In cooperation with the U.S. National Park Service

2005 Annual Progress Report: Elk and Bison Grazing Ecology in the Great Sand Dunes Complex of Lands

By Kate Schoenecker, Bruce Lubow, Linda Zeigenfuss, and Julie Mao

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Preface

Many individuals, representing five resource management agencies and one nonprofit organization, assisted in the development and implementation of this research. As co-investigators, their participation has been and continues to be essential to the successful completion of this work, which overlaps jurisdictions. Following is a list of these partners and cooperators.

National Park Service Partners

Steve Chaney, Superintendent, Great Sand Dunes National Park
Fred Bunch, Chief, Resource Management, Great Sand Dunes National Park
Phyllis Bovin, Resource Management, Great Sand Dunes National Park
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USDA-Forest Service and BLM Partners

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2005 Annual Progress Report: Elk and Bison Grazing Ecology in the Great Sand Dunes Complex of Lands

By Kate Schoenecker[1], Bruce Lubow[2], Linda Zeigenfuss[1], and Julie Mao[3]

Introduction

In 2000 the U.S. Congress authorized the expansion of the former Great Sand Dunes National Monument by establishing a new Great Sand Dunes National Park and Preserve in its place, and establishing the Baca National Wildlife Refuge. The establishment of Great Sand Dunes National Park and Preserve and the new Baca National Wildlife Refuge in the San Luis Valley (SLV), Colorado was one of the most significant land conservation actions in the western U.S. in recent years. The action was a result of cooperation between the National Park Service (NPS), U.S. Fish and Wildlife Service (USFWS), Bureau of Land Management (BLM), U.S. Forest Service (USDA-FS), and The Nature Conservancy (TNC). The new national park, when fully implemented, will consist of 107,265 acres, the new national preserve 41,872 acres, and the new national wildlife refuge (USFWS lands) 92,180 acres (fig. 1). The area encompassed by this designation protects a number of natural wonders and features including a unique ecosystem of natural sand dunes, the entire watershed of surface and groundwaters that are necessary to preserve and recharge the dunes and adjacent wetlands, a unique stunted forest, and other valuable riparian vegetation communities that support a host of associated wildlife and bird species.

When the National Park was initially established, there were concerns about over-concentrations and impacts on native plant communities of the unhunted segments of a large and possibly growing elk (*Cervus elaphus*) population. This led to the designation of the Preserve as a compromise solution, where the elk could be harvested. The Preserve Unit, however, will not address all the ungulate management challenges. In order to reduce the current elk population, harvests of elk may need to be aggressive. But aggressive special hunts of elk to achieve population reductions can result in elk avoidance of certain areas or elk seeking refuge in areas where they cannot be hunted, while removals of whole herd segments and abandonment or alterations of migration routes can occur (Smith and Robbins, 1994; Boyce and others, 1991). Elk may seek refuge from hunting in the newly expanded Park Unit and TNC lands where they might over-concentrate and impact unique vegetation communities. In these sites of refugia, or preferred loafing sites, elk and bison could accelerate a decline in woody riparian shrubs and trees. This decline may also be due to changes in hydrology, climatic, or dunal processes, but ungulate herbivory might exacerbate the effects of those processes.

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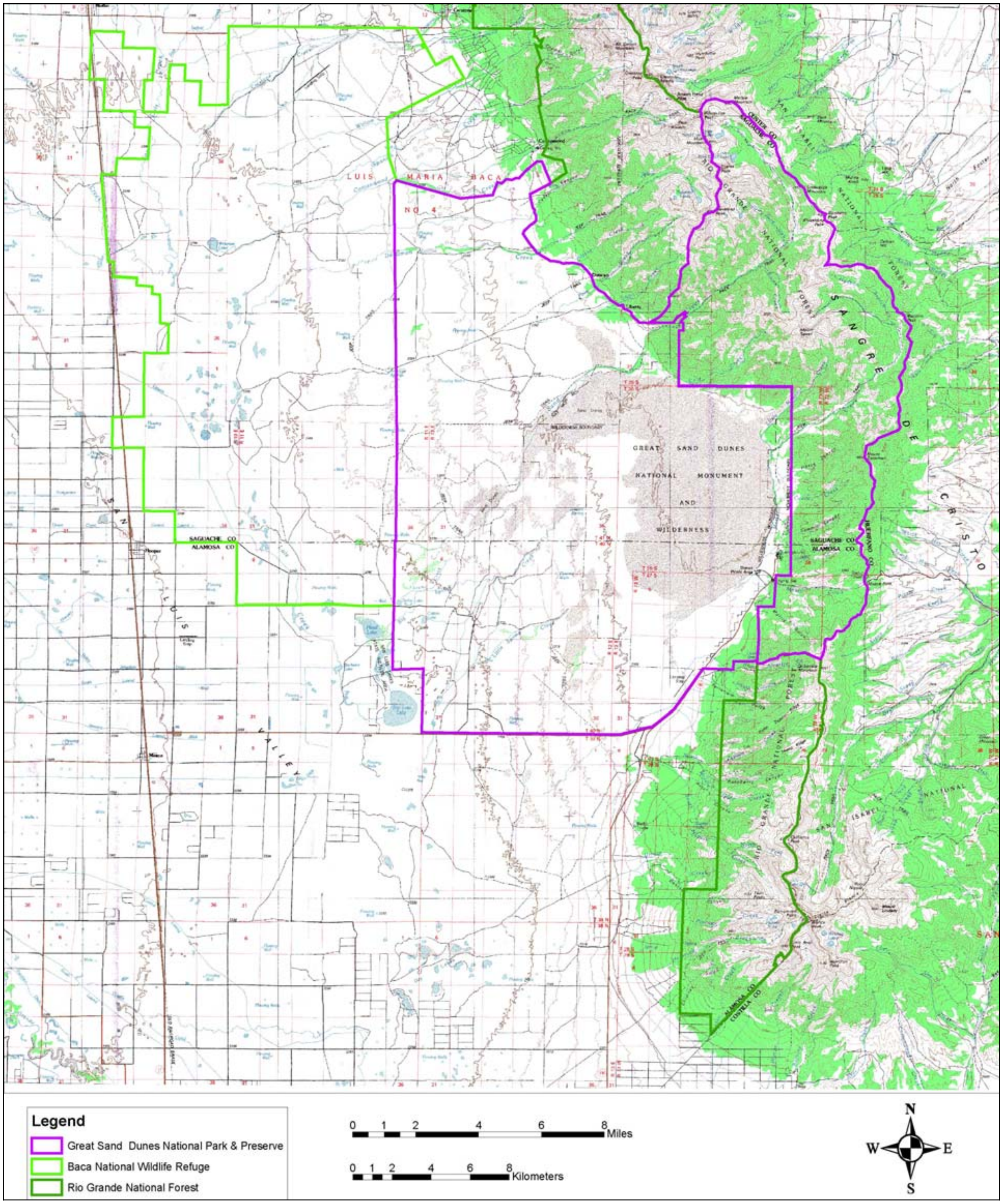

Figure 1. The eastern section of the San Luis Valley, Colorado, showing Great Sand Dunes National Park and Preserve, the Sangre de Cristo Mountains, U.S. Fish and Wildlife Service lands (Baca National Wildlife Refuge), and the Rio Grande National Forest.

To address the questions and needs of local resource managers, a multi-agency research project was initiated in 2005 to study the ecology, forage relations, and habitat relations of elk and bison in the Great Sand Dunes–Sangre de Cristo–Baca complex of lands. Meetings and discussions of what this research should include were started in 2001 with representatives from NPS, USFWS, TNC, the Colorado Division of Wildlife (CDOW), and USDA-FS/BLM. The final study plan was successfully funded in 2004 with research scheduled to start in 2005. The research was designed to encompass three major study elements: (1) animal movements and population dynamics, (2) vegetation and nutrient effects from ungulate herbivory, and (3) development of ecological models, using empirical data collected from the first two components, that will include estimates of elk carrying capacity and management scenarios for resource managers.

Objectives

The objectives of our study are to:

1. Determine the current population status of elk, including year-round distribution, movements, population size, carrying capacity, and herd projection into the future, as well as the herd movements and potential migrations of bison.
2. Evaluate the effects of bison and elk herbivory on plant communities, including shrub and tree recruitment, annual aboveground net production (AANP), plant species diversity, and plant nutrients.
3. Provide information on current levels of consumption in target plant communities of concern to managers.
4. Develop an ungulate grazing model that includes grazing as a significant natural ecological process and estimates carrying capacity (modeling will be at the end of the study after empirical data is collected).
5. Develop a body condition model for elk to assess impacts to the elk herd from drought, density, and potential differences in subpopulation.
6. Monitor the effects of treatments and new experiments on the distribution and movements of elk. Experiments and treatments that have been discussed include special hunts to move elk from certain areas, cessation of irrigation, removing fences, and adding fences (e.g., to keep elk from crossing Highway CO-17 and reaching adjacent seed potato farms).
7. Evaluate the effect of bison and elk grazing on soil nitrogen processes.
8. Evaluate the role of hydrology in potentially exacerbating the effects of high ungulate herbivory; and investigate the interaction of climate and ungulate herbivory on cottonwood and willow communities, using dendrochronology to estimate establishment dates, recruitment dates, and correlations to water tables and precipitation patterns.
9. Potentially evaluate the effects of management treatments on target plant communities, such as movement, harassment, and hunting of elk.

Overall Progress

In the first year of the study we radiocollared elk and bison and began ground and aerial tracking with radio-telemetry. We conducted an aerial elk population survey, analyzed elk population dynamics, and conducted elk population modeling (B. Lubow). We collected data on elk body condition in three consecutive elk captures conducted in early and late summer. We conducted genetic analysis of bison to determine hybridization, if any, with cattle. We established more than 20 ungulate exclosures in various vegetation communities and began vegetation measurements for both summer and winter, and we conducted a preliminary survey of the alpine areas used by elk to get a general idea of elk utilization in summer (L. Zeigenfuss). In cooperation with our study, a Ph.D. student completed nutrient analysis on soils in areas used by bison versus areas used by elk and bison (A. Przeszlowski, Colorado State University). Results of these initial investigations are presented in this report.

Study Area

The study area is defined as the low elevations of Great Sand Dunes National Park and adjacent lands west to Highway CO-17 (including the Baca National Wildlife Refuge [NWR]), north to Highway T, and south to include the Medano-Zapata Ranch to Highway CO-160. Elk population surveys and radiocollar tracking were conducted up to Poncha Pass, including the Sangre de Cristo Range, as well as on the east side of the Sangre de Cristos when radiocollared elk are found there.

The valley floor and dunes ecosystem is a dry land area where water, primarily from snow melt and springs, is rare. There are basically three unique vegetation types of the Great Sand Dunes complex.

1. Active dunes and swale area: grasses such as blowout grass (*Redfieldia flexuosa*) grow in low densities on the dunes. The swales are flooded ephemerally during spring from snowmelt off the mountains, and support a dense ground cover of sedges and wet grasses. Water sources in this complex include the Sand Creek, Little Spring, and Big Spring. Cottonwood stands that occur along Sand Creek are considered unique for the southern Rockies, since they are pure narrow-leaved cottonwood (*Populus angustifolia*), while most other stands are hybrids of narrow-leaf and broadleaf.
2. Ephemeral wetlands: these form the western boundary of the complex and are watered from the springs and Sand Creek. The only large population of the endangered slender spider flower (*Claeome multicaulis*) occurs in these meadows. Only a few records for the spider flower exist outside of this population.
3. Sand sheet: this area surrounds the active dunes complex and is dominated by greasewood (*Sarcobatus vermiculatus*) and rabbitbrush (*Chrysothamnus viscidiflorus*). Cottonwoods and willows (Coyote willow, *Salix exigua;* Mountain willow, *Salix monticola;* Interior willow, *Salix interior)* grow on top of some dunes (the dunes may support a pyramid water supply), along Sand Creek, and near the springs.

Historically, bison, elk, mule deer, and pronghorn antelope were native to the area until about the 1840s when both bison and pronghorn were extirpated. Livestock, mostly cattle, have been grazed in the area, especially in the Sand Sheet type. The NPS portion of the Baca ceased cattle grazing in 2005. The wet meadow type was irrigated and hayed to increase cattle production. In 1937, there were 114 interdunal ponds in the Sand Creek drainage, but presently there are only ~51 such ponds. Sand Creek has downcut 1.0−1.5 m in some areas, thus dewatering local willow patches. Recent sand deposits are burying many interdunal willow patches. A dry period of several decades resulted in a decline in the water table and wetlands near Sand Creek (Wurster and others, 2003). Dune movement increases during dry periods, which may explain the burial of some willow patches.

Methods

Elk Distribution and Home Range

We captured and radiocollared ~45 adult cow elk (Quicksilver Air, Colorado Springs, Colorado) using a net gun in conjunction with CDOW in February 2005. In addition, CDOW used corral traps and clover traps to increase the sample size of radio collars, for a total of 65. Eighteen of the collars are GPS collars (Lotek Inc., Ontario, Canada; and Advanced Telemetry Systems, Isanti, Minnesota) and the remaining 47 collars are VHF beacon (Advanced Telemetry Systems and Lotek Inc.). Helicopter capture crew surveyed the study area, placing collars on groups according to group size: if <30, 1 animal was collared; if the group was 50–99, 2 elk were collared; if the group was 100+, 3–4 elk were collared. We attempted to saturate groups in the periphery of the population (especially at the northern end) to get a good representation of animals outside of the core herd area. When the capture crew could no longer locate new (uncollared/unmarked) groups in the north, the remaining collars were placed west and just north of the dunes. One animal died shortly after trapping, so we redeployed the collar via helicopter. During the capture, we observed animals for condition, collected blood for pregnancy analysis, and determined body condition score by John and Rachel Cook (Cook and others, 2004a). After collaring, we radio-located animals twice per month using a fixed-wing aircraft to determine extent and range of movements. We also tracked animals with ground crews gaining 1 additional location/collar/month using a random method to select which collar to locate per day. We plotted elk group locations to determine distribution and analyzed locations with kernel density estimates (Silverman, 1986).

Elk Population Size

We estimated elk population size by flying an aerial survey in winter 2004–2005 using a helicopter (pilot E. Tracy, NewAir Helicopters) and collecting additional data on radiocollar locations via fixed-wing aircraft (pilot D. Felix, Olathe Spray). Survey conditions were very poor in winter 2005–2006 due to low precipitation (lack of snow); thus, the survey was cancelled. We plan to survey the population again in winter 2006–2007.

We conducted the survey on 4 March 2005 in the eastern San Luis Valley and lower elevations of the western slope of the Sangre de Cristo Mountains, including the Great Sand Dunes National Park. The survey extended north to Poncha Pass and south to the plains west of Mount Blanca. The survey extended up the mountains to approximately 2,900 m on the east side and westward to within sight of the major north-south highways CO-17 and US-285 (fig. 2).

We flew predefined transects with a Bell 206B-III helicopter using an onboard global positioning system (GPS). Transects were flown ¼–½ mile apart on the flats, and along contours at closer spacing (<1/8 mile) in the mountains. A U.S. Geological Survey (USGS) observer was located in the front-left seat of the helicopter. A second USGS observer switched positions between the left and right rear seats during the flight to make observations in the same direction as the helicopter reversed direction. Observers worked independently, searching for groups of elk within their view. When a group was spotted, the observer recorded (1) the size of the group; (2) the presence or absence of trees; (3) the presence or absence of shrubs; (4) percentage of the area surrounding the group covered by vegetative canopy as described by Unsworth and others (1994);

and (5) the percentage of the area surrounding the group covered by snow. The time, presence of radiocollars, and a GPS location of each sighting were also recorded.

No communication, visual or verbal, was permitted or occurred between front and rear observers until after both observers had adequate opportunity to detect each elk group independently. However, after the group had passed abeam of the helicopter, observers could notify the entire crew if they felt that it was necessary to circle the group to obtain a better count. If this was done, all crewmembers participated in the count and also took digital photographs of the group for more careful recounting after the flight.

