THE ECOLOGY OF BISON MOVEMENTS AND DISTRIBUTION IN AND BEYOND YELLOWSTONE NATIONAL PARK

A Critical Review
With Implications for Winter Use and Transboundary Population Management

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The history and enormity of issues leading to this study have touched the professional or personal lives of a broad spectrum of Americans, including federal and state civil servants and citizens who care passionately about the integrity of Yellowstone National Park, bison conservation, or protection of livestock against reinfection with a zoonotic organism nearing eradication in the industry. Given the strong polarization among interests involved in these environmental conflicts, the authors feel privileged to have been welcomed by key informants to engage in exploration of their knowledge and insights, and in many cases to have been provided with unpublished data contributing to our assessment and recommendations. Foremost among those we wish to acknowledge as contributing to the assessment is Dr. Mary Meagher, whose passionate concerns for the conservation of Yellowstone bison and the integrity of the Yellowstone Park ecosystem have been uncompromising. We encourage her to continue analyzing the as yet unrealized potential of a data set spanning more than 30 years, complimented by experience in the Yellowstone ecosystem exceeding the duration of most professional careers in wildlife management. In contrast, Rick Wallen, the current bison biologist with the National Park Service, is just beginning to develop a research and management program. We thank Rick for contributing information and his insights to the assessment and hope in return that the report contributes to the development of his program. We are grateful to both Rick Wallen and Dr. Doug Smith for the experience and insights we gained while riding the Mary Mountain Trail with them in October 2004. Finally, we wish to acknowledge the enormous contribution to the project by Traci Weller of Bozeman, Montana. Traci organized and scheduled the interviews and workshops, recorded the dialogue and prepared transcripts. Her competency and humor sustained us through the arduous interview schedule.

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BISON POPULATION DYNAMICS AND SPATIAL ECOLOGY

Yellowstone National Park is not a self contained ecosystem. It covers 8,983 km^2 or slightly more than 10% of the Greater Yellowstone Ecosystem (> 80,503 km^2; Baden and Leal 1990, Clark et al. 1999). The movements and population dynamics of large mammal populations, including elk, grizzly bears, wolves, pronghorn, mule deer and bison, need to be viewed at spatial scales significantly larger than the park itself. In particular, herbivores can be expected to respond to regional environmental gradients in forage quality and availability, which are influenced by climate, seasonal weather, snow cover, elevation, vegetation cover, plant phenology, and herbivory. Understanding factors influencing bison movement and density distribution patterns is important for predicting range expansion and transboundary movements, and to form bison management decisions within and outside the park (Cheville et al. 1998). The influence of human activities and infrastructure in the park on bison movement and distribution patterns is also an important matter. The effects of road grooming in winter on bison movements and population dynamics is particularly controversial, and was the subject of several legal undertakings[1] and recent management decisions (National Park Service et al. 2000). Human infrastructure influences bison movements in other seasons as well.

The bison is the largest herbivore among ungulates occurring in the Greater Yellowstone Ecosystem. Typical of the species throughout its distributional range (Reynolds et al. 2003), the bison in Yellowstone National Park is an obligate grazer in winter (Meagher 1973). Its winter diet consists almost entirely of grasses and sedges (Delgiudice et al. 2001) and it is dependent on grasslands in the park and in areas where it is tolerated in surrounding jurisdictions. The ecological roles of bison include grazing, carbon and nitrogen cycling (Frank 2000), vegetation and soil disturbance (Coppedge and Shaw 2000), resource competition with elk (Delgiudice et al. 2001), prey for wolves (Smith et al. 2000), and food for bears, coyotes and other scavenging species (Green et al. 1997). The influence of bison on ecological processes and other species with which it interacts in an area can be expected to vary with abundance. During the past 100 years the number of bison in the park has ranged from > 23 to > 4,000. The population provides a valuable opportunity to study the dynamics of a recolonizing large herbivore population.

In 1968, Yellowstone National Park moved from a 33 year (1934-1967) period of controlling ungulate populations at predetermined stocking levels by culling to a regime of ecological management under which wildlife populations are allowed to fluctuate in the park without human intervention (Houston 1982). Subsequently, the bison population increased in size and area used (Taper et al. 2000), exhibiting characteristics of an erupting population (see Caughley 1970*a*). Spatial equilibria and regulation of colonizing

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[1] The legal history is summarized in a complaint filed against the Secretary of the Interior and Director, National Park Service by The Fund for Animals and other plaintiffs to the United States District Court for the District of Columbia, Case Number 1:04CV0193, 11/04/2004.

ungulate populations have been important topics in ecology since Riney (1964) and Caughley (1970*b*, 1977) established the theoretical foundations for understanding eruptive oscillations. An eruptive oscillation starts when there is a large surplus of resources available relative to resources required by animals present in a system. In established populations, such discrepancies can arise under three circumstances: by an environment becoming more favorable, e.g. following logging or fire; by a population being temporarily reduced by management interventions (hunting or culling) to well below per capita resource availability; or by a rare natural catastrophe, such as a flood or an exceptionally severe winter causing high adult female mortality. Once the source of perturbation is removed, a relatively low density population experiences high fecundity and survival, a high rate of increase, followed by increasing intraspecific competition for forage which serves as the stimulus for expansion into unoccupied range. This is followed by a new phase of population increase in the new range, and the pattern is repeated until available ranges are occupied. This pattern of pulsed expansion was first described by Caughley (1970*a,b*) for an exotic ungulate introduced to New Zealand. Pulsed expansion has also been demonstrated for recolonizing indigenous North American species: muskox in Alaska (Reynolds 1998), Northern Quebec (Le Henaff and Crete 1989) and Greenland (Oleson 1993); elk in Yellowstone (Lemke et al. 1998); and wood bison in Northern Canada (Gates and Larter 1990, Larter et al. 2000).

The substantial body of historical data available for bison in Yellowstone National Park provides a unique opportunity to examine long term spatial and demographic patterns in an expanding population subject to perturbations (management removals and variable winter severity). Historical observations predate establishment of the park (Meagher 1973). Population estimates varying in quality exist from 1902 to the present. Ecological studies have been carried out since 1963 (Meagher 1971, 1973, 1974, 1994, 1998, Meagher et al. 1997, Taper et al. 2000), creating a remarkable data set that has been only partially analyzed. Meagher (1993) reviewed changes in bison abundance, distribution and movements between 1970 and 1993. Long term data for the period 1970 to 1997 were recently analyzed and published by Taper et al. (2000, and *in press*). Cheville et al. (1998) and Klein et al. (2002) also reviewed population dynamics and factors influencing movements of bison within the park and movements to the boundaries of YNP in the Gardiner basin and West Yellowstone area.

Plowing and grooming of snow on roads in the Park for winter access management is claimed to influence bison ecology. In a paper reviewing the pattern of range expansion exhibited by the Northern YNP bison herd, Meagher (1989*b*:674) offered the first testimony concerning the effects of roads on winter range expansion: “Use of the plowed road for relatively easy and energy-efficient travel probably facilitated learning and a rapid increase in numbers.” The argument was further developed in a review of movements and range expansion in the Central Park in which Meagher (1993:2) claimed that groomed roads in YNP had the following effects on the YNP bison population:

- groomed roads provide movement corridors facilitating travel within traditional foraging areas;
- groomed roads induce major shifts among previously isolated population sub-units;
- groomed roads induce range expansion;

- groomed roads reduce the energy cost of displacing snow during movements within and between winter ranges;
- energy saved from the reduced cost of transport mitigates winter kill and enhances calf survival, resulting in a higher rate of population increase than would otherwise occur.

Meagher et al. (2000, 2002) further elaborated these notions in their "domino effect" hypothesis:

> "In the early 1980's, gradual but escalating changes in the bison population became apparent. Annual winter use of foraging areas by the Pelican bison expanded west from traditionally used, geothermally influenced places near the shore of Yellowstone Lake to sedge areas near the mouth of Pelican Creek, Lake area, and on the Hayden Valley. Because Hayden Valley (part of the Mary Mountain unit) was occupied already by wintering bison, as more shifted from Pelican Valley, more bison moved into the Firehole. They also moved earlier. The process of winter range expansion was coupled with a population increase, and more bison moved further west to Madison Junction and beyond, to spill over the park's west boundary into Montana. We term this cascading pattern of population increase the domino effect." (Meagher et al 2002:135).

However, the authors were ambiguous about the role of road grooming as the cause of the domino effect concluding, "The use of snow packed or plowed roads certainly represents some energy savings to the Central herd, and even provides access to areas that would otherwise be inaccessible to bison. It is unclear if these energy savings have merely facilitated a population and range expansion that would have occurred anyway, or if an apparently minor change has upset a delicately balanced demography and caused the expansion." (Meagher et al. 2002:145,146).

We reviewed these key sources and examined other available information, including key informant knowledge, on the spatial and demographic patterns of the Yellowstone bison population to address the following questions:

1. Does this erupting population experience density dependence?
2. Does the population follow a pattern of gradual or episodic/pulsed expansion?
3. Are boundary removals influenced by population size and winter conditions in the park?
4. Is there or has there been spatial independence of population sub-units?
5. Have patterns of movement and interchange among population subunits changed?
6. Has road grooming influenced spatial patterns and population dynamics in the ways described by Meagher (1993) and Meagher et al. (2002)?
7. Do bison management actions at the boundaries influence range expansion and demographic patterns differently on the northern and central ranges?

We address these questions by examining available information on the spatial patterns and population dynamics of the Yellowstone bison population over a century-long period during which management interventions and weather have perturbed the system. In the next chapter, we employ a population and distribution simulation model to test sensitivity of the system to assumptions presented in this chapter and ecological conditions described in Chapter 3.

Population and Density Trends

Ecological conditions differ between the Northern and Central ranges in Yellowstone National Park (Chapter 3), making it necessary to consider population and distribution trends of Northern and Central bison subpopulations separately. Two previous analyses have considered YNP bison as if they were one population (Cheville et al. 1998, Klein et al. 2002). Lumping population subunits ignores important gradients in environmental conditions between YNP bison ranges that differentially influence reproduction and survival, and spatial ecology of bison, elk and their predators.

The Northern range provides a marked elevation gradient from the Upper Lamar Valley down to the Gardiner basin, where a precipitation shadow creates drier conditions in the summer (Chapter 3) and lower amounts of snow in the winter relative to the middle and upper Lamar Valley (Figure 5.1). The value of the Gardiner basin as refuge habitat for bison in harsh winters has long been understood (see Chapter 4; Albright 1944, Cahalane 1944*a*). Unlike the Central Range, there is an insignificant area of geothermally influenced bison habitat in the Northern range. The Central ranges experience a longer period of continuous snow cover and deeper snow than the Northern range (Despain 1987, 1990). Unlike the elevation gradient in snow depth on the Northern range, there is no significant gradient in mid winter snow cover (depth, density, SWE) between West Yellowstone and the Pelican Valley in areas not subject to geothermal influence (Chapter 3 and Figure 5.1). However, snow melt and spring greenup occur earlier in the West Yellowstone area than in the Hayden and Pelican Valleys (Despain 1990). Significant areas of geothermally influenced habitat are present in the Firehole, Gibbon and Norris Geyser Basins, Hayden Valley and in the Pelican Valley winter ranges (see Chapter 3 and note red polygons in Figure 5.1) in which diminished snow cover increases access to forage, and reduces the cost of thermoregulation and movements. In addition, Craighead et al. (1973:38) described thermal springs in the Duck Creek and Cougar Creek area used by elk in the winter during the 1960s and early 1970s. In addition to providing foraging opportunities, geothermal areas and streams in the Central range are used as movement corridors by bison and elk (Aune 1981, Bjornlie and Garrott 2001). Similar to the Northern Range where reduced snow cover in the grassland habitat of the Gardiner basin provides refuge habitat for bison, the geothermally influenced areas in the Central Range provides refuge for a significant part of the subpopulation in harsh winters. Meagher (1971, 1973, 1976) refers to geothermally influenced areas as the survival habitat for the Central Range bison.

There are major differences in the structure of ungulate assemblages on the Northern and Central ranges and differential intensity of seasonal grazing related to herbivore species abundance and composition (Singer and Norland 1994, Delguidice et al. 2001). Elk and bison are the dominant herbivores on these ranges. Since 1970, the Northern range elk population has varied from a low of < 5,000 to > 20,000 (Klein et al. 2002). In contrast, relatively few elk winter in the Central bison ranges, except in the Duck Creek-

Madison-Firehole area where 300 to 800 elk reside in winter (Craighead et al. 1973, Singer 1991, Garrott et al. 2002). Few elk winter in the Pelican Valley (Smith et al. 2000:1131, DelGuidice et al. 2001:8). The number of bison on the Northern range varied from > 100 in the late 1960s to >1200 in 2004. On the Central range the number of bison also varied 10 fold during this period, from >300 to >3,000. Elk and bison exhibit moderate habitat (Barmore 2003, Singer and Norland 1994) and dietary overlap (DelGuidice et al. 2001) in winter on both the Northern and Central ranges during the late 1980s. The mean dietary overlap between bison and elk during the winters of 1987-1990 was 0.59 for the Northern Range (DelGuidice et al. 2001). Dietary overlap was higher in the Madison-Firehole area (0.69) where elk and bison shared geothermally influenced habitat when snow was deep. Because bison are behaviorally dominant to elk (McHugh 1958) resource competition on geothermal habitat patches in winter may disadvantage elk, exacerbating the population effects of geochemically induced senescence (Garrott et al. 2002) of this species in the Central ranges of YNP.

By the early 1940s, a few years after the reintroduction of 71 bison into the Mary Mountain range (1936), the YNP bison population was considered structured into three wintering subunits, the Lamar herd, the Mary Mountain Herd (Hayden Valley and Madison-Firehole) and the Pelican Valley herd (Meagher 1973). Meagher (1993:2) reported interchange among subpopulations during the winter was minimal because of topography and deep snow between the wintering Valleys. However, the Lamar and Pelican herds shared common high elevation summer range in the Upper Lamar Valley and east slopes of the Absaroka Mountains, and late fall interchanges between the Lamar and Pelican herds were inferred from unexpected variations in the number of bison on either winter range (Meagher 1973: 87). Movement between the Pelican and Hayden Valleys was known in the summer and fall (Figure 5.2). Therefore, Pelican Valley bison were familiar with both the Hayden and Lamar areas.

There were long periods of relatively constant growth of the bison population within each range when management interventions and weather had little influence on population growth. These periods can be considered to represent the inherent capacity of each range to support population growth below levels where density dependence is exerted. At low densities, bison should have access to adequate forage, except during severe winters, and growth rate should be relatively stable and high. At high densities, productivity can be expected to decrease and juvenile mortality increase, lowering recruitment and population growth. Growth of the Northern population between 1902 and 1952 was excluded from consideration because the herd was subsidized by winter feeding to some extent throughout this period and it was intensively managed (Chapter 4). The only period during which growth of the Northern population was relatively unaffected by management interventions was between 1967 and 1988[2]. During 1970 to 1988 the Northern range population increased at an exponential rate of 0.072 (Figure 5.3). The period ended with the harsh winter of 1989 when a large proportion of the population moved into the Gardiner basin and 581 were removed near the Northern boundary (Meagher 1989*b*).

There were two periods in the history of the Pelican Valley herd without major perturbations to population growth, 1902-1954 and 1968-1995 (Figure 5.4). Rates of increase were not significantly different between these periods; r = 0.056 and 0.051,

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[2] Bison were removed from the Northern range in 1976 (8), 1985 (88), 1986 (41), and in 1988 (2).

respectively. At the end of these periods, first in 1956 then again in 1996 and 1997, culling and harsh winter weather reduced the size of the population (Meagher 1973, Taper et al. 2000).

The Mary Mountain subpopulation experienced a period of relatively constant growth between 1936 and 1955 before managers intervened to reduce the herd in 1956; a severe winter that year further affected the population (Meagher 1973). The highest observed growth capacity of the Mary Mountain population was 0.156 during 1936-1954 (Figure 5.5). 1970 to 1981 was another period free of perturbations and the Mary Mountain bison herd increased at a slightly lower rate of 0.13 (Figure 5.5).

Taper et al. (2000) proposed range expansion as a mechanism explaining stable population growth; we refer to this as 'the density-equalization effect'. As the Central (Mary Mountain and Pelican) and Northern range populations increased in size (prewinter maximum count), the area they occupied in mid winter expanded within available grassland and meadow habitat (Figures 5.6 and 5.7). The pattern of range expansion was gradual and linear, differing from the pulsed pattern described for the Mackenzie wood bison population in the Northwest Territories (Gates and Larter 1990, Larter et al. 2000), the only other documented bison population eruption. In that case, population growth rate declined as density approached a threshold of approximately 0.55 bison /km^2. Then bison spilled over into the next available habitat temporarily reducing density, increasing per capita resources, with renewal of the growth rate of the population (Larter et al. 2000); the cycle was repeated twice. This pattern of increase to high density followed by expansion into new range is similar to that described for exotic ungulates in New Zealand (Caughley, 1970*a*,*b*) and for muskox reinvading their historic native range (Reynolds, 1998).

Differences in landscape composition and configuration between the Mackenzie and YNP bison ranges explain the different patterns of range expansion. Bison foraging habitat in the Mackenzie range occurs in discrete, widely spaced patches representing <6% of the landscape within a boreal forest matrix (Larter et al. 1991*a*,*b*, Matthews 1992). In contrast, the Northern and Central bison ranges of YNP consist of large tracts of continuous grassland and meadows connected by corridors containing foraging habitat and relatively short distances of non-foraging habitat (Chapter 3). The connected landscape of YNP bison ranges permits gradual expansion whereas the fragmented landscape in northern Canada supported pulsed expansion. We found evidence of only one exception to this rule. In the harsh winter of 1996-1997 a cow/juvenile of six dispersed south of the park following the groomed road out the south entrance, joined the Jackson herd and never returned[3]. Of interest, three mature bulls from Mary Mountain moved to near Jackson Lake the previous year; they returned to the Hayden Valley for the rut and repeated the migration for several years[4]. Exploratory movements by some mature bulls is characteristic of bison populations (Gates and Larter 1990).

Temporal patterns of density and population growth also differed between bison in northern Canada and YNP. Larter et al. (2000) described a cyclical pattern when population density was plotted against instantaneous growth rate. Population growth rate and density increased until population density exceeded approximately 0.55 animals/km^2. Once this point was reached both rate of growth and density decreased and the cycle

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[3] Interviews with R. Wallen (23 July 2004) and Steven Cain (11 August 2004).

[4] *Supra* note 3.

began again. In YNP, growth rate (r values from Taper et al. 2000) showed an inverse relationship to prewinter population size and density as a function of habitat area for the Central range subpopulation (Figure 5.8 and 5.9) but not for the Northern range population (Figures 5.10 and 5.11).

After increasing through the first decade of the ecological management era, instantaneous winter densities, calculated as bison within 95% kernel areas (Taper et al. 2000), remained relatively steady in YNP bison ranges as the population subunits increased (Figure 5.12). The mean instantaneous density of bison on the northern range between 1971 and 1997 was 3.17 ± 0.19 (s.e.), and 4.20 ± 0.26 for the Central Range bison (data source: Taper et al. 2000); the means were significantly different, t = 3.21, 52 d.f., P = 0.002. However, density calculated as a function of available grassland and meadow habitat area within ranges necessarily increased with population size (Figure 5.13).

