient around zero. In general agreement with the global model, there was a strong selection for water. Five of the 6 wolves selected strongly for proximity to rivers (all $\beta > -3.434 \pm 0.202$, all $P < 0.01$), and the 6th individual, NW047, for which the home range encompassed the most water bodies, showed a strong selection for all water features ($\beta = -3.530 \pm 0.683$, $P < 0.01$). Given an overall selection by most individuals for water, there was an interesting contradiction in selection coefficients for lakes among individuals. Members of the Leg Hold pack (NW051, NW052) showed an affinity for lakes ($\beta > -0.525$, $P < 0.01$), which was reflected in their late-winter movements. All other individual wolves tended to avoid lakes (all $\beta > 0.556$, $P < 0.01$).

Although snow depths increased in late winter (64.1± 1.7 cm, mean ± SE), snow was included only in models describing resource selection for 2 wolves. Only wolf NW047 in the Tolsona Pack selected for areas with less snow depth and harder snow surfaces. Despite the fact that the Moore Lake Pack had the fewest linear features available within the annual home range (0.068 km/km^2) relative to all other packs, wolf NW040 selected areas with a higher density of linear features and for low-activity trails, while avoiding areas with relatively high prey density. Snow depth and snow hardness were also parameters in this individual's selection, but the coefficients did not differ from zero (all $P > 0.263$).

Summer

Slope, aspect, and distance to water were the most important parameters for 8 wolves in summer, as reflected by the global model (Table 3.4, Figure 3.8, Appendix B1: Table B.3). To a lesser degree, elevation was also important as summer was the only season where elevation was present in numerous individual models (3 selections for, 1 selection against). Wolves tended to select south-facing terrain (all $\beta > -0.067$, $P < 0.05$) with little or no slope (all $\beta > -0.005$, $P < 0.038$), although 2 wolves did select northern exposures (all $\beta > 0.119$, $P < 0.01$). The distance to water was equally important for all wolves as all 8 models identified a strong selection for both the linear (n = 7; all $\beta > -0.612$, $P < 0.01$) and quadratic terms (n = 8; all $\beta > 0.230$, $P < 0.05$).

Although human activity levels were not available for the summer, the presence of linear features was significant for 2 wolves (NW042, NW043). Wolf NW042 showed selection for areas with higher densities of features, for linear features, and more specifically, for trail-type features. Wolf NW043 also showed this selection for linear features, but not significantly and avoided areas with higher densities of linear features.

Discussion

As human development and activity encroach into the backcountry, understanding animal response is increasingly important. This is particularly true for wolves in the Nelchina Study Area where human exploitation created a high risk of mortality (Mysterud and Ims 1998; Frid and Dill 2002; Merrill and Hebblewhite 2008).

The presence of wolves is generally dependent on prey density and minimal human disturbance (Fritts et al. 2003; Ciucci and Boitani 2003). The establishment and distribution of packs in the Nelchina area are defined by the boundaries of neighboring packs and the level of human exploitation (Ballard et al. 1987; Thurber et al. 1994; Paquet and Callaghan 1996; Ciucci et al. 2003). As wolves negotiate their range, they must make trade-offs between selecting travel routes that minimize energetic expenditures and encounters with human activity while simultaneously maximizing encounters with prey (Alexander et al. 2005). In winter, the constraints of travel imposed by snow further compound these trade-offs.

Resource selection models are an important tool in understanding the resources that animals select and avoid across the landscape in human-wildlife interfaces. Previous resource selection studies have concluded that individual wolves respond to human activity more similarly within packs than between packs (Merrill and Hebblewhite 2008) and substantial differences in seasonal selection exist for habitat generalists such as wolves (Boyce et al. 2002; Manly et al. 2002). Although global seasonal models are commonly used to make population level inferences, models for individual wolves in the Nelchina Study Area exemplify variation in selection within and across seasons. I did not examine selection at the pack level because of discontinuity in pack sizes and membership.

Variation in selection was high among individual wolves in this study, but some general patterns of use did emerge. In winter, individual wolves avoided higher elevations and selected southwest exposures with little slope; the global models reinforced this. Similarly, other wolf studies have shown that wolves commonly travel in areas with $\leq 15^{\circ}$ slopes and southwest aspects in winter (Ballard 1987; Singleton 1995; Kunkel 1997;

Whittington et al. 2005). Although the deep snow found at higher elevations increases prey vulnerability, wolves tend to avoid deep snow because of energetic constraints and because steeper slopes actually decrease prey vulnerability (Paquet and Callaghan 1996). Moreover, moose and other large ungulates migrate to lower elevations and congregate in valley bottoms where snow is shallower and access to high-quality forage is greatest (Peek 1998; Alexander et al. 2004). In northern Italy, wolves responding to prey density avoided higher elevations, steeper slopes, and northeast aspects (Ciucci et al. 2003). Ballard (1987) observed that wolves followed the seasonal migration in elevation by moose and caribou within territories and concluded that wolves in the Nelchina area were more vulnerable to human harvest at higher elevations because of low vegetation and deeper snow.

Wolves also showed a strong affinity for frozen hydrologic features across both winter seasons in the NSA. Wolves commonly use windswept features and frozen waterways to facilitate winter travel (Mech 1970; Fritts and Mech 1981; Bergerud et al. 1984; Thurber et al.1994; Singleton 1995; Paquet and Callaghan 1996; James and Stuart-Smith 2000; Kunkel and Pletscher 2001; Creel et al. 2002; Ciucci et al. 2003). In addition, these riparian areas may serve as a surrogate parameter for moose habitat and occupation. Rivers were selected in both winter seasons, although to a higher degree in late winter. There was a change in the role that lakes played throughout the winter. In early winter, 2 of 4 wolves showed significant selection for lakes; in late winter, significant avoidance of lakes was demonstrated by these same individuals. The 2 wolves that did select for lakes in late winter were members of the Leg Hold pack in the control area, south of the predator management activities. Therefore, it is realistic to surmise that since the majority of wolves taken in same-day-airborne hunting are chased out on to lakes, wolves that have been harassed by humans (via snowmachine or aircraft) avoid these broad open areas by late winter.

Snow morphology did not appear to have a significant influence on the choices wolves made in the NSA, given other parameters in the models. This may have been a result of attempting to model snow parameters across a large area, although my techniques did identify the trends in snow morphology. Snow hardness and snow depth were significant for only one wolf in late winter. I believe that more snow data with less extrapolation potentially could have contributed to better model performance. Nonetheless, the annual mean density of snow (0.17 ± 0.017 g/cm^3) in the NSA rarely exceeded the minimum supportive thresholds of 0.21g/cm^3 described by Nasimovich (1955) and probably provided very little support. The average snow depth in the NSA was 57 cm during the years of this study. Overall selection by wolves for lower elevations identified in the late-winter global model, and individual early and late-winter models implies an avoidance of areas with high snowfall.

Four out of 5 wolf packs had access to all categories of linear features, with an average density of 0.31 km/km^2 during the course of this study (the St. Anne Lake pack moved north out of the control area). Although few anthropogenic parameters did surface in 2 individual models in winter, the global models did not identify any anthropogenic parameters as being significant. Wolf NW040 was the only individual that selected for both low-activity trails and avoided areas with higher densities of linear features at a significant level. This selection can be attributed to the location of its territory, which lacked the higher density features and human activity of more southern areas. This response to low-level and predictable activity has been repeatedly identified in previous studies (Thurber et al. 1994; James and Stuart-Smith 2000). In Banff National Park in Alberta, Canada, resource selection by wolves was independent of human activity in areas when little human activity existed (Merrill and Hebblewhite 2008).

Whittington et al. (2005) noted that the lack of hunting/trapping and very high snow depths encouraged the use of trails by wolves in Jasper National Park in Alberta, Canada, during winter. They also concluded that wolves responded more to the level of human activity on trails rather than to the density of linear features. Even though most of the activity in the Nelchina Study Area was of a low and predictable level (see Chapter 2), wolves did not select for linear features even in areas with higher densities. In fact, the lack of selection for, and the subtle avoidance of linear features, suggests that possible mortality risks associated with use of linear features may have outweighed the potential energetic-reducing benefits.

