DISSERTATION

ECOLOGY OF BISON, ELK, AND VEGETATION IN AN ARID ECOSYSTEM

Submitted by

Kathryn Alyce Schoenecker

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Doctoral Committee:

Advisor: N. Thompson Hobbs

David M. Swift
Michael C. Coughenour
Alan K. Knapp

ABSTRACT

ECOLOGY OF BISON, ELK, AND VEGETATION IN AN ARID ECOSYSTEM

Herbivory has profound effects on vegetation production and structure in many different plant communities. The influence of herbivory on plants and ultimately ecosystem processes is shaped by the types of plants consumed, the intensity of herbivory, the evolutionary history of grazing, and the availability of water and nutrients to plants. The effect of ungulate herbivores on vegetation is of great interest to ecologists, land managers and agriculturalists. In addition, the Department of Interior recently established a Bison Conservation Initiative to provide for the conservation and restoration of North American plains- and wood bison, which includes establishing new populations and expanding existing populations. The San Luis Valley, Colorado, is being considered as a potential location for a bison conservation herd. Resource managers need to know the vegetation impacts of adding a second large ungulate to a system that already has elk.

In Chapter 1 I conducted a landscape-scale observational study comparing areas with bison and elk grazing to areas with just elk grazing. I studied 6 vegetation communities to evaluate differences between ungulate strata, elk-bison versus elk-only, in herbaceous and woody vegetation production, and ungulate utilization. I found few differences in herbaceous production or utilization between the two ungulate strata. Herbaceous production was lower in elk-bison than elk-only wet meadows and cottonwood stands, but no production differences were found in mesic meadow, greasewood, or rabbitbrush communities. Willow communities were not comparable in soil substrate and species composition, so I could not compare production between elk-bison and elk-only willow communities. Average winter percent offtake in wet meadows was higher with both ungulates but not summer utilization. These meadows are highly resilient, not water-limited, and the most able to sustain grazing pressure of all the vegetation types I evaluated. Mesic meadows had higher summer and winter utilization in meadows with both ungulates compared to meadows with just elk. In woody communities, there was no change in cottonwood sapling density at elk-bison grazed areas over the 4-year study period, but sapling density decreased from 2005 to 2009 in elk-only cottonwood communities. I found higher browsing levels of cottonwood saplings in areas with both ungulates, but no differences between ungulate strata in willow utilization. I found higher summer than winter browsing in both cottonwood and willow communities suggesting ungulates are utilizing woody species in the summer for shade in the hot, arid climate of the San Luis Valley and browsing while present, as opposed to relying on winter browse as their primary food source as they do in temperate systems. My finding that annual willow utilization was slightly lower in some years in sites with both elk and bison browsing than sites with only elk, suggests bison may spatially exclude elk from willow stands when bison are present. There is evidence in the literature for competitive interactions between these two ungulates. Areas with both elk and bison mostly did not incur greater levels of utilization than areas with just elk, suggesting that spatially ungulates are segregating on the landscape or the additional forage needed by a second large herbivore is coming from mesic meadows or other communities. Greasewood percent offtake was higher in areas with two ungulate grazers than one, but was not statistically significant likely due to low sample size. I propose that forage utilization by a second large ungulate is being absorbed in mesic meadow and greasewood communities.

In Chapter 2 I focused on plant responses to herbivory, using an ungrazed (exclosed) treatment to test theory on grazing optimization and plant compensation. I conducted research to understand the response of plants to herbivory and identify potential constraints on plant compensation in the arid San Luis Valley ecosystem. Arid systems pose challenges to grazing theory because it is assumed external factors such as moisture have a more dominant role than internal interactions, such as herbivory. I used a replicated herbivore exclusion experiment to evaluate herbaceous plant and woody species response to grazing by large ungulates, and to study longer-term trends in ungulate-vegetation dynamics. I measured N-yield, and herbaceous and woody species production in wet meadows, cottonwood stands, and willow communities. I used fenced exclosures to conduct ungrazed treatments from 2005 to 2009 in areas with elk plus bison and paired areas with elk-only. Grazed herbaceous production and N-yield in wet meadows was greater than ungrazed, showing evidence for overcompensation by plants to tissue losses from herbivory. Herbaceous plants in willow and cottonwood communities exhibited equal compensation, showing plants can tolerate and compensate for levels of herbivory incurred during my study period. In woody species, browsing suppressed some elements of willow structure. Cottonwood sapling heights increased over time in both elk-bison and elk-only communities protected from grazing. The density of cottonwood saplings decreased from 2005 to 2009 in elk-only grazed sites, but did not increase within fenced pairs despite complete cessation of browsing for 5 years. Small diameter cottonwood trees also decreased at grazed sites, but did not increase within fenced pairs, suggesting water and climate drivers influence recruitment of these woody plants more strongly than herbivory. Cottonwood stand age-structure measurements indicated the lack of recruitment of saplings and smaller age classes has been in place for some time.