Based on these patterns we propose that YNP bison attempt to compensate for declining per capita food resources by increasing the area used, hence maintaining a relatively stable instantaneous density (Taper et al. 2000). However, compensation is not exact; r declines because high quality winter foraging patches (sedge meadows) are limited in overall area (0 to 9.4% of ranges, Chapter 3), they are patchily distributed and depleted first, forcing bison to shift to poorer quality patches as density increases, with the demographic consequences of decreased fecundity and increased juvenile mortality. There is limited evidence from YNP and other populations to test this hypothesis.

Several geographically disparate studies have demonstrated that given a choice, bison preferentially forage in high biomass lowland meadows dominated by sedges and grasses in the winter, including the Mackenzie bison range (Larter and Gates 1991*a*,*b*) and the Slave River Lowlands (Reynolds et al. 1978) in the Northwest Territories, Elk Island National Park in central Alberta (Cairns and Telfer, 1980, Telfer and Cairns, 1986), and in YNP (Barmore 2003, DelGuidice et al. 2001). In 1970, when spring greenup was delayed on the Northern range in YNP, bison continued to forage in areas with deep snow in lowland areas, despite the availability of relatively snow free uplands (Barmore 2003). It is important to consider that bison density in YNP in 1970 was the lowest it had been in many decades; winter grazing would not have depleted standing biomass in lowland meadows to the same extent as at higher densities.

In Elk Island National Park where density was high, foraging bison shifted to snow free upland grasslands in late winter before green up (Van Camp 1975). This may be attributable to reduction of forage biomass in meadows by winter grazing, which by the end of the winter reduced forage availability to a level lower than or similar to the upland meadows. Evidence from the Mackenzie Bison Range (Larter et al. 2000) indicated that the winter diet of a recently established bison population subunit in an expansion area was higher in quality than for the core population. Unpublished results from YNP[5] indicate an increase in use of upland habitats and decrease in use of sedge habitat after the mid 1980s, coincident with a high population size. Between 1968 and 1988 the Northern bison subpopulation in YNP increased from < 100 to > 800. Singer and Norland (1994) compared diet composition and habitat selection for 1967-1970 and 1986-1988 finding that bison consumed less sedge and more grasses at the higher population level,

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[5] Interview with Chris Jerde, 24 June 2004, Edmonton, Alberta. Analysis of survey data series 1970 to 1997 collected by M. Meagher.

increased their habitat breadth, and increased habitat and diet overlaps with other herbivores. In particular, there was moderate diet overlap but high habitat overlap between bison and elk.

Heavy use in summer and winter has been recorded on YNP grasslands. Dawes and Irby (2000) studied forage production and utilization during two years, 1996 and 1997, in the Madison, Gibbon and the Firehole drainages at a time when the Central bison population was close to a record maximum and severe winter conditions induced high losses from starvation and a record number of management removals from boundary ranges in Montana. They found plant biomass was 54% lower in exposed compared to exclosed plots in high use areas. This apparent high utilization was similar to winter forage removal by herbivores recorded during 1986-1990 on the Northern Range (55%) by Singer and Harter (1996). Working in grassland communities in the Hayden Valley in the late 1990s, Olenicki[6] recorded grassland forage summer offtake of approximately 35%. Meagher (1993) referred to "loss of functional winter range" in the Hayden Valley resulting from heavy grazing during the summer and fall. Taper et al. (2000) reiterated this explanation and in addition suggested that soil compaction by large numbers of bison was causing damage to geothermal areas on Fountain Flats.

The mechanisms underlying regulation of YNP bison subpopulations have received limited attention by researchers. Food mediated density dependent effects on calf survival were suggested in a review of available information by Cheville et al. (1998). DelGuidice et al. (2001) studied the nutritional status of bison on different ranges, concluding the Pelican Valley was the harshest environment based on metabolic indicators. Extreme winter severity has caused significant starvation mortality, primarily of calves (DelGuidice et al. 2001). In a study conducted between 1963 and 1969 when the YNP bison population was small, Meagher (1973) found pregnancy rates for cows 2.5 years and older was only 52% and most cows did not reach sexual maturity until 4 years. Taper et al. (2000) suggested delayed maturity and low fecundity in Yellowstone bison are likely responses to severe winter climate and sub-optimal forage availability. In contrast, 82% of 45 females culled at West Yellowstone in winter 2001-2002 were pregnant (Gogan et al. 2002). The different rates obtained at these two times may indicate a high degree of lability in pregnancy rates in response to variable nutrition, or differences in methods. The reader is referred to Reynolds et al. (2003) for a review of pregnancy rates in other bison populations.

Predation on bison by wolves can also be an important limiting factor for bison populations and is the subject of current research in the central and northern portions of the park and the Pelican Valley. Similar to the numerical response seen in other wolf–prey systems (Messier 1996), wolf populations in the Mackenzie Bison Range, Northwest Territories (Larter et al. 1994) and Wood Buffalo National Park (Joly and Messier 2000) were shown to respond numerically to increasing bison population size. In the Mackenzie bison range, wolf predation became a significant mortality factor, particularly for bison calves, about 20 years after bison were reintroduced to the area (Larter et al. 1994). Predation is a significant limiting factor for bison in Wood Buffalo National Park in the presence of tuberculosis and brucellosis (Joly and Messier 1998). Wolves attack bison calves preferentially over older age classes of this species (Larter et al. 1994, Carbyn and Trottier 1998, Smith et al. 2000, Jaffe and Garrott 2001).

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[6] Interview (July 22, 2004) with Tom Olenicki and unpublished data.

Elk are the dominant herbivore and the primary prey of wolves in YNP (Smith et al. 2004*b*). Elk represented 92% of 1582 wolf kills recorded from 1995 to 2001 (Smith et al. 2004*b*). Unlike bison, wolves are more readily able to kill adult elk; calves represented 43% of wolf-killed elk, cows 36% and bulls 21% while these classes represented 15%, 60% and 25% of the population (Smith et al. 2004*b*). Bison are rarely killed by wolves on the Northern Range; typically only when individuals are weakened by starvation or injury (Smith et al. 2000). Most bison killed by wolves have been recorded in Central YNP where elk are substantially less abundant during the winter months than on the Northern Range. A numerical response by wolves to bison is possible in the Central Range of the park where bison is becoming increasingly important in their diet. Wolves prey almost exclusively on bison in the Pelican Valley where elk are not available during the peak of winter (Smith et al. 2000, 2004a). Similarly, bison are a significant component of the winter diet of wolves in the Mary Mountain range and Cougar meadows area near West Yellowstone.

Wolves are more successful killing elk than bison; bison were killed in 7% of 57 interactions compared to 21% of 372 interactions between wolves and elk (Smith et al. 2000). Elk outnumbered bison in YNP 5.6:1, yet the ratio of elk:bison killed by wolves between 1995 and 1999 was 47.6:1 (Smith et al. 2000). In three years of study in the Madison-Firehole area, Jaffee and Garrot (2001) located 101 definite and 29 probable wolf kills, including 70 elk calves, 34 cow elk, nine bull elk, one unknown adult elk, 13 bison calves, one cow bison, and one unknown bison.

Future effects of predation on bison population dynamics in YNP is an important research focus. We suggest that wolf predation on bison will continue to increase in the Central ranges, but not on the northern range as long as elk are relatively more abundant there. In systems where wolves show a numerical response to an abundant prey species that is difficult to kill, predation rate on easier prey can be inversely proportional to their density (Dale et al. 1994; Messier 1996), which could lead to extirpation of easier prey species. Examples of this phenomenon include woodland caribou (*Rangifer tarandus*) in a wolf–moose system (Seip 1992) and moose in a wolf-bison system (Larter et al. 1994). To critically evaluate if wolf predation on elk is acting or will act in an inverse density-dependent fashion in the Central YNP bison ranges will require measurement of both the numerical response of wolves and the killing rate per predator, i.e. the functional response. It is important to emphasize that, as with plant-herbivore dynamics, predator prey relationships are different on the Northern and Central YNP ranges.

Distribution and Movement Patterns

With cessation of management interventions to control population size after 1967, bison began to increase in each subpopulation unit in YNP. Winter distribution and movement patterns changed over time as the population increased in size (Figure 5.14). Meagher et al. (2002) provided a thorough description of changes in distribution and movement patterns and suggested winter road grooming may have “...upset a delicately balanced demography and caused the expansion” (Meagher et al. 2002:146). Considering the evidence, we suggest the plausible mechanism underlying changes in winter distribution was the density-equalizing effect of range expansion described above, whereby density remained relatively constant as the population increased owing to an increase in area occupied (Taper et al. 2000). Although groomed roads facilitate movements within and among winter habitat patches, range expansion would have occurred regardless as bison responded to intraspecific exploitative competition. In only one instance (Firehole to Mammoth corridor) might a road have been the factor underlying range expansion into areas that would not otherwise have been used. The evidence for this is presented below.

Patterns of range expansion during 1970 to 1997 were analyzed by Taper et al. (2000). They mapped changes in the mid winter utilization distribution of bison using kernel home range analysis (Seaman and Powell 1996) and kindly shared the distribution maps with us. The key temporal changes in the pattern of winter distribution evident in Figure 5.14 were:

- the instantaneous area occupied increased with population size as previously noted;
- when population subunits were small, there were four primary wintering areas: the Pelican Valley, Hayden Valley, the Firehole, and the Lamar Valley;
- range use west of Tower Junction on the Northern range was first evident in the 1975 distribution, then increased thereafter;
- range expansion into the Mammoth-Gardiner area by the Northern population subunit was first evident in the 1983 distribution and increased thereafter;
- the entire Northern Range subpopulation may move to the Gardiner basin under harsh winter conditions (e.g. February distributions 1992 and 1997) where it may be subject to significant management actions;
- when Central subpopulations were small, the distance between Pelican Valley and Hayden Valley winter distributions was shorter than the distance between the Hayden Valley and the Firehole distributions;
- The areas used by bison in the Pelican and Hayden Valleys increased with population size and gradually coalesced;
- expansion of the Lamar subpopulation to Madison Junction was first evident in the mid 1970s;
- range expansion in the Madison River drainage towards the park boundary north of West Yellowstone progressed gradually thereafter, encompassing the park boundary by 1987 and every winter thereafter;
- the distribution maps illustrate the first measurable use of the Norris Geyser Basin occurred in 1986 and at Swan Lake Flats in 1991;
- bison used the Norris to Swan Lake area every winter after 1991;
- geothermal habitat in the Central Ranges is always used by a significant portion of the Central subpopulation.

The combined area from Madison Junction to the western boundary and north from Madison Junction is referred to as the West Side[7]. Forty to 50 bison had been reported wintering in the Cougar meadows (located in the West Side area) in 1956 and some were seen again in 1959 (Meagher 1973:36), but were not recorded again until 1974; there were no records indicating surveys during the intervening years. Two were observed in

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[7] Definition provided by M. Meagher.

1974 and again in 1978 (data source: M. Meagher survey data series). Six were counted in 1980; numbers increased thereafter. The number of bison using the West Side increased linearly (natural log transformed) with the number of bison in the Central subpopulation between 1978 and 1997 (Figure 5.15; data series provided by M. Meagher, M. Taper and C. Jerde), consistent with the pattern of range expansion by which density was equalized. The threshold Central Range population above which expansion into the West Side occurred was approximately 1,000 bison (converted x axis intercept, Figure 5.15). There was no detectable effect of mid February snow cover (SWE) on the number of bison occurring on the West Side. In contrast, Bjornlie and Garrott (2001) found a positive correlation between SWE at the Canyon SNOTEL site and the number of bison in the Madison-Gibbon-Firehole area during the winters of 1997-1998 and 1998-1999, with peaks in the number of bison in April both years.

Cheville et al. (1998) found that movements to the boundary of YNP (represented as removals) were influenced by total population size above 3,000 and snow conditions (SWE). We argue (see above) that winter ecology of bison on the Northern and Central Ranges is different and separate examination of bison trophic ecology and population dynamics is warranted. Accordingly, removals at the western boundary occurred at Central Range prewinter populations above 1500 (Figure 5.16). Consistent with Cheville et al. (1998), we found snow conditions and population size contributed significant effects in the Central Range. Similarly, on the Northern Range we found at populations above 550, population size and snow had significant effects on removals at the northern boundary (Figure 5.17).

Movements of bison between the Central Range and the Northern Range have been reported historically via the Mirror Plateau corridor (Chapter 4; Meagher 1973). The exchanges occurred in the late fall to early winter period before deep snow precluded movement in the high country. Since the 1990s, bison have migrated along the road allowance and adjacent habitat between the Firehole (Taper et al. 2000, Meagher et al. 2002) and the West Yellowstone area[8] and to the Northern Range near Gardiner Montana. In some recent winters, large numbers of bison have used this migration pathway (Meagher et al. 2002). Bison from the Central Range may reach and be subject to management actions at both the western and northern boundaries. To date there is no evidence that Northern Range bison have moved to the western boundary. Because of inter-range movements, it is important to look at the overall relationship between bison population size and total removals (Figure 5.18). Similar to Cheville et al. (1998), we found significant effects for total prewinter population size and average snow conditions in February on total removals; the model explained 73% of overall variance in boundary removals (Figure 5.18).

Until recently, when radio transmitters were used to monitor the movements of individuals[9], inferences about subpopulation interchange and movement patterns were based on anecdotal observations, limited records of neck banded bison, observations

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[8] Interview with Peter Gogan and Ed Oelexa, USGS, 21 July 2004: commented that radio collared bison captured and released in November 1996 13 km north of West Yellowstone were later captured 3 km from Gardiner, Montana.

[9] Keith Aune (Montana Fish Wildlife and Parks) and Tom Roffe (U.S. Fish and Wildlife Service, Bozeman, MT) deployed 52 VHF radio collars and 11 GPS collars on bison in YNP during 1995-1998. Pete Gogan and Ed Olexa radio collared (VHF collars) approximately 100 bison in YNP during late 1997 and March 1998. Rick Wallen, NPS, Yellowstone NP) deployed 13 GPS collars on bison in late 2003.

made during periodic aerial surveys (Meagher 1973, 1993, Taper et al. 2000, Meagher et al. 2002), and one specific study that examined winter movements in the Firehole-Madison-Norris area (Bjornlie and Garrott 2001). Meagher (1973) summarized historical information on distribution and movement patterns of Lamar and Pelican bison prior to 1936. Bison wintered in separate areas in the central Lamar Valley and in the Pelican Valley. Some time between 1915 and 1920, the summer ranges of Lamar and Pelican bison overlapped on the Mirror Plateau and Upper Lamar drainage. The pattern was one of mixing on the summer range followed by return to the respective winter ranges in the fall or early winter. There was little evidence that Pelican Valley bison ranged into the Hayden Valley before bison were reintroduced there in 1936. Meagher (1973:31) refers to one file report containing a penciled notation about "some bison in the Hayden Valley in 1930-31".

Within a decade of the reintroduction of 35 bison into the Lower Geyser Basin at Fountain Flats and 36 into the Hayden Valley in 1936, winter movements between the Hayden Valley and the Firehole were noted. McHugh (1958) reported 54 bison moved 10 km over the Mary Mountain Trail through 107 cm of snow in March 1945. As the number of bison in the Hayden Valley and the Firehole increased the areas they occupied increased and movements between ranges occurred during all seasons including the rut. The herds were considered merged into one population first given the cumbersome name of the Hayden Valley-Nez Perce-Firehole herd (Franke in press). It was later dubbed the Mary Mountain herd, referring to the height of land between the two ranges over which bison maintain a trail (Meagher 1973: 86).

Frequent interchanges between the Lamar and Pelican populations were evident from survey data. Meagher (1973: 87) noted significant shifts between these populations during 6 of 15 years between 1935 and 1950 when decreases in the number of bison on Lamar winter range coincided with increases in Pelican Valley or vice versa. Meagher (1973) explained that such shifts occurred less frequently (2/15 years: 1941 and 1946) between the Pelican and Hayden Valleys during the same period. In the harsh winter of 1956 a mixed herd of about 24 bison broke a trail from the Pelican Valley to the Hayden Valley through deep snow along the east side of the Yellowstone River (Meagher et al. 2002:140). Notably, the number of bison counted in the Pelican Valley that year was approximately the same as the number present in the early 1980s when bison from the Pelican Valley were again observed to move in winter to the Hayden Valley (Meagher 1993). Movement of a significant number of bison into the Pelican Valley was suspected in 1964-65 (Meagher 1973: 88).

As the Mary Mountain and Pelican Valley populations increased after 1970, the area they occupied gradually increased, eventually coalesced (Figure 5.14), and movements between ranges became fluid throughout the year, including the winter. Consistent with the high rate of bi-directional movement observed in winter over the Mary Mountain Trail connecting Hayden Valley and the Firehole (Bjornlie and Garrott 2001), VHF radio collared bison were documented moving between the Pelican and Hayden valleys continuously in most seasons during 1997-1998 and 1998-1999 including the winter months[10]. The movements of radio collared bison during mid summer 1998 and 1999 were consistent with the observation by Meagher et al. (2002) that Pelican Valley bison

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[10] P. Gogan and E. Olexa of the U.S. Geological Survey monitored the movements of 103 radio collared bison during 1997 - 1999

no longer moved up into the Mirror Plateau and slopes of the Absaroka Mountains where they previously had shared summer range with the Lamar herd for > 60 years. However, in 1998 and 1999 some radio collared bison moved to the Mirror Plateau from the Pelican Valley in the fall, after the rut[11]. The Central Range subpopulation, including the Pelican Valley herd, has developed a pattern of nearly exclusive aggregation in the Hayden Valley during the rutting season (Figure 5.19).

The scale of movements dramatically changed with population size. Although Central Range bison return to the Hayden Valley for the rut, the scale of movements in other seasons is extensive. Individual radio collared bison may move from the Hayden Valley to the western and the northern boundaries within the same year. Examples from recently GPS collected collar data[12] illustrate some of the variety of individual movements occurring in the Central Range (Figure 5.20 – 5.24). One cow remained entirely within the Mary Mountain range (Figure 5.20). Another included the Madison Valley and habitat in the western boundary area (Figure 5.21). Three others included parts of the Northern Range (Figure 5.22 – 5.24). The last two movement patterns (Figures 5.23 and 5.24) illustrate novel movements between Canyon Junction and Norris Junction and from Norris Junction north to Blacktail Deer Plateau following routes not identified by key informants in this study.

The data now being obtained from GPS collars will allow key questions about movement ecology to be addressed, including the timing and extent of movements in relation to plant phenology, snow conditions, forage production and utilization. In addition, with this technology research is now possible to address questions about the effects of roads and other anthropogenic or natural features on movements about which some uncertainty remains.