According to Alexander et al. (2005), the movement of wolves in winter is related to the maximum encounter rate with prey. The Nelchina Study Area has a low-density moose population that has been in decline since the mid-1990s (ADF&G, unpublished data). Testa (2004) identified low twinning rates (9-24%) and a delayed age of first reproduction (3.4 yr) in the Nelchina area as evidence of a moose population constrained by nutrition. In winter, moose in this area have been observed moving to habitats of lower browse production to access greater forage availability in shallower snow depths (Ballard et al. 1991). Although direct comparisons to the prey populations in similar studies are difficult (i.e., others often did not enumerate prey populations), most point out that movements of ungulates to valley bottoms are in response to deepening snow at higher elevations (Paquet and Callaghan 1996; Alexander et al. 2004; Whittington et al. 2005). The Nelchina Study with its moderate snow depths appears to have a more dispersed and less restricted moose population with fewer aggregations, as evidenced by our survey data in late winter.

The distance to areas of high prey was a significant parameter for only 1 individual wolf in late winter. There are numerous potential factors that may have influenced this apparent lack of response to prey. First, the change in moose abundance observed in early winter and late winter could be attributed to a lower detectability of moose in late winter (i.e., low-angle high-intensity light, and contrasted shadows); however, the effects of predation, low-quality forage, and winter mortality (previously estimated as high as 71% in the Nelchina Basin; Ballard and Gardner 1980) cannot be ruled out as factors affecting the numbers and distribution of moose. Model performance might have been improved if the prey surveys provided a more complete coverage across the study area. I believe the search intensity was adequate; however, the surveys were flown prior to acquiring the majority of wolf locations. Combined with weather constraints, the prey layer covered approximately 44% (80% of the core wolf use area) of the study area. This was further compounded by large extraterritorial movements by wolves. In addition to potentially being more cost-effective, a vegetation layer specifically identifying cover classes important to moose could have helped to compensate for areas not covered by the surveys and for any dynamic territories.

There are very few trails navigable by ATVs in the NSA during summer because of the wet, bog-like terrain. As a result, human activity exists at negligible levels and I assumed that wolf use of linear features might have increased during the summer months with the decreased likelihood of human encounters. Compared to other seasons, wolves did use trails more in summer than in the winter months (although not significantly). The distance to linear features, trails, and the density of linear features were significant factors for only 2 wolves from the Little Nelchina and Tolsona packs. Much of this selection can be explained by the fact that these two adjoining packs occupied the region with the highest density of linear features during periods of negligible human activity and may have taken advantage of that.

Both the individual and global models overwhelmingly identified southern exposures with little or no slope, and a close proximity to all water features as important parameters for wolves in summer. The shift to higher elevations and the affinity for riparian areas are likely in response to moose and the influx of seasonal caribou using these features. Moose move to higher elevations in the Nelchina area in May and June as snow melts and to even higher elevations after calving (Ballard et al. 1991). Caribou are second to moose in the diet of Nelchina wolves during summer (Ballard 1987) and can be captured and killed more easily by individual wolves and small packs than moose. Brown bears (*U. arctos*) are generally assumed to be the primary predators on moose and moose calves in the Nelchina Basin (Ballard 1987; Ballard 1987; Testa and Becker 2002); thus, because of the declining wolf densities in the NSA from 7.4 ± 1.10 wolves/1000 km^2 in 2002 to 3.9 wolves/1000 km^2 in 2006 (Golden 2005; ADF&G, unpublished data), wolves may take advantage of the more readily available caribou given the constraints of reduced pack size.

The absence of overt selection patterns by wolves on the landscape may have more to do with the dynamic recolonization of wolf populations than shortcomings in sampling design given my large GPS dataset and extensive feature layers. Small packs and recolonizing wolves exemplify typical opportunistic and generalist behaviors when wolves cannot establish specific hunting patterns or define reliable areas of concentrated prey to the degree that larger or long-established packs can.

There appears to be high variation among individuals of a social species such as wolves in exploited populations. New emerging techniques for modeling wildlife-human relationships in social species using mixed-effects resource selection models (Merrill and Hebblewhite 2008) show promise in addressing the issues of variation around the social structure of wolves and the functional response to human activity.

Management Implications

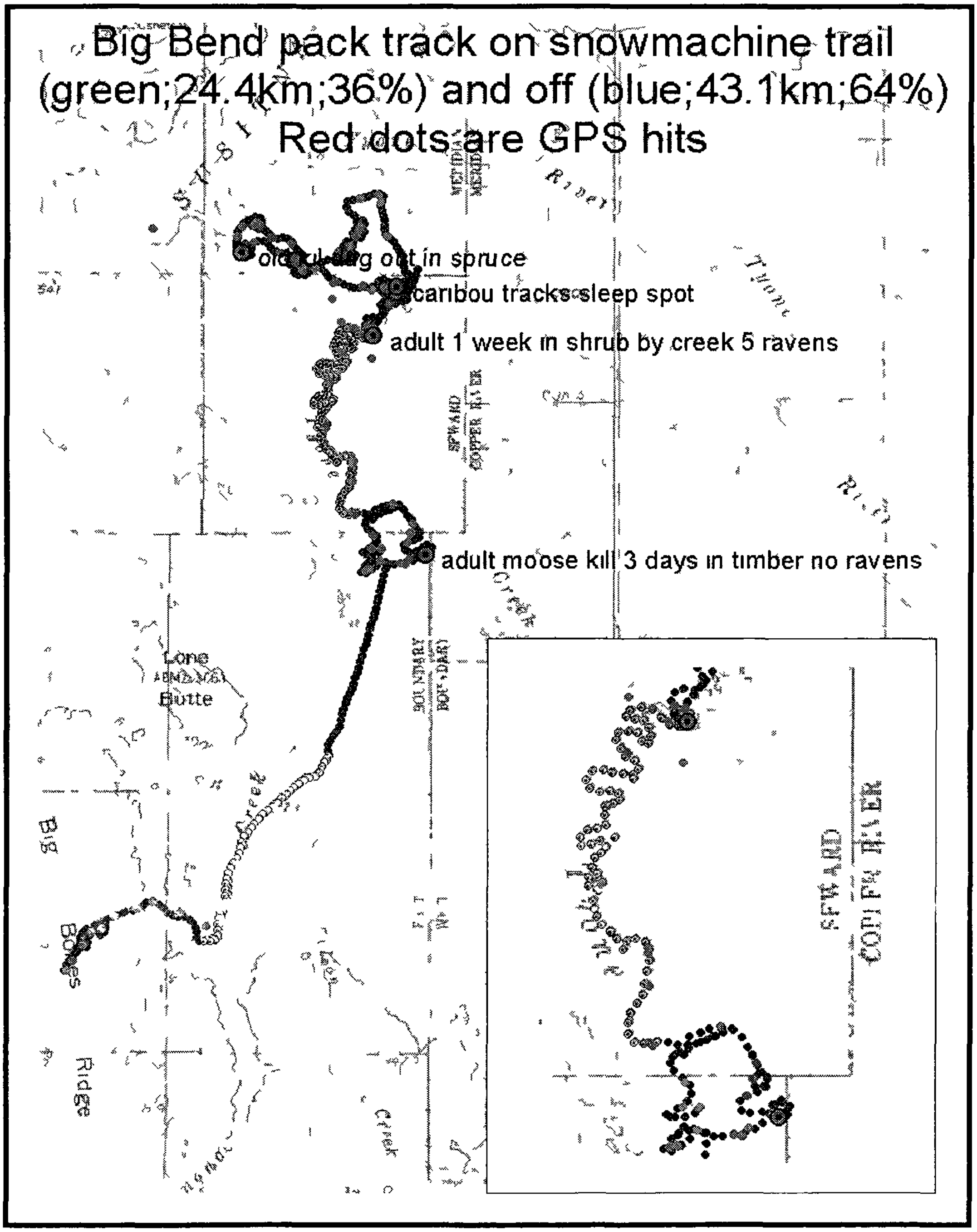
The effects of snow, the distribution of prey, and the availability of linear features may affect the selection of resources by wolves. If the level of human activity is low and predictable, the presence of trails and their use may minimize energetic expenditures and aid in hunting efficiency. However, for recolonizing wolves in a heavily exploited ecosystem where encounters with humans typically lead to harassment or death, the cost of utilizing linear features may outweigh any potential energetic benefits associated with winter travel and prey capture.