In addition, a fixed-wing aircraft, occupied only by the pilot, flew near but above the helicopter to locate elk with radiocollars. The fixed-wing pilot recorded covariates for all radiocollared elk. At the end of the survey we compared the group size, time of observation, presence of radiocollars in a group, and Universal Transverse Mercator (UTM) locations to determine which groups with radiocollars were seen or not seen by the observers in the helicopter.

Following the flight, observers reviewed the time, size, location, and characteristics of each group in order to determine which groups had been independently detected by each observer. This created a mark-resight dataset with individual covariates, in which groups could be sighted by one, two or all three observers. We used the Huggins closed capture estimator for mark-resight data with individual covariates in program MARK (White and Burnham, 1999) to fit models of the elk survey. Thirty-nine models with different combinations of the available covariates, ranging in complexity from 1 to 12 parameters, were fitted and compared using Akaike Information Criterion (AIC*c*).

The objects of interest in the mark-resight model were elk *groups*, not individual elk, because only groups are sighted independently. The model was structured with 3 capture occasions, corresponding to the three possible observers (front seat, rear seat, and fixed-wing pilot).

Elk groups were divided into four categories:

1. Those available to all three observers (fixed wing, front seat, and rear seat); i.e., groups containing elk with radiocollars and on the same side of the helicopter as the rear-seat observer.
2. Available to the fixed wing and front seat only; i.e., groups containing elk with radiocollars and *not* on the same side of the helicopter as the rear-seat observer.
3. Available to front and rear seats, but not fixed wing; i.e., groups *not* containing elk with radiocollars and on the same side of the helicopter as the rear-seat observer.
4. Available to the front seat only; i.e., groups *not* containing elk with radiocollars and *not* on the same side of the helicopter as the rear-seat observer.

Sighting probabilities for some observers for some groups were fixed at constant values. The first two groups have 100% sighting probability, by definition, because of the radio collars. The third group has sighting probabilities computed based on the fitted model and the detection history (front only, rear only, or both). The final group has sighting probability based only on the modeled sighting probability for the front seat observer (table 1).

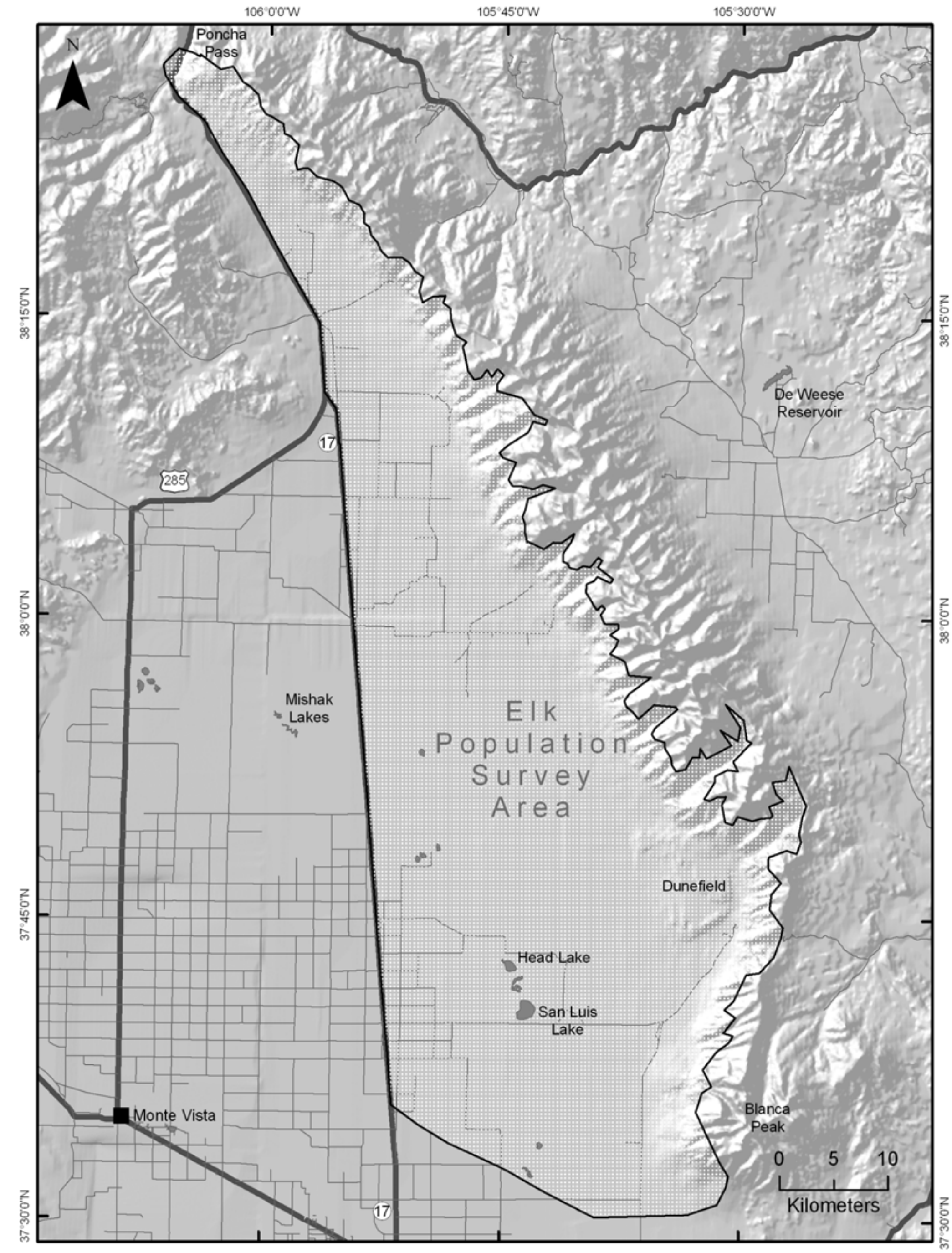

Figure 2. Survey area for elk population flight in the San Luis Valley, Colorado, extending from Poncha Pass south to the plains west of Mount Blanca, and from the Sangre de Cristo Mountains west to Highway CO-17 and US-285.

Table 1. Probabilities of seeing elk groups for each observer on the helicopter population survey of elk in the Great Sand Dunes study area, San Luis Valley, Colorado, 2005.

	Observer		
	Fixed Wing	Front Seat	Rear Seat
Available to all	1.0	1.0	1.0
Available to fixed wing and front seat	1.0	p_f	0.0
Available to front and rear seats	0.0	p_f	p_r
Available to front seat only	0.0	p_f	0.0

The model for aerial sighting probability for an elk group by a particular group *i* by observer *j* was:

$$p_{ij} = \frac{1}{1+e^{-(\boldsymbol{\beta}\mathbf{x}'_{ij}+\mathbf{x}'_{ij}\boldsymbol{\Sigma}\mathbf{x}_{ij})}} \quad , \qquad (1)$$

where:

$'$ = indicates a matrix transpose;
$\boldsymbol{\beta}'$ = a vector of fitted coefficients for the logistic model;
$\mathbf{x}_{ij}'$ = a vector of observed covariates for group *i*, observer *j;* and
$\boldsymbol{\Sigma}$ = the variance-covariance matrix of estimated logistic model parameters.

The sighting probabilities apply only for groups *available* to a given observer. The rear seat observer could not see groups located on the opposite side of the helicopter or along the centerline. The sighting probability for the rear observer conditioned on availability was adjusted to obtain unconditional probability by computing the proportion of groups known to be present that were available to the rear observer. In other words:

g = # groups available to rear / # groups seen
$p_{i,obs2} = g\, p_r$

Sighting probability for groups seen by multiple observers was computed as

$$p_{i,\text{comb}} = 1 - (1 - p_{i,1})(1 - p_{i,2}).$$

Each group seen was assumed to represent $1/p_{i,comb}$ actual groups, to account for those not seen. This adjustment was applied separately to each group, and the adjusted estimates were summed to obtain a total population estimate.

In planning the survey, we attempted to define survey area boundaries that would encompass the entire elk population that uses the East San Luis Valley. However, several radiocollars were not located in the defined study area covered by the aerial survey. We assumed that these represented a proportion of the population that was unavailable due to temporary movement beyond the home range we assumed when we planned the survey. The proportion of the total working radiocollars not located within the survey boundaries by the fixed-wing pilot relative to the total number of known working radiocollars was computed as a correction for unavailable elk. Precision of this proportion was estimated based on the assumption of a binomial probability distribution for group presence versus absence.

Elk Population Model

Data

We used the population estimate produced by the current project, along with data provided by CDOW from annual aerial surveys of the elk population in SLV covering biological years (BY) 1983–2004 (surveys were actually conducted in February–March of the following calendar year). These data consist of annual estimates of ratios of bulls to cows and calves to cows, along with standard errors for each estimate. In addition, annual harvest data for the three age-sex classes based on mailed hunter surveys were provided by CDOW.

Model Structure and Assumptions

A stage-structured population projection model was built for the elk population in SLV for bulls, cows, and calves at the time of the annual mid-winter survey. The population was projected with an annual time step. Calves were recruited into the population each year at the time of the survey, when they were approximately 0.5 years old. Calves were advanced to adult age classes in the following year at an age of approximately 1.5 years. Sex ratio at recruitment was either an estimated parameter fitted to the data or assumed to be 50% male. In all models, and the population was assumed to be closed to immigration and emigration.

Survival (excluding harvest) of calves, $S_c(t)$, adult females, $S_f(t)$, and adult males, $S_m(t)$, in year t is estimated based on the following general model:

$$\begin{aligned} S_c(t) &= S_c^{\,m(t)} \\ S_f(t) &= S_a^{\,m(t)} \\ S_m(t) &= S_f^{\,a}(t) \end{aligned} \tag{2}$$

The base survival rates S_c and S_f were fitted parameters. The mortality factor $m(t)$ was a (possibly) time-varying value that affected both age classes, forcing a strong correlation between annual survival by age classes. The exponent, a, was an additional fitted parameter that related male to female survival. Aside from the most general (complex) model in which $m(t)$ was estimated independently by year, all other models fixed this value at $m = 1$ to force survival to a constant value determined by the age-specific parameters S_c and S_a and the sex effect, a. The male survival exponent, a, was fixed at 1.0 by default in models in which it was not estimated, thereby forcing male and female survival to be equal.

Recruitment of calves was based on the model:

$$R = \frac{\beta_c}{1 + e^{-(\beta_0 + \beta_1 t + \beta_2 N)}} \quad , \tag{3}$$

where:

R = recruitment rate (calves/cow),
t = the year of the model (1 represents the year 1983),
N = the total population of elk in year t-1,
β_c = maximum possible recruitment,
β_0 = intercept of logistic recruitment function,
β_1 = slope of logistic recruitment function with respect to time (year),
β_2 = slope of logistic recruitment function with respect to population size (no. elk).

Alternative, simpler, models were considered in which β_1, β_2, or β_0, β_1, and β_2 were fixed at zero. These cases model, respectively, a density effect only (β_1=0), a time effect only (β_2=0), and a constant recruitment rate (β_0, β_1, and β_2 =0). This limited set of models was chosen *a priori* because temporal and density effects were suspected and of interest to management. More complex models, including alternatives that use weather covariates to explain some of the annual variation in rates, were not considered due to both the limited extent of the dataset and the project budget. More elaborate models may be considered in future years.

A correction for possible negative bias in the field estimates of bull-to-cow ratios was also considered in one model where the field estimate is increased by a fixed percentage, which is an additional fitted parameter. Separate male and female wounding loss rates were also considered. These proportions were applied to the reported harvest to increase the removal of adults from the population. Actual wounding by hunters is only one of several possible causes of such an effect, which also includes underreporting of harvest and dispersal emigration, all of which would be mathematically equivalent in the model. All of the models also contained a required parameter for the initial population size in 1983.

Bison Habitat Use and Genetics

Ten bison (four bulls, six cows) were radiocollared with VHF collars (Advanced Telemetry Systems) during annual round-up operations in November 2004. In addition, we radiocollared four female bison with GPS collars (Habit Research, British Columbia, Canada) for frequent monitoring and better habitat use information. GPS collars were set to collect a fix or location every four hours. The Nature Conservancy assisted with collaring in 2004, and Duke Phillips and staff (Zapata Partners) assisted in 2005. During the round-up, bison are brought into nearby pastures using ATVs, then moved through a chute for counting and processing. Once in the chute, adult bison were restrained for radiocollaring. Animals were randomly selected with an effort made to space collars so different bison groups would be represented. Because of the tendency for bison to remain in large groups (100+) and an estimated population size of ~1000–1200 individuals, we determined that 10–15 collars would adequately represent movements of the herd, assuming the majority of groups were "marked" with at least a single radiocollar. All bison collars were located and recorded 1x/week by ground observers for a year. To evaluate overlap in habitat, ground locations were analyzed using kernel density estimates and compared with elk locations of the same sampling period.

To evaluate herd genetics, particularly hybridization with cattle, we collected tail hair samples from >200 bison (randomly selected as they were rounded up) for genetics evaluation in November 2004. Dr. Jim Derr, who has evaluated most of the bison herds in the western United

States, conducted tail hair sample analyses at Texas A&M University. Genetics tests involved analyzing mitochondrial DNA (mtDNA), which represents the genetic contribution from mothers only, for evidence of hybridization with cattle. Based on those results, we collected additional samples in November 2005 for nuclear DNA (nDNA) analysis (which represents genetic contribution from fathers) in order to further evaluate the genetic status of the bison population.

Vegetation Study

Experimental Design

In the original study plan, four vegetation communities were identified for study–swale, wet meadow, cottonwood, and willow. Field trips to the study area were made in July, August, and October 2004 by Kate Schoenecker, Linda Zeigenfuss, and Francis Singer of USGS. These site visits resulted in a refocusing of the vegetation study design. It was noted that three distinct strata of large ungulate herbivory were evident on the landscape–elk as the primary ungulate grazer, elk and bison, and elk and cattle. Changes of ownership and subsequent management of the lands on the Baca Ranch from private to government ownership brought an additional herbivory stratum to the landscape–elk as the primary ungulate with recent heavy cattle grazing. Additionally, many of the sites that were identified with swale and wet meadow characteristics according to the study plan overlapped upon field investigation. Since a scientifically appropriate number of study sites was not available in all strata and because of funding and labor limitations with such an expansive design, we focused the design on the vegetation communities of greatest interest to all partners that would answer the most biologically critical questions. Two strata of major ungulate use were selected, (1) elk only with no recent cattle grazing, and (2) elk and bison together. These designations do not imply that herbivory on these sites is exclusive of other large ungulates, such as mule deer. Three vegetation types were selected for study: (1) cottonwood, (2) wet meadow and riparian areas, and (3) willow.

With the input of NPS and TNC biologists, a total of 23 potential exclosure sites were selected in cottonwood, willow, and wet meadow communities on the Medano Ranch, NPS lands, and the Zapata Ranch. Twenty of these sites were selected for construction of exclosures (4 each in elk and bison willow, cottonwood, and wet meadow; 4 each in elk-only cottonwood and wet meadow). There was limited availability of comparable sites for replication in each vegetation type. As a result, the wet meadow/riparian sites are grouped along Little Spring and Big Spring Creeks. Selection of cottonwood sites was restricted to areas with a sufficient amount of regeneration (root sprouts and saplings) to indicate that the site had some potential to show signs of recruitment into the tree canopy within the timeframe of the study. Cottonwood within the bison areas are limited to Lower Sand Creek. Outside of the bison fence, cottonwood are found along upper Sand Creek near the old townsite of Liberty, near the Zapata Ranch, and along Medano Creek. Willow sites along Medano Creek receive a confounding amount of park visitor activity, so this site was dropped from consideration. Willow along lower Sand Creek occur in large enough concentrations to replicate study sites, where both elk and bison graze. Willows on the Baca NWR (where there are elk but no bison) are mostly a different species and are recovering from recent heavy cattle grazing; some cattle grazing may continue. Thus, these sites were not comparable to the lower Sand Creek willows. Other willows in the study area are scattered in the interdunal wetlands, but these willow patches are too small to allow comparative study of grazed and exclosed treatments. As a result, there are no comparable sites in the willow elk-only strata.