The influence of roads on movements has been questioned since the early 1990s (Meagher 1993; Meagher et al. 2002). Evidence presented above for the Northern Range indicates that population size above a threshold of about 550 is a driver of movement to lower elevation range in the Gardiner basin and egress is positively correlated with snow pack (SWE). A large proportion of the population has been documented to move to the Gardiner basin in harsh winters when the population exceeds 550. Roads were plowed in the Northern Range starting in the late 1940s. Bison follow either the plowed road or a natural corridor along the Yellowstone River (Figure 5.1). Stress induced movement to the Gardiner basin along the Yellowstone River corridor was documented before road plowing began (Cahalane 1944*b*); at 750 head in winter 1942-1943. It is evident that closure of the road in winter will not prevent movements of bison to the Gardiner basin. Indeed, 12 years of attempting to control and contain bison movements failed, e.g. bison detoured around obstacles placed along the corridors (Meagher 1989*a*). The Gardiner basin is at the lower end of an ecological gradient. It can be considered refuge habitat in harsh winters much the same as geothermal habitat serves this ecological role for bison in the Central Range. Bison are familiar with the Gardiner basin (Meagher 1989*b*) and there are no evident biophysical barriers to movement. Under current management, a large proportion of the Northern herd could be subject to removal in a harsh winter, particularly if bison from the Central Range arrive early and defined thresholds for

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[11] *supra* note 11

[12] To illustrate types of movements currently occurring we selected GPS location data for 5 of 13 bison provided by R. Wallen of NPS/YCR on February 25, 2005.

holding and tolerance of free-ranging bison are reached before Northern Range bison arrive. The bison population on the Northern range has existed as a semi-independent subunit and exhibits biological traits distinctive from Central range bison[13], including genotypes (Halburt 2003), fetal growth rates (Gogan et al. accepted, revision submitted), and tooth wear patterns (Christainson et al. *in press*). Assessment of an objective minimum viable population for the Northern Range is an important outstanding task under the adaptive management intent of the current bison management plan.

Under current policies, range expansion beyond the boundaries is limited by management interventions, primarily culling or hazing. Tolerance for bison in the Gardiner basin and West Yellowstone areas outside the park is defined in the current management plan as the modified preferred alternative. The plan does not provide for unlimited range expansion, a density-related phenomenon. Management zones 2 and 3 outside the western boundary of YNP have 25 km^2 and 7.3 km^2 of bison habitat, which if available could support 100 and 29 bison respectively at the instantaneous density typical of Central Range bison. Management zones 2 and 3 outside the Northern boundary offer 17.6 km^2 and 83.3 km^2 of habitat and would support 56 and 266 bison respectively at the typical winter density of the Northern Range bison subpopulation. We consider the Gardiner basin to be refuge habitat and an important component of the Northern winter range.

In contrast, the Hebgen Lake area offers no unique ecological value as winter range; we consider it an expansion area for the Central subpopulation. Even if this area is used to capacity, at densities above 4 /km^2 bison would continue expanding into adjacent range to equalize density, if permitted to do so. In 2003, in an effort to create winter range opportunities for bison where there are no conflicts with livestock, the National Wildlife Federation paid two Idaho based ranchers for their grazing rights to an allotment in the Caribou-Targhee National Forest, thus providing an alternative for cattle grazed in the Horse Butte grazing area[14]. Even if additional habitat is acquired in this area and bison are permitted to occupy it, the question remains about the extent to which continued range expansion is desirable in this area of Montana; moving the boundary will simply delay the required debate, but not for long.

Under the Interagency Bison Management Plan, state and federal agency officials either haze bison that leave YNP back into the park, or bison are captured and tested for brucellosis and those testing positive are slaughtered. Removals at the boundary temporarily reduce the density of the park population, diminishing the magnitude of density dependent effects on survival and reproduction from resource limitation within the park bison ranges. Either range expansion or removals at the boundaries compensate for forage limitation effects within the park on fecundity and particularly juvenile survivorship. Hazing bison back into the park should result in maintaining density dependent effects caused by exploitative competition. The additional energetic cost induced by hazing should accentuate the negative effects of resource limitation for bison

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[13] Interview with Peter Gogan, USGS and John Gross, NPS, 21 July 2004.

[14] National Wildlife Federation and the Montana Wildlife Federation. 2003. Yellowstone Bison Given More Room to Roam. Outdoor News, http://www.huntingandfishingjournal.org/archives/issues/wcr_horsebutte_ens_4-2003.php, Copyright Environment News Service (ENS) 2003. Republished with permission from ENS online at: http://ens-news.com.

exposed to this action. The ethical question of increasing physiological stress by hazing is a matter for deliberation.

Biophysical conditions are more complex in the Central Range than the Northern Range (e.g. refuge geothermal habitat is embedded within the winter range; ranges are separated by linear corridors), making it challenging to readily distinguish between the alternative hypotheses proposed by Meagher et al. (2002)[15]. The central question to be addressed is: In the absence of road grooming would bison in the original winter ranges in the Central Range (Firehole, Hayden, Pelican) have remained spatially isolated and demographically independent owing to deep snow in the movement corridors separating them?

Snow cover is an important determinant of ungulate trophic ecology, energetics, population dynamics and spatial ecology (Turner et al. 1994). Systematic research has not been carried out on the ability of bison to move through snow under the variety of circumstances present in Yellowstone National Park. All available information for YNP is anecdotal or the opinion of experts. Meagher (1973:73) commented that cow/juvenile (mixed) herds travel in line through deep snow, plunging to create trenches several feet deep, "frequently for more than a mile". In Pelican Valley bison were observed foraging through snow 102-114 cm and moving to areas with lower snow cover when depths exceeded 127 cm (Meagher 1971). Snow depths in interior YNP exceed those recorded for bison ranges in Elk Island National Park (< 70 cm, Van Camp 1975) and the Slave River Lowlands (< 65 cm, Reynolds and Peden 1987), hence data from those studies provide little inference about maxima at which foraging or movements become severely restricted. Van Camp (1975) suggested impediment of movement by adult bison starts at snow depths < 65-70 cm. For their model, Turner et al. (1994) used a maximum depth of 180 cm at which foraging ceased, based on expert opinion.

We inferred from the available information, key informant interviews and technical workshops, that the factors influencing movements important for designing research include the following:

- snow depth, density, and hardness (crusting);
- terrain (slope, ruggedness);
- habitat, including forage attributes (species, biomass, quality), patch size and dispersion;
- geothermal influence on snow depth and dispersion of low snow patches or linear thermal features such as streams;
- class of bison (e.g. mixed groups vs. mature bulls);
- group size of moving bison, and their behaviour (dominance and changing lead);
- distance attributes, e.g. length of the corridor between origin and destination ranges;
- index of bison condition;
- familiarity with destination;
- quality of destination;

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[15] Meagher et al. (2002:145) proposed 1) winter road grooming facilitated range expansion that "would have occurred anyway", or 2) alternatively, "an apparently minor change [road grooming] has upset a delicately balanced demography and caused the expansion".

- trails broken previously by bison moving in the corridor;
- number of bison on either side of a corridor; and
- per capita forage availability in ranges on either side of a corridor.

Three studies on use of groomed roads by bison and interactions with Over Snow Vehicles (OSVs) have been conducted in Yellowstone National Park in recent years (summarized in Appendix III). There is sufficient evidence from these studies and other sources (e.g. Meagher 1993) to conclude that groomed roads facilitate travel within traditional foraging areas and between ranges, where they are present. However, bison appear to use sections of road in winter where they are convenient. As a testable hypothesis we suggest bison do not typically use roads where they are not aligned with pathways that can be predicted based on terrain and habitat features and bison behaviour. Consistent with this hypothesis, bison rarely use the following groomed road sections: Canyon to Norris; the east entrance road to Sylvan Pass; the south entrance road south of Old Faithful; or the western half of the groomed road between Seven-Mile Bridge (on the Madison River) and West Yellowstone. Friction modeling is one method that can be used to predict movement pathways for bison based on preliminary information or expert opinion (Gates et al. 2001). Such modeling would allow comparison of pathways predicted based on decision rules in the virtual absence of roads with actual pathways selected by bison under varying conditions (GPS locations) including groomed roads.

The Pelican to Hayden Valley corridor has been of particular interest to some stakeholders. At 8.3 km, this corridor is the shortest of the Central Range corridors (Figures 5.1, 5.25); by comparison, the Mary Mountain Trail is 19 km. There is slightly more habitat in the Pelican-Hayden corridor than the Mary Mountain Trail (51% vs. 44%), and less snow on average (SWE 13 vs. 20 cm). The west face of Mary Mountain represents a long, steep incline while there is little elevation gradient in the Pelican-Hayden corridor. Other than the greater amount of geothermally influenced terrain in the Mary Mountain Trail we see no reason to consider the Pelican-Hayden less permeable than the Mary Mountain Trail, indeed it appears more permeable. It is instructive to repeat that in winter 1956, long before roads were groomed, a mixed group of about 24 bison was observed to break trail in the deep snow through the Pelican-Hayden corridor (McHugh 1958). Meagher (1993:12) also observed a major trail in unconsolidated snow along the east side of the Yellowstone River in winter 1991-1992. In August 2005, we observed a well used bison trail on the power line located < 1km west of the Yellowstone River in the Pelican-Hayden corridor (Figure 5.25). Open linear features such as this have been observed to influence movements of other ungulate species. Their influence on bison movements in any season in YNP has not been examined.

Roads were used by snow coaches (heavy tracked vehicles) many years before road grooming began. The first permit for a snowcoach operator to bring tourists intoYNP (Yochim 1998*a*) was granted to a businessman in West Yellowstone in 1955 (Aune 1981, Bjornlie and Garrott 2001). The packed snow in the trails of these vehicles would have had snow hardness similar to groomed road surfaces and could have provided movement pathways for bison. Cheville et al. (1998) questioned why groomed roads were not used by bison for inter-range movements when first available in the Central Range. They suggested the delay may have been due to a threshold density effect above which expansion to new ranges occurred and population pressure induced bison to maintain pathways between ranges. They explicated that attributing population increase to road grooming rather than the use of groomed roads to population pressure reverses cause and effect. Given the evidence, we concur for the most part with their assessment. However, groomed roads may have induced range expansion and development of a migration corridor by the Central subpopulation into the Northern Range along the Madison Junction to Swan Lake Flats corridor section where in the absence of road grooming, snow and topography of the Gibbon Canyon could otherwise have been a barrier to movement.

There is however some uncertainty about the nature of the effect of the Gibbon Canyon section of the corridor that cannot be resolved without further study. Key informants expressed conflicting opinions about the effect that closing the road to grooming would have on bison migrating to the Northern Range. Some commented that despite the rugged terrain in Gibbon Canyon, the geothermally influenced drainage provides reduced snow depth and affords opportunity for bison to navigate through the canyon, a distance of approximately 6 km (Figure 5.26). Most suggested that in the absence of road grooming, bison would not be able to push through deep snow on the road allowance in the canyon. The areas surrounding the canyon are steep and heavily forested and appear to offer limited potential for winter movements. A power line located approximately 1 km east of the road could provide an alternative pathway (Figure 5.26). In August 2005, we walked the power line to determine if it was used by bison and found no evidence to suggest it is used in the winter; there were few droppings and all appeared to be loose stool typical of summer rather than well formed droppings characteristic of winter. We concluded the power line is not currently used by bison moving to and from the Gibbon and Norris Geyser Basins in winter and there is very limited use of the power line in other seasons at the present time.

Despite the absence of specific research on bison movements in snow, we consider there is sufficient anecdotal evidence to suggest that once bison are familiar with destination ranges within the Central Range, range expansion will occur as a function of population size. If numbers are sufficient, bison will maintain trails (trenches in the snow) in most corridors, except the Pelican-Lamar and Firehole-Northern Range corridors, in the absence of road grooming, and movements between Central ranges will be fluid. However, the ability of bison to move through the Gibbon Canyon and further north to the Mammoth area in the absence of road grooming is an important consideration. The Gibbon Canyon could serve as a topographic gate preventing Central Range bison from migrating to the Northern Range once snow accumulates. Given the large number of Central Range bison moving in some years to the north boundary and the potential consequence for inequitable culling of the Northern subpopulation, the role the Gibbon Canyon as a potential barrier to movement is an important research question.

Finally, it is necessary to comment on the hypothesis that groomed roads reduce the energy cost of displacing snow during movements within and between winter ranges and energy saved from the reduced cost of locomotion mitigates winter kill and enhances calf survival, resulting in a higher rate of population increase than would otherwise occur (Meagher 1993). The effect, if any, was not registered in a detectable difference in the rate of increase in the Pelican Valley population during long periods before and after road grooming occurred (Figure 5.4). Bjornlie and Garrott (2001:560 and 570) posited that any energy saved by not displacing snow during travel on roads may be countered by losses associated with stress induced by a high encounter rate with OSVs. The proposed mechanism for this hypothesis is complex and it would be difficult if not impossible to design an experiment(s) to test it. However, it is worthy of investigation through systems modeling, the subject of the next chapter.

Conclusions

The long term data set on bison population size and distribution in an area as large as YNP spanning more than a century is unparalleled in large animal ecology. Mary Meagher is to be credited with compiling much of the available data, first in her seminal publication of 1973, then systematically collecting data annually for over 30 years. Her attention to detail generated a data set for the period 1970 to 1997 that is not yet fully explored. In particular, population rates of increase presented in Taper et al. (2000) should be recalculated based on annual changes in the adult population (> 1 year old), rather than on the maximum annual count, to account for variation in annual productivity (calves/100 cows) related to winter severity and previous summer forage production. Since 1997, population monitoring has been somewhat inconsistent and data do not provide the same opportunity for continued analysis. A population monitoring program is needed that will provide for: 1) annual estimates of adult population size (< 1 year); 2) fecundity (calf production); 3) winter density distribution, i.e. during the period when distribution is most responsive to forage limitation; 4) inter-annual population rate of increase; and 4) seasonal and annual calf and adult mortality.

Ecological conditions are markedly different on the Northern and Central bison ranges requiring separate consideration of population and trophic ecology. On the Northern Range, reduced snow cover in the grassland habitat of the Gardiner basin provides refuge habitat for bison during harsh winters. In contrast, there is no range-wide gradient in snow conditions on the Central Range. Rather, geothermally-influenced areas provide refuge for a significant part of the Central subpopulation in harsh winters.

The data compellingly support the interpretation that YNP is a forage-limited system, where bison density coupled with snow conditions are the key drivers of bison distribution and movements. The evidence indicates that the population experiences density dependent effects on population growth despite range expansion that equalizes instantaneous density as the population increases. With two exceptions, the pattern of range expansion is gradual rather than pulsed. On both ranges, the instantaneous area occupied in winter (aerial survey data) increased linearly as a function of population size. Removals at the western and northern boundaries to control egress of bison from the park were a direct function of population size, influenced by snow conditions. The relationships were strongest for populations above 1500 for the Central Range and 550 for the Northern Range.

The only period in the Park’s history when a subpopulation may have been completely isolated and spatially independent of others was in the early years (before 1920) when the Pelican Valley population was the only free-ranging population in the park. Apparent isolation of bison in separate winter ranges when populations were small likely reflected high per capita availability forage and the low pressure to move or expand. From the evidence, we infer that as populations grew, the area they used expanded, and distributions eventually coalesced. Anecdotal information on bison movements suggests they can break trail for considerable distances through deep snow, but in addition to forage limitation, knowledge of destination is likely an important motivation. At the present time, there remain two relatively separate subpopulations, one on the Northern Range and the other on the Central Range. Some exchange has occurred since the 1920s via the Mirror Plateau. In recent years, there have been major migrations from the Central Range to Gardiner basin via the road allowance between Madison Junction and Swan Lake Flats. The Gibbon Canyon may not be navigable by bison in the absence of snow grooming.

With the possible exception of the Madison Junction Mammoth road section, road grooming likely has not induced range expansion although roads facilitate bison movements within and between winter ranges where aligned with natural movement corridors. Given the evidence, we concur with the assessments made by Cheville et al. (1998): 1); there is a threshold density effect above which expansion to new ranges occurred and population pressure induced bison to maintain pathways between ranges; and, 2) attributing population increase to road grooming rather than the use of groomed roads to population pressure may reverse cause and effect (except for the Madison Junction to Mammoth road segment). There is no evidence to suggest that groomed roads have changed population growth rates relative to what may have happened in the absence of road grooming. Furthermore, the bison population of YNP is likely approaching or has recently reached a state of dynamic equilibrium possibly not seen since the early 1800s. Conclusions formed about spatial and population ecology of bison when the population was increasing or at low densities cannot be readily applied to the dynamics of a population in dynamic equilibrium around a higher range of densities. The system is dynamic and continues to evolve, thus requiring systematic monitoring of key state variables and continuation of basic research on system properties.