Chapter 4 : Wolves in an Exploited Ecosystem: Implications for Management

Introduction

Top carnivores such as wolves with broad habitat requirements need large home ranges to maximize the likelihood of encountering prey. Many have hypothesized that the presence of linear features could define the distribution of wolves, as well as dictate how they move across their ranges (Thurber et al. 1994; James and Stuart-Smith 2000; MacKenzie 2008). My study was built on this suggestive evidence and reinforced by preliminary empirical and anecdotal observations of wolves using anthropogenic linear features, and specifically snowmachine trails (Figure 4.1; ADF&G, unpublished data). I developed my hypotheses on the assumption that the presence of linear features could define the spatial arrangement of wolves across the landscape. If the human activity on that trail network was low and followed predictable patterns (see Thurber et al. 1994), anthropogenic trails could also facilitate expeditious travel, minimizing energetic expenditures while maximizing the likelihood of encountering prey. Further, the role of linear features should be more important during winter when the constraints on energetics are greatest. Although it has been suggested frequently that wolves do use trails, the existing empirical evidence has only defined potential associations and the potential costs of those relationships (i.e., proximity analyses, mortality, and displacement) (Mech et al. 1988; Thurber et al. 1994; Musiani et al. 1998; Merrill 2000; Whittington et al. 2005; Mackenzie 2008). I used GPS collars, programmed for short fix-intervals (15-min), to quantify the fine-scale movements of wolves and reveal the degree of actual trail use by wolves.

A)



Big Bend pack track on snowmachine trail (green;24.4km;36%) and off (blue;43.1km;64%)
Red dots are GPS hits
caribou tracks sleep spot
adult 1 week in shrub by creek 5 ravens
adult moose kill 3 days in timber no ravens
Lone Butte
Big Bones Ridge
SEWARD COPPER RIVER

B)

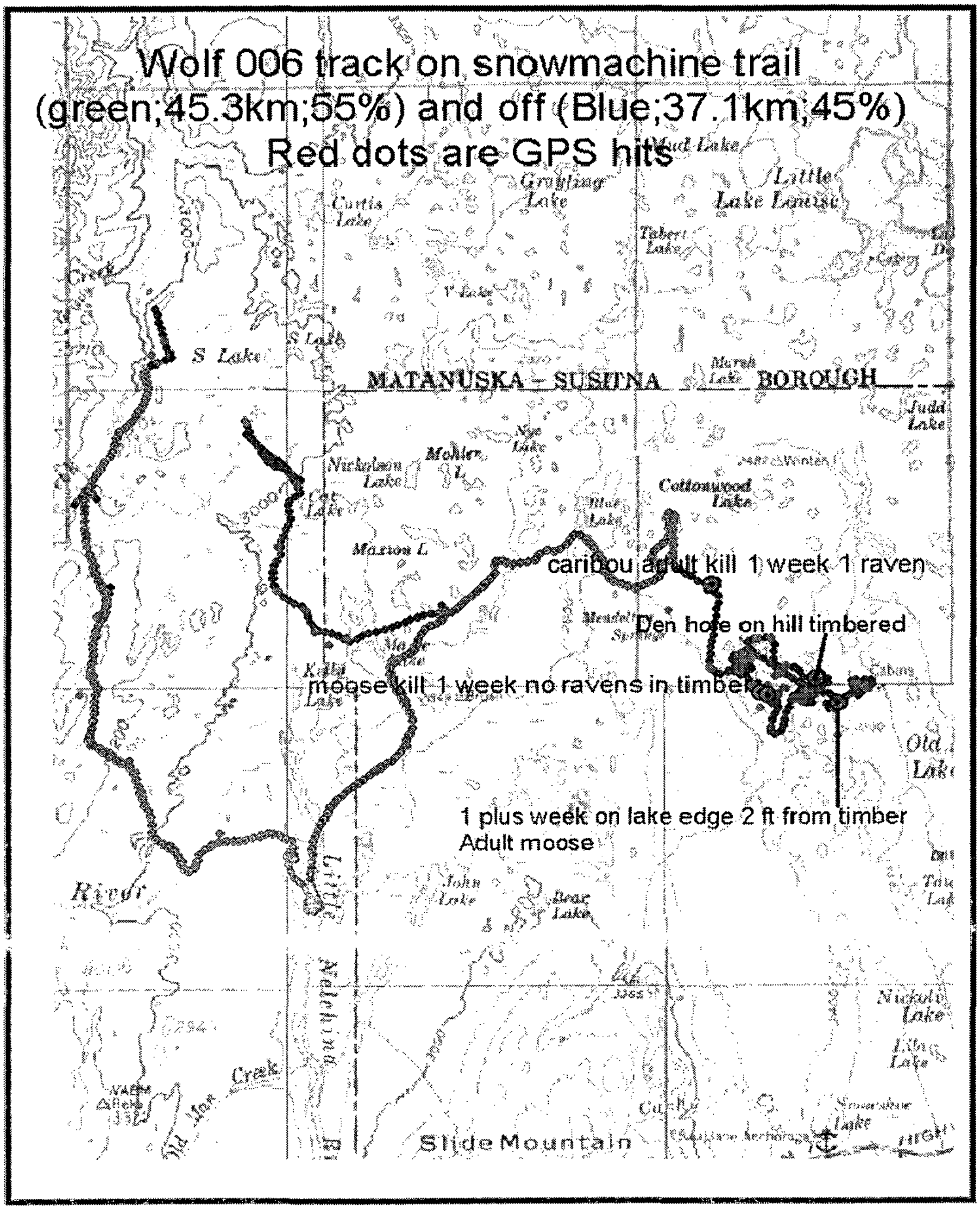


Figure 4.1. Preliminary observations of snowmachine trail use by wolves in the Nelchina Basin of south-central Alaska, March 2002. A) The Big Bend Pack travelled on trails for 24.4 km or 36% of the total locations over a 1-week period. B) Wolf 006 travelled for 45.5 km on trails or 55% of the total locations for 1-week. GPS fix intervals were 30 min.

The Nelchina Basin in south-central Alaska has a long history of research and intensive management (see Rausch 1969; Stephenson and Johnson 1973; Ballard et al. 1987; Ballard et al. 1991; Testa and Becker 2002; Testa 2004). Since 1994, portions of the Nelchina Study Area have been under a legislatively mandated intensive management strategy to actively reduce the number of predators and thereby increase populations of ungulates for human harvest. In 2003, ADF&G implemented a wolf-predation control program that extended beyond the liberal harvest of wolves to allow the taking of wolves via same-day-airborne methods. This action proved to be effective and resulted in a sudden increase in the annual harvest of wolves in the Nelchina Basin from 125 in 2002 to 224 in 2003 (ADF&G, unpublished data), disrupting pack dynamics and stability of the wolf population. Those hunting methods continued throughout the years of my study with a mean harvest of 129 wolves annually, reducing the population from 7.4 ± 1.10 wolves/1000 km^2 in 2002 to 3.9 wolves/1000 km^2 in 2006 (Golden 2005; ADF&G, unpublished data).

In this study, I determined the movements and ranges of 5 wolf packs in relation to the temporal and spatial distribution of prey, snow, linear features, and snowmachine-based human activity. I summarize findings in this chapter and present them in the context of overlying predator management activities.

Effects of Anthropogenic Disturbance on Movement and Home Ranges

The directed movement rate of wolves in the Nelchina Study Area averaged 2.7 ± 0.01 km/h, which is similar to other estimates (Mech 1970). Rates were highest in the summer (2.9 ± 0.02 km/hr) and lowest in late winter (1.98 ± 0.02 km/hr), coinciding with the greatest snow depths. The maximum distance travelled in 15 min was also greatest in summer (6.7 km), but lowest in early winter (4.5 km).