In Chapter 3 I focused entirely on bison to evaluate their population dynamics using hierarchical Bayesian modeling. Little is known about the ecology and habitat interactions of bison in areas outside the Great Plains, especially arid habitats. Population dynamics of bison are poorly understood and quantitative data are scarce. I estimated population demographics of bison in the cold desert ecosystem of the San Luis Valley. This study provides the first vital rates for bison inhabiting an arid ecosystem. Survival rates of all age/sex classes during study years were ≥75%. The highest survival was in adult females and the lowest in yearling females. Calf and adult female survival probabilities were both >89%, and yearling plus adult male survivorship was 0.87 (0.72 - 0.98). Female yearling survival was the most variable (credible intervals 0.61 - 0.96). Sex ratio at birth slightly favored females ($m = 0.52$) but studies in other habitat types have indicated equal sex ratios at birth in bison. Recruitment averaged 0.63± 0.05. Vital rates estimated in my model were consistent with current knowledge of bison life history, but differed somewhat from vital rates of bison inhabiting more temperate habitats.

These 3 studies, along with other research conducted simultaneously and published elsewhere, provide the first evaluation of ungulates in the San Luis Valley. Prior to this research, there were little or no data on ungulates and their ecology in this special ecosystem; an ecosystem protected because of its awe inspiring geology, strong cultural heritage, and beauty in natural resources. My hope is that this research will support resource managers in their efforts to manage these amazing natural resources, and protect the richness of the San Luis Valley, Colorado for the enjoyment of future generations.

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CHAPTER 1: ELK AND BISON HERBIVORY IN AN ARID ECOSYSTEM

Herbivory frequently and independently evolved in terrestrial vertebrates about 300 million years ago (Sues 2000), and grazer–graminoid coevolution tracked the advent of grasslands in North America ~20 million years ago (Janis 1989; McFadden 1997). At many archeological sites, herbivore fossils co-occurred and therefore species were believed to be sympatric (Sues 2000). However, contemporary landscapes have been changed dramatically by humans. Populations of large herbivores on those landscapes are intensively managed; even "natural" areas such as National Parks and National Wildlife Refuges are influenced by humans directly by manipulations within the natural area, or indirectly by activities outside the boundary. These human activities impact the population size, movement, migration, and foraging behavior of herbivores. Whether multiple large herbivores can coexist in this changed and managed modern-day environment is not always clear, especially with regard to their potential impacts on vegetation.

Herbivory has profound effects on vegetation production and structure in many different plant communities (Augustine and McNaughton 1998, Hobbs 1996, Wisdom et al. 2006). Herbivores directly (Knapp et al. 1999) and indirectly influence ecosystem processes, in plant structure and function, in both aboveground and belowground processes (Bardgett and Wardle 2010, Schoenecker et al. 2004). The influence of herbivory on ecosystem processes is shaped by the types of plants consumed, the intensity of herbivory, the evolutionary history of grazing, and the availability of water and nutrients to plants (Milchunas and Lauenroth 1993).

The effect of ungulate herbivores on vegetation is of great interest to ecologists, land managers and agriculturalists. I conducted a study to determine the effects of elk (*Cervus* *elaphus*) and bison (*Bison bison*) herbivory on plant communities in a high-elevation arid landscape in Colorado. My objective was to measure ungulate consumption rates and vegetation production under different combinations of elk and bison utilization in 6 different vegetation communities. Communities selected were of specific concern to managers because of the presence of the endangered slender spider flower (*Claeome multicaulis;* Pineda et al. 1999) and because of concerns about possible elk overpopulation or overconcentration in sensitive woody shrubs. In addition, the Department of Interior recently initiated a Bison Conservation Initiative (DOI 2008) that outlined conservation and restoration goals for North American plains bison (*Bison bison bison*) and wood bison (*Bison bison athabascae)*. Goals of the Initiative include locating and determining suitable areas for new bison conservation herds or expansion of existing herds. But many of the suitable areas for bison are already habitat for migratory herds of elk. Decision makers need to understand the impacts of adding a second large-bodied ungulate (bison) to new communities and ecosystems, especially sensitive arid systems. I assessed herbaceous grazing intensity and browsing intensity among plant and ungulate communities, and ungulate grazing/browsing effects on herbaceous and woody plant production in an arid ecosystem. Based on diet differences between elk and bison, I hypothesized that areas with both elk and bison would have higher levels of herbaceous offtake than areas with just elk because of the addition of a second grazer. I hypothesized that woody species would have similar utilization between strata because bison are not primarily browsers and would unlikely utilize woody browse the way elk do (Hansen and Reid 1975, Hobbs et al. 1981).