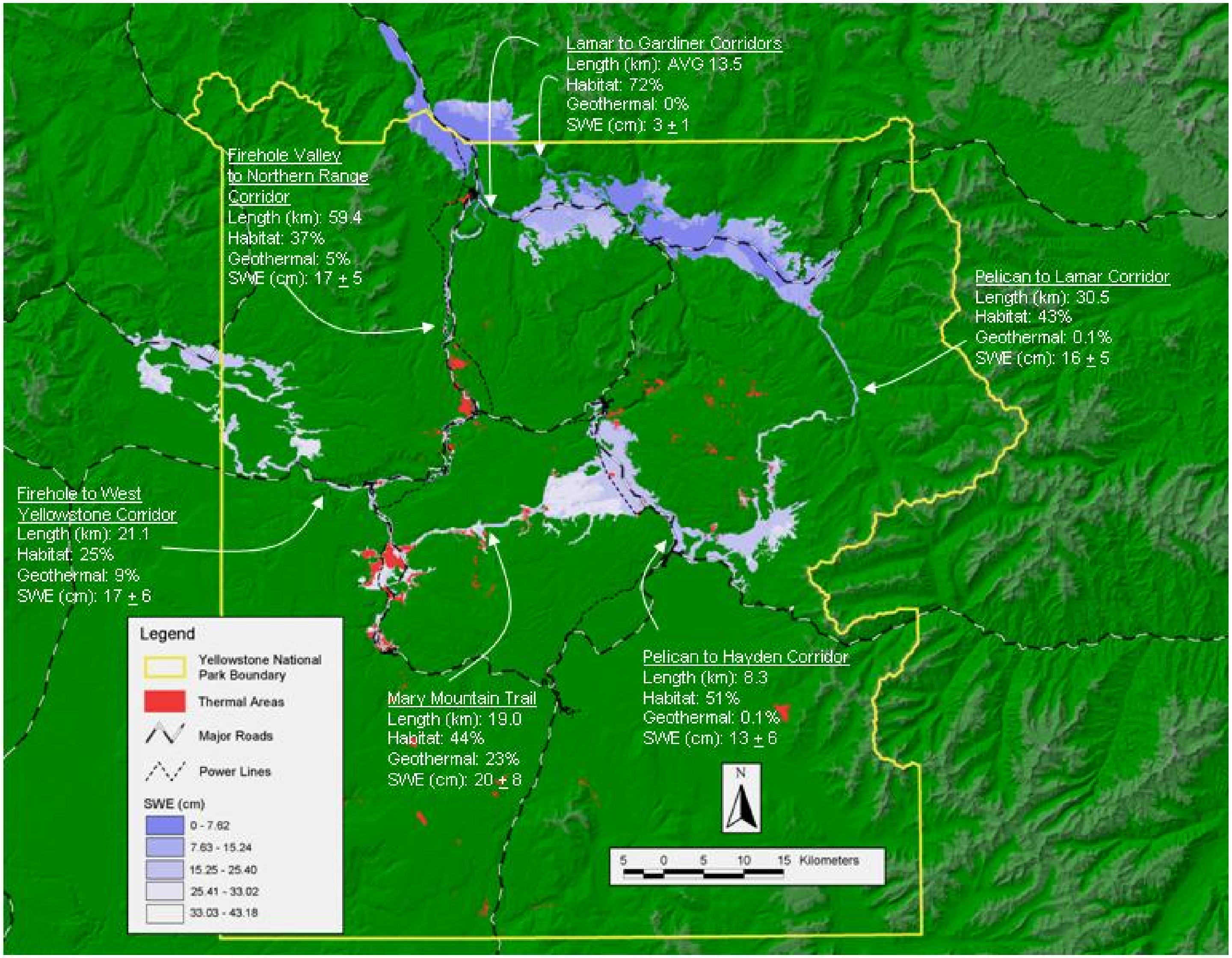
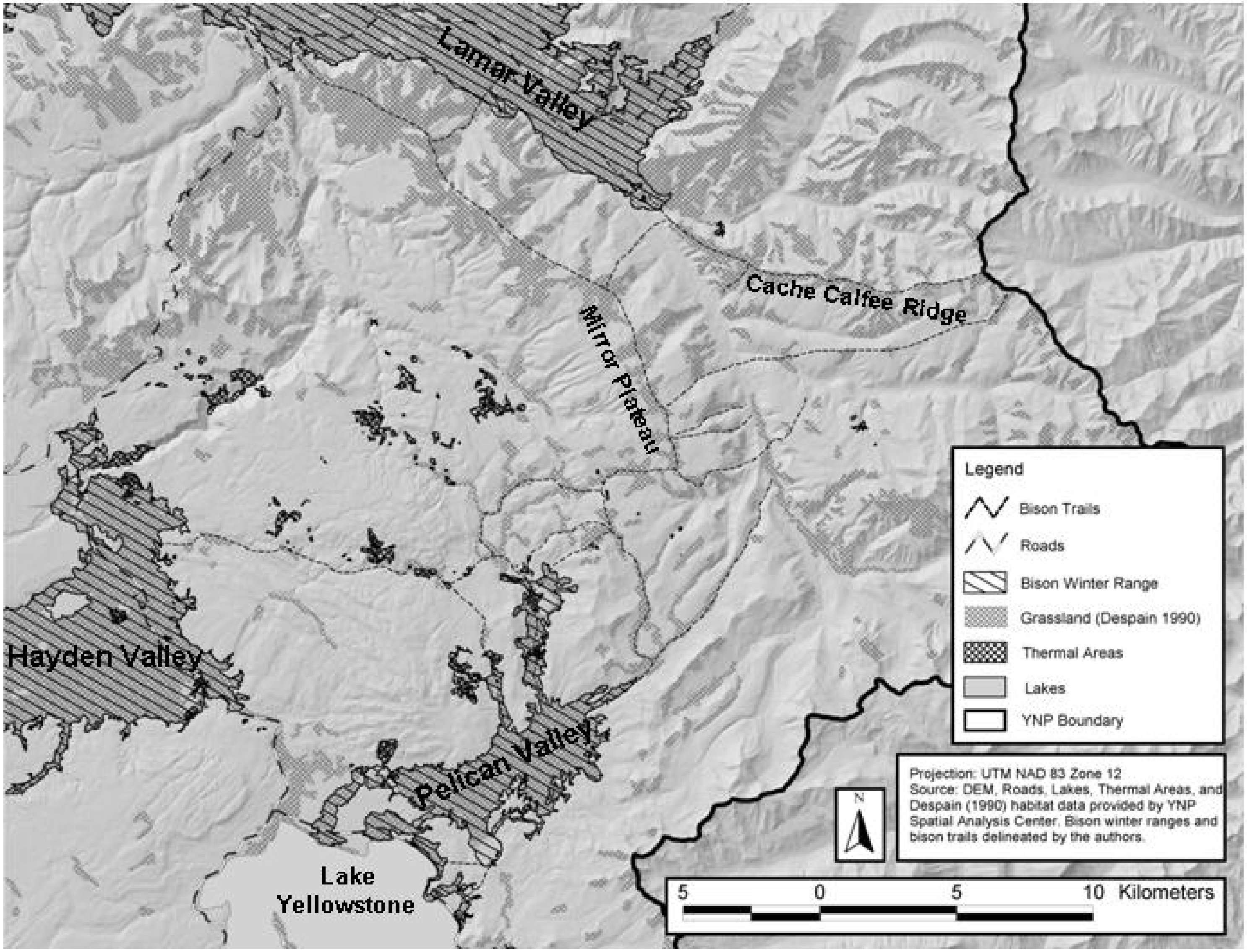


Figure 5.1 Bison winter ranges and movement corridors defined by key informants. Snow conditions (SWE in cm) are represented as shading for February 15th, 1995, an average to slightly above average winter. Corridor characteristics are indicated. SWE is the mean value of Snow Water Equivalence (SWE) on February 15th for the period 1982 to 1999 ± s.d.



Projection: UTM NAD 83 Zone 12
Source: DEM, Roads, Lakes, Thermal Areas, and Despain (1990) habitat data provided by YNP Spatial Analysis Center. Bison winter ranges and bison trails delineated by the authors.

Figure 5.2. Location of historic bison trails between, Hayden Valley, Pelican Valley and Lamar Valley mapped by Mary Meagher during an interview, July 15, 2004.

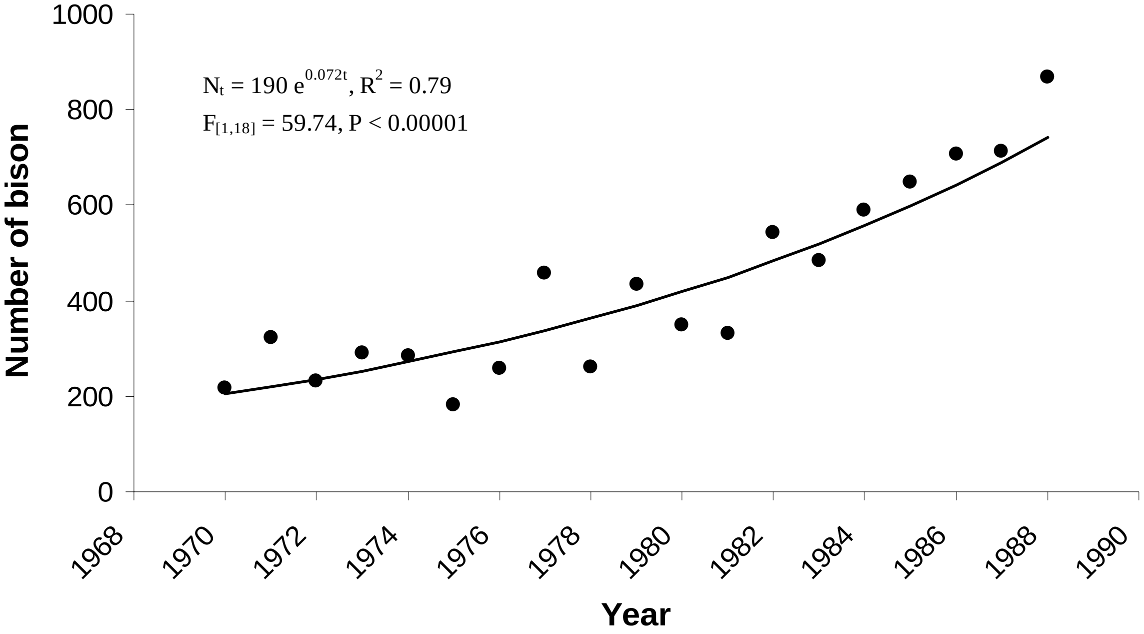


Figure 5.3. Increase in the YNP Northern Range bison subpopulation during 1970 – 1988. Data source: M. Meagher, M. Taper and C. Jerde pers. comm.

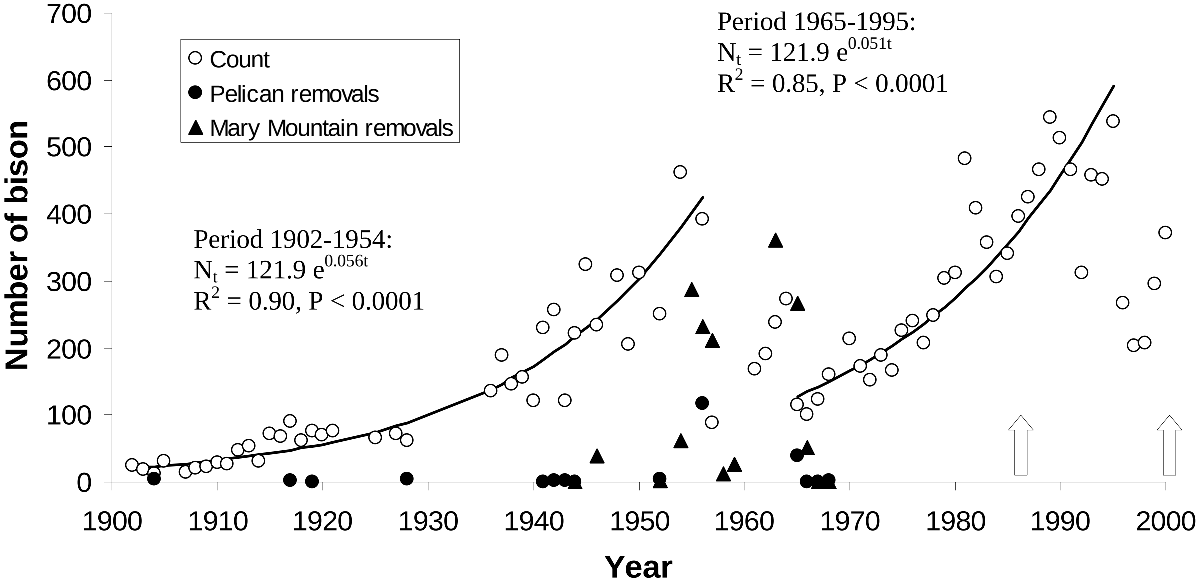
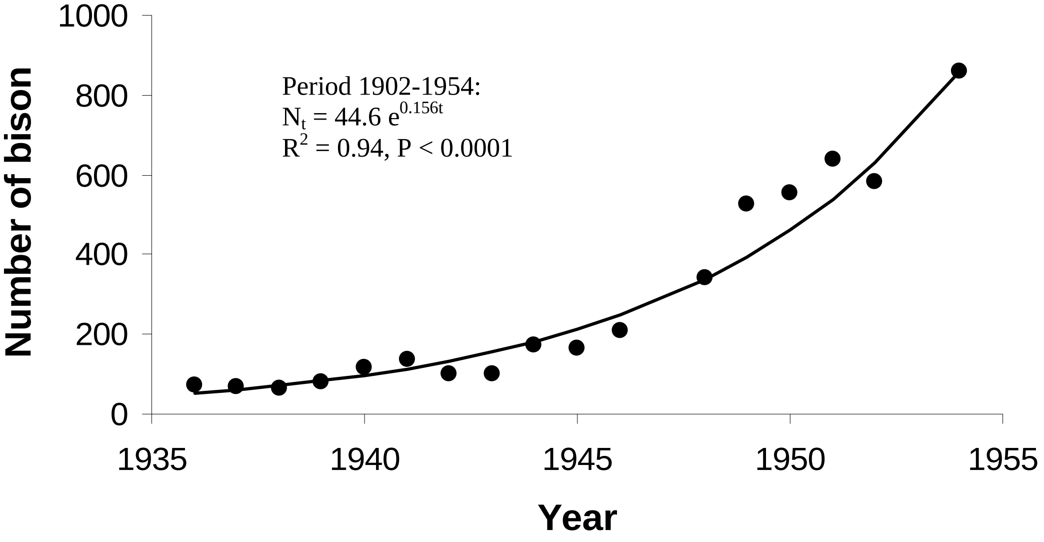


Figure 5.4. Growth of the Pelican Valley bison population during 1902 to 1997 based on mid-winter counts (data sources: Meagher 1973 for 1902 - 1968; M. Meagher, M. Taper and C. Jerde pers. comm. for 1970-1997; Hess 2002 for 1998-2000). Removals prior to the ecological management era (mostly culling and translocations) are indicated for the Pelican and other Central bison ranges. 38 bison removed in 1946 from Mary Mountain are likely those reported by Beal (1950) as falling through the ice on the Yellowstone River. The arrows indicate the harsh winters of 1981/82, 1995/96 and 1996/97. In the latter winter > 1,000 bison were removed at the boundaries of the park. Exponential rates of increase (r) of the Pelican Valley population (mid-winter counts) did not differ between the periods 1902-1954 and 1965-1995 (t = 1.762, 37 df).



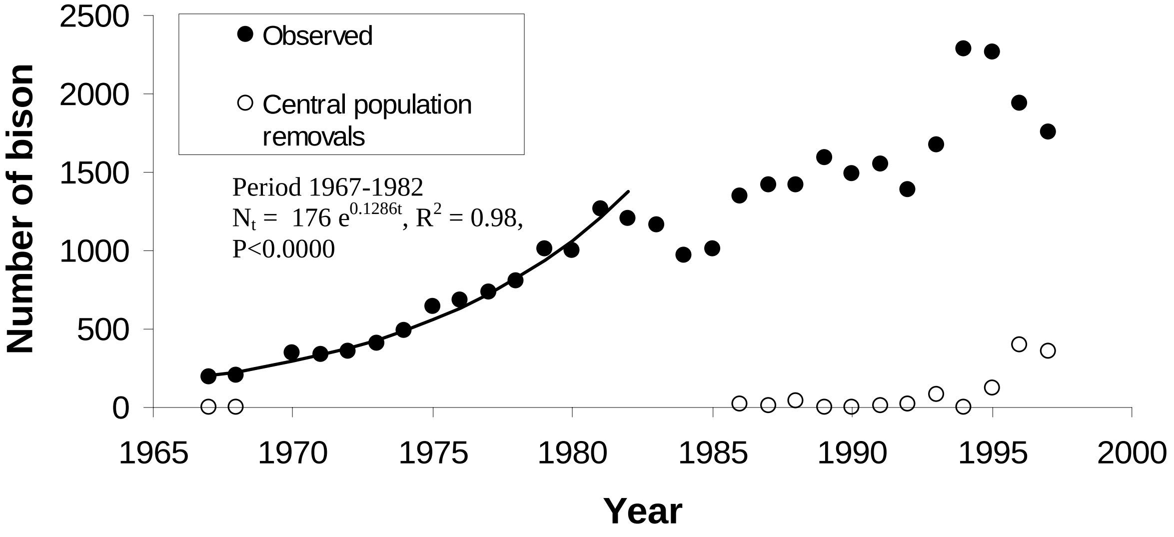


Figure 5.5. Growth of the central bison population excluding bison enumerated in the Pelican Valley during the periods 1935-1954 and 1967 to 1997. Equations represent growth of the population during the periods 1936-1954 (top graph) and 1967 to 1982 (bottom graph

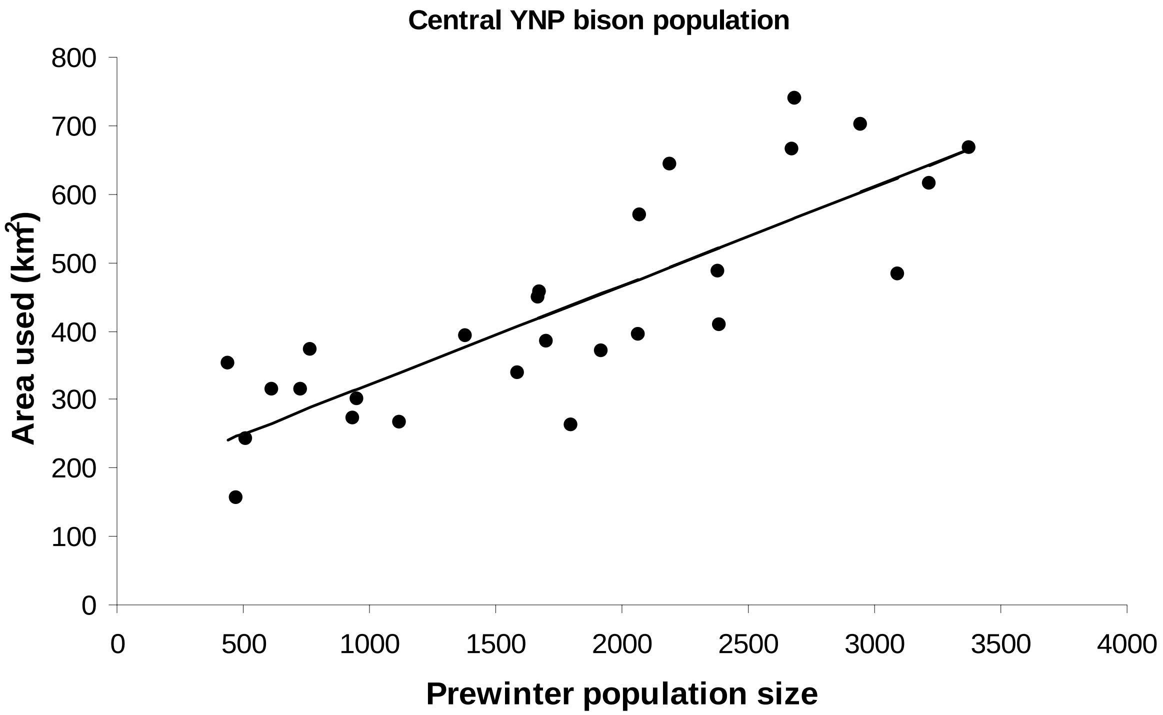


Figure 5.6. Relationship between the instantaneous area occupied (95% kernel; Taper et al. 2000) and prewinter population size for the Central YNP bison population. $Y = 177.2 + 0.140\ CPOP$, $R^2 = 0.666$, $P < 0.0001$.