Use of linear features was defined by any location that fell within the area defined by actual trail width and the additional buffers of 15 m on each side of the trail to compensate for wolf GPS location error. Even though all wolves used linear features at some point, use of linear features was minimal (1.5% of all locations) and wolves did not select for linear features. This use was lowest in late winter (<1%) when I expected use to be highest. The proportion of use more than doubled to 3.5% when wolves exhibited directed travel, suggesting that when wolves are moving longer distances, they could benefit from travel on linear features as reflected in the differences in movement rates (4.2 ± 0.05 km/h on trail vs. 2.7 ± 0.01 km/h off trail). The trade-offs of trail use warrant further investigation because as trail use increases by wolves, the likelihood of encountering humans also increases, which may result in negative interactions or death. Although the levels of human activity were nominal and followed predictable patterns by day, week, and season, the wolves appeared to respond even to this pressure by using trails when activity was least (i.e., nighttime, weekdays, early winter, and summer). Five of the 9 mortalities of collared wolves during the study resulted from trapping on or in immediate proximity to trails, and 5 of the 9 wolf mortalities also occurred in late winter when human activity was greatest. The use of linear features by wolves might be greater in other areas where the potential for human encounters is lower and does not lead to indirect or direct mortality.

Annual home ranges of wolves in the Nelchina Study Area ranged between 1434 and 13,799 km^2 and there was considerable overlap. Ranges were largest in summer and most restricted in late winter, coinciding with the rates of movements. These estimates are larger than what others have reported at similar latitudes (Stephenson and James 1982; Peterson et al. 1984; Hayes 1995; Mech et al. 1998), but those investigations were not conducted in areas with active wolf control programs. After the initial federal wolf control program in the Nelchina Basin prior to statehood, Burkholder (1959) reported a pack occupying an area of 6272 km^2. One possible reason for this reported variability in home-range size could be attributed to poor habitat quantity and quality, characteristic of low moose densities (Ballard et al. 1987; Ballard et al. 1997). The influx of seasonal prey such as caribou during the summer when wolf movements are greatest may further increase variability; however, given the degree of overlap, the large home ranges and fluid boundaries are more likely a result of wolves recolonizing and adjusting to unoccupied or poorly defended territories (Ballard 1987). In other exploited systems, wolves have taken advantage of open areas and also established territories many times larger than what would be needed to support their small pack sizes (Peterson et al. 1984; Hayes et al.1991).

Following removal of the alpha male in the St. Anne Lake pack, which appeared to disrupt pack dynamics temporarily, some of the remaining pack members travelled 660 km round trip over 2 months in late summer and early winter. The application of 95% MCPs to calculate home range sizes did not accommodate this extra-territorial movement well and as a result, inflated the annual, summer, and early winter MCPs. With the St. Anne Lake pack removed from the pool of annual home ranges, the average annual home range for the 4 remaining packs in the NSA was 1958 km^2, which is more comparable to Ballard's (1987) estimate of 2308 km^2 for packs in the same areas. The fine scale of 15-min GPS locations appears to identify the true use areas of wolves, which the 95% MCP masked in the calculation for the St. Anne Lake pack and possibly others, (i.e., Moore Lake and Tolsona). For this reason, MCPs may not be the most appropriate tool to describe the ranges of wolves in exploited populations or for data sets with fine-scale movement data. I encourage exploring the application of other techniques that avoid inflated estimates to define the home ranges of wolves such as parametric and nonparametric kernel-density estimators (Getz and Wilmers 2004; Getz et al. 2007).

Many wolf packs in the predator control area (north of the Glenn Highway) were eliminated or reduced to single individuals between 2002 and 2006, opening large areas to recolonization. Ballard (1987) observed that the distribution of wolf packs in the Nelchina Basin was similar before and after wolf reduction. In my study, individual wolves originally observed south of the Glenn Highway recolonized historic territories identified in previous studies north of the Highway (Ballard et al. 1987; ADF&G, unpublished data). These packs, the Little Nelchina and the Tolsona, occupied home ranges with the highest density of linear features and levels of human activity, and were separated and bounded by roads, providing some evidence that linear features influenced their distribution. There was some, albeit minimal, movement across the Glenn Highway by the Little Nelchina, Tolsona, and St. Anne Lake packs early in the study which appeared to be related to recolonization. The St. Anne Lake pack also appeared wary of crossing the Alaska Pipeline corridor, as evidenced by the large number of GPS locations along the west side of the corridor (See Figure 2.3). The resource selection models incorporating density of linear features, distance to trails, and indices of human activity did not identify significant relationships with linear features or a response to the varying levels of human activity. However, it is probable that, because of the exploitation associated with trails, linear disturbance was exerting some influence on the movements of wolves.

Prey Distribution

The Nelchina moose population is considered to be a low-density population with larger home ranges than those reported elsewhere in North America (Ballard 1987). After showing steady growth over the previous 20-30 years, the moose population in the Nelchina Basin began to show a decline from 594 moose/1000 km^2 in 1990 to 384 moose/1000 km^2 in 2000 (ADF&G, unpublished data). Because I did not have access to a surrogate for prey distribution such as a classified vegetation map, I chose to quantify the relative distribution and abundance of moose in early and in late winter by conducting aerial surveys using a grid-based approach. These prey surveys identified few aggregations of moose in early winter and fewer in late winter. Although it is conceivable that the detectability of moose from an airplane was more difficult in late spring due to the incidence of light, the apparent random and broad dispersion of moose seemed more likely to be an indication of the low numbers of moose and poor habitat quality. The efficacy of survey results versus the application of vegetation classification to identify moose occurrence is questionable. One can assume that moose observed on the landscape were generally found in preferred habitats, whereas the reliance on a vegetation layer is dependent on localized knowledge of moose foraging behavior. Analyses of plant communities in the Nelchina Study Area have revealed high levels of tannins in readily available willow species (*Salix spp.*), such as felt leaf willow (*Salix alaxensis*), limiting protein availability (Collins 2002). In most other areas in Alaska, it is accepted that these willows are preferred by moose. To maximize digestible protein, however, moose in the Nelchina Study Area have been observed digging down through many feet of snow to access dwarf birch species *(Betula spp.)*. If vegetation classifications can differentiate different shrub types, and knowledge of localized foraging behavior exists, then the use of such a layer could be more effective in identifying the potential distribution of prey.

Topography, Hydrology, and Snow

Elevation, slope, aspect, and distance to water features were important to wolves in all seasons. Similar to other studies in winter, wolves preferred lower elevations with southwest exposure and little slope (Ballard 1987; Singleton 1995; Kunkel 1997; Whittington et al. 2005). Wolves also showed selection for frozen hydrologic features, which when combined with the topographic variables, suggests that these relationships are an indication of moose habitat and occupation. In late winter, however, wolves in the predator control area avoided lakes. Because of the landing access provided by lakes, many of the wolves taken by same-day-airborne hunting were pushed out on to lakes, giving the hunters an opportunity to take unobstructed, longer distance shots. It seems likely that if these wolves were harassed by hunters or same-day-airborne teams on or near lakes, they would avoid lakes in winter. In summer, wolves shifted to higher elevations and disproportionately used southern exposures with little or no slope, coinciding with the elevational shift in habitat use by moose and the influx of seasonal caribou. It seems plausible that caribou would become more important in the summer diet of wolves as pack sizes decline due to predator reduction efforts that could limit the wolves' ability to successfully capture and kill moose.

Snow parameters are difficult to extrapolate across a large area and require a frequent sampling routine. Despite sampling up to 29 numerous sites every 2 weeks, sampling did not prove adequate to create high-resolution raster layers. This appears to be a major gap in both the snow sciences and wildlife literature and warrants much attention (R. McClure, Natural Resources Conservation Services (NRCS), personal communication). From my measurements, I observed an increase in snow depth, density, and hardness with the progression of winter. The annual mean snowpack during study years was 57 cm and contained very little water (0.17 ± 0.017 g/cm^3). Although the snow provided little support for wolves, this depth is negotiable for wolves with chest heights of 50-60 cm. Snow hardness values (R_i) were 23.6 times greater on snowmachine trails than in adjacent areas, emphasizing the supportive structure of these anthropogenic compacted features.