STUDY AREA

I conducted research in the San Luis Valley of south-central Colorado (Figure 1.1). The San Luis Valley is a high elevation desert and lies within the Great Basin desert zone (Barbour and Billings 2000) and the Southern Rocky Mountains floristic zone (Daubenmire 1943). West (1988) describes a saltbrush (*Atriplex* spp.)-greasewood (*Sarcobatus vermiculatus*) vegetation type that dominates lowlands of the upper Rio Grande drainage. The vegetation is correlated with halomorphic soils, where vegetation composition and production is closely linked to soil characteristics (West 1988). In the San Luis Valley both rabbitbrush (*Ericameria spp*) and saltbrush/greasewood vegetation types predominate. Precipitation averages 28 cm annually and falls mostly during monsoonal rains in July through September. Summers are warm with average daytime temperatures ranging from 26.5 ^{o}C to 29.5 ^{o}C on the valley floor. Winters are cold and relatively dry with average valley daytime temperatures ranging from -9.5 ^{o}C to 1.5^{o}C. Elevations on the valley floor range from 2,285 m to 2,440 m. The study area includes the lower elevations of Great Sand Dunes National Park, the Baca National Wildlife Refuge, and The Nature Conservancy's (TNC) Medano-Zapata Ranch (Figure 1.1).

This landscape contains the highest sand dunes in North America (229 m) with associated vegetation. The sand dunes contain blowout grass (*Redfieldia flexuosa*) growing in low densities atop dunes. Swales are flooded ephemerally during spring from snowmelt off the mountains, and support a dense ground cover of sedges (*Carex* spp.) and wet meadow grasses. Ephemeral wetlands form the western boundary of the dunes complex and are watered from natural springs and Sand Creek. Cottonwood stands occurring along Sand Creek are considered unique for the southern Rockies because they are pure narrow-leaved cottonwood (*Populus angustifolia*), while most others are hybrids of narrow-leaf and broadleaf cottonwood species. The only large population of the endangered slender spider flower (*Claeome multicaulis*) in North America occurs in ephemerally flooded meadows (Dixon 1971).

Sand sheet surrounds the active dunes complex and is dominated by greasewood and rabbitbrush. Cottonwoods and willows (primarily Coyote willow, *Salix exigua)* grow atop some dunes (the dunes may support a pyramid water supply), along Sand Creek, and near springs. This area is interspersed with wet meadows along creeks and mesic meadows (some formed by irrigation) away from riparian areas. Dominant graminoids include arctic rush (*Juncus balticus*), needle and thread grass (*Hesperostipa comata*), Indian rice grass (*Achnatherum hymenoides*), sand dropseed (*Sporobolus cryptandrus*), saltgrass (*Distichlis spicata*), slender wheatgrass (*Elymus trachycaulus*), and beardless wildrye (*Leymus triticoides*).

Eight major streams traverse the study area from east to west. All of these streams have limited flow during the year with streams disappearing underground at their lower reaches. Flowing water typically reaches the lower end of streams for a period of 1-2 weeks in late spring if winter snow conditions provide snowmelt runoff. Most of the streams have been manipulated for irrigation at some point in the past century.

Bison, elk, mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocapra americana*) were native to the area until about the 1840s when bison, pronghorn and elk (Swift 1945) were extirpated. Bison were returned to SLV via ranching in the 1980s. Pronghorn and elk likely moved into the area from surrounding populations to the north and south, and mule deer populations have varied through time. Livestock, including sheep (*Ovis aries*) and cattle (*Bos taurus*), were grazed historically throughout the study area especially in the sand sheet type that now comprises the National Park. The former Luis Marie “Baca” Ranch, which makes up the northern part of Great Sand Dunes National Park and all of the Baca National Wildlife Refuge (Figure 1.1), was actively grazed by cattle through 2004.