In January 2005, we conducted a field trip and visited several willow and cottonwood sites on the Baca NWR with USFWS personnel. Several potential sites were chosen in willow communities for exclosures as well. Four exclosure sites were finalized during August 2005, and USFWS personnel erected three of the exclosures in spring 2006. Sampling of these sites commenced in spring 2006. Although these sites are not comparable to those on lower Sand Creek, the addition of these sites will provide baseline information on these willow communities and their response to removal of cattle grazing, and changes in elk management, as well as elk herbivory response to changes in cattle grazing regime.

Fig. 3 illustrates the locations of the ungulate exclosures. At each site, two plots were selected and one randomly chosen to be excluded from large ungulate grazing (where the exclosure fence would be built). Both plots are approximately 0.4 ha (1 acre) in size and approximately square or rectangular in shape. Exclosure fences are 2.4 m (8 ft) in height. NPS contracted the building of the exclosures, and construction was completed by October 2005. The unfenced plots are at least 30 m distant from the exclosed plot in order to avoid fenceline effects that may occur (trampling due to animal trailing along the fenceline, potential drifting of snow, etc.) and are subject to ambient levels of ungulate herbivory.

Herbaceous Production and Consumption

A total of 100 grazing cages were placed on the initial 20 grazed sites (5 cages/site) adjacent to the exclosure sites in April 2005. These small, movable grazing exclosures were used to protect ~1-m^2 areas from grazing for short periods. Annual aboveground herbaceous production and consumption was sampled by clipping all vegetation within 0.25-m^2 circular plots inside and outside the movable grazing exclosures. All graminoids, forbs, and sub-shrubs within the plot were clipped and sorted into dead and live portions to measure annual peak standing crop. Vegetation was oven dried at 55^o C for at least 48 hours and then weighed. Sampling was conducted twice during the growing season (June and August) in 2005, but ideally will be sampled 3–4 times over the 2006 growing season. Cages are randomly placed again after each sampling to protect a new area from further grazing. We will use the difference method to determine cumulative consumption and production over the growing season (Frank and McNaughton, 1992). Production is calculated by summing the significant increments of standing crop inside the grazing cage for each sampling interval. Consumption is defined as significant differences in standing crop biomass inside the cage versus outside the cage at any given time period. These differences are summed over all sampling intervals to determine consumption over the growing season. Winter consumption is determined over a single time interval by placing the cages at the end of the growing season and then sampling before spring green-up.

Species Composition

We measured species composition in the grazed and exclosed plots at each site in order to determine the similarity in vegetation composition between each pair and to acquire baseline data on species composition prior to the beginning of the study treatments. Plots will be surveyed again using the same methods in year 4 of the study to determine if exclusion of elk and bison caused changes in plant species composition/diversity. Plot surveying was determined to be the most effective and comprehensive method of conducting the species composition study of the established plot locations. Each composition plot encompassed 400 square meters. To determine the placement of composition plots, we conducted rapid, ocular estimates of the vegetation community(ies) to ensure that plots would represent the vegetation community of interest. For example, in the case of the wet meadow/riparian communities along the Big and Little Spring Creeks, we wanted to capture a representation of palustrine systems, although the exclosures, for reasons of practicality in installation, typically included portions of dry greasewood/rabbitbrush upland communities. In the case of these wet meadow communities, many of the species composition plots also included small portions of the upland species due to steep cutbanks or species encroachment into the riparian strip. Plots were laid out to capture the target vegetation community and were either a 11.3-m radius circle or a 20 x 20 m square, although occasionally rectangles were necessary. The UTM coordinates of the center of the survey plot were recorded using a handheld GPS unit.

We first conducted a basic ocular estimate of ground cover by percentage. Categories included wood, sand, bare soil, rock, bedrock, water, plant basal area, litter/duff, and "other." Species were then recorded using scientific name following Weber's *Colorado Flora, East Slope*. Any discrepancies regarding species were verified using Hobart N. Dixon's *Keys to the Vascular Plants of the San Luis Basin, The Taos Plateau, and the Surrounding Mountains, Colorado and New Mexico*, as well as *The Intermountain Flora vol. 6*, and Janet Wingate's *Illustrated Keys to the Grasses of Colorado*. Species were placed into a strata class that was broken down into eight categories: emergent (trees that extend beyond the average height of the canopy), canopy (trees that form the most distinct tree stratum), sub-canopy (trees that establish an obvious or distinct sub-canopy beneath the uppermost layer), tall shrubs (shrubs and shorter statured trees 2−5 m in height), short shrubs (shrubs 0.5−2.0 m tall), dwarf shrubs (shrubs under 0.5 m tall), herbaceous (forbs and graminoids), and non-vascular (non-vascular plants). Each species was assigned cover classes based on ocular estimates (<1%, 1−5%, 5−15%, 15−25%, 25−45%, 45−75%, >75%).

Cottonwood Sites

Measurements were taken to estimate percent leader use of cottonwood saplings, seedlings, and resprouts unprotected from elk and bison browsing as well as recruitment rates of protected cottonwoods. Because exclosures weren't completed at all the cottonwood sites until October 2005, measures at exclosure sites are intended to provide pre-treatment data as well as expanding the sample size for determining summer browsing rates. Measurements were taken on all cottonwood plants that fell within each of two 10-m radius circles (5-m radius circles were used in extremely dense vegetated areas) at each site and grazing treatment. Plot locations were selected by moving a random direction and distance from the center of the grazed or exclosed treatment at each site. These circular plots were chosen within the cottonwood stand, such that they did not overlap other plots and were a minimum of 3 m from the exclosure fence. A rebar post was installed to mark the center of each circular plot and was tagged with a plot identification label. UTM coordinate locations of the plots were determined using a handheld GPS unit.

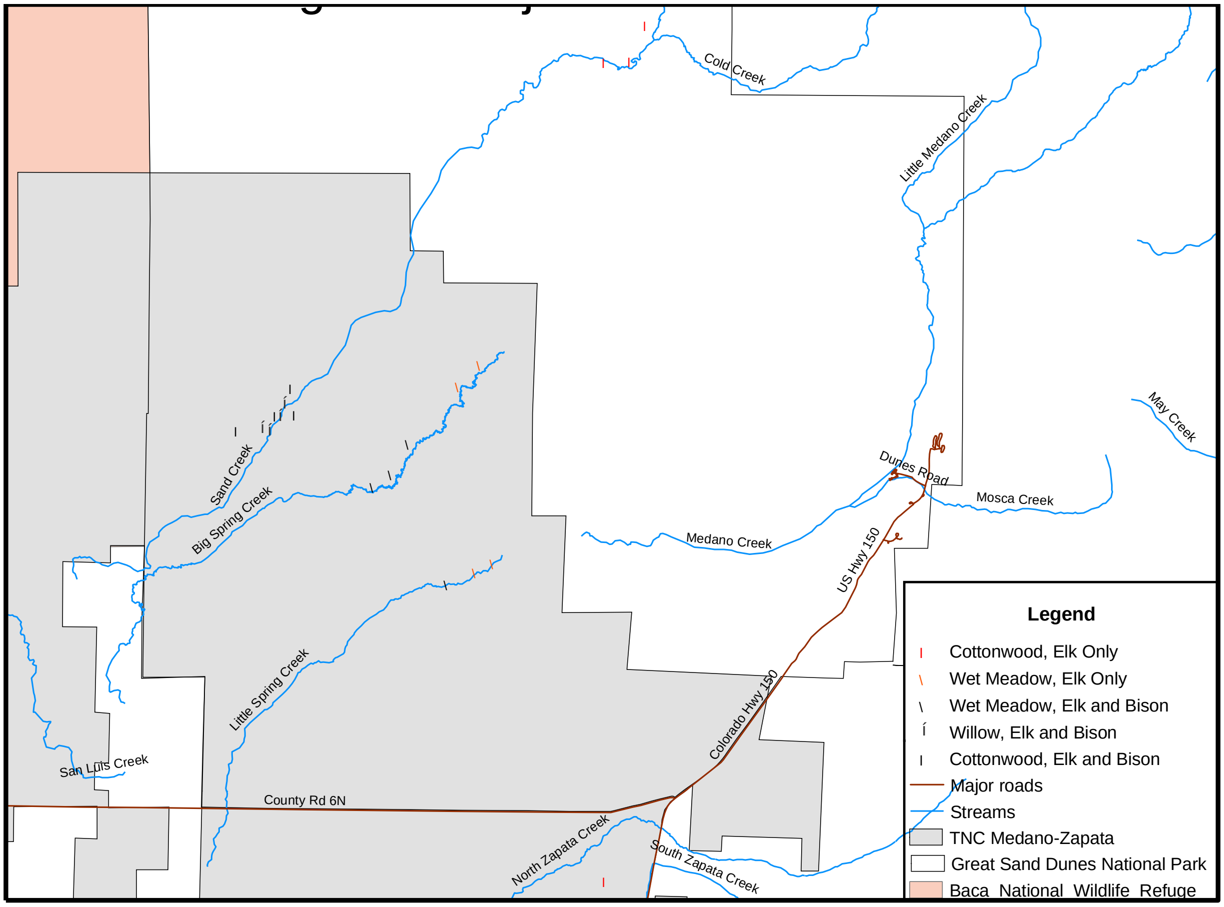

Figure 3. Locations of willow, cottonwood, and wet meadow ungulate exclosure sites in the Great Sand Dunes complex of lands, San Luis Valley, Colorado.

Data were collected at each plot for each tree with a DBH (diameter at breast height, or 1.4 m from ground) of greater than 2.5 cm. We recorded the number of trunks, DBH, estimated canopy diameters, and percent of dead canopy. For each tree that had basal sprouts, we recorded the height, canopy diameters, stem diameter where the sprout exited the trunk, and number of browsed and unbrowsed current annual growth (CAG) shoots. For branches within 200 cm of the ground, number of browsed and unbrowsed CAG shoots were recorded. Data collected for saplings and resprouts (all cottonwood plants less than 1.4 m in height) included height, number of stems, diameter at root crown, canopy diameters, number of browsed and unbrowsed CAG shoots, and percent dead canopy. Percent leader use was determined using the equation:

$$\%\ leaderuse = \frac{a}{a + b}\ (100)\quad , \qquad (4)$$

where: a = number of browsed CAG shoots, and b = number of unbrowsed CAG shoots.

Willow Sampling

Two fixed-radius,10-m^2 circular plots were randomly located within the willow community of each grazed and exclosed treatment at each site. The center of each circular shrub plot was marked with rebar. All plants that grew completely or more than 50% within the plot were measured. In the case of indistinct plants where large numbers of shoots or small stems were emerging from the ground side by side, only the part of the clump's canopy that fell within the radius of the plot were measured. Data collected on each willow in all plots included species, shrub canopy diameters (widest and perpendicular to widest diameter), shrub height, number of stems, an estimate of percent of dead canopy, a subsample of the number of browsed and unbrowsed CAG shoots, leader length, and diameters at shoot base, tip, and point of browse.

On lower Sand Creek, the willow communities consist almost exclusively of coyote willow (*Salix exigua*). This species tends to have shoots that branch multiple times within a single season's growth. In cases of multiple branching shoots, the length of the longest part of the shoot plus the length of all side shoots from branching point to tip were totaled to give the total shoot length. Basal shoot diameter measurements on such shoots were taken only from the base of current year's growth where the previous year's bud scar was located, not from branch points along the shoot. Tip diameters were taken from the current year's apparent main growth shoot, not from branching shoots. For browsed shoot counts on such shoots, browsing on any part of the shoot was counted as only one browsed shoot.

In 2005, due to labor shortage, many of these willow sites were not surveyed until November-December. Percent leader use will be considered cumulative and will be measured in spring 2006, but we were striving to get some baseline data on these sites shortly after the exclosures were constructed. Percent leader use was estimated using formula (4) described for cottonwood sites. Average percent twig removed was determined using the method of Jensen and Urness (1981) and Pitt and Schwab (1990) following the formula:

$$\%twiguse = \frac{100(D_p - D_t)}{D_b - D_t} \quad , \qquad (5)$$

where: D_p = twig diameter at point of browsing, D_t = diameter of a representative sample of unbrowsed twig tips, and D_b = basal diameter of the current year's twig growth. Total consumption was determined by multiplying percent leader use by percent twig use.

Vegetation Field Work for 2006

Field data collection for 2006 is scheduled to begin the last week of March and will continue through the end of September. At this time, we project that winter consumption sampling of herbaceous vegetation will occupy most of April, followed by willow and cottonwood consumption in May 2006. The first sampling of herbaceous production and summer consumption will begin in June 2006, and sampling will continue cyclically for 3−4 sample periods throughout the growing season. Cottonwood recruitment and willow production measures will begin in mid to late August and continue through the end of September. Sampling will be conducted at all exclosure sites and their paired grazing treatments. We hope to increase the number of plots sampled at each site and treatment to decrease the variance of the data.

If time and funding allows, we will place grazing cages in several other target communities on the Medano Ranch to try to capture consumption levels in other key communities used heavily by bison. We also plan to conduct a survey of willows growing in interdunal wetlands. Data exists as to the location and hydrology associated with these wetlands. We plan to use a GPS unit to map willow patches (both live and dead) in these wetlands, estimate depth to which willows are buried in sand to index dune encroachment, and measure consumption on live willows to determine the amount of utilization occurring in these communities. Laboratory sorting and weighing of 2005 herbaceous samples will continue through spring 2006, and processing of 2006 samples will commence in fall 2006.

Alpine Willow Herbivory in the Upper Deadman Creek Drainage

Rio Grande National Forest and CDOW managers were concerned about potential high use of willows by ungulates in the alpine areas of Deadman Creek drainage compared to other nearby alpine areas. In September 2005, at the request of USDA-FS, CDOW, and NPS partners, a field crew visited alpine areas of Deadman Creek and Deadman Lakes. Alpine areas above Cottonwood Creek were selected for comparison and visited the following week. Information on heights and leader use of alpine willows was collected in an effort to index use of these areas.

Willows were measured using a line-intercept method (Canfield, 1941) along 30-m transect lines. Eleven transect lines were measured in the alpine areas of Deadman Creek drainage and encompassed areas of short alpine willows as well as areas of taller subalpine willows near treeline. This drainage appeared to have high elk use as well as bighorn sheep activity. Four transect lines were measured in alpine areas of the Cottonwood Creek drainage, an area with apparently lower levels of elk and bighorn sheep herbivory. General observations were made as to the number of elk and bighorn sheep fecal pellets in relation to the measured willow patches.

Transect lines were laid out along a random bearing running through willow patches to be measured. Lines began at the edge of a willow patch to ensure inclusion of heavier levels of browsing that may occur near patch edges. At any place where the line intercepted the canopy of a willow, the length of that intercept was recorded, along with the average height and species of the willow. For each clump, we recorded the species of willow and the number of browsed and unbrowsed CAG shoots on the plant. Only browsing on current year's twigs was counted. When willow clumps were continuous (which makes it difficult to distinguish individual plants), or when the growth consisted of many single shoots emerging from the ground, a 0.5 m x 0.5 m plot was used for counting browsed and unbrowsed shoots, instead of counting on the entire plant/clump. UTM coordinates of each transect line were recorded using a handheld GPS unit.

Due to continued concern about alpine willow use by elk and potential displacement of bighorn sheep from elk overconcentrations in summer, we intend to repeat the alpine survey in 2006 and develop a broader experimental design. Some contribution of time and personnel (field technicians) will be requested from partner and cooperating agencies since this addition to the original study plan is not funded.

Interactions of Herbivory, Climate, and Water Table

Aging of both cottonwood and willow (willows aged at basal root crowns) to determine the year they were established will commence in 2006. We plan to establish water wells at each paired exclosure/grazed site and attempt to correlate fluctuations in water tables and precipitation to periods of woody establishment to attempt to evaluate whether herbivory is correlated to declining water tables or to partial sand burial. Damaged or stressed plants are often more susceptible to browsing and are often more palatable to ungulates during periods of stress. Thus, drought could exacerbate the effects of herbivory. Winter 2005−2006 was one of the driest years in the past 50 (F. Bunch, pers. commun., 2006), so an opportunity exists to evaluate the effects of a severe drought year. We are currently investigating the potential for an additional study of plant physiology of the willows and cottonwoods (Andersen and Cooper, SSP proposal, 2006).