Summary

The active wolf-control program initiated coincidentally at the onset of this research undoubtedly influenced the wolf population in the Nelchina Study Area. It is uncertain how it affected patterns of use and the selections that wolves made on the landscape. Predator management was effective at rapidly reducing the wolf population, but wolves recolonized areas quickly. This instability in the population combined with the low density of moose is most evident in non-detectable relationships with moose in selection models, large territories with dynamic boundaries, and extensive extraterritorial movements. As a result, the movements of wolves observed in this study may not be representative of other wolf populations in North America. My observation of little trail use by wolves highlights both the advantages of expeditious travel on linear features, as well as the increased risks of mortality from that use.

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Appendix A: Distribution of snow survey sites in the Nelchina Study Area of south-central Alaska, 2004-2006

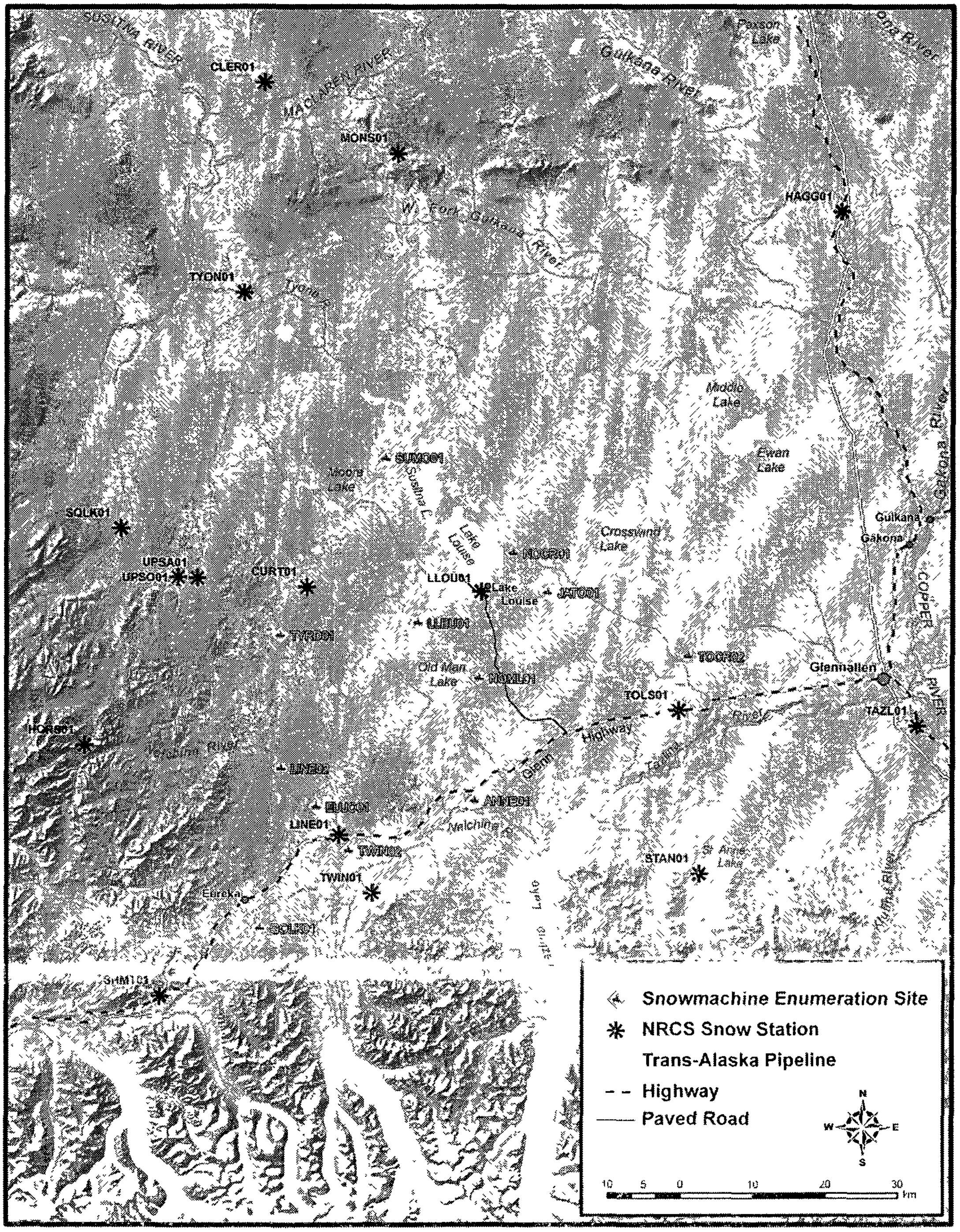

Figure A.1. Distribution of snow survey sites (12 snowmachine enumeration sites and 16 Natural Resources Conservation Service (NRCS) snow stations) in the Nelchina Study Area, south-central Alaska, 2004-2006.

Table A.1. Early winter snow characteristics (depth, snow water equivalent (SWE), density, and hardness defined by an integrated ram hardness number R_i on and off trails) as measured at 14 Natural Resources Conservation Service (NRCS) snow stations across the Nelchina Study Area, south-central Alaska, 2004-2005.

Year	Season	SITE ID	Elevation (m)	Date (mo/day/yr)	Depth (cm)	SWE (cm)	Density (g/cm^3)	R_i Off	R_i On
2004	**Early Winter**	CURT01	869	12/1/2004	53.34	9.1	0.17		
		HORS01	1311	12/1/2004	73.66	12.4	0.17		
		LINE01	808	12/1/2004	45.72	7.9	0.17	56.3	
		LLOU01	732	12/1/2004	35.56	7.6	0.21	249.0	
		TAZL01	373	12/1/2004	45.20	2.3	0.05		
		TOLS01	610	12/1/2004	27.94	4.6	0.16	22.9	
2005		CURT01	869	1/1/2005	68.58	12.7	0.19		
		HORS01	1311	1/1/2005	99.06	17.8	0.18		
		LINE01	808	1/1/2005	71.12	12.2	0.17	56.3	
		LLOU01	732	1/1/2005	60.96	11.2	0.18	22.0	
		MONS01	945	1/1/2005	78.74	15.2	0.19		
		SHMT01	884	1/1/2005	78.80	14.7	0.19		
		SQLK01	899	1/1/2005	55.88	9.9	0.18		
		STAN01	607	1/1/2005	61.00	10.7	0.18		
		TAZL01	373	1/1/2005	40.64	8.1	0.20		
		TOLS01	610	1/1/2005	53.34	8.1	0.15	16.4	
		TYON01	747	1/1/2005	50.80	8.6	0.17		
		UPOS01	960	1/1/2005	63.50	11.4	0.18		
		UPSA01	945	1/1/2005	76.20	14.0	0.18		
		CURT01	869	2/1/2005	60.96	11.7	0.19	202.8	
		HORS01	1311	2/1/2005	81.28	23.9	0.29		
		LINE01	808	2/1/2005	58.42	13.5	0.23	27.4	

Table A.1. Continued

Year	Season	SITE ID	Elevation (m)	Date (mo/day/yr)	Depth (cm)	SWE (g/cm^3)	Density (g/cm^3)	R_i Off	Ri On
2005	**Early Winter**	LLOU01	732	2/1/2005	66.04	14.0	0.21	36.4	
		SQLK01	899	2/1/2005	58.42	12.7	0.22		
		STAN01	607	2/1/2005	55.90	11.4	0.20	16.0	
		TAZL01	373	2/1/2005	38.10	8.1	0.21		
		TOLS01	610	2/1/2005	50.80	10.7	0.21	22.1	
		TWIN01	738	2/1/2005	71.12	13.5	0.19		

Table A.2. Late winter snow characteristics (depth, snow water equivalent (SWE), density, and hardness defined by an integrated ram hardness number R_i on and off trails) as measured at 16 Natural Resources Conservation Service (NRCS) snow stations and 13 snowmachine enumeration sites across the Nelchina Study Area, south-central Alaska, 2005.