METHODS

Study Design

I studied six vegetation types including wet meadows, mesic meadows, cottonwood communities, willow communities, rabbitbrush, and greasewood. I evaluated these communities in relation to two strata of ungulate use: elk as the primary grazer ("elk-only"), and elk and bison together ("elk-bison"). Elk inhabit and move freely across the ~125,000 ha study area, while free-roaming bison are fenced within the 20,000 ha Medano Ranch (Figure 1.1). Mule deer and pronghorn are also present in the study area, but are not considered primary herbivores due to their smaller body size (100 lbs for pronghorn, 150 lbs for mule deer, versus 1,250 lbs for bison and ~800 lbs for elk; Wassink 1993) and lower forage intake based on their density in the study area. The mule deer population during my study period was estimated at 3,230 (CDOW 2008a), the pronghorn population ~2160 (CDOW 2008b), bison ~1200-1500 (C. Pagues, TNC, personal communication), and elk ~4,500 (K. Schoenecker, *unpublished data*). Ungulates have an average forage demand of 2% of their body weight/day (Holechek and Pieper 1992), so the larger-bodied elk and bison have much greater forage demands than deer and pronghorn.

I selected study sites from a group of randomly generated points within target vegetation types in the two ungulate strata (Figure 1.1). I evaluated each point to ensure there was enough area for a grazed plot that could contain 3-5 grazing cages within the vegetation type. These small, movable cages protected ~1-m^2 areas from grazing for short periods. I established 4 replicate sites in each vegetation type and sampling began in 2005 (Table 1.1), with the exception of rabbitbrush and greasewood sites which were sampled once in 2009.

Table 1.1. Experimental design and schedule of vegetation sampling in the Great Sand Dunes ecosystem, Colorado, 2005-2009.

			No. Replicates	Years sampled				
Variable measured	Vegetation Type	Ungulate Strata	(Cages/replicate)	2005	2006	2007	2008	2009
Summer herbaceous production and offtake	Cottonwood	Elk-only	4 (5)	X	X		X	
		Elk-bison	4 (5)	X	X		X	
	Wet meadow	Elk-only	4 (5)	X	X		X	
		Elk-bison	4 (5)	X	X		X	
	Willow	Elk-only	4 (5)		X		X	
		Elk-bison	4 (5)	X	X		X	
	Mesic Meadow	Elk-only	5 (3)		X		X	
		Elk-bison	4 (3)				X	
	Greasewood	Elk-only	4 (3)					X
		Elk-bison	2 (3)					X
	Rabbitbrush	Elk-only	10 (3)					X
		Elk-bison	6 (3)					X
Winter herbaceous offtake	Cottonwood	Elk-only	4 (5)		X	X	X	
		Elk-bison	4 (5)		X	X	X	
	Wet meadow	Elk-only	4 (5)		X	X	X	
		Elk-bison	4 (5)		X	X	X	
	Willow	Elk-only	4 (5)		X	X	X	
		Elk-bison	4 (5)		X	X	X	
	Mesic Meadow	Elk-only	4 (5)		X	X	X	
		Elk-bison	4 (5)			X	X	
Woody structure (Height, density, cover)	Cottonwood	Elk-only	4 (5)	X	X		X	X
		Elk-bison	4 (5)	X	X		X	X
	Willow	Elk-only	4 (5)				X	
		Elk-bison	4 (5)	X	X		X	X
	Cottonwood	Elk-only	4 (5)	X	X		X	X
		Elk-bison	4 (5)	X	X		X	X

			No. Replicates			Years sampled		
Variable measured	Vegetation Type	Ungulate Strata	(Cages/replicate)	2005	2006	2007	2008	2009
Summer browsing	Willow	Elk-only	4 (5)				X	X
		Elk-bison	4 (5)	X	X		X	X
Winter browsing	Cottonwood	Elk-only	4 (5)		X	X	X	
		Elk-bison	4 (5)		X	X	X	
	Willow	Elk-only	4 (5)		X	X	X	
		Elk-bison	4 (5)		X	X	X	

Some areas were removed from consideration in the study design due to confounding factors. Areas of cottonwood along Pole and Deadman Creeks had been grazed by cattle for many years and were eliminated due to historical effects. Areas of cottonwood and willow along Medano Creek receive ~90% of the total park visitor activity reducing ungulate use due to human presence, so this area was also eliminated.