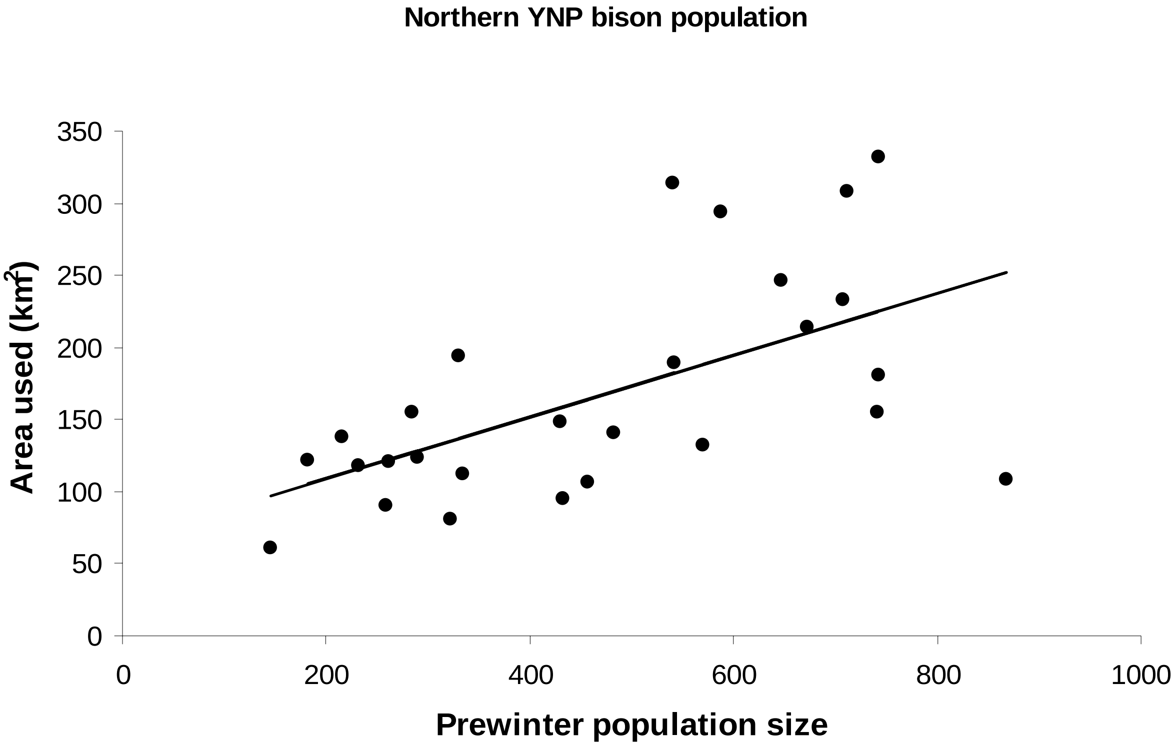


Figure 5.7. Relationship between the instantaneous area occupied (95% kernel; Taper et al. 2000) and prewinter population size for the Northern YNP bison population. Y = 66.9 + 0.316 NPOP, $R^2 = 0.316$, P = 0.0013.

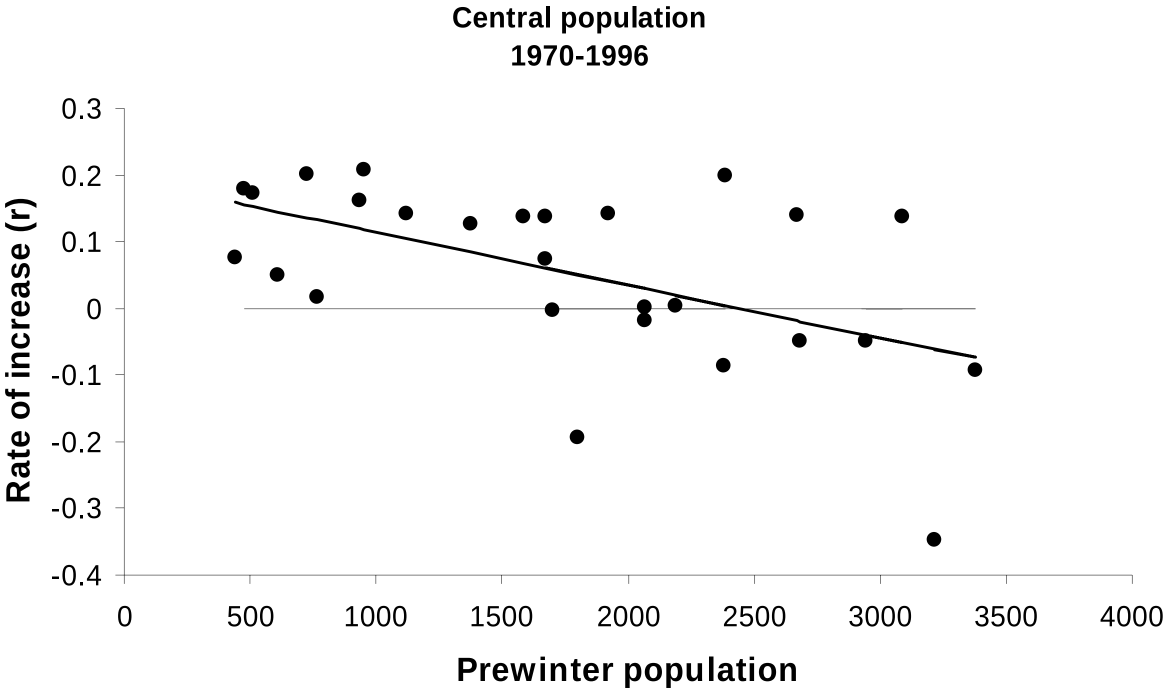


Figure 5.8. Relationship between the rate of increase (r) (Taper et al. 2000) and prewinter size of the central bison subpopulation: $Y = 0.193 - 0.000079\ CPOP_{max}$, $R^2 = 0.29$, $P = 0.0038$.

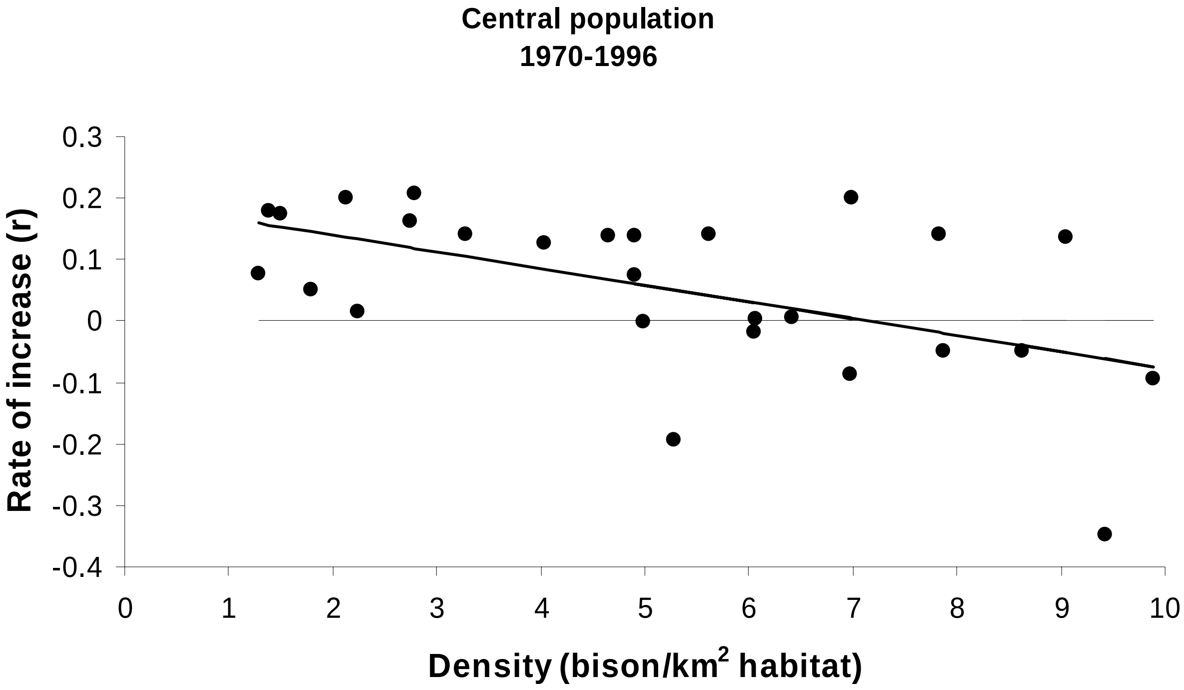


Figure 5.9. Relationship between rate of increase (r) (Taper et al. 2000) and density of the central bison subpopulation where density was calculated from the maximum number of bison counted in the central range prior to winter and the area of grassland habitat present in the maximum winter range area used by the population: Y = 0.193 – 0.0271 Density, R^2 = 0.25, P = 0.0038.

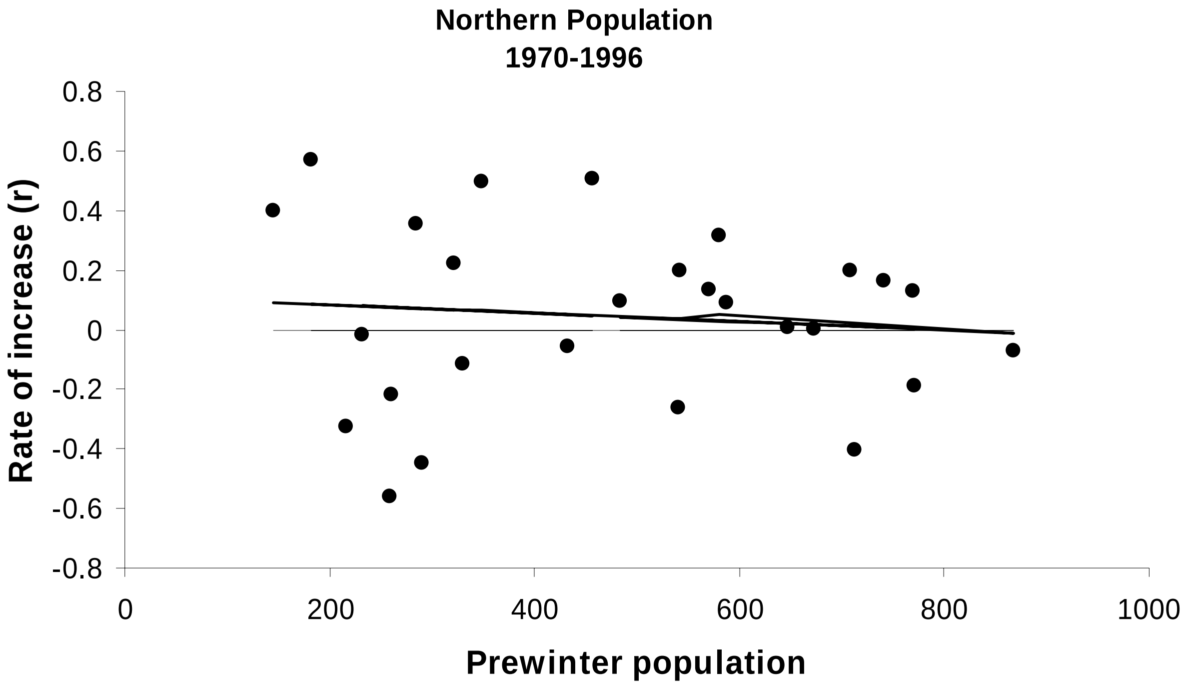


Figure 5.10. Relationship between the rate of increase (r) (Taper et al. 2000) and prewinter size of the northern bison subpopulation. The relationship was not significant ($F_{[1,25]}$ = 0.24, P = 0.63).

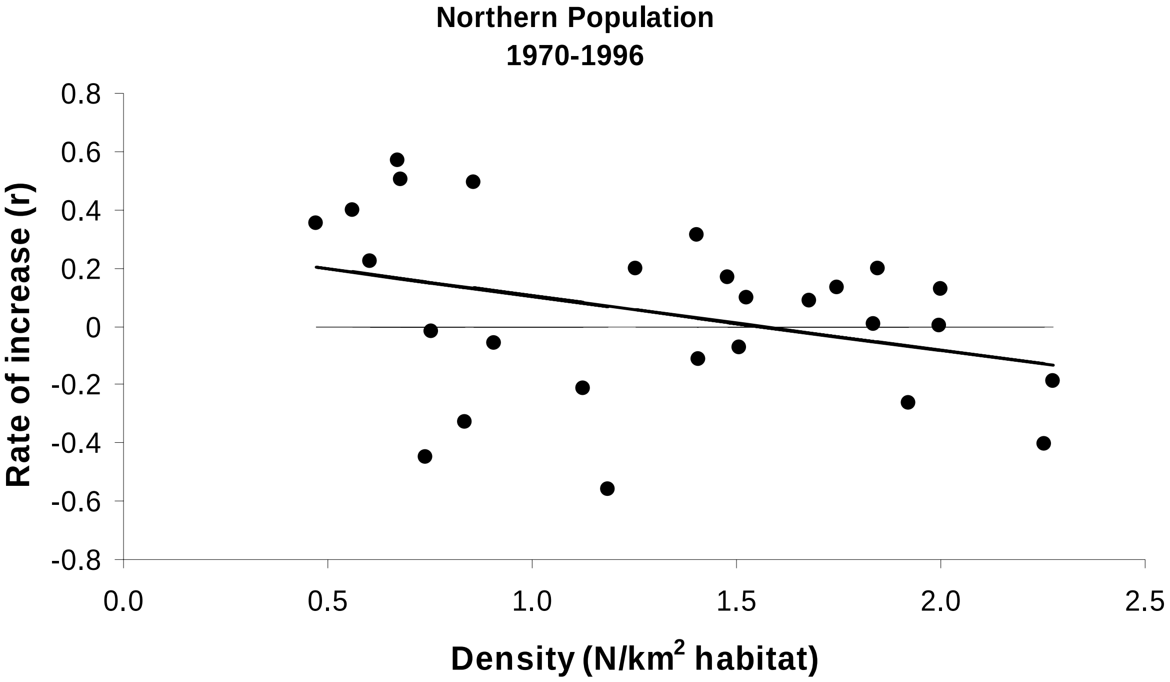


Figure 5.11. Relationship between rate of increase (r) (Taper et al. 2000) and density for the northern bison subpopulation where density was calculated from the maximum number of bison counted on the Northern Range prior to winter and the area of grassland habitat present in the winter range of the population. The relationship approached significance: $Y = 0.291 – 0.1869$ Density, $R^2 = 0.12$, $P = 0.0754$.

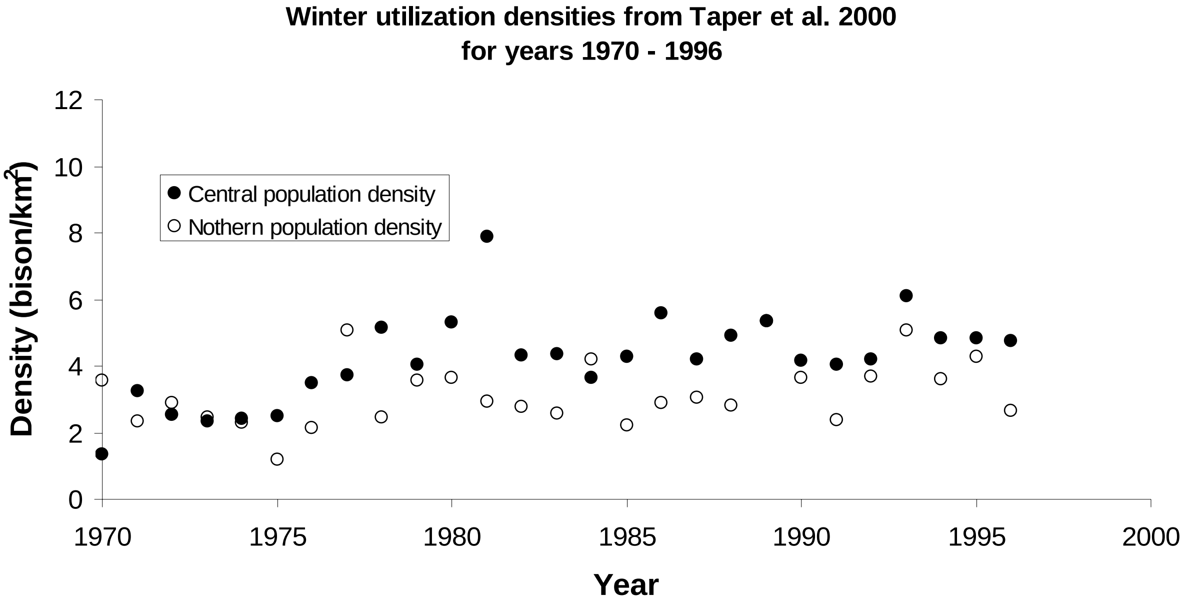


Figure 5.12. Trends in bison density (bison/km^2) calculated from the number counted within the observed 95% probability distribution in mid-winter in the Northern and Central Ranges of Yellowstone National Park between 1970 and 1996 based on Tables A2 and A3 presented in Taper et al. (2000).

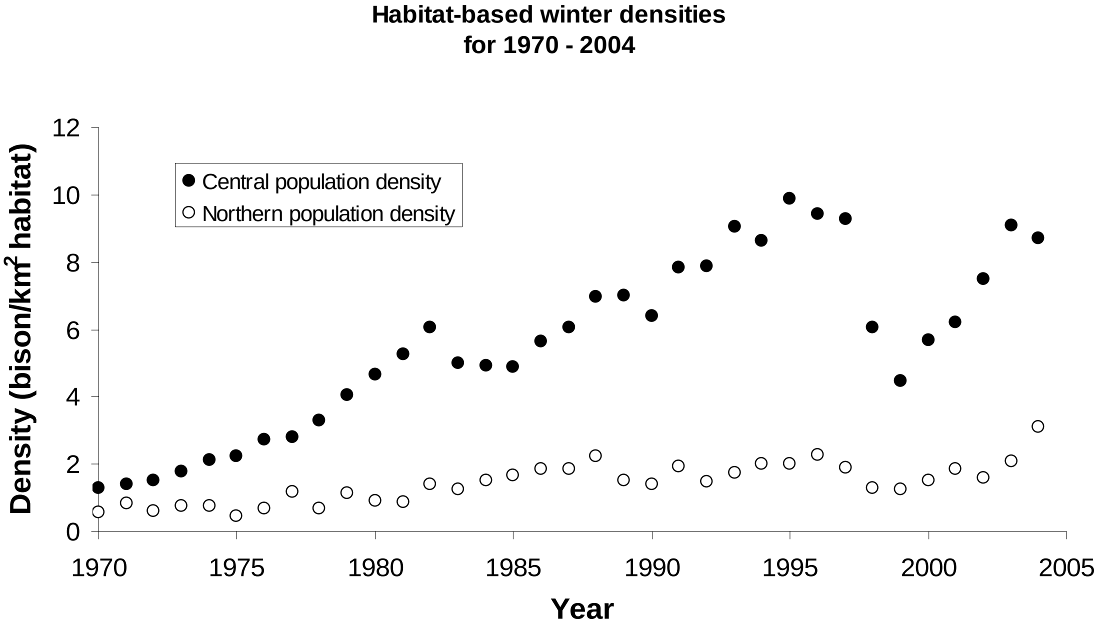


Figure 5.13. Density trends of the Central and Northern Range bison populations where density was calculated from the maximum number of bison counted in the range prior to winter and the area of grassland habitat present in the winter range of the population.