Elk and Bison Grazing Model and Estimates of Carrying Capacity

Ecological model development will commence in 2007 because it relies on inputs from empirical data collections in 2005, 2006, 2007, and possibly 2008.

Carrying capacity is defined as the maximum number of animals, in this case ungulates, the resources of the area can support (McCullough, 2003). It refers strictly to the capability of the land and is expressed in number of animals that can inhabit the area, without regard to limiting factors such as predation rates. We will estimate carrying capacity using three methods. First, we will use the method of forage biomass-based estimate of carrying capacity for elk that has been used for elk and bison in the Greater Teton Ecosystem (Hobbs and others, 2003). This method uses available forage, estimated offtake levels, and forage requirements to estimate ungulate numbers that can be supported across large landscapes. Using GIS technology, this method will be coded into a model that will allow simulation of the needed management scenarios outlined in the next section. Inputs for this model will be products derived from the vegetation studies described in the previous section, existing Park and area vegetation maps, and estimates of ungulate forage requirements derived from previous research in similar systems. Second, we will estimate carrying capacity using the mathematical approach outlined by Hobbs and others (1982). This spreadsheet/mathematical method relies on forage quantity/quality and ungulate nutritional needs to derive an estimate. Inputs for this model will come from sampling of forage quality (nitrogen concentrations) in key elk habitats, as well as prior research in similar systems. These first two methods proved highly successful in a very similar project in the Greater Teton Ecosystem and met the needs of project stakeholders, including USFWS, NPS, Wyoming Game and Fish, and the USDA-FS. Third, we will use a population-based model that incorporates a nonlinear density feedback. Population modeling in this report presents the population-based estimate. When the herd is far from carrying capacity, this is a rougher estimate than other methods, but still useful. We plan to use all three methods to gain confidence in our estimates of carrying capacity for the area.

Body Condition Model for Elk

In order to develop a model of elk body condition for the Great Sand Dunes–Crestone–Sangre de Cristo complex, we requested the collaboration of John Cook and Rachel Cook, who have developed techniques for measuring nutritional condition of elk and have published numerous papers on the subject (Cook and others, 2001a,b; 2004a,b). Our goal is to investigate the effects of the following parameters on elk condition: (1) elk population density (the density may be greatly reduced in the next few years), (2) drought (the area is subject to periodic severe drought, as occurred in 2005–2006), and (3) subpopulation or area (how do elk fare in the more typical higher summer range of the Sangre de Cristos versus the less typical low-elevation summer range that most elk select in the valley floor). We collected body condition score from aerially captured elk cows in February and November 2005, and March 2006. We plan to measure body condition of elk cows again in November 2006. Although calf condition and calf survival are the most sensitive class to respond to environmental change, we were not able to measure calves. Our model will portray the importance of these three variables to elk condition and to potentially project scenarios. Modeling for elk body condition will be completed in 2008, but initial elk body condition results are presented here.

John Cook and Rachel Cook led data collections during each of the elk captures. We sampled elk body condition using a score developed by John Cook and colleagues (Cook and others, 2001b). This score combines a measure of the palpation of the wither, ribs, and rump (= BCS score) combined with a measure of subcutaneous rump fat thickness, the latter measured using ultrasound (Stephenson and others, 1998). We sampled the catabolism of lean mass of elk by measuring the thickness of the longissimus dorsi (loin) muscle between the 12th and 13th rib. The BCS score is converted to an estimate of body fat (%) and gross energy using the equations developed by Cook and others (2001a, b).

Using the ultrasound for subcutaneous rump fat depth is the "best" live animal index available; however, it has its limitations. Once rump fat is depleted (about 5–6% body fat), the ultrasound measurement cannot be used. For many herds, this poses a problem in the spring. A body condition score works well for all levels of condition but has been criticized for being subjective. Thus, we followed Connolly's (1981) approach by combining kidney fat index (KFI) and femur marrow fat into a new index and combining the rump fat thickness and the rump body condition score. To address limitations associated with each index, the estimate of body fat relies on a combination of the two values until rump fat thickness is depleted; beyond that point the estimate relies solely on the body condition score.

Heart girth (chest girth) measurements were taken on hobbled elk in the field and then converted to sternal girth values for estimating mass using equations in Cook and others (2003). Mass estimates are also dependent on pregnancy status (due to the weight of the fetus), so mass was calculated using the following formulas:

If pregnant: $mass = 2.296*stgirth + 1.299*\%fat - 133.455$
If non-pregnant $mass = 1.877*stgirth + 1.840*\%fat - 89.458$

And for yearling cows,
If pregnant: $mass = 2.296*stgirth + 1.299*\%fat - 133.455$
If not pregnant: $mass = 0.740*stgirth + 2.499*\%fat - 45.484$

Specific body condition indices that were measured on each helicopter net-gun captured elk include maximum rump fat thickness, depth of longissimus dorsi muscle (which is essentially an index to protein catabolism and is useful in looking at change of condition over a given time period), withers body condition score, rump body condition score, and calculated ingesta-free body fat.

Pregnancy rates are also an indicator of the nutritional status of elk. This is particularly true for yearling cows, where the pregnancy rate may be high in herds in good condition or almost zero in herds that are not. Therefore, we collected serum from captured cows for pregnancy evaluation using pregnancy-specific protein B (Noyes and others, 1997).

Data Analysis

We used SAS statistical software V8 (SAS Institute, 1988) for data analysis, and we used multivariate methods and ANOVA procedures to evaluate differences in treatment effects.

Ungulate consumption was determined using the difference method (Bonham, 1989). Herbaceous biomass differences were analyzed using ANOVA procedures.

Results and Discussion

Elk Distribution and Home Range

Elk distribution from month to month is shown in fig. 4. Elk appear to have distinct and separate ranges in summer (north vs. south) and are more contiguous in winter, although we may learn differently with the addition of more years of data. A difference in distribution is seen from winter 2004−2005 to winter 2005−2006 (fig. 5), likely due to the lack of precipitation in the SLV in winter 2005−2006. Winter 2004−2005 appears to have been a fairly heavy year for precipitation; while 2005−2006 was at the opposite extreme, according to SNOTEL precipitation data collected at Medano Pass (fig. 6). Elk remained at higher elevations where they had access to what are normally snow-drifted areas in winter. Since forage was available along the slopes of the Sangre de Cristo Mountains throughout the winter, elk may not have concentrated on the valley floor in winter 2005−2006 as they did the previous year. However, the groups that did winter on the Baca NWR in 2005−2006 were highly concentrated in two large groups of 1,000−2,000 individuals for about 1 month in early/mid-winter.

Elk were observed using areas west of Highway CO-17 during summer (fig. 4). We found 6 of 60 radiocollar locations west of the highway, although collared elk were not observed in or near irrigation circles to the north. In 2006 CDOW is potentially placing more radiocollars on elk in the area of the irrigation circles to further determine their movements.

Elk summer (June-August) home ranges varied depending on whether they migrated. Home ranges were larger for elk summering on the valley floor than for elk that migrated to high-elevation summer range ($P < 0.05$). The shape of home ranges was more elongated for elk using high-elevation summer habitat, and more rounded for elk summering on the valley floor ($P = 0.01$), when comparing perimeter:area ratios of minimum convex polygons. Since elk prefer to move horizontally (Skovlin and others, 2002; Kie and others, 2005), we would expect home ranges to be more elongated in hilly areas. Forage availability within a given home range must meet energy and nutritional needs of elk, otherwise the home range size must be increased to include additional resources (Ford, 1983; Relyea and others, 2000). Therefore we would expect winter home range size to be larger than summer in areas where there is heavy snow cover or reduced forage availability. We will calculate winter home range sizes to test this in 2006−2007.

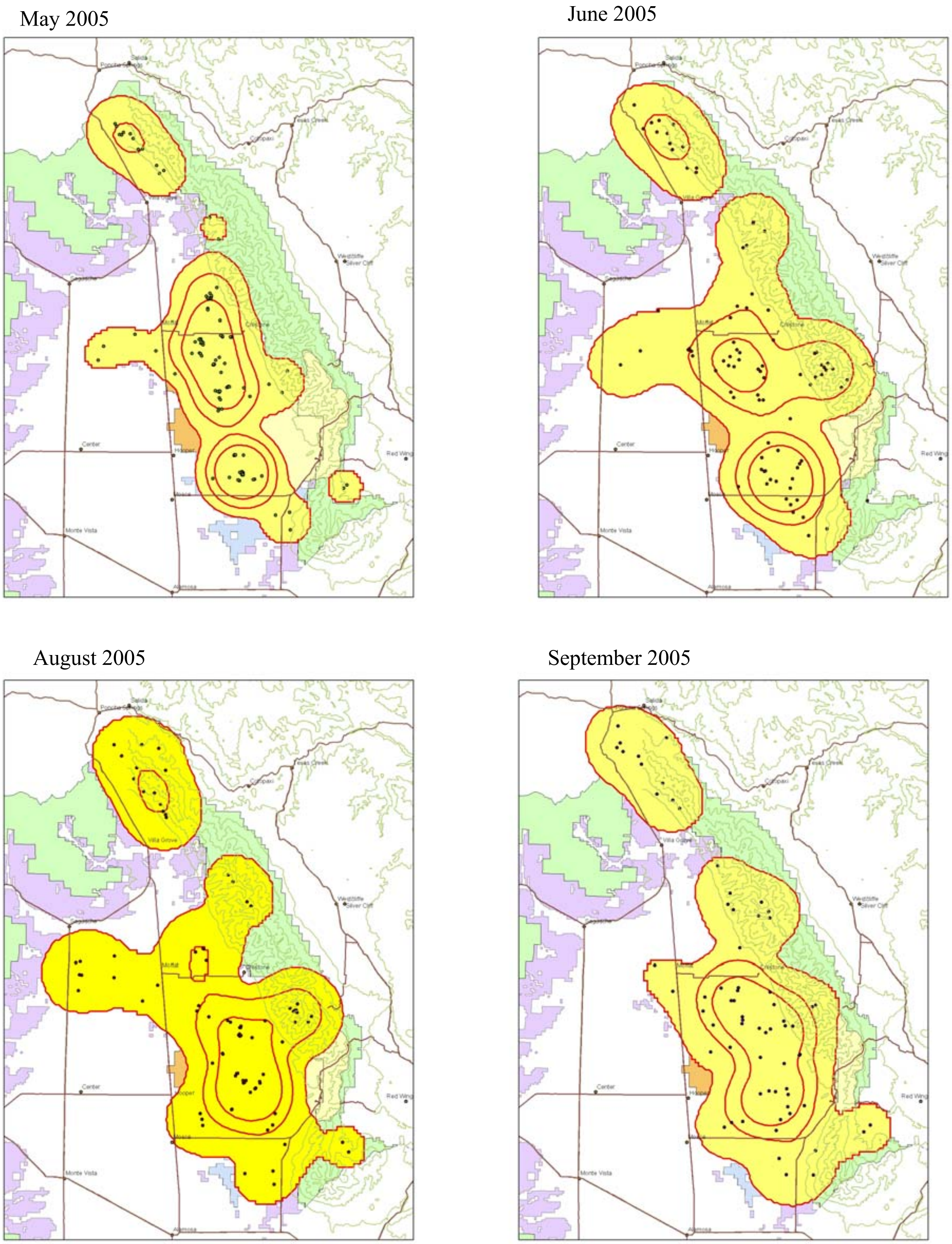

Figure 4. Elk kernel density estimates showing locations of 50% kernels (outer circle) and 95% kernels (inner circle) in several key summer months in the Great Sand Dunes study area, San Luis Valley, Colorado, 2005.

February 2005 February 2006

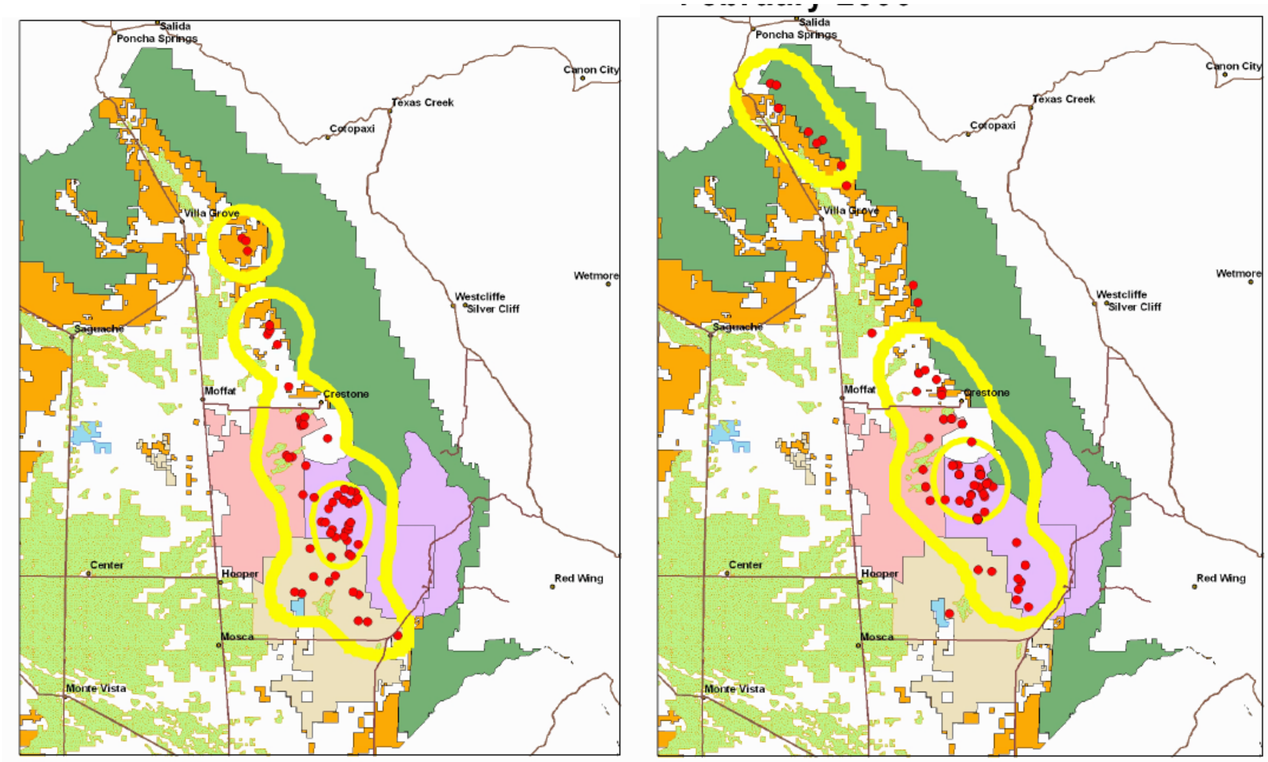

Figure 5. Change in winter elk distribution in the Great Sand Dunes study area from 2005 to 2006, comparing elk kernel density estimates in February 2005 with February 2006, San Luis Valley, Colorado. Note the lack of concentration of elk on the Medano Ranch (shown in beige) in 2006. Land area in pink is the Baca NWR, purple is NPS, and dark green is USDA-FS.