Year	Season	SITE ID	Elevation (m)	Date (mo/day/yr)	Depth (cm)	SWE (cm)	Density (g/cm^3)	R_i Off	R_i On
2005	**Late Winter**	ANNE01	688	3/1/2005	73.30			111.4	
		CLER01	807	3/1/2005	78.74	17.0	0.22		
		CURT01	869	3/1/2005	66.04	13.0	0.20	87.3	
		GOLK01	957	3/1/2005	87.00			139.0	
		HORS01	1311	3/1/2005	109.22	26.7	0.24		
		JATO01	716	3/1/2005	64.50			48.6	
		LINE01	808	3/1/2005	71.12	15.2	0.21	70.4	
		LLEU01	747	3/1/2005	56.30	0.0		29.4	
		LLOU01	732	3/1/2005	73.66	14.5	0.20	96.3	
		MONS01	945	3/1/2005	93.98	21.8	0.23		
		SHMT01	884	3/1/2005	78.74	17.0	0.22		
		SQLK01	899	3/1/2005	66.04	14.7	0.22		
		STAN01	607	3/1/2005	83.80	17.0	0.20	94.8	
		TAZL01	373	3/1/2005	53.34	11.4	0.21		
		TOLS01	610	3/1/2005	71.12	13.7	0.19	45.3	
		TWIN01	738	3/1/2005	81.28	15.7	0.19		
		TWIN02	763	3/1/2005	69.00			53.9	
		TYON01	747	3/1/2005	66.04	13.2	0.20		
		UPOS01	960	3/1/2005	137.16	33.0	0.24		
		UPSA01	945	3/1/2005	81.28	17.0	0.21		
		ANNE01	688	3/15/2005	57.60			93.9	
		EUJO01	897	3/15/2005	60.00			67.0	2496.0
		EUJO01	897	3/15/2005	73.50				

Table A.2. Continued

Year	Season	SITE ID	Elevation (m)	Date (mo/day/yr)	Depth (cm)	SWE (cm)	Density (g/cm^3)	R_i Off	R_i On
2005	**Late Winter**	GOLK01	957	3/15/2005	91.00			123.7	
		JATO01	716	3/15/2005	71.50			149.2	
		LLEU01	747	3/15/2005	60.00			41.9	
		NOCR01	760	3/15/2005	65.00				
		NOML01	769	3/15/2005	67.60				
		SUMO01	777	3/15/2005	58.00				
		TOCR01	826	3/15/2005	68.30			68.0	
		TWIN02	763	3/15/2005	67.00			72.2	
		TYRD01	964	3/15/2005	76.50				
		CLER01	807	4/1/2005	81.28	18.3	0.23		
		CURT01	869	4/1/2005	68.58	14.7	0.21		
		HAGG01	762	4/1/2005	71.12	15.5	0.22		
		HORS01	1311	4/1/2005	121.92	30.0	0.25		
		LINE01	808	4/1/2005	73.66	16.0	0.22	61.4	
		LLOU01	732	4/1/2005	71.12	15.2	0.21	69.0	
		MONS01	945	4/1/2005	78.74	21.8	0.28		
		SHMT01	884	4/1/2005	83.82	20.3	0.24		
		SQLK01	899	4/1/2005	71.12	16.0	0.22		
		STAN01	607	4/1/2005	78.74	16.5	0.21	84.9	
		TAZL01	373	4/1/2005	35.56	9.7	0.27		
		TOLS01	610	4/1/2005	66.04	13.2	0.20	60.3	
		TWIN01	738	4/1/2005	86.36	16.8	0.19		
		TYON01	747	4/1/2005	60.96	13.9	0.23		
		UPOS01	960	4/1/2005	81.28	17.8	0.22		
		UPSA01	945	4/1/2005	81.28	18.3	0.23		

Table A.3. Early winter snow characteristics (depth, snow water equivalent (SWE), density, and hardness defined by an integrated ram hardness number R_i on and off trails) as measured at 16 Natural Resources Conservation Service (NRCS) snow stations and 12 snowmachine enumeration sites across the Nelchina Study Area, south-central Alaska, 2005-2006.

Year	Season	SITE ID	Elevation (m)	Date (mo/day/yr)	Depth (cm)	SWE (cm)	Density (g/cm^3)	R_i Off	R_i On
2005	**Early Winter**	LINE01	808	12/1/2005	37.00	2.5	0.07		
		SHMT01	884	12/1/2005	34.20	2.5	0.07		
		TAZL01	373	12/1/2005	35.50	2.5	0.07		
		TOLS01	610	12/1/2005	31.50	2.5	0.08		
		GOLK01	957	12/15/2005	48.00				
		TOCR02	826	12/15/2005	29.20	1.3	0.04		
2006		CLER01	807	1/1/2006	43.18	8.3	0.19		
		CURT01	869	1/1/2006	38.10	6.1	0.16		
		GOLK01	957	1/1/2006	63.00	0.0		41.3	
		HAGG01	762	1/1/2006	53.34	9.3	0.17		
		LINE01	808	1/1/2006	40.60	6.9	0.17		
		LLOU01	732	1/1/2006	35.50	3.8	0.11		
		NOCR01	760	1/1/2006	33.00				
		SHMT01	884	1/1/2006	33.00	5.8	0.18		
		SQLK01	899	1/1/2006	38.10	5.6	0.15		
		STAN01	607	1/1/2006	43.20	8.4	0.19		
		SUMO01	777	1/1/2006	31.80	3.3	0.10		
		TAZL01	373	1/1/2006	25.40	6.6	0.26		
		TOCR02	826	1/1/2006	29.50	5.8	0.20	23.3	
		TOLS01	610	1/1/2006	30.50	4.1	0.13		
		TWIN01	738	1/1/2006	43.20	8.6	0.20		
		TYON01	747	1/1/2006	39.50	7.0	0.18		
		UPOS01	960	1/1/2006	38.10	5.8	0.15		

Table A.3. Continued

Year	Season	SITE ID	Elevation (m)	Date (mo/day/yr)	Depth (cm)	SWE (cm)	Density (g/cm^3)	R_i Off	R_i On
2006	**Early Winter**	UPSA01	945	1/1/2006	53.34	8.4	0.16		
		EUJO01	897	1/15/2006	48.30	5.8	0.12	25.3	
		GOLK01	957	1/15/2006	66.00	11.7	0.18	41.3	
		JATO01	716	1/15/2006	38.60	4.1	0.11	24.8	
		LINE02	826	1/15/2006	38.60	5.1	0.13	28.1	
		NOCR01	760	1/15/2006	36.30	3.3	0.09	24.7	
		NOML01	769	1/15/2006	34.30	6.4	0.19		
		SUMO01	777	1/15/2006	35.00				
		TOCR02	826	1/15/2006	29.50	2.5	0.08	30.8	
		TWIN02	763	1/15/2006	42.70	5.1	0.16	19.0	
		TYRD01	964	1/15/2006	46.50	5.8	0.14	26.7	
		CLER01	807	2/1/2006	43.20	7.6	0.18		
		CURT01	869	2/1/2006	40.60	6.4	0.17	202.8	
		EUJO01	897	2/1/2006	52.10	7.1	0.14	70.8	
		GOLK01	957	2/1/2006	75.90	14.0	0.18	130.1	
		HORS01	1311	2/1/2006	91.50	15.7	0.17		
		JATO01	716	2/1/2006	38.10	5.1	0.13	39.4	
		LINE01	808	2/1/2006	48.30	7.1	0.15	47.9	
		LINE02	826	2/1/2006	47.80	7.1	0.15	36.9	
		LLEU01	747	2/1/2006	41.10	5.1	0.12		
		LLOU01	732	2/1/2006	33.00	5.6	0.17	36.4	
		MONS01	945	2/1/2006	40.60	6.9	0.17		
		NOCR01	760	2/1/2006	38.10	6.1	0.16	42.6	
		NOML01	769	2/1/2006	41.70	6.4	0.15		