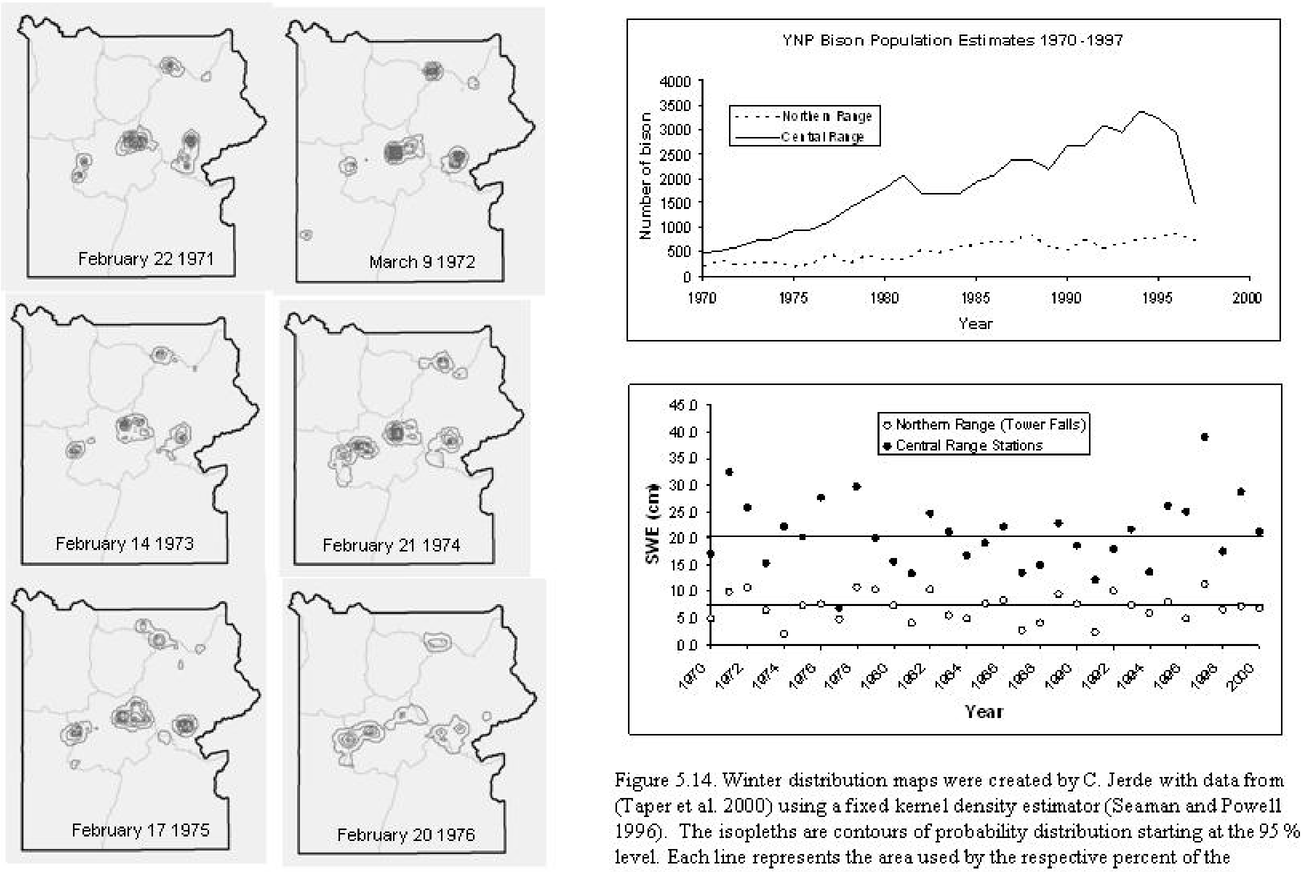
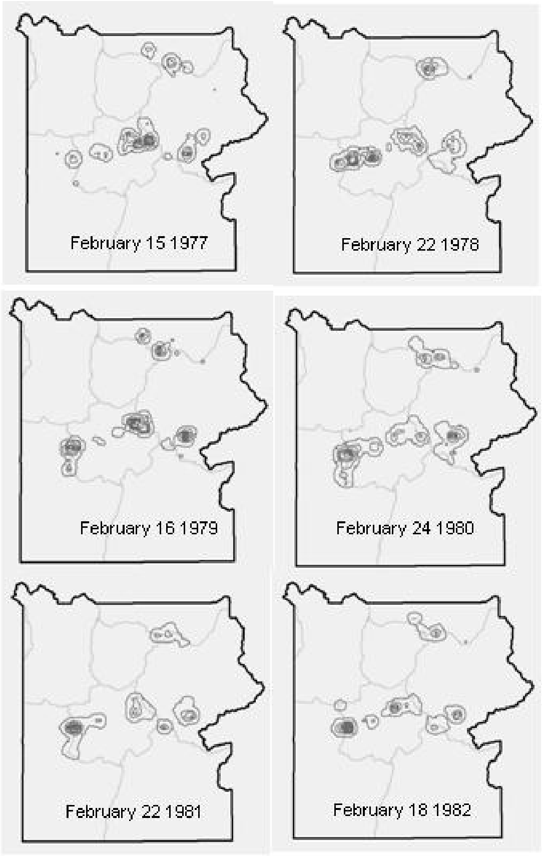
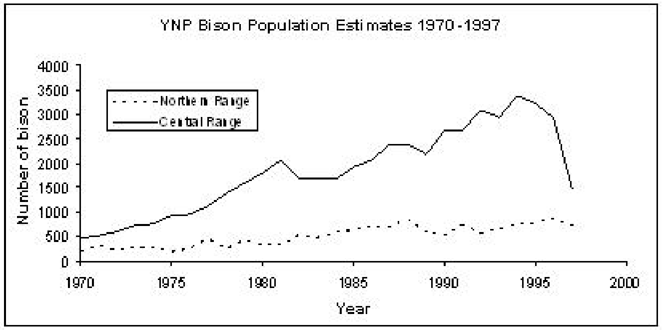
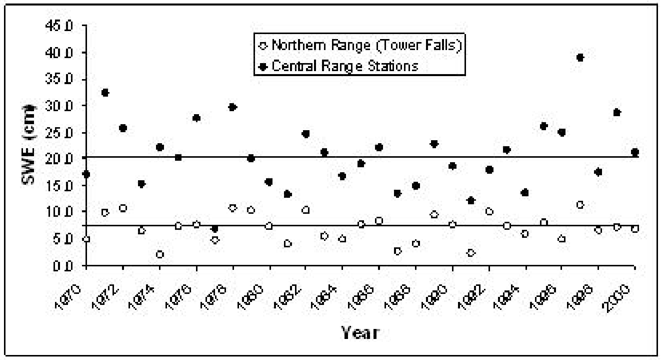
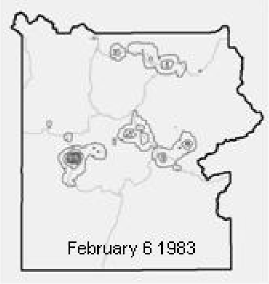


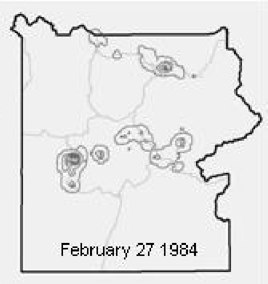
Figure 5.14. Winter distribution maps were created by C. Jerde with data from (Taper et al. 2000) using a fixed kernel density estimator (Seaman and Powell 1996). The isopleths are contours of probability distribution starting at the 95 % level. Each line represents the area used by the respective percent of the population. Jackknife cross validation was used to optimize the routine.

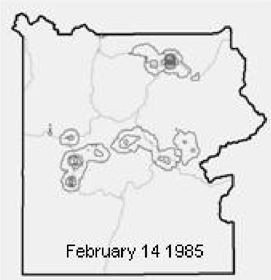

February 15 1977
February 22 1978
February 16 1979
February 24 1980
February 22 1981
February 18 1982


YNP Bison Population Estimates 1970-1997
Number of bison
4000
3500
3000
2500
2000
1500
1000
500
0
1970
1975
1980
1985
1990
1995
2000
Year
Northern Range
Central Range

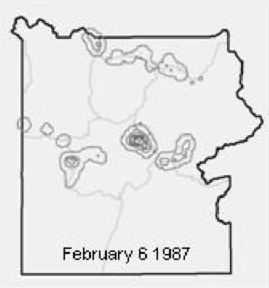

SWE (cm)
45.0
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
○ Northern Range (Tower Falls)
● Central Range Stations
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
Year

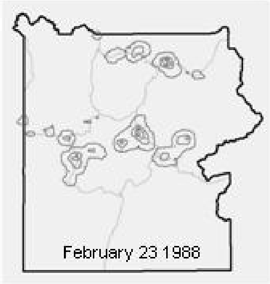

February 6 1983

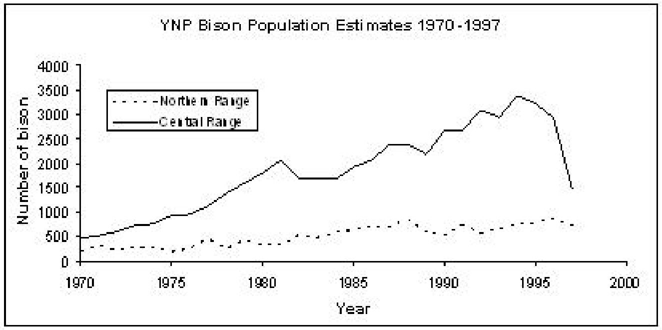

February 27 1984

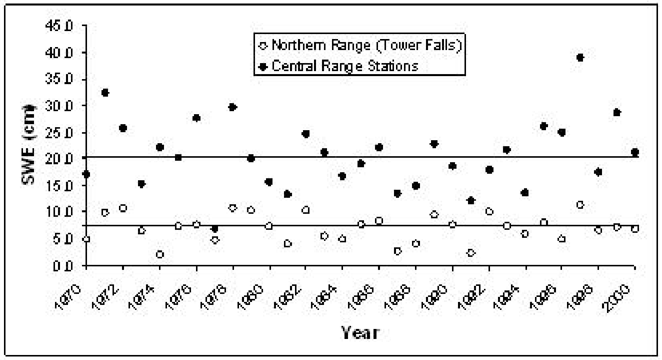

February 14 1985


February 11 1986


February 6 1987


February 23 1988


YNP Bison Population Estimates 1970-1997
Number of bison
4000
3500
3000
2500
2000
1500
1000
500
0
Northern Range
Central Range
1970
1975
1980
1985
1990
1995
2000
Year


SWE (cm)
45.0
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
Northern Range (Tower Falls)
Central Range Stations
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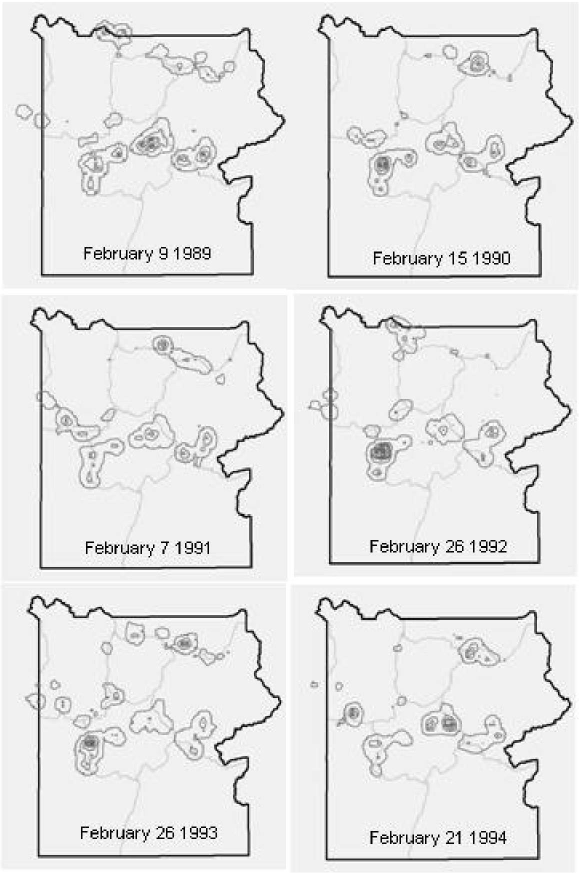
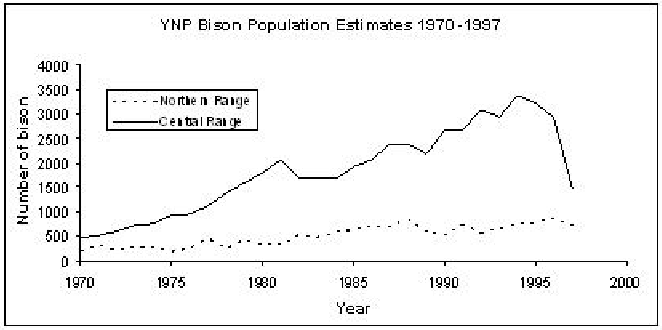
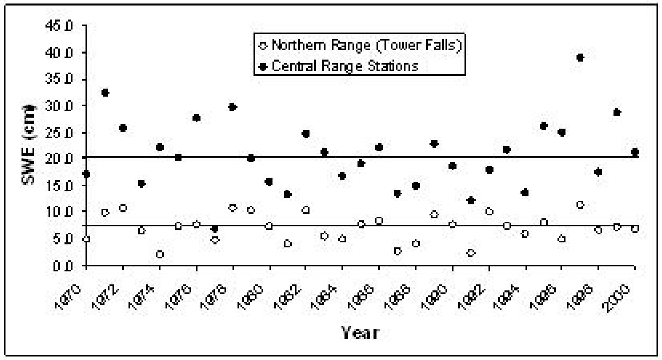
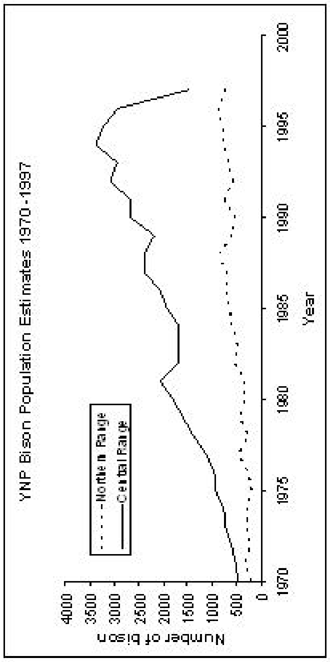
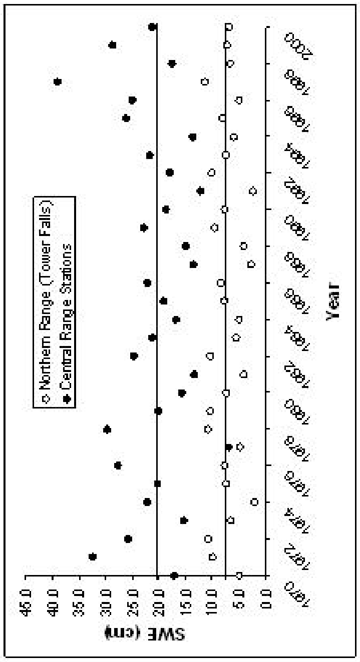
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
Year

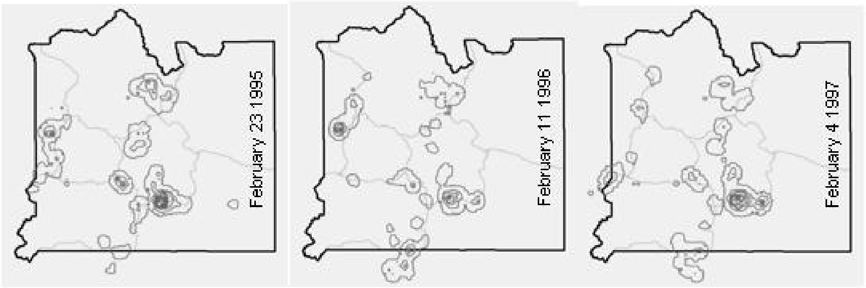

February 9 1989
February 15 1990
February 7 1991
February 26 1992
February 26 1993
February 21 1994


YNP Bison Population Estimates 1970-1997
Number of bison
4000
3500
3000
2500
2000
1500
1000
500
0
Northern Range
Central Range
1970
1975
1980
1985
1990
1995
2000
Year


SWE (cm)
45.0
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
Northern Range (Tower Falls)
Central Range Stations
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
Year


YNP Bison Population Estimates 1970-1997
Number of bison
4000
3500
3000
2500
2000
1500
1000
500
0
1970
1975
1980
1985
1990
1995
2000
Year
Northern Range
Central Range


SWE (cm)
45.0
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
Year
○ Northern Range (Tower Falls)
● Central Range Stations


February 23 1995
February 11 1996
February 4 1997

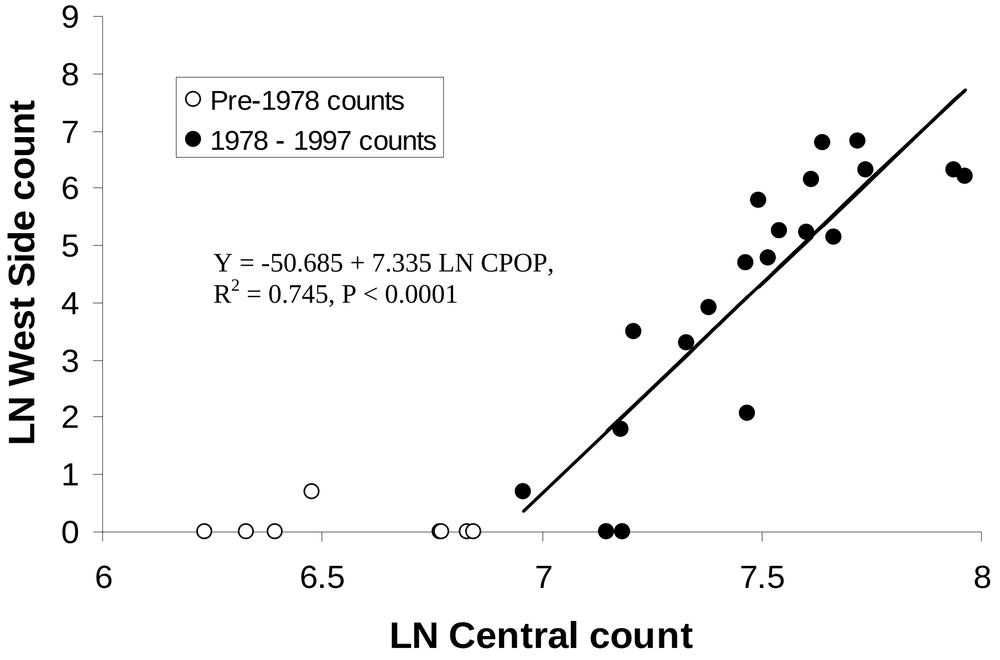


Figure 5.15. Relationship (natural log values) between the number of bison counted in the Central Range (includes West Side) and the number counted on the West Side of YNP for the years 1970 to 1997. Data source: M. Meagher, M. Taper and C. Jerde pers. comm.