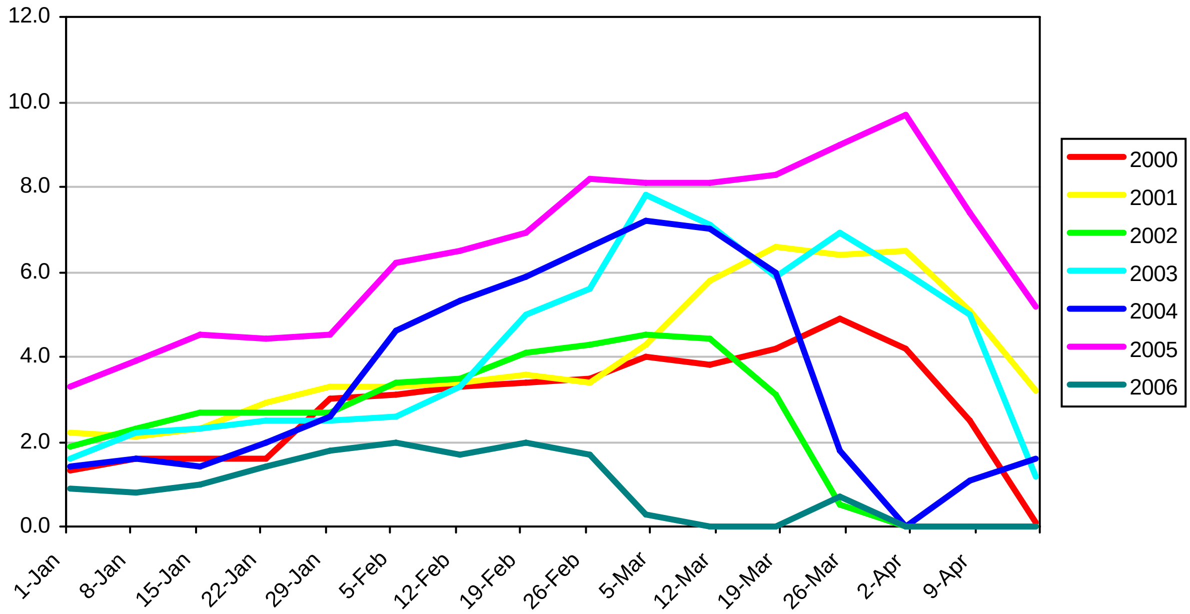

Figure 6. Precipitation levels from the SNOTEL site in Medano Pass (snow water equivalent (SWE) in inches at ~9,600 ft), San Luis Valley, Colorado, in winters 2000–2006. Note the lack of precipitation in winter months for 2006.

Elk Population Size

Observed Elk

The front-seat observer in the helicopter detected 39 elk groups, and the rear-seat observer detected 22 groups. Seventeen of these groups were common to both observers; so, combined, they saw 44 groups. The fixed-wing aircraft located 4 groups of elk with radiocollars present that were not seen by the helicopter crew. Thus, 48 groups were known to be present in the survey area. In addition, 8 radiocollars were not found within the survey area boundaries during the time of the survey. One of these was located in the Crestone residential development area, which was off-limits to helicopter overflight. The remaining 7 collars could not be located, but were relocated subsequent to the flight, confirming that they were still functioning.

The front-seat observer in the helicopter counted 2,904 elk in the field; however, this number was revised to 3,196 based on a careful scrutiny of photographs of the largest groups. The helicopter crew together (front and rear observers combined, excluding duplicates) counted 2,952 elk in the field, which they revised to 3,244 after a careful review of the photographs. In other words, 292 elk were later determined to be present in groups seen, but were not counted during the flight. The fixed-wing aircraft counted an additional 170 elk in the 4 groups with collars that were available to, but not detected by, the helicopter. In all, combining data from all sources and using photograph-based counts, the field crews observed 3,414 elk.

Sightability Model Based on MARK Analysis

The best model of elk group sighting probability contained three parameters: an intercept, a slope for group size, and a slope for the presence of vegetation (either shrubs or trees). This model received 9.6% of the model weight. Many alternative models received nearly equal support.

In total, 75.0% of the AIC*c* model weight supported models with the group size covariate; shrub cover received 40.8%; tree cover 35.5%; front versus rear seat position 29.7%; percent snow cover only 11.6%; and percent vegetation cover only 9.1% of model weight. A composite variable that indicated presence or absence of vegetation cover of either shrubs or trees was found to be a better indicator than either of these alone or both included together, with or without interactions between them.

The estimated best model for aerial sighting probability, p_i, for an elk group, *i,* was:

$$p_i = \frac{1}{1+e^{-(\boldsymbol{\beta}\mathbf{x}_i' + \mathbf{x}_i'\boldsymbol{\Sigma}\mathbf{x}_i)}} \quad ,$$

where:

$'$ = indicates a matrix transpose,
$\boldsymbol{\beta}'$ = [1.36554, 0.00646, -1.15087] was a vector of fitted coefficients for the logistic model,
$\mathbf{x}_i'$ = [1, n_i, v_i] was a vector of observed covariates for group *i* (the 1 is for the intercept term),
n_i = number of elk counted in a group, *i*,
v_i = 1 if elk group, *i*, was located in an area of shrubs *or* trees and 0 otherwise, and

$$\boldsymbol{\Sigma} = \begin{bmatrix} 0.46103 & -0.0025 & -0.4227 \\ -0.00254 & 0.0001 & 0.0018 \\ -0.42265 & 0.0018 & 0.7374 \end{bmatrix}$$

was the variance-covariance matrix of estimated logistic model parameters.

Sighting probability for groups seen by multiple observers was computed as:

$$p_{\text{comb}} = 1 - (1 - p_{\text{obs1}})(1 - p_{\text{obs2}}).$$

The sighting probabilities from the chosen model apply to both front- and rear-seat observers, but only for groups *available* to those observers. The rear-seat observer could not see groups located on the opposite side of the helicopter or along the centerline. During the survey, 7 of the 44 groups seen from the helicopter were recorded as being on the centerline, leaving 37 available to observers viewing only out of rear side windows (note that these values are actual observed numbers of groups, not bias-adjusted estimates). With a single rear observer, only half of these (on one side) would be available, leaving 42.0% of all groups available to the single rear observer. In other words, sighting probability for a group seen by the rear observer was computed as $0.42p_r$. This correction assumes that elk were randomly distributed on either side of the aircraft. We believe that this assumption was met both because the rear observer switched sides and because transects were largely perpendicular to ecological gradients.

Population Estimate

When corrections for sighting probabilities were applied to all known elk groups, the estimated number of elk present in the survey area was 3,460 ± 66.7 (SE) elk with a 95% log-normal confidence interval of 3,420–3,783. This represents a low coefficient of variation or error rate of 1.9%. Of the 64 working radiocollars, 7 were not located by the fixed-wing pilot and one was in Crestone where it was unavailable to helicopter observers. We assumed the 7 missing radiocollared elk were not within the boundaries of the survey area during the flight. We suspect these animals moved higher into drainages of the Sangre de Cristo Mountains after being captured and radiocollared two weeks prior to our survey, and were not found by either the fixed-wing or helicopter observers. This may or may not be a valid assumption, as these 7 radiocollared elk were located on the lower slopes of the Sangres or on the valley floor two weeks later. However, the composition of radiocollared elk groups were not the same for any group from our survey to the next one, so we cannot be sure. In either case, to obtain an estimate of the full population, including those temporarily missing or thought to be outside of the survey area boundaries, we applied the estimated availability rate of (64–8) / 64 = 87.5 ± 6.5% to produce our final estimate of the full elk population. A composite standard error was computed using the delta method based on the two component error estimates. A 95% confidence interval was computed based on a log-normal probability distribution. The final estimated population, including elk not present in the survey area, was 3,955 ± 304 (SE), 95% log-normal CI = (3,608–4,919) elk, which represents a 7.7% CV error rate.

Survey Biases and Error Rates

Compared to the final estimate of 3,955 elk, a single highly experienced observer in the front seat of the helicopter counted only 2,904, or 73.4% of the total population, while in the air (although digital photography increased the percentage to 82.0%). In other words, the actual population was 1,051 elk, or 36.2% larger than would have been indicated by just the raw field count. This large difference between raw and statistically estimated population size is the result of the combined effects of five different sources of error in the raw counts (table 2), which are discussed in the following sections.

Table 2. Sources and sizes of biases affecting the final population estimate for elk in the Great Sand Dunes study area, Colorado, 2005.

Factor/Correction	Estimated Bias Correction	Cumulative Estimate[1]	% of Total Population (3,955)	% of Available Population[2]
Raw, single observer count		2,904	73.4%	83.9%
Single observer bias	48	2,952	74.6%	85.3%
Large group field count bias (photo)	292	3,244	82.0%	93.7%
Aerial group sightability bias	216	3,460	87.5%	100.0%
Availability bias (survey area/elk movement)	494	3,955	100.0%	114.3%

[1] The cumulative estimate column is the total of the raw count plus bias corrections in each row, showing the estimate after correction. Only the estimate in the final row is a fully corrected estimate of the elk population.

[2] Population present within survey area during flights, based on proportion of radiocollared elk thought to be outside of survey area at the time.

Survey Area and Elk Movement Bias

The results of this survey illustrate the important biases present in raw field data (table 2). The largest single bias in the field count was caused by what we assumed was the movement of elk outside of the pre-defined study area (radiocollared elk groups not found by the fixed-wing pilot). This bias represented 494 elk, or 12.5% of the population. Without radiocollared animals, this bias could not have been corrected in this survey and would not even have been known. To avoid the continued use of radio collars during future surveys, a valid option is to ensure that the survey area encompasses all of the locations where elk could be at the time of the survey. Enlarging the survey area may involve prohibitively high survey costs, so timing the survey with careful attention to snow conditions so that elk are known to be concentrated in the smallest possible areas of winter range is recommended. However, it may be necessary to at least partially sub-sample areas outside the normal winter range of this herd to obtain an estimate of the portion of the population that may stray beyond the regular survey boundaries. In years with below-normal snow, accurate surveys may be impossible or too expensive to justify.

Large Group Field Count Bias

The second largest bias was caused by the undercounting of large elk groups in the field, as compared to more intensive counts of high-resolution digital photographs of those same groups. An additional 292 elk, or 7.4% of the population, would have been missed without the use of photographs. Elk groups in this population during winter are often very large. The largest group during this survey contained 667 elk. The combined motion of the elk and the helicopter makes accurate counting of groups this large unlikely without the use of high-resolution photographs. Consequently, we recommend use of photography for all large groups during future surveys.

Aerial Group Sightability Bias

Aerial sightability bias refers to the imperfect detection (missing) of elk groups (not individuals within groups) by aerial observers. This bias was similar in magnitude to the large–group–field–count bias. Without statistical corrections for sightability of groups, an additional 216 elk, or 5.5% of the population would have been unaccounted for. This bias can be corrected through the regular use of two (or, preferably three) aerial observers on all surveys so that sightability correction models can be calculated based on the observers and field conditions specific to that survey. The sightability model estimated in the current study could be applied to a single aerial observer in a future survey; however, this will introduce unknown bias due to variation among surveys related to different environmental conditions and observers. For this reason, it is not a good idea to apply the population estimation model to future surveys, although the data regarding sightability from this survey and future surveys could potentially be pooled to obtain a larger sample size and greater precision, if statistical models support such pooling.

Single Observer Bias

The additional bias that would have arisen by using only a single observer in the helicopter, rather than two, accounted for 48 missed elk, or 1.2% of the population. Although this bias can be corrected using a sightability correction model, that model itself can only be estimated for a particular survey if a rear observer is present. Without the second observer, corrections can only be made by placing unwarranted faith in the applicability of the sightability corrections estimated from different flights, with different observers, under different conditions.

"Full" Sightability Model Applied to Helicopter Data Only

To build the “full” sightability model that was used for the final population estimate above, we used data collected from the observers in the helicopter and the additional data collected by the fixed-wing pilot. We then used this "full" model to analyze the survey data again, but without including data collected by the fixed-wing; this enabled us to examine how well the "full" model would have performed in the absence of supplemental data from the radiocollared elk. Using this sightability model with the helicopter-based dual-observer data alone, we estimated 3,340 ± 100.5 (SE) elk. This is 3.5% lower than the best estimate of the available elk (3,460) based on all available data, including radiocollars. Without radiocollar data, the error estimate increased from 1.9 to 3.0%. This is the rate of error that could be expected on future surveys after radiocollar data is no longer available. Note that this estimate uses the sightability model developed with radiocollar data included, but applied only to the helicopter observations.

"Partial" Sightability Model Based on Helicopter Data Only

For comparison to the "full" model above, we reconstructed the model as if we never had the radiocollars to begin with. In other words, we didn't use fixed-wing data to build this alternative sightability model in order to see what our population estimate would have been if we had relied only on helicopter data and observations. In this analysis we considered only the data collected by the two helicopter observers, both for fitting/building the sightability model and for correcting the observations to obtain a population estimate. This differs from the analysis in the previous section, where the sightability model was built using the complete data set (both fixed-wing and helicopter), but was applied only to helicopter data. The most strongly supported model included the same two covariates as the model developed with radiocollar data, but had separate intercepts for front and rear observers. The model for sighting probability for group *i* by observer *j* was:

$$p_{i,j} = \frac{1}{1 + e^{-(\boldsymbol{\beta}\mathbf{x_i} + \mathbf{x_i'}\boldsymbol{\Sigma}\mathbf{x_i})}} ,$$

where:

′ = indicates a matrix transpose;
β′ = [1.20332, 2.81276, -2.71248, 0.03848], which is a vector of fitted coefficients for the logistic model;
x_i = [$I_{i,f}$, $I_{i,r}$, n_i, v_i] is a vector of observed covariates for group *I;*
I_f, = front seat indicator variable: 1 if front observer, 0 if rear;
I_r= rear seat indicator variable: 1 if rear observer, 0 if front;
n_i = number of elk counted in a particular group;
v_i = 1 if elk group is located in an area of shrubs *or* trees and 0 otherwise; and

$$\boldsymbol{\Sigma} = \begin{bmatrix} 0.9370 & 0.7370 & -0.6951 & -0.0253 \\ 0.7370 & 1.737 & -0.6951 & -0.0253 \\ -0.6951 & -0.6951 & 1.9065 & 0.0058 \\ -0.0253 & -0.0253 & 0.0058 & 0.0024 \end{bmatrix}$$

is the variance-covariance matrix of estimated logistic model parameters.

The estimated population using this "partial" model was 3,307 ± 288 (SE) elk with a 95% lognormal confidence interval of [3,246–5,212]. This estimate is 4.4% lower than the one (3,460) obtained using the sightability model based on the full data set (including radiocollar data), and the estimated error rate is 4.3 times higher.

Helicopter Observations Without Radiocollar Data

There was no significant bias in estimating the available population using the sightability model developed with the combined helicopter and radiocollar data, but using only helicopter data to estimate the population size. These estimates differed by only 3.5%. The error rate increased from 1.9% to 3.0% CV using only helicopter observations, which is still very good.

However, using only the helicopter data from this single flight to fit the sightability model produced a substantially less precise estimate (4.3 times larger error rate and confidence interval width). This is an unsurprising consequence of the small sample size for estimating the sightability model based only on this single helicopter flight. There were only 27 elk groups available to the rear observer in the helicopter (this number is the bias-corrected number of estimated groups available to the single rear observer, not the number actually seen), which is the effective sample size for the sightability model based on helicopter data alone. Had radiocollars not been available, a second flight (either in the same or a subsequent year) would have been required to obtain more precise sightability corrections. With the possibility in the future of pooling data from surveys in multiple years, the total sample size for fitting the sightability model should be adequate without the need for ongoing use of radiocollars.

Comparison to "Idaho" Sightability Model

Models of visibility bias for elk have previously been calibrated and published (Samuel and others, 1987; Unsworth and others, 1994). Software called "*Aerial Survey*" is freely available to analyze such data. For comparison, we used this software to compute estimates of the elk population in SLV using the sightings from the current survey. Observations for front and rear observers were combined for this analysis. In *Aerial Survey* software, the population estimation models have been calibrated for specific aircraft: the Hiller 12E and Bell 47G helicopters, and a Piper Supercub. None of these is comparable to the Bell Jet Ranger used in our survey. Unlike our best model, which includes group size and an indicator of the presence of vegetation, both models for helicopters in *Aerial Survey* use group size, the percentage of vegetation cover and percentage of snow cover as covariates.

We estimated the elk population in SLV using pre-calibrated helicopter models in *Aerial Survey*. Using the Hiller 12E model, *Aerial Survey* estimated 3,310 ± 29.6 (SE) elk. The Bell 47G model estimated 3,288 ± 21.9 (SE) elk. Compared to our best estimate of the available elk (excluding those thought to be not present in the study area) of 3,460 ± 66.7 (SE) elk, both estimates from *Aerial Survey* are low. The Hiller 12E model is 4.3% too low and the Bell 27G model is 5.0% too low. These differences are statistically significant ($P = 0.039$). A more equal comparison, however, is to our estimate based only on helicopter data (the “partial sightability” model, presented above). This estimate (3,307 ± 288 (SE) elk) is very similar to the Hiller model, but 5.7% higher than the Bell model. However, the error estimate is >10 times higher in our estimate (CV for Hiller = 0.9%, Bell = 0.7%, our “partial” model = 8.7%).