Table A.3. Continued

Year	Season	SITE ID	Elevation (m)	Date (mo/day/yr)	Depth (cm)	SWE (cm)	Density (g/cm^3)	R_i Off	R_i On
2006	**Early Winter**	SHMT01	884	2/1/2006	38.10	5.6	0.15		
		SQLK01	899	2/1/2006	40.60	6.1	0.15		
		STAN01	607	2/1/2006	53.30	9.1	0.17	16.0	
		SUMO01	777	2/1/2006	38.10	5.1	0.13	50.1	
		TAZL01	373	2/1/2006	32.00	7.1	0.22		
		TOCR02	826	2/1/2006	37.30	4.6	0.12	47.7	
		TOLS01	610	2/1/2006	38.10	5.1	0.13	21.5	
		TWIN01	738	2/1/2006	48.30	9.1	0.19		
		TWIN02	763	2/1/2006	39.62	6.4	0.16	44.7	
		TYRD01	964	2/1/2006	46.70	5.4	0.12	38.7	
		UPSA01	945	2/1/2006	58.40	9.9	0.17		
		EUJO01	897	2/15/2006	60.20	11.7	0.19	60.6	
		GOLK01	957	2/15/2006	106.70	19.3	0.18	25.6	
		JATO01	716	2/15/2006	41.90	5.8	0.14	26.4	
		LINE02	826	2/15/2006	61.00	8.4	0.14	53.7	
		LLEU01	747	2/15/2006	47.20	7.6	0.16	37.7	
		NOCR01	760	2/15/2006	47.20	8.4	0.18	27.8	
		SUMO01	777	2/15/2006	46.50	8.4	0.18	22.9	
		TOCR02	826	2/15/2006	39.60	5.1	0.13	15.6	
		TWIN02	763	2/15/2006	66.04	9.1	0.14	48.9	
		TYRD01	964	2/15/2006	53.30	7.6	0.14		

Table A.4. Late winter snow characteristics (depth, snow water equivalent (SWE), density, and hardness defined by an integrated ram hardness number R_i on and off trails) as measured at 16 Natural Resources Conservation Service (NRCS) snow stations and 11 snowmachine enumeration sites across the Nelchina Study Area, south-central Alaska, 2006.

Year	Season	SITE ID	Elevation (m)	Date (mo/day/yr)	Depth (cm)	SWE (cm)	Density (g/cm^3)	R_i Off	R_i On
2006	**Late Winter**	CLER01	807	3/1/2006	55.90	9.1	0.16		
		CURT01	869	3/1/2006	48.30	8.6	0.18	54.9	
		EUJO01	897	3/1/2006	58.90	10.2	0.17	22.1	1446.0
		GOLK01	957	3/1/2006	95.30	20.3	0.21	146.5	2170.0
		HAGG01	0	3/1/2006	58.40	11.4	0.20		
		HORS01	1311	3/1/2006	76.20	19.1	0.25		
		JATO01	716	3/1/2006	48.30	6.6	0.14	29.4	2015.5
		LINE01	808	3/1/2006	61.00	10.2	0.17	53.9	
		LINE02	826	3/1/2006	57.20	10.2	0.18	33.6	1502.5
		LLEU01	747	3/1/2006	46.20	6.6	0.14	29.8	1072.5
		LLOU01	732	3/1/2006	45.70	7.4	0.16	96.3	
		MONS01	945	3/1/2006	58.40	10.4	0.18		
		NOCR01	760	3/1/2006	46.00	6.6	0.14	25.2	864.0
		SHMT01	884	3/1/2006	61.00	10.2	0.17		
		SQLK01	899	3/1/2006	45.70	7.9	0.17		
		STAN01	607	3/1/2006	61.00	12.4	0.20	60.6	
		SUMO01	777	3/1/2006	43.40	5.8	0.13	31.4	549.5
		TAZL01	373	3/1/2006	35.60	8.9	0.25		
		TOCR02	826	3/1/2006	39.40	5.1	0.13	33.1	1438.0
		TOLS01	610	3/1/2006	43.20	5.1	0.12	60.5	
		TWIN01	738	3/1/2006	50.10	13.7	0.27		

Table A.4. Continued

Year	Season	SITE ID	Elevation (m)	Date (mo/day/yr)	Depth (cm)	SWE (cm)	Density (g/cm^3)	R_i Off	R_i On
2006	**Late Winter**	TWIN02	763	3/1/2006	58.90	9.1	0.15	51.6	868.5
		TYON01	747	3/1/2006	50.80	8.1	0.16		
		UPSA01	945	3/1/2006	68.60	12.2	0.18		
		EUJO01	897	3/15/2006	57.20	8.4	0.15	67.0	2496.0
		GOLK01	957	3/15/2006	92.70	21.8	0.24	165.5	2459.0
		JATO01	716	3/15/2006	40.60	6.6	0.16	23.8	949.0
		LINE02	826	3/15/2006	53.80	8.4	0.16	29.3	1397.5
		LLEU01	747	3/15/2006	46.20	7.6	0.16	21.1	1247.5
		NOCR01	760	3/15/2006	44.50	6.6	0.15	24.3	1992.0
		SUMO01	777	3/15/2006	41.40	5.8	0.14	48.6	1334.5
		TOCR02	826	3/15/2006	42.20	7.1	0.17	26.5	1332.5
		TWIN02	763	3/15/2006	58.42	7.9	0.14		
		CURT01	869	4/1/2006	50.80	10.2	0.20	26.0	
		EUJO01	897	4/1/2006	58.90	12.2	0.21	44.3	1312.0
		GOLK01	957	4/1/2006	94.00	15.7	0.17	204.4	1502.5
		HORS01	1311	4/1/2006	99.00	20.3	0.21		
		JATO01	716	4/1/2006	53.80	30.7	0.57	35.0	1669.0
		LINE01	808	4/1/2006	61.00	12.7	0.21	44.2	
		LINE02	826	4/1/2006	57.20	13.5	0.24	31.9	1267.5
		LLEU01	747	4/1/2006	46.00	9.1	0.20		
		LLOU01	732	4/1/2006	50.80	9.1	0.18	69.0	
		NOCR01	760	4/1/2006	52.10	9.1	0.17	73.4	1583.5
		SHMT01	884	4/1/2006	58.40	11.2	0.19		
		SQLK01	899	4/1/2006	48.30	9.4	0.19		

Table A.4. Continued

Year	Season	SITE ID	Elevation (m)	Date (mo/day/yr)	Depth (cm)	SWE (cm)	Density (g/cm^3)	R_i Off	R_i On
2006	**Late Winter**	STAN01	607	4/1/2006	68 60	13 7	0 20	65 4	
		SUMO01	777	4/1/2006	54 00	9 1	0 17	86 0	1590 0
		TAZL01	373	4/1/2006	35 60	9 4	0 26		
		TOCR02	826	4/1/2006	45 70	5 6	0 12	33 7	1541 0
		TOLS01	610	4/1/2006	48 30	8 9	0 18	33 6	
		TWIN01	738	4/1/2006	61 00	89 4	1 47		
		TWIN02	763	4/1/2006	58 42	5 7	0 10	65 3	769 5
		UPOS01	960	4/1/2006	48 30	9 1	0 19		
		UPSA01	945	4/1/2006	71 12	14 0	0 20		
		EUJO01	897	4/11/2006	59 70	12 3	0 21	63 7	147 5
		GOLK01	957	4/11/2006	87 90	19 6	0 22	138 5	2429 5
		JATO01	716	4/11/2006	49 80	9 1	0 18	42 6	1019 0
		LINE02	826	4/11/2006	58 90	10 9	0 19	31 9	1267 5
		LLEU01	747	4/11/2006	50 10	8 4	0 17	51 8	1161 0
		NOCR01	760	4/11/2006	52 10	9 7	0 19	37 7	610 5
		SUMO01	777	4/11/2006	52 30	9 7	0 19	40 4	1221 5
		TOCR02	826	4/11/2006	42 20	7 2	0 17	71 5	1337 0
		TWIN02	763	4/11/2006	63 50	13 0	0 20	53 3	1096 0

Appendix B: Selection coefficients (β) and standard errors (SE) of attributes in final individual and global (pooled) models that describe resource selection by wolves in the Nelchina Study Area, 2005-2006

Table B.1. Resource selection coefficients (± SE) representing seasonal selection patterns for all wolves (global) and by individual wolf in the Nelchina Study Area of south-central Alaska in early winter (15 November – 14 February). Values in bold indicate significant selection (positive values) or avoidance (negative values) at $P \leq 0.05$. Blanks indicate those parameters that were not included in final models rankings or could not be tested because of an absence of data. All models validated by k-fold cross validation.