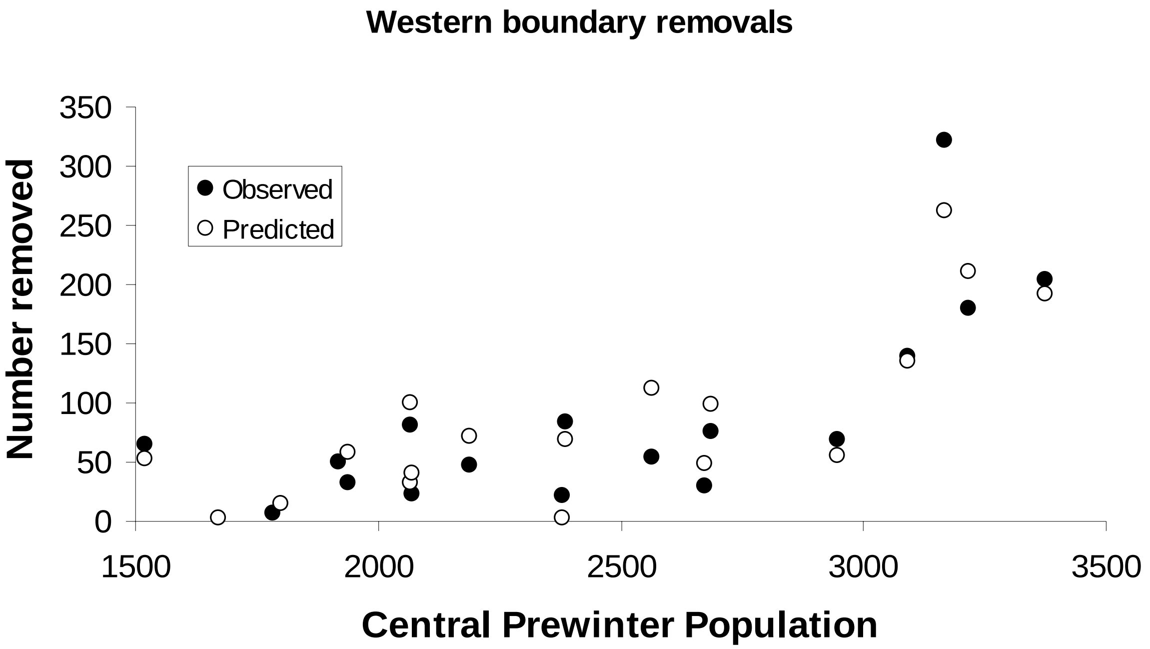


Figure 5.16. Bison removals at the western boundary of Yellowstone National Park in relation to the number of bison on Central Ranges prior to winter in years when the population exceeded 1500. Y = -312 + 0.91 CPOP + 9.58 SWE, $R^2 = 0.576$, $P < 0.001$, where SWE is average snow water equivalence (cm) at Central Range meteorological stations in mid-February, and NPOP is the number of bison on Central ranges prior to winter.

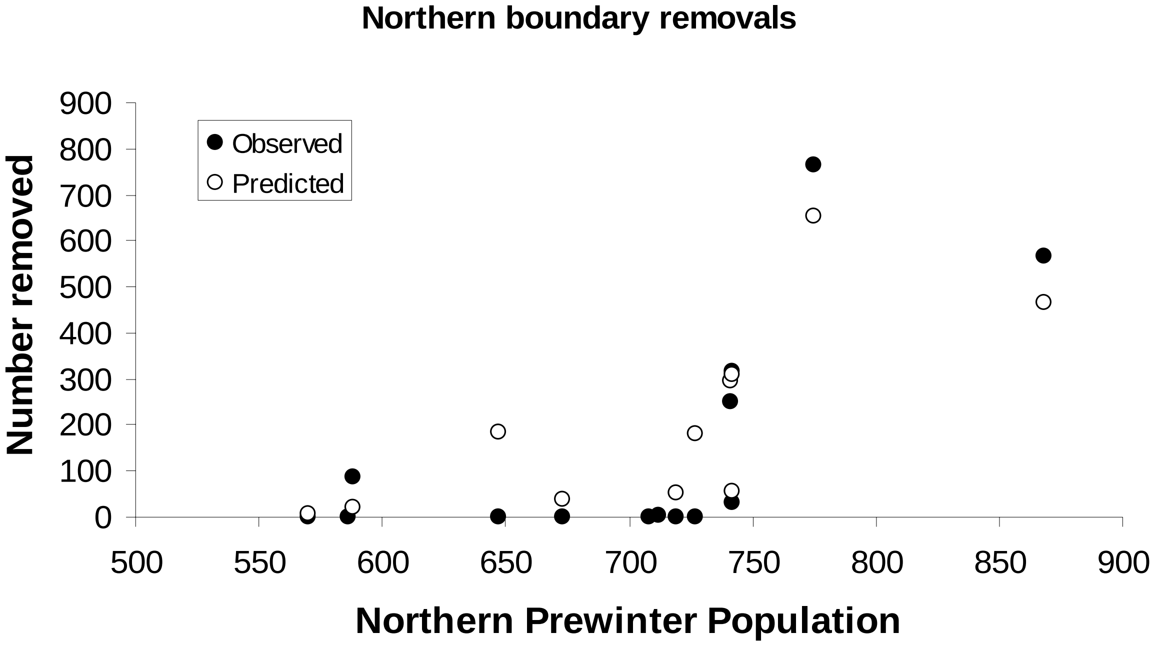


Figure 5.17. Bison removals at the northern boundary of Yellowstone National Park in relation to the number of bison on the Northern Range prior to winter in years when the population exceeded 550. Y = -1211 + 47.32 SWE + 1.337 NPOP, $R^2 = 0.793$, $P < 0.000$, where SWE is average snow water equivalence (cm) at Tower Falls meteorological stations in mid-February, and NPOP is the number of bison on the Northern Range prior to winter.

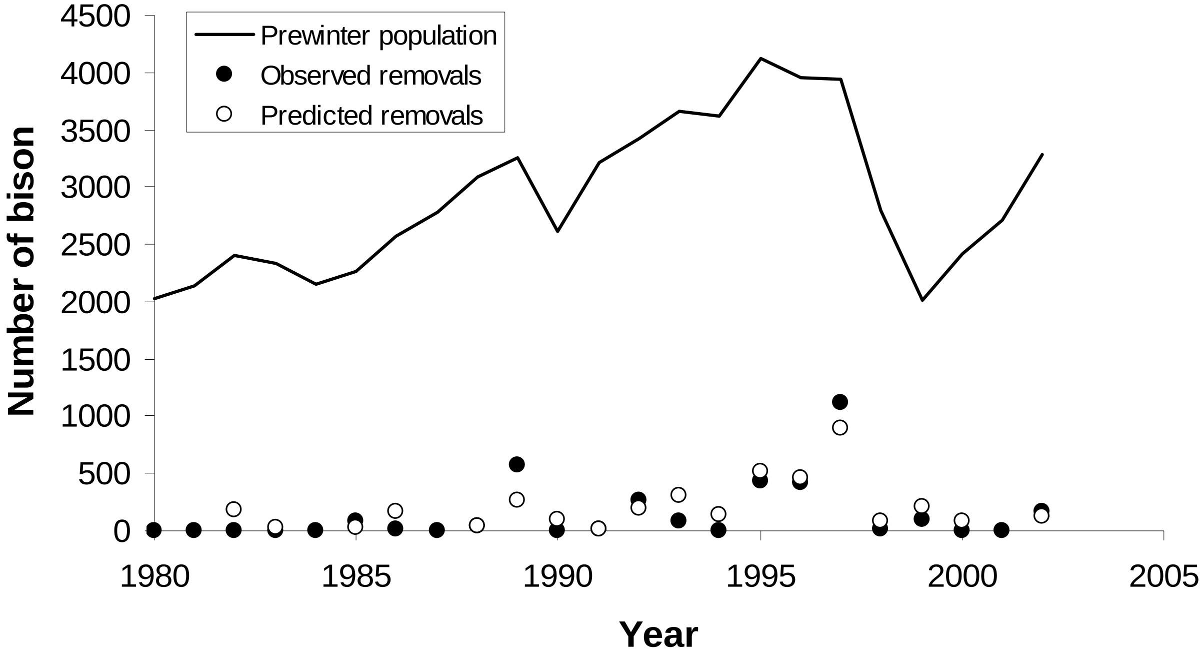


Figure 5.18. Total bison removals at the western and northern boundaries of Yellowstone National Park in relation to the number of bison present in the park prior to winter and snow. Y = -869 + 28.84 SWE + 0.183 TPOP, $R^2 = 0.734$, $P < 0.000$, where SWE is the average snow water equivalence (cm) in mid-February at Central Range meteorological stations and the Tower Falls station in the Northern Range.

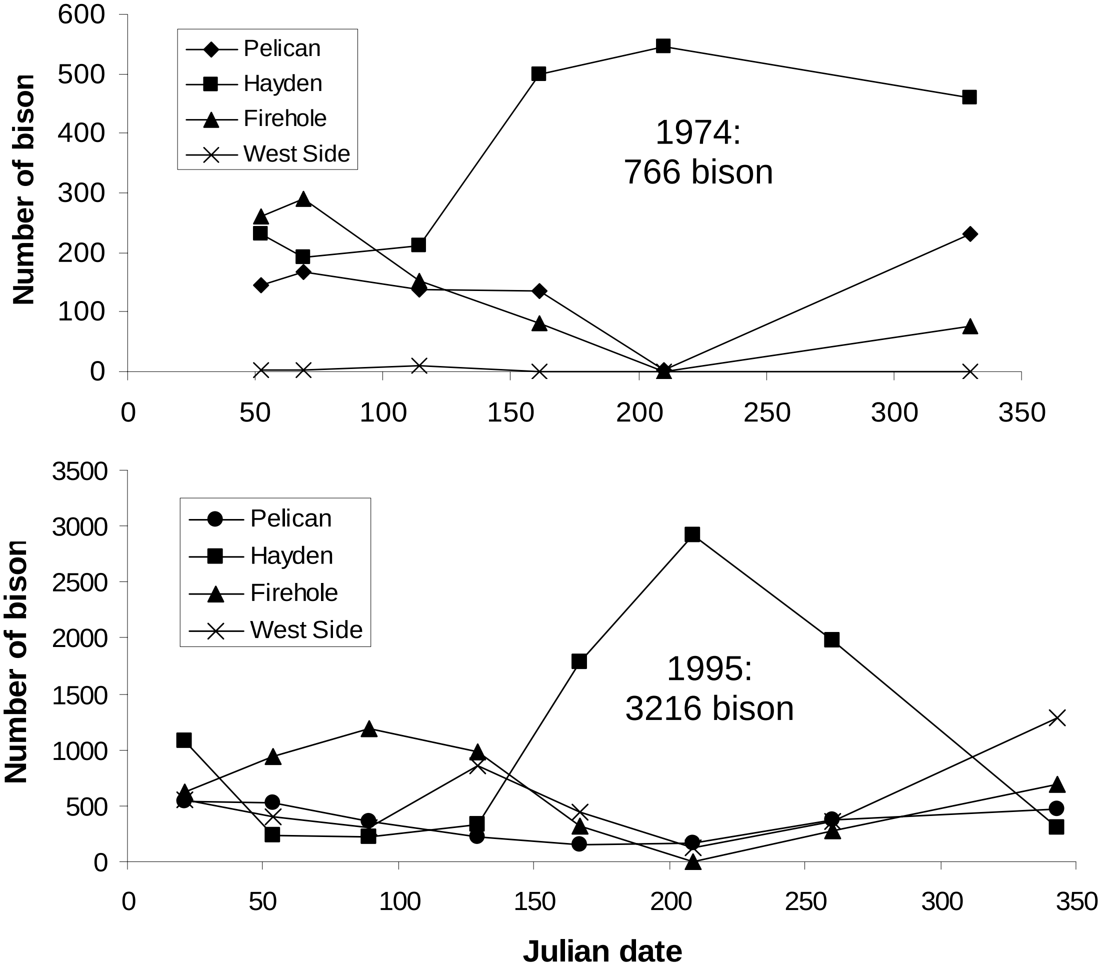


Figure 5.19. Distribution of bison in the Central Range during representative years 1974 and 1995. The maximum number of bison counted in the year in the Central Range is indicated. Data source: survey data of M. Meagher compiled by C. Jerde.

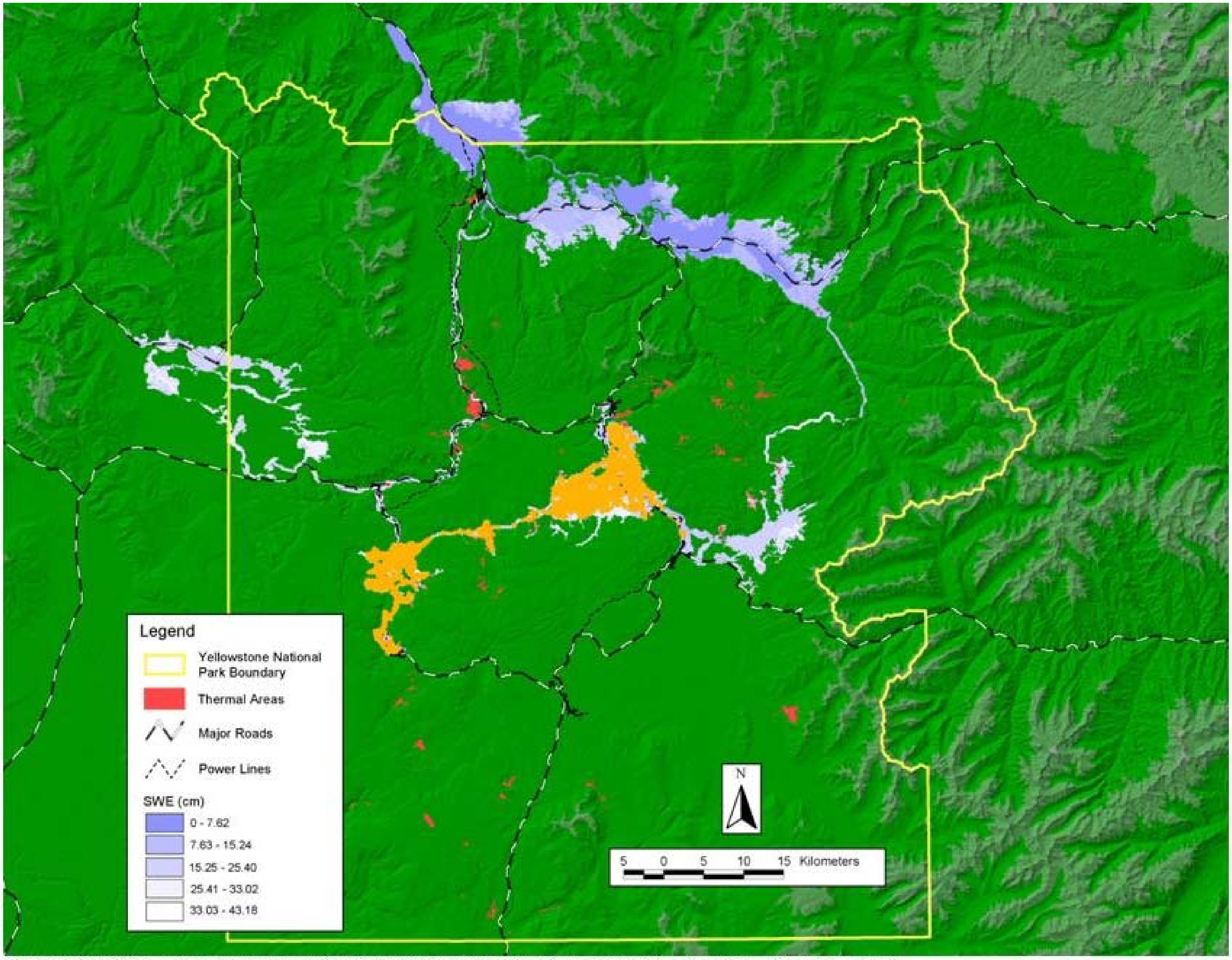


Figure 5.20. GPS locations (orange points) of bison YELL003 during the period November 2003 – December 2004.

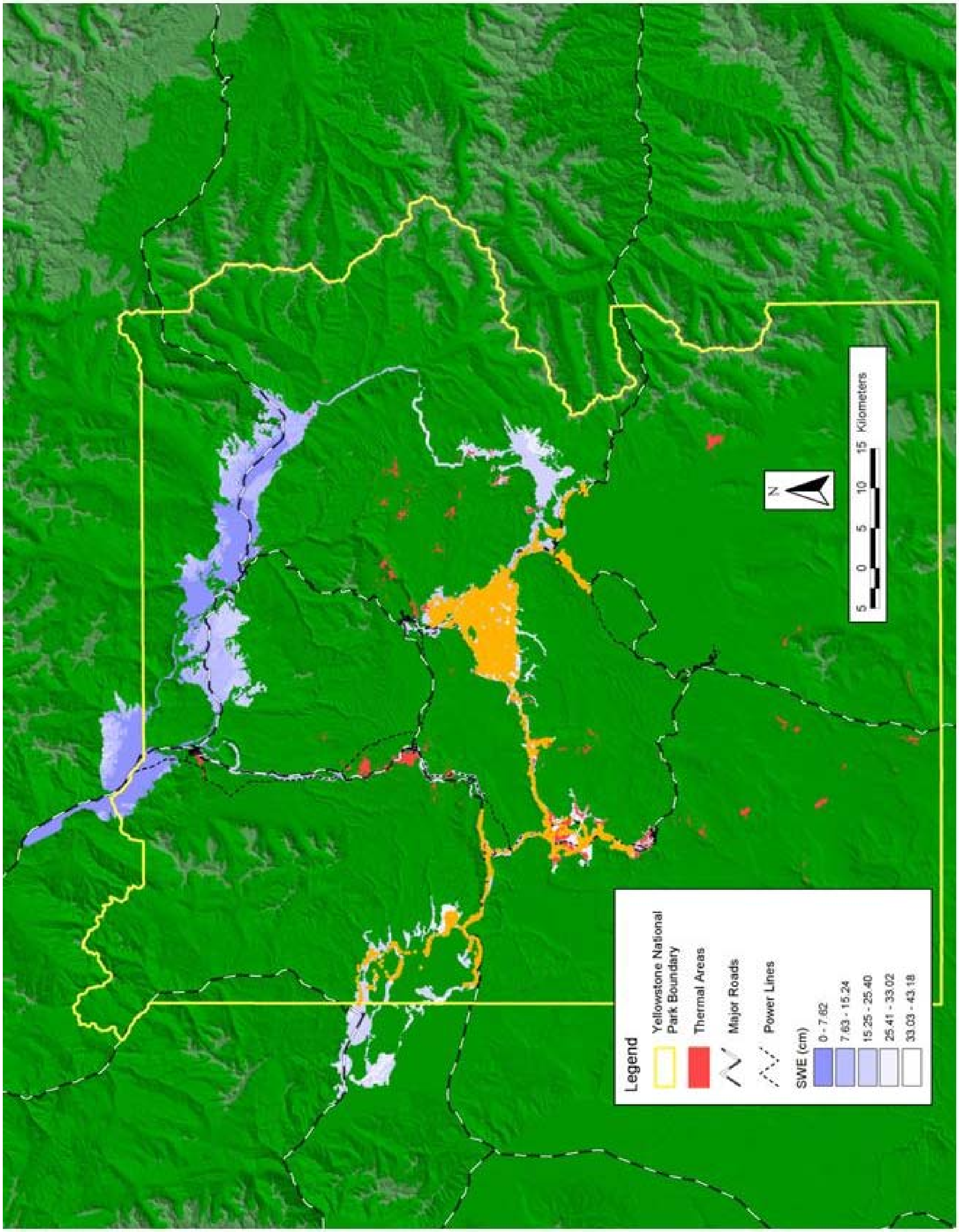


Figure 5.21. GPS locations (orange points) of bison YELL007 during the period November 2003 – December 2004.