Aside from differences in estimates of the population size, the *Aerial Survey* models produced implausibly low estimates of the error rate; both are <0.9%. These very low error estimates would mislead managers into thinking they had a much more precise estimate of the true population than they really did. The error rate estimated for this survey based on our “full” model (including radio collar data), but applied only to helicopter data (excluding radiocollar data), is 3.0% (>3 times higher than the least precise *Aerial Survey* error estimate). Our error estimate is more reasonable, although still somewhat low for typical aerial surveys of large mammal populations. We suspect that the range of variation among elk group sizes in the SLV is much larger than in the areas used to calibrate the “Idaho” models, contributing to these severe underestimates of the statistical error rates. The error calculation procedures used by *Aerial Survey* do not fully account for all sources of error, which our methods do. Our higher, but still modest, error rate gives a more realistic assessment of the true degree of uncertainty about the population size.

We recommend that the “Idaho” models – developed by different observers for use in different habitat with different aircraft and different survey procedures and conditions – not be applied to the elk population in SLV. In fact, a pre-calibrated sightability model—even one built specifically for this population with the aircraft used in this survey—is unnecessary if the simultaneous double count method used in our study is used for future surveys. This method has all of the advantages of sightability models but does not rely on an unnecessary leap of faith that models developed once at a different time, in some other location, by different observers, and using different aircraft will work just as well anywhere, anytime, with anyone. There is no advantage to using the pre-calibrated “Idaho” sightability models when better and equally cost-effective methods are readily available.

Elk Population Model

Model Fitting and Selection

Models were fitted to the field data by the method detailed in White and Lubow (2002). The most general (detailed) model fit the data well, producing a variance inflation factor of 1.59 compared to an expected value of 1.0. Values <2.0 indicate adequate fit and do not require variance adjustments to the estimates.

AIC*c* was used to compare and weigh models. The results of this analysis (table 3) indicated that the best model included an effect of time on calf recruitment but not an effect of population size (density). In fact, 89.3% of the model weight supported a decline in calf recruitment over time. The best model also included sex proportion at recruitment that differed from a nominal 0.50. This difference in recruitment by sex was supported by 75.2% of model weight. Effects of wounding losses were very weakly supported (14.2% for males, 0.0% for females) as were sex differences in adult survival (2.4%). The effect of annual variation in survival rate was not supported at all by the data (0.0%); therefore, constant rates for each age class were preferred.

Although not present in the best model, the effect of density was supported by 28.8% of the model weight and was estimated to have a magnitude that would be of substantial biological importance if confirmed by additional data. The modest weight of evidence supporting the density effect was probably due to the fact that only a single population size estimate has so far been made for this population as part of the current project, and juvenile survival rates have never been directly estimated (for example, with a radiocollar study). Additional years of data on population size should improve the ability to estimate a density effect.

Table 3. Results of AIC*c* analysis to compare and weigh different models for population modeling of elk in the Great Sand Dunes study area, Colorado.

Model[1]	AIC*c*	No. parameters in model (K)	Difference between best and this model (D-AIC*c*)	Relative weight (rel-w_i)	Normalized weight of the model (w_i)
R(T) SR	73.94	7	0.00	1.000	54.7%
R(D,T) SR	76.84	8	2.90	0.235	12.8%
R(D) SR	77.88	7	3.94	0.139	7.6%
R(T) W	77.91	7	3.97	0.137	7.5%
R(T)	77.98	6	4.04	0.133	7.2%
R(D) W	79.77	7	5.83	0.054	3.0%
R(D,T)	80.00	7	6.06	0.048	2.6%
R(D,T) W	80.56	8	6.62	0.037	2.0%
R(T), S(Sex) W	80.80	8	6.86	0.032	1.8%
R(D,T), S(Sex) W	82.87	9	8.93	0.011	0.6%
R(D)	86.66	6	12.72	0.002	0.1%
General x/annual	91.02	12	17.08	0.000	0.0%
Simple	91.24	4	17.30	0.000	0.0%
SR	93.76	5	19.82	0.000	0.0%
General	352.80	34	278.86	0.000	0.0%
				1.828	100.0%

[1] Symbols: R = recruitment rate, T = temporal effect (slope parameter) included; D = density effect included; SR = sex-ratio parameter estimated rather than fixed at 50%; W = wounding loss rates for adults included; S(Sex) = different adult survival rate by sex included. Simple model includes a constant recruitment rate, a single adult survival rate, a single calf survival rate, and the initial population size. General model has all effects including annual mortality factors for survival rates, $m(t)$.

Model Results

We used AIC*c* model weights to compute weighted average values for each model parameter across the complete set of models (table 4). This procedure takes into account both model-specific estimation error and error due to model structural uncertainty. For example, the composite model estimated initial 1983 population size at 1,473 (95% CI = 906, 2394) elk. Several parameters that were not strongly supported by the data have very poor precision (table 4), such as male wounding loss rate. The negative values of β_1 and β_2 indicate that recruitment decreased in response to larger population size (β_1) and over time (β_2), although the decrease due to temporal effects is more strongly supported by the data. More females survive to recruitment age (appearance in their first winter count). Adult males have slightly lower survival rates than adult females independent of harvest, and calves have substantially lower survival than adults, as expected.

Table 4. AIC*c* model-weighted parameter estimates across all models considered for elk in the Great Sand Dunes study area, Colorado.

	Estimate	SE	CV	LCL[1]	UCL[1]
Recruitment max (β_c)	44.9	4.08	9%	36.9	52.9
Recruitment intercept (β_0)	4.12	2.18	53%	-0.1	8.4
Recruitment density slope (β_1)	-0.00021	0.00040	190%	-0.000019	-0.002369
Recruitment time slope (β_2)	-0.150	0.058	39%	-0.264	-0.036
Sex ratio (% female)	61%	7.7%	12%	46.5%	76.5%
Calf survival rate	76.7%	26.8%	35%	24.3%	129.2%
Adult female survival rate	92.8%	6.9%	7%	79.2%	106.4%
Adult male survival exponent[2]	1.13	0.252	22%	0.63	1.62
Initial population	1473	371	25%	906	2394
Male wounding loss	3.25%	15.1%	465%	0.1%	104%

[1] Confidence intervals are computed assuming a log-normal distribution for parameters that cannot have negative values (density slope, initial population size, and male wounding loss).

[2] Adult male survival is computed as $S_m = S_f^a$, where a is the estimated exponent parameter. This yields S_m = 91.9%.

We constructed a model based on the weighted parameters in table 4. This model, which we refer to as the "composite" model, includes both time and density effects on recruitment and serves as the basis for projections and sensitivity analysis presented below. The model appears to be an adequate fit (within the confidence intervals) for most of the observed values (figs. 7-9).
The estimated population over the period of the study ranged from 1,473 in 1983 to 5,077 in 1999, ending at 4,101 in 2004 (fig. 10). The model takes the entirety of the dataset into account in estimating the final population size, rather than just the single observation from our aerial survey. This results in some smoothing of the population curve from year to year, so the modeled population size in 2004 (4,101 elk) is slightly higher than our population survey estimate of 3,955 elk.

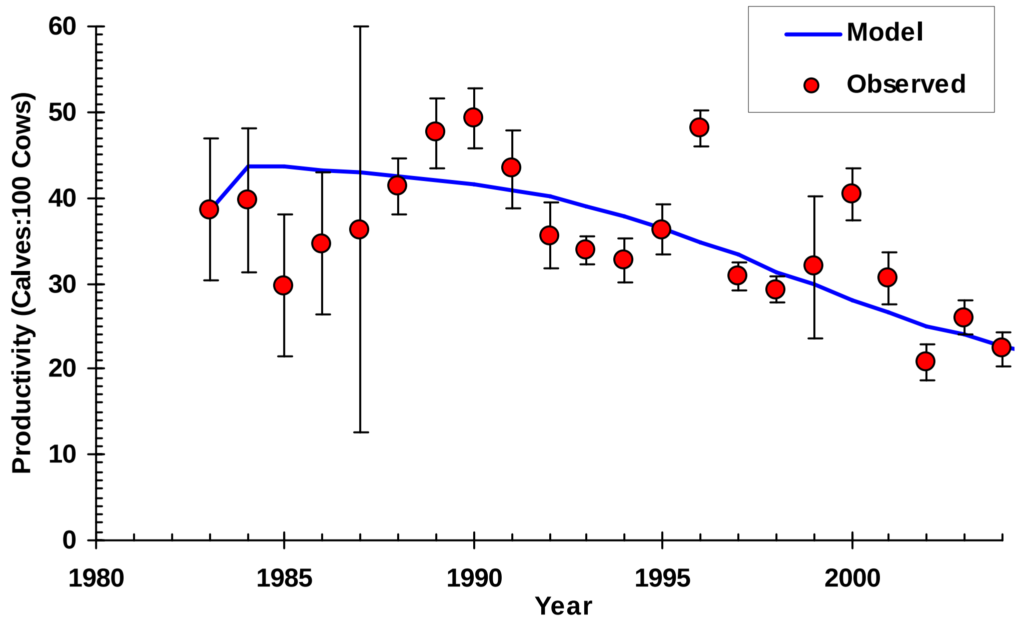

Figure 7. Comparison of modeled and observed ratios of calves per 100 cows for the elk population in the Great Sand Dunes study area, Colorado, from biological years 1983 to 2004 (calendar years 1984–2005). Observed ratios are from CDOW aerial surveys. Error bars depict 1 SE (not 95% CI).

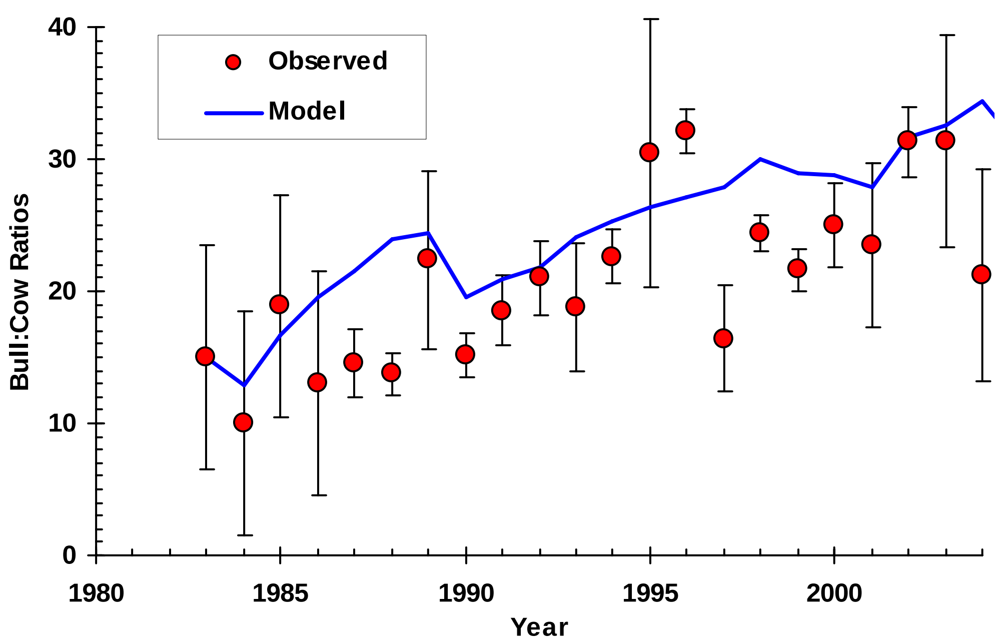

Figure 8. Comparison of modeled and observed ratios of bulls per 100 cows for the elk population in the Great Sand Dunes study area, Colorado, from biological years 1983 to 2004 (calendar years 1984–2005). Observed ratios are from CDOW aerial surveys. Error bars depict 1 SE (not 95% CI).

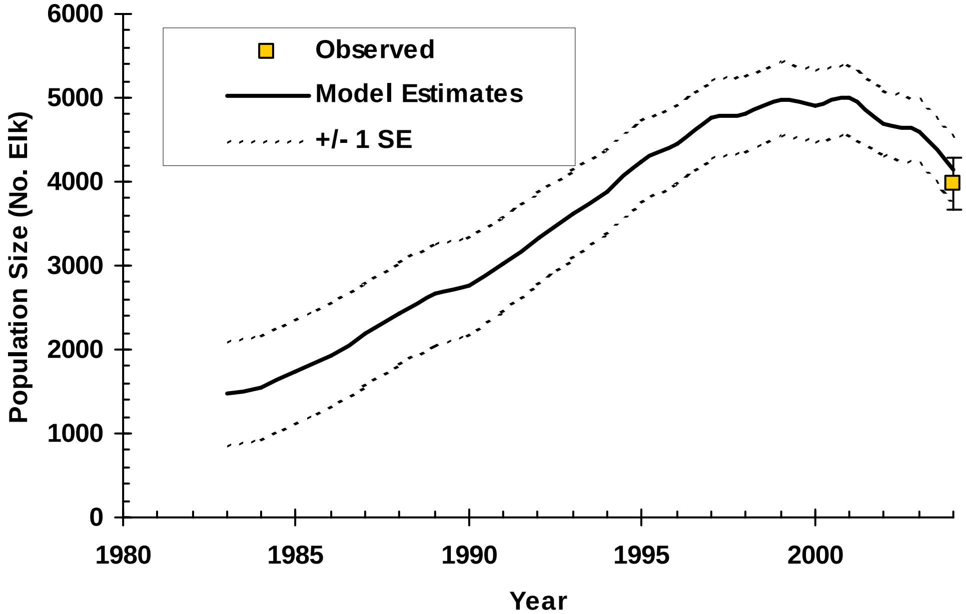

Figure 9. Comparison of modeled and observed population estimates for the elk population in the Great Sand Dunes study area, Colorado, from biological years 1983 to 2004 (calendar years 1984–2005). Error bars depict 1 SE (not 95% CI).

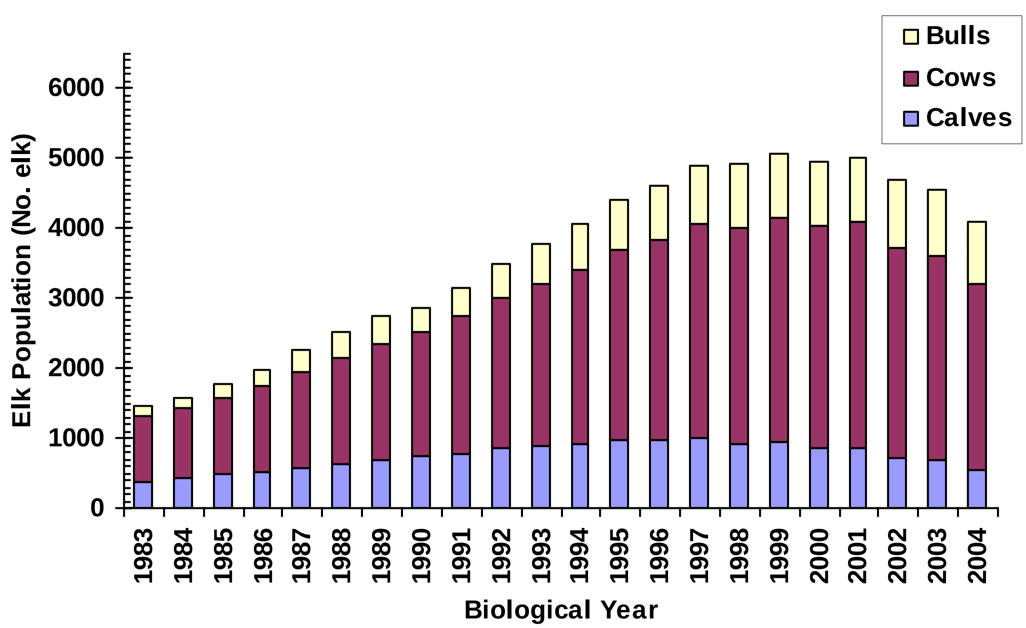

Figure 10. Estimated elk population size in the Great Sand Dunes study area, Colorado, by age and sex class for biological years 1983–2004 (calendar years 1984–2005).