EARLY WINTER[a]	**GLOBAL**	**NW042[b]**	**NW044**	**NW047**	**NW049**
Elevation		**-0.001 (0.000)**			**-0.001 (0.000)**
Slope		**0.048 (0.005)**			**0.007 (0.002)**
Eastness		-0.06 (0.032)			-0.004 (0.020)
Northness		0.033 (0.033)			**0.061 (0.022)**
Depth	-0.001 (0.001)		-0.001 (0.003)	-0.003 (0.003)	0.000 (0.000)
Hardness	0.003 (0.007)	0.033 (0.033)	0 .000 (0.001)	0.000 (0.004)	0.000 (0.000)
Early Prey$_c$	0.001 (0.001)		-0.033 (0.020)	0.022 (0.020)	0.000 (0.001)
Linear Density					-0.031 (0.020)
Rivers$_c$		-0.099 (0.060)			**-1.288 (0.090)**
Rivers^2_c		0.043 (0.022)			**0.51 (0.045)**
Lakes$_{ec}$		0.393 (0.255)			**-0.942 (0.135)**
Lakes^2_c		**-1.504 (0.409)**			**0.592 (0.099)**
Water$_c$	**-2.742 (0.197)**		**-3.919 (0.332)**	**-5.412 (0.533)**	
Water^2_c	**2.023 (0.196)**		**3.172 (0.317)**	**3.545 (0.715)**	
Trails$_c$		**-0.287 (0.060)**			
Trails^2_c		**0.068 (0.015)**			
Low Activity Feature$_c$					**-0.011 (0.004)**
Low Activity Feature^2_c					**0.001 (0.000)**
High Activity Feature$_c$					0.000 (0.000)
High Activity Feature^2_c					0.000 (0.000)

[a] There were no data available for wolves NW040, NW041, NW043, NW051, and NW052 in early winter; and no significant models for NW045.
[b] Individual models did not meet threshold values and were averaged as in Burnham and Anderson (2002: 150, 162).
$_c$ Parameter is defined as a 'distance to' feature.

Table B.2. Resource selection coefficients (± SE) representing seasonal selection patterns for all wolves (global) and by individual wolf in the Nelchina Study Area of south-central Alaska in late winter (15 February – 15 April). Values in bold indicate significant selection (positive values) or avoidance (negative values) at $P \leq 0.05$. Blanks indicate those parameters that were not included in final models rankings or could not be tested because of an absence of data. All models validated by k-fold cross validation.

LATE WINTER[a]	GLOBAL	NW040[b]	NW043	NW044	NW047	NW051	NW052
Elevation	**-0.000 (0.000)**	0.00 (0.000)	**0.004 (0.001)**	0.002 (0.001)		0.000 (0.001)	0.001 (0.001)
Slope	**0.011 (0.001)**	**-0.001 (0.000)**	**0.041 (0.005)**	**0.027 (0.005)**		**0.025 (0.005)**	**0.027 (0.005)**
Eastness	**-0.073 (0.021)**	**0.028 (0.007)**	0.028 (0.062)	0.034 (0.063)		**-0.555 (0.063)**	**-0.682 (0.065)**
Northness	**-0.188 (0.023)**	**-0.038 (0.009)**	**-0.161 (0.061)**	-0.044 (0.063)		**-0.530 (0.086)**	**-0.566 (0.087)**
Depth		0.000 (0.000)			**-0.013 (0.003)**		
Hardness		0.000 (0.000)			**0.009 (0.0020**		
Late Prey$_c$		**0.078 (0.005)**			0.017 (0.012)		
Linear Density		**-0.208 (0.032)**					
Rivers$_c$	**-0.715 (0.052)**	**-3.434 (0.080)**	**-1.123 (0.202)**	**-1.537 (0.248)**		**-2.717 (0.259)**	**-2.855 (0.247)**
Rivers^2_c	**0.189 (0.018)**	**1.522 (0.039)**	**0.434 (0.088)**	**0.691 (0.123)**		**0.764 (0.122)**	**0.801 (0.115)**
Lakes$_c$	**-0.18 (0.041)**	**0.567 (0.086)**	**0.556 (0.265)**	**1.004 (0.260)**		**-0.525 (0.106)**	**-0.532 (0.108)**
Lakes^2_c	0.017 (0.010)	**-0.108 (0.038)**	**-0.317 (0.146)**	**-0.539 (0.136)**		**0.060 (0.025)**	0.049 (0.025)
Water$_c$					**-3.530 (0.683)**		
Water^2_c					**3.053 (0.763)**		
Low Activity Feature$_c$		**-0.164 (0.027)**					
Low Activity Feature^2_c		**0.007 (0.003)**					

[a] There were no data available for wolves NW045 and NW049 in late winter; and no significant models for NW041and NW042.

[b] Individual models did not meet threshold values and were averaged as in Burnham and Anderson (2002: 150, 162).

$_c$ Parameter is defined as a 'distance to' feature.

Table B.3. Resource selection coefficients (± SE) representing seasonal selection patterns for all wolves (global) and by individual wolf in the Nelchina Study Area of south-central Alaska in summer (16 April – 14 November). Values in bold indicate significant selection (positive values) or avoidance (negative values) at $P \leq 0.05$. Blanks indicate those parameters that were not included in final models rankings or could not be tested because of an absence of data. All models validated by k-fold cross validation.

SUMMER[a]	GLOBAL	NW040	NW041	NW042[b]	NW043[b]	NW044	NW045	NW047	NW049
Elevation	**0.000 (0.000)**	**-0.001 (0.000)**	0.000 (0.000)	-0.001 (0.000)	**0.003 (0.000)**	**0.002 (0.000)**	**0.000 (0.000)**	0.000 (0.000)	0.000 (0.001)
Slope	**-0.015 (0.001)**	**-0.017 (0.002)**	**-0.016 (0.000**	**-0.005 (0.000)**	**0.006 (0.002)**	**-0.008 (0.004)**	**-0.014 (0.003)**	**-0.021 (0.004)**	**-0.029 (0.008)**
Eastness	0.002 (0.012	-0.042 (0.032)	-0.065 (0.036)	-0.034 (0.004)	**0.09 (0.019)**	**0.134 (0.031)**	**-0.088 (0.033)**	0.012 (0.031)	0.064 (0.105)
Northness	-0.061 (0.013)	**-0.067 (0.034)**	**0.135 (0.037)**	**-0.077 (0.007)**	**-0.186 (0.026)**	**-0.096 (0.036)**	**0.119 (0.034)**	-0.165 (0.030)	**-0.356 (0.096)**
Linear Density				**-0.003 (0.000)**	**0.001 (0.000)**				
$Water_c$	**-0.219 (0.036)**	**-0.612 (0.208)**	**-0.909 (0.090)**	**-1.256 (0.314)**	**-4.435 (0.135)**	**-2.324 (0.204)**	**-1.225 (0.088)**	**-2.078 (0.238)**	-0.418 (0.735)
$Water^2_c$	**0.087 (0.014)**	**0.668 (0.169)**	**0.23 (0.028)**	**0.524 (0.3510)**	**4.483 (0.103)**	**2.531 (0.166)**	**0.297 (0.026)**	**1.422 (0.272)**	**1.363 (0.646)**
Linear $Feature_c$				**-0.037 (0.004)**	-0.004 (0.002)				
Linear $Feature^2_c$				**0.004 (0.000)**	0.000 (0.000)				
$Trails_c$				**-0.011 (0.001)**					
$Trails^2_c$				**0.001 (0.000)**					

[a] There were no data available for wolves NW051 and NW052 in summer..

[b] Individual models did not meet threshold values and were averaged as in Burnham and Anderson (2002: 150, 162).

$_c$ Parameter is defined as a 'distance to' feature.