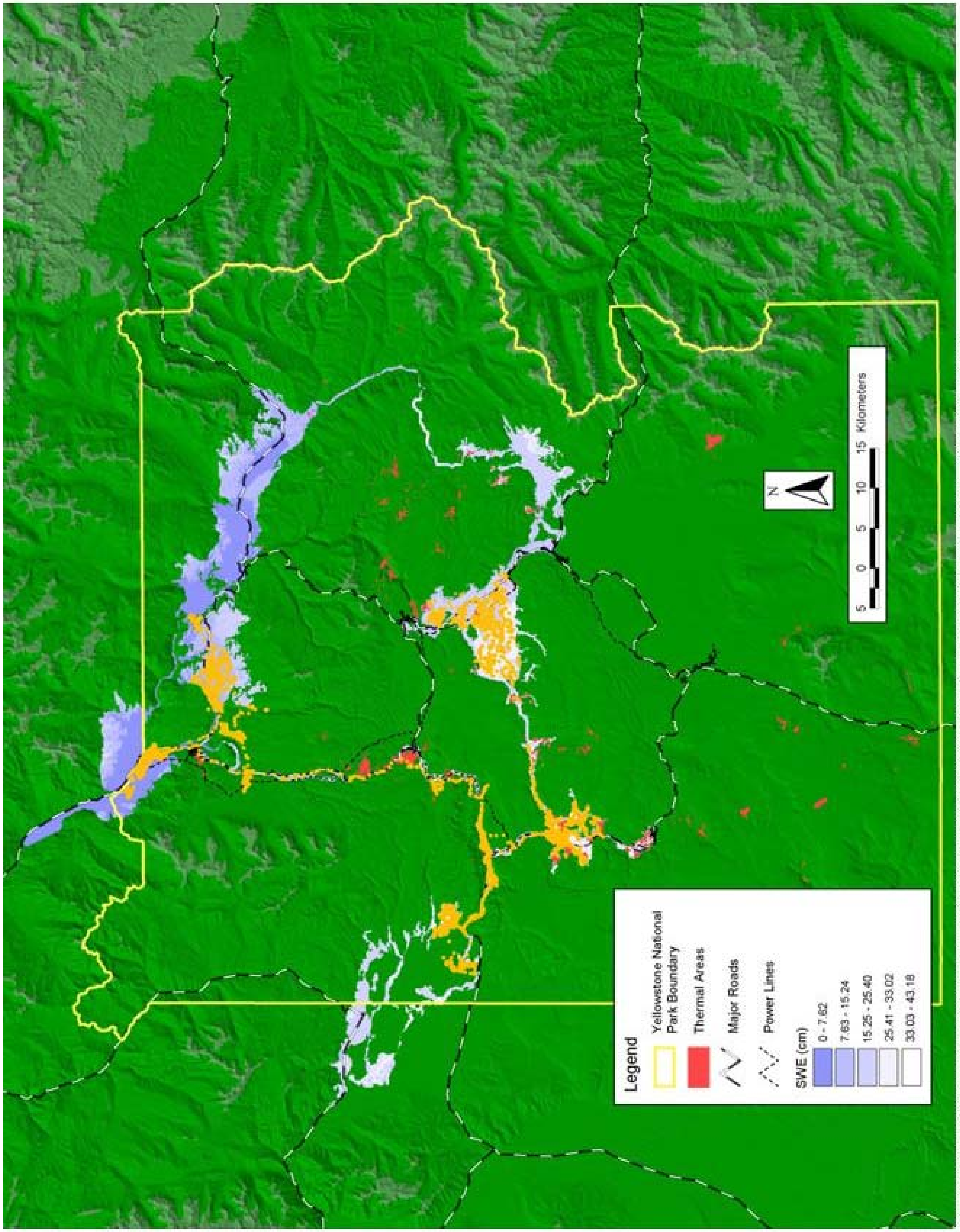


Figure 5.22. GPS locations (orange points) of bison YELL014 during the period November 2003 – December 2004.

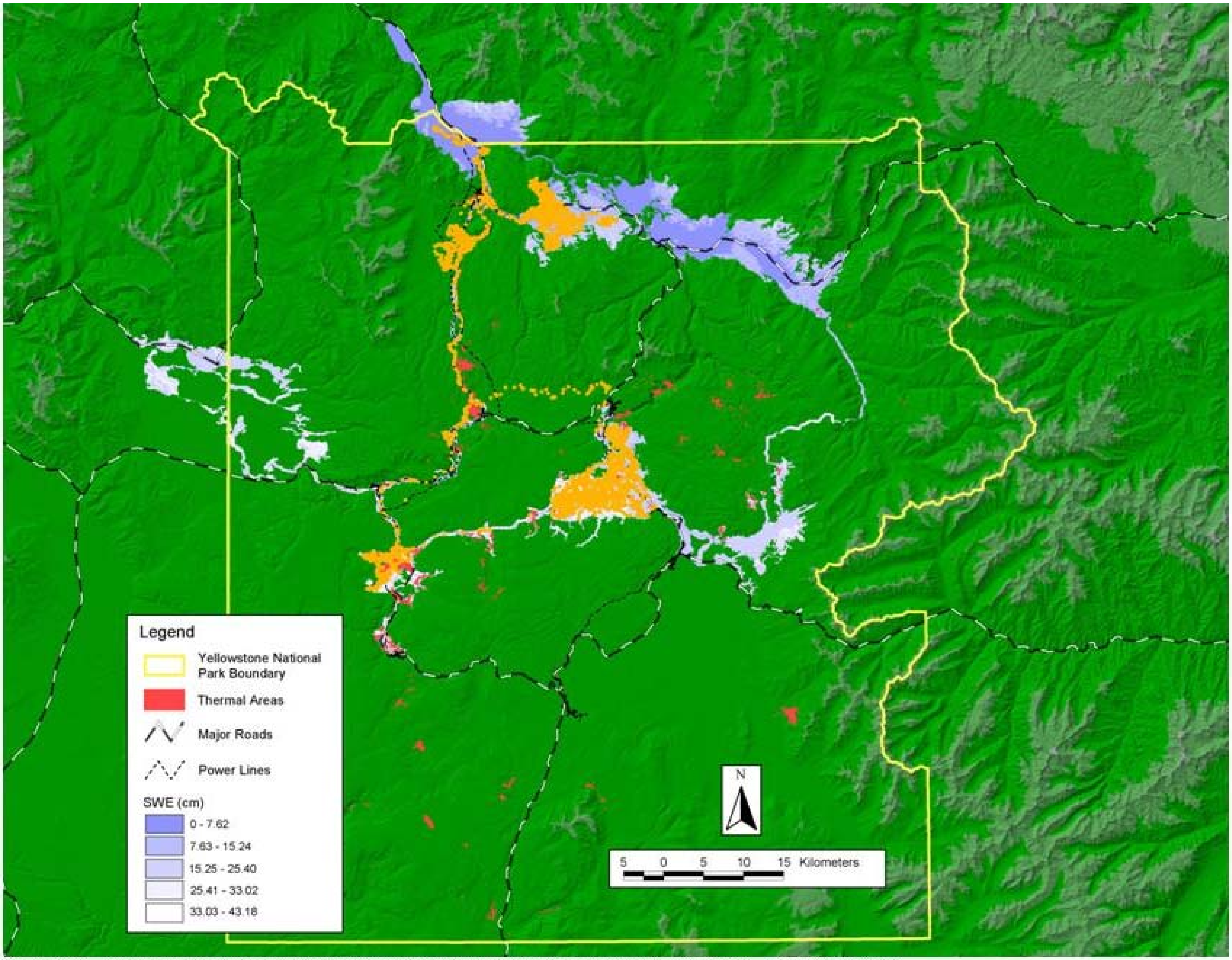


Figure 5.23. GPS locations (orange points) of bison YELL011 during the period November 2003 – December 2004.

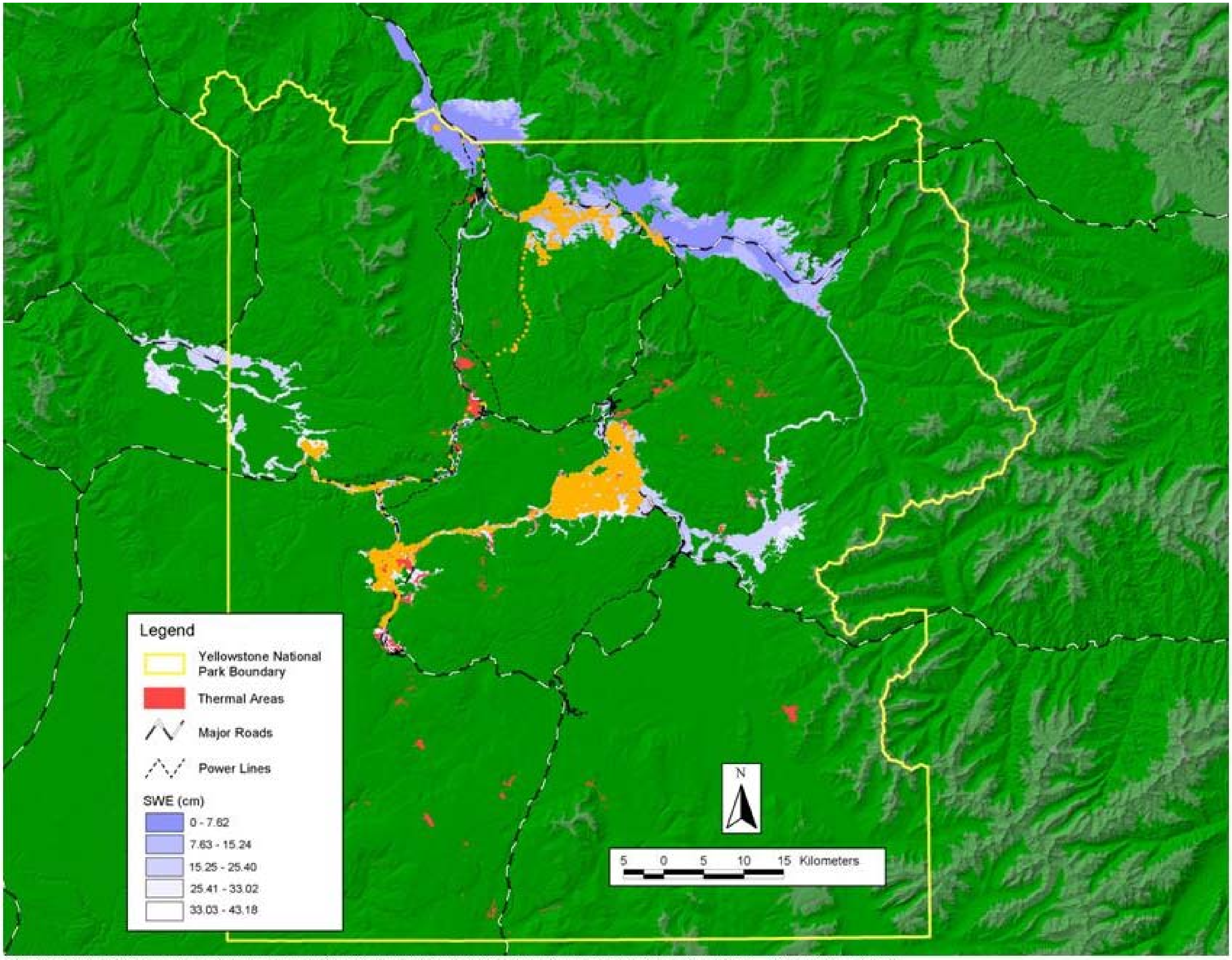


Figure 5.24. GPS locations (orange points) of bison YELL490 during the period November 2003 – December 2004.

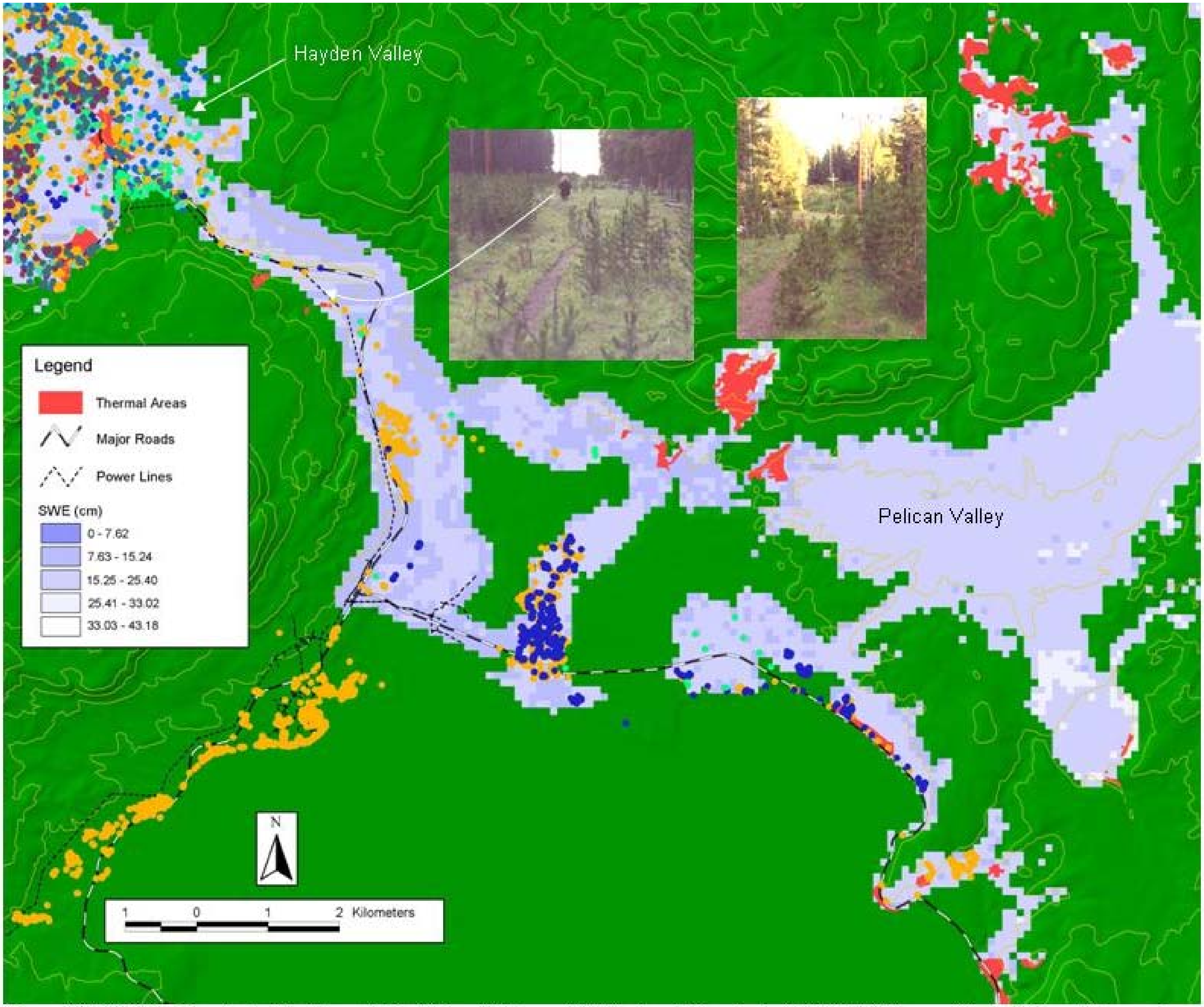


Figure 5.25. GPS locations (points) of bison in the Pelican Valley and SE Hayden Valley during 2003-2004. The corridor is 8.3 km. 50 m contour lines are indicated. Photographs of a bison trail deeply cut into power line were taken in August 2004; the location of the bison is indicated. Data source: R. Wallen, YCR.

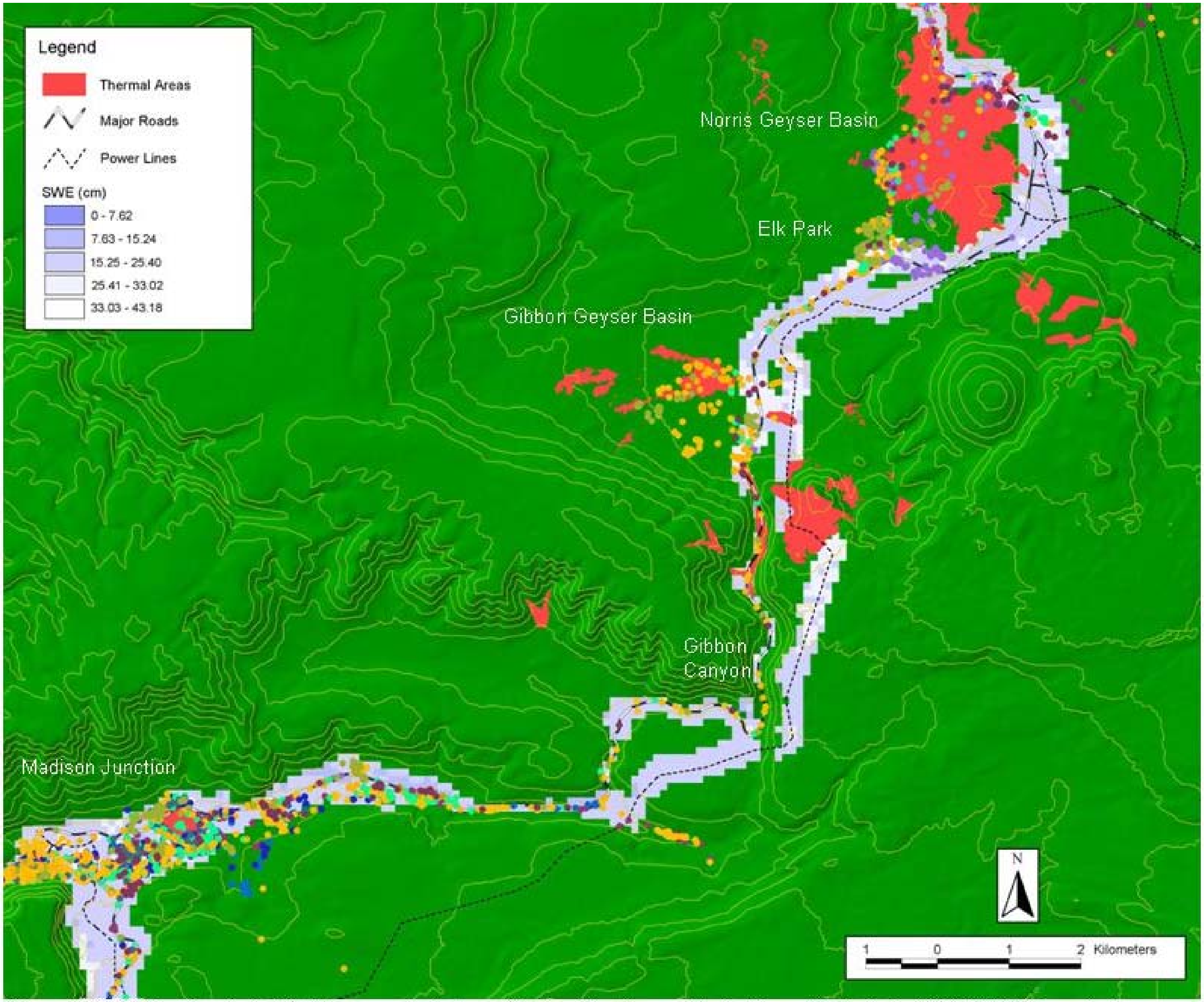


Figure 5.26. GPS locations (points) of bison moving between Madison Junction and Norris Geyser Basin during 2003-2004. Distance between Madison Junction and Norris Junction is 21.5 km. 50 m contour lines are indicated. Data source: R. Wallen, YCR.