Despite relative population stability (from ~1997–2001) followed by a decline (2001–2004), calf recruitment has continued to decline. We conclude that density is not a complete explanation for declining recruitment.

Projecting the population into the future, including determining an equilibrium population size (ecological carrying capacity) is problematic because of the strongly supported temporal decline in calf recruitment rate. Population projections depend strongly on the future temporal pattern of calf recruitment, independent of the density effect. To investigate further, we examined the recruitment function for several levels of maximum recruitment rate (βc) shown in fig. 11. These projections of the population into the future assumed that bulls would be harvested at the same rate (percentage of bulls present) as the average over the last 5 years of the study (BY 1999–2004), which was 17%. Similarly, we assumed the calf harvest would remain at the same average level relative to cow harvest as during the past 5 years (7.7%).

We also estimated the population size that would result in MSY for a range of assumed maximum recruitment rates (fig. 12). MSY is determined by finding the rate of antlerless harvest that maximizes the equilibrium total harvest (all age and sex classes). Projected equilibrium population size with no female harvest is zero for recruitment rates below 15.2 calves/100 cows (fig. 12). Equilibrium population varies widely for calf recruitment rates between this minimum up to about 20 calves/100 cows, and much more gradually for higher calf recruitment rates.

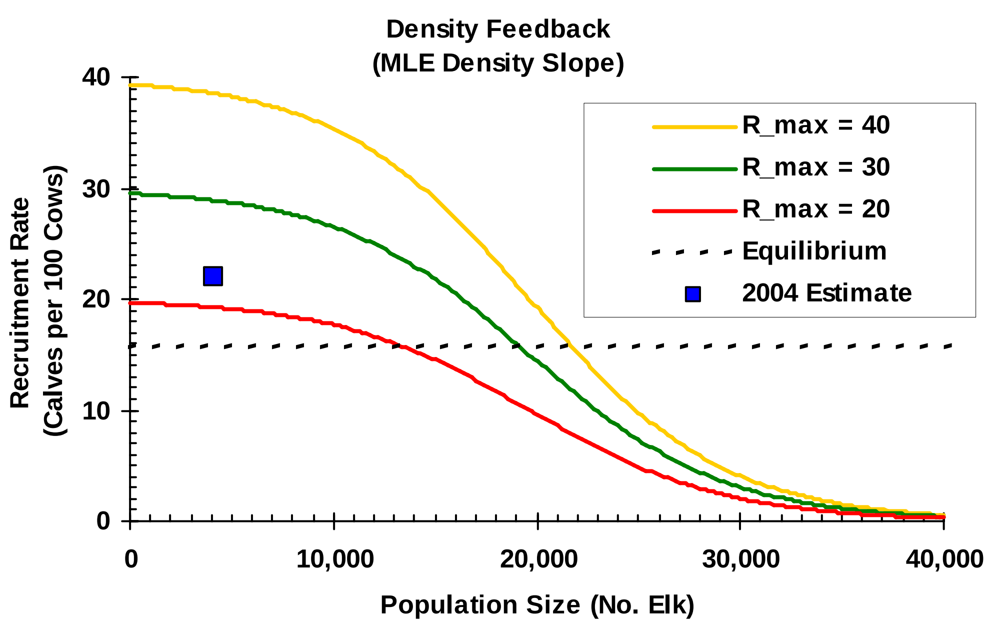

Figure 11. Sensitivity of the model of calf recruitment (eqn. 1) to a range of predictions about potential future maximum calf recruitment rates, *c*, with no temporal effect (t = 0) and assuming the model-weighted maximum likelihood estimate (MLE) for the density effect slope, $_{2}$, illustrating what the population would be at various recruitment rates. The dotted line is the recruitment rate at equilibrium herd size, and the intersection of the three colored lines shows the population size at equilibrium for each recruitment rate.

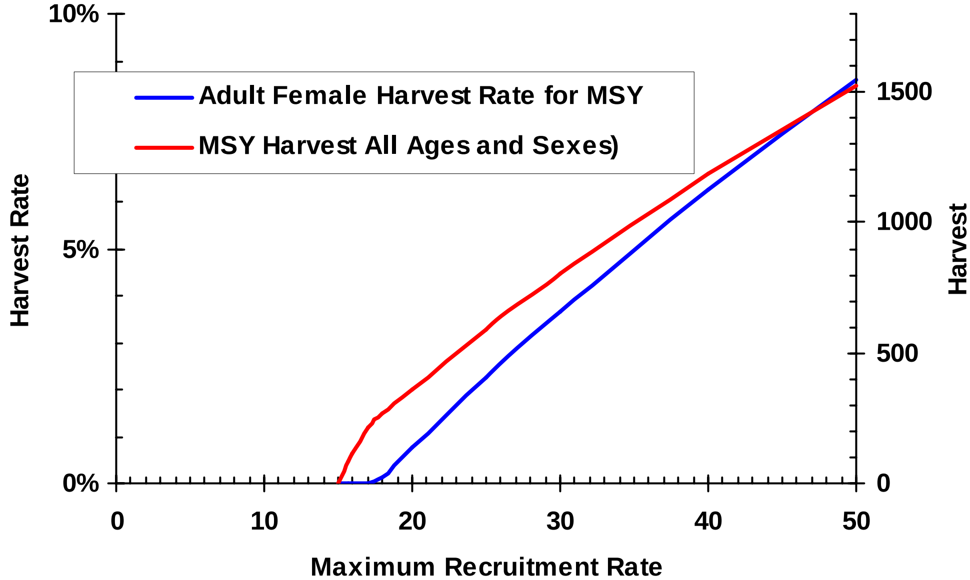

Figure 12. Rate of adult female harvest required to produce the maximum sustained yield (red line, left axis) and the total annual elk harvest of all age and sex classes (blue line, right axis) at equilibrium under the MSY harvest rate for a range of assumptions about future maximum calf recruitment rate, *c*. MSY population sizes corresponding to these harvests are shown in fig. 13.

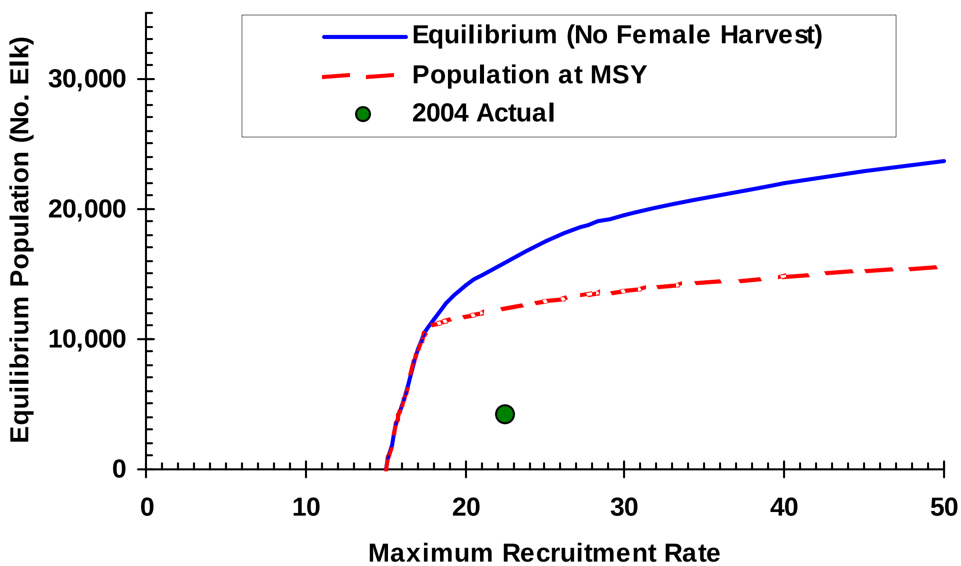

Figure 13. Effect of a range of plausible calf recruitment rates on forecasted equilibrium population size with (1) no female harvest and (2) female harvest that would produce maximum sustained yield for elk in the Great Sand Dunes study area, Colorado.

The low precision of the estimated density effect slope makes any projections uncertain. To better examine this uncertainty, we conducted a sensitivity analysis with respect to the density effect slope with no temporal effect (fig. 14).

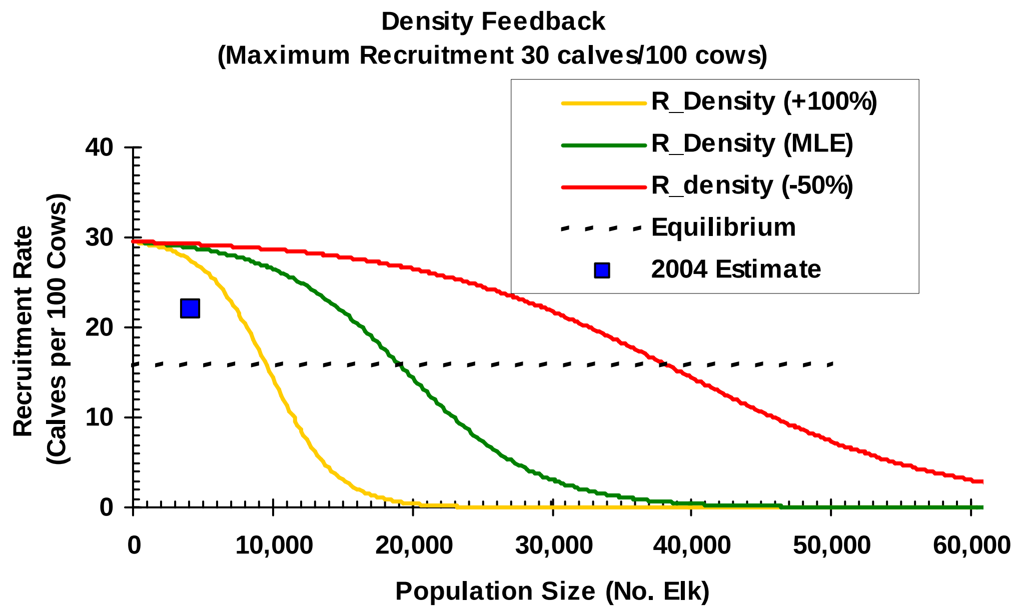

Figure 14. Sensitivity of the model of calf recruitment (eqn. 1) to density effect slope, $_2$, with no temporal effect (t = 0) for an assumed value of maximum calf recruitment *c* = 30 calves/100 cows. Values for $_2$ (R_Density in legend) are the model-weighted maximum likelihood estimate and values twice and half as large.

Despite the uncertainty about future recruitment rates and the lack of strength of the density feedback, it appears from this analysis that the current population is almost certainly well below both its equilibrium level and the level that would produce MSY. Consequently, density effects are minimal; if calf recruitment improves, only sustained harvest of adult females can limit the population to its current level or lower. However, if calf recruitment continues to decline independent of population size, the herd size will also continue to decrease.

Population Model Discussion

The results of our population modeling should be interpreted carefully. The available data represent the bare minimum necessary to adequately model a biological population. Survival rates have never been directly estimated (using radiocollars) for any age or sex class in this population. The population size has only been estimated once (as part of this investigation) in the history of the population. Only harvest data from voluntary mail-in surveys and age- and sex-class ratio estimates are available for most of the period covered. Furthermore, there has never been an experimental manipulation or a dramatic change in management that would produce a measurable response that could be strongly associated with that intervention.

We emphasize that a density feedback effect was only moderately supported by the available data, so the equilibrium population projection and maximum sustained yield levels based on this mechanism should be treated as tentative until additional data are available. It is entirely possible, in fact likely, that the full response of this population's vital parameters to increasing population size has not yet been observed, because the population has not reached a size close to ecological carrying capacity. As this level is reached, it is common first to see a decline in recruitment, as was weakly evident here, followed by declines in other vital rates, such as the first full year calf survival rate and possibly even adult survival rates. In order to detect these feedback responses, the population would have to be close to ecological carrying capacity and more data than is currently available would be required. Thus, while we are confident that the carrying capacity is above the current population size, it may be lower than projections based on current evidence.

The estimated initial population size of 1,473 [906–2,394] for this herd in 1983 was a model parameter fitted to the available data in our analysis, not merely an assumed value. However, backward projection of the population size to the beginning of the period modeled is less reliable than would be the case if even one population survey had been conducted earlier in the history of this population. Nevertheless, the confidence interval of our estimate encompasses an earlier estimate of 1,750 elk made from these same data by CDOW.

The decline in calf recruitment over time detected in this analysis appears to be independent of density feedback. We have no data regarding the cause or causes of this decline. To our knowledge, there have been no obvious large-scale changes in habitat, endemic diseases, or predation that would explain this decline. We projected population into the future for a range of plausible assumptions about the future level of this recruitment rate, but our assumptions are not supported by direct evidence. Thus, it is especially important that management and research efforts focus on the recruitment rate in the future. An intensive study of calf mortality rates and causes, beginning with the neonatal period (<1 week postpartum) through the first winter of life, would be especially valuable in understanding the dynamics of this population. Such a study would provide not only direct data to better estimate the recruitment rate, but also the sex ratio of calves at the age of recruitment—another important parameter in our population model for which we currently have only indirect evidence.

The maximum sustained harvest rate is very sensitive to the juvenile recruitment rate, for which projections are difficult. Furthermore, our model indicates that maximum sustained yield would not be achieved unless the population size was allowed to grow much larger than its present level, which is unlikely due to risk of agricultural damage. Consequently, the population will likely be held below MSY, which is an unstable state that can only be maintained by careful monitoring and management response to prevent overharvest and rapid population decline. One option is to set harvest rates by adaptive management using regular monitoring of the population response to harvest. Such responsive management, as well as improving our understanding of the dynamics of this population, requires regular (although not necessarily annual) population surveys like the one done in this study.

Bison Habitat Use and Genetics

Areas of habitat overlap between elk and bison are shown during several key months (fig. 15). Because elk are highly concentrated on the Medano Ranch during the months of April and May, the kernel is small. They disperse for calving in June, widening the kernel. The bison locations are taken strictly from ground observations. The GPS collars from Habit Research did not perform, and no GPS data was collected in the first year of the study. We have acquired new bison GPS collars and intend to deploy them in November 2006. Once we collect additional data, we intend to conduct cluster analysis (ClustanGraphics 5.25, Edinburgh, Scotland) to evaluate whether bison are exhibiting any migratory behavior or site fidelity within the Medano Ranch boundaries. TNC is interested in potentially expanding the bison population. Ungulate consumption rates, impacts from both elk and bison to the plants and soils, movement patterns, bison herd genetics, evidence of natural behaviors by the bison herd, and other factors will be used by TNC to evaluate the potential for a free-roaming bison population in SLV.

Results of the mtDNA analysis indicate there is a 5.2% hybridization of bison with cattle genes in the population. Five percent hybridization is extremely low for a private herd, although we suspect the percentage will increase once results of the nuclear DNA analysis are available. This analysis will reflect the addition of 60 bulls from other private herds into the TNC population in the 1980s. Nationally, there are several bison herds with no cattle hybrids, and they are all federally managed herds (Yellowstone National Park, National Bison Range, etc.). Historically, most private bison herds were intentionally bred with cattle to produce "uber" cows, or super-bison. Thus, the low level of cattle genes in the TNC bison population is encouraging in terms of the purity of the herd. We will have further conclusions on genetic status of the bison population after the nDNA analysis is completed.

Vegetation Study

Herbaceous Production and Consumption

Sorting and weighing of the herbaceous data is currently underway. We will conduct analysis for pre-treatment differences between grazed and exclosed treatment plots at each site and to determine summer consumption rates when this laboratory work is complete.

Species Composition

Data is currently being entered into electronic format and will be analyzed in fall 2006.

Cottonwood

Cottonwood resprouts and saplings were taller in areas subject to elk browsing alone compared to sites browsed by both elk and bison ($P = 0.027$, fig. 16). While the density of these smaller trees was slightly greater in areas browsed only by elk, this difference was not significant ($P = 0.44$). No significant differences were found in the density of overstory cottonwood trees (either dead or live). Summer utilization of cottonwoods (percent leader use) was significantly higher ($P < 0.0001$, fig. 17) in areas subject to both elk and bison browsing.

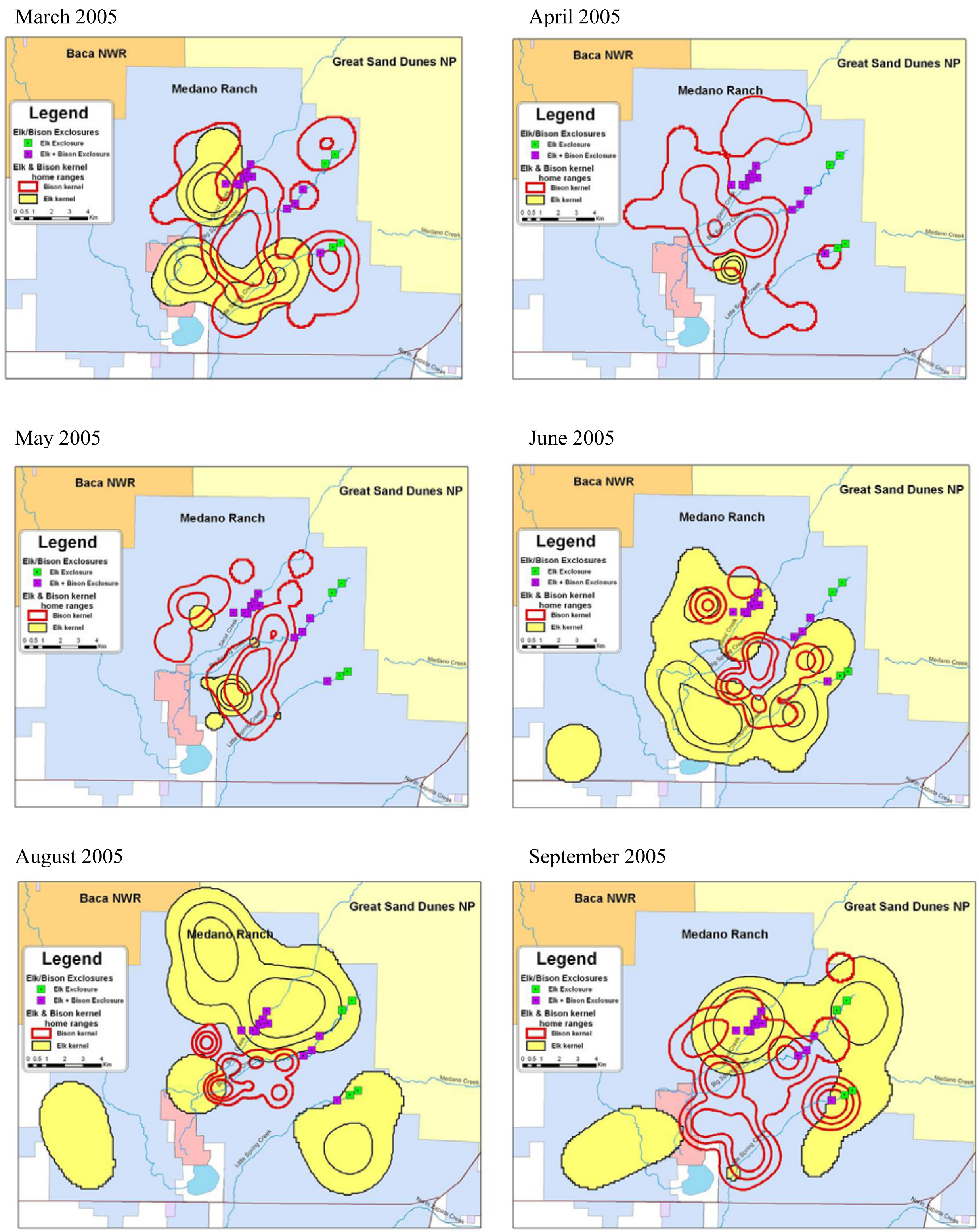

Figure 15. Kernel density estimates for bison and elk on the Medano Ranch, TNC, Colorado, in key spring/summer months in 2005. Outer circles indicate 50% density and innermost lines delineate a 95% kernel density estimate. Ungulate exclosure locations are also shown for reference.

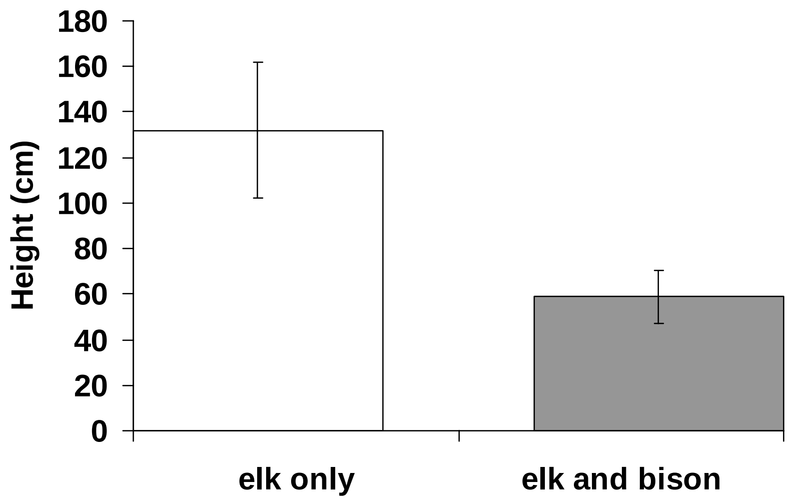

Figure 16. Average height of cottonwood resprouts and saplings (less than 2.5 m total height) in areas browsed by elk and areas browsed by elk and bison in the Great Sand Dunes study area, Colorado, 2005.

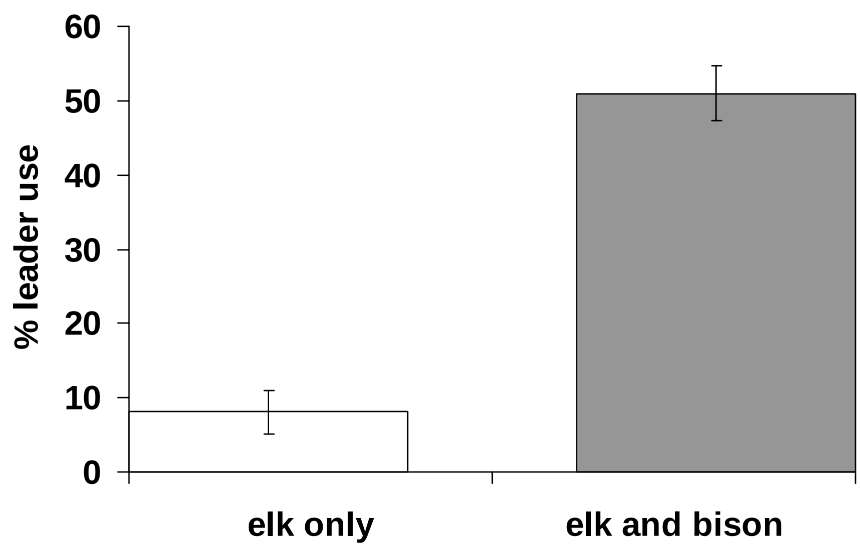

Figure 17. Average utilization (percent leader use) of cottonwood resprouts and saplings (less than 2.5 m total height) in areas browsed by elk and areas browsed by elk and bison in the Great Sand Dunes study area, Colorado, 2005.

Willows

Summer/fall consumption levels ranged from 12.6% to 28.4% of current annual growth (fig. 18). No significant differences were found in grazed/exclosed pairs prior to construction of the exclosures. It is important to keep in mind that exclosures in these willow areas were not complete until October 2005; therefore, areas listed in fig. 18 as ungrazed were in fact grazed during the 2005 growing season. In subsequent years, we will not report “offtake” levels in exclosed (ungrazed) sites, as it will be zero because herbivory will be prevented due to exclosures. No significant differences in pre-treatment willow canopy area or volume were observed, though the variation was quite high. Average heights were variable, ranging from 31 to 120 cm (fig. 19). Greater average heights pre-treatment in one grazed plot at site 2 will be accounted for when analyzing data from future years of study, but overall, heights were relatively similar between treatments at each site.

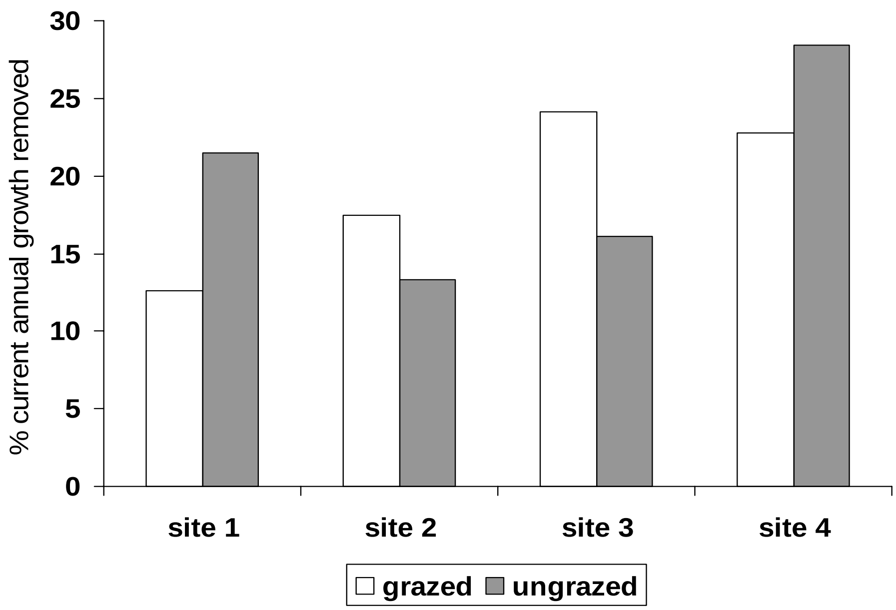

Figure 18. Average consumption (percent current annual growth removed) of willow (*Salix exigua*) in sites browsed by elk and bison in the Great Sand Dunes study area, Colorado, 2005. Note that exclosures were not established until October 2005, so some herbivory did occur in “ungrazed” sites in 2005, evidenced by higher numerical offtake levels at sites 1 and 4 in ungrazed plots.

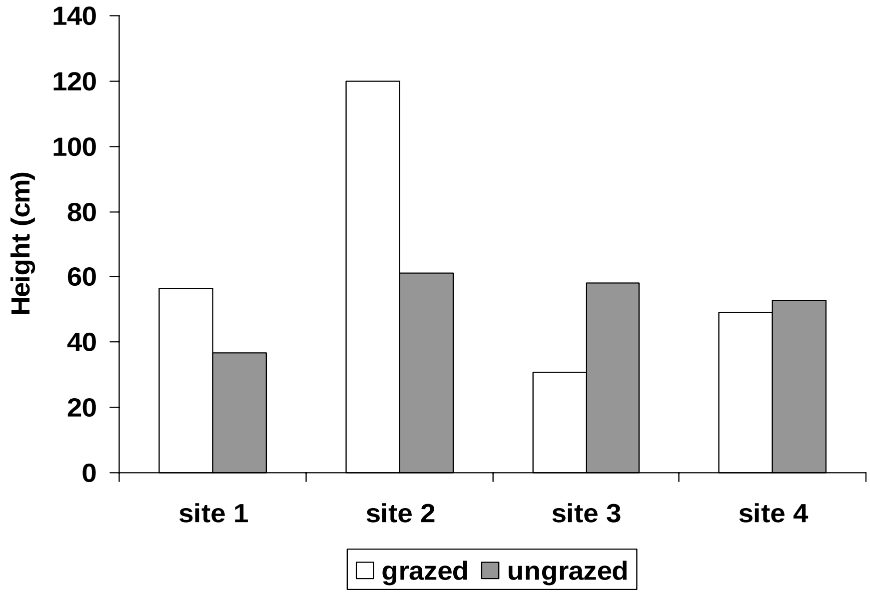

Figure 19. Average height (cm) of willow (*Salix exigua*) in sites browsed by elk and bison in the Great Sand Dunes study area, Colorado, 2005. This is pretreatment data, showing no significant differences in heights between ungrazed and grazed treatments.

Alpine Willow Herbivory in the Upper Deadman Creek Drainage

Fresh scat and tracks of both bighorn sheep and elk were observed throughout Deadman drainage and around Deadman Lakes. Only bighorn sheep sign was observed along measured transect lines around Cottonwood Lakes, and only at one of four lines. There is likely a greater degree of human activity in the area around Cottonwood Lakes as popular trails are close by and offer some access. Topography and lack of maintained trails make Deadman Lakes much less accessible to humans.

Average willow cover was more than three times greater in areas around Cottonwood Lake where only a small amount of ungulate sign was observed. Heights of both *Salix brachycarpa* and *S. planifolia* were greater at the Cottonwood Lake site than Deadman Lake and upper reaches of Deadman Creek (fig. 20). Percent leader use was less than 5% on willows at Cottonwood Lake, but ranged from 30-60% in the upper Deadman drainage (fig. 20). The recommended sites are not entirely comparable, as the Cottonwood Lake site had very little observed sign of either bighorn sheep or elk. Observational, diet, and radiotelemetry studies are necessary to discern the relationship of ungulate species throughout the area, not just in isolated drainages. High levels of leader use are occurring in at least one drainage, and levels this high have been found to lead to loss of willow in less sensitive montane and subalpine environments.

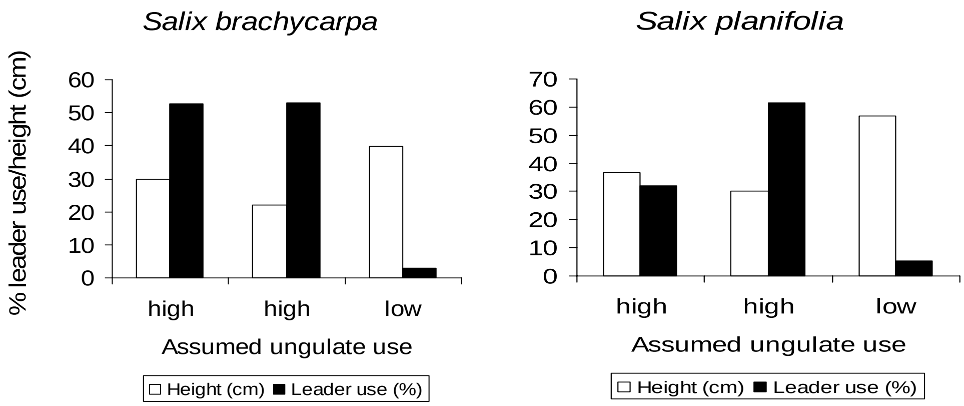

Figure 20. Average utilization (percent leader use) and height (cm) of willow (*Salix brachycarpa* and *Salix planifolia*) in three alpine willow sites near Deadman Lakes (high ungulate use) and Cottonwood Lake (low ungulate use) on the Rio Grande National Forest, Colorado.

Elk Body Condition

We compared February (late winter/early summer) body condition of elk cows to November (early winter/late summer) condition to evaluate whether their condition improved over summer. Most body condition indices increased significantly from February to November, including ingesta-free body fat ($P = 0.0348$), overall body condition score (the calculated rLIVINDEX; $P = 0.0465$), maximum subcutaneous rump fat thickness ($P = 0.0201$), withers body condition score ($P = 0.001$), and rump body condition score ($P = 0.0683$). In February, all but 1 of 27 cows (96%) were pregnant, and 2 of 27 (7%) were lactating. In November, 88% were pregnant, and 44% were lactating.

Depth of longissimus dorsi muscle is an index to protein catabolism and can be used to evaluate change of condition over a given time period. In general, animals with loin depths <4.4 cm are in a state of extreme protein catabolism and depending on the time of year, probability of survival is lower. No elk in the SLV was found in this range.

We compared elk cows that migrate to higher-elevation summer range in the Sangre de Cristo Mountains to those that remain on the valley floor (non-migratory) and found no differences in body condition. Differences may be discernible after we increase the sample size with more data in year 2. There were no differences in pregnancy rates between elk that migrate and those that do not, although sample sizes were small with only one year of data.

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