Herbaceous Production, Utilization, and Offtake

I sampled annual aboveground herbaceous production and offtake by clipping all vegetation within 0.25-m^2 circular plots inside and outside grazing cages, which were then randomly relocated for the next sampling. I clipped all graminoids, forbs, and sub-shrubs within plots at ground level, oven-dried vegetation at 55^o C for 48 hours, and weighed it. I sorted a subsample of plots to separate live and dead plant material, separating previous from current year dead.

I conducted sampling twice during the growing season (June and August) in 2005, and three times (mid-late June, late July-early August, and late August-mid-September) in 2006 and 2008 to determine total production and summer offtake rates (Table 1.1). I sampled over-winter offtake of standing crop remaining at the end of the growing season in April 2006, 2007, and 2008 by placing cages at the end of the growing season and sampling before spring green-up.

I estimated total herbaceous production using a modification of the difference method (McNaughton 1985, Bonham 1989):

$$B = P_1 + \sum_{i=1}^{T} (P_{c(i+1)} - P_{ui})$$

where B =total herbaceous biomass produced, $P_{c(i+1)}$ is the average amount of biomass in caged plots at time $i+1$ and P_{ui} is the amount of biomass outside the cage at time . For the first time interval, P_1=P_{ci}. Both positive and negative differences in production for each interval were added to the initial caged biomass to determine production. Sample sizes for each site were chosen following recommendations in Waddington and Cooke (1971) where authors determined that reduced sample sizes could be used based on 90% confidence intervals rather than power tests. Bonham (1989) recommended 25 cages/site, which was not achievable for my study. I used 5 cages/site (Table 1.1).

I determined summer ungulate consumption (utilization) of forage using the equation,

$$U_s = \sum_{i=1}^{T} (P_{ci} - P_i),$$

where U_s is amount of forage used, P_{ci} is the average amount of biomass in caged plots at time i and P_i is the amount of biomass in uncaged plots at time i. Percent offtake for the growing season was calculated as $O_s=(U_s/B)*100$.

Winter utilization was determined by caging plots at the end of the growing season and comparing remaining biomass to that in grazed plots using the equation,

$$U_w = \left(P_{ci} - P_i\right),$$

where U_w is the amount of standing crop remaining at the end of the growing season that is removed overwinter, P_{ci} is the amount of biomass in caged plots at the end of winter and P_i is the amount of biomass in uncaged plots at the end of winter. Winter percent offtake was calculated as $O_{\mathrm{w}}=U_w/B*100$. Total annual percent offtake was calculated as $O_t=O_w+O_s$ (Bonham 1989).

Willow Production and Browsing

I randomly placed 2 fixed-radius 10 m^2 circular plots within the 8 willow sites and marked the center with rebar. I measured that which fell completely or greater than 50% within the plot. In the case of indistinct plants where large numbers of shoots or small stems were emerging from the ground side by side, I measured only the portion of the clump's canopy which fell within the radius of the plot. For each willow I recorded species, canopy diameters (widest and perpendicular to widest diameter), shrub height, number of stems, an estimate of percent dead canopy, a subsample of the number of browsed and unbrowsed current annual growth (CAG) shoots, diameters at shoot base, diameters at shoot tip, diameters at point of browse, and leader length.

On lower Sand Creek (elk-bison sites) the willow communities consist almost exclusively of coyote willow (*Salix exigua*). This species tends to have shoots that branch multiple times within a single growing season. In cases of multiple branching shoots, I totaled the length of the longest part of the shoot, plus the length of all side shoots from branching point to tip to give the total shoot length. I took basal shoot diameter measurements on such shoots only from the base of current year's growth where the previous year's bud scar is located, not from branch points along the shoot. I took tip diameters from the apparent main current year's growth shoot, not from branching shoots. For browsed shoot counts on such shoots, I considered browsing on any part of the shoot as one browsed shoot. I estimated percent leader use using the formula:

$$\% leaderuse = \left(\frac{a}{a+b}\right) \times 100 \quad ,$$

where a = number of browsed CAG shoots and b = number of unbrowsed CAG shoots. I determined average proportion of shoot (twig) removed following Jensen and Urness (1981) and Pitt and Schwab (1990) with the formula:

$$proportion\_twig\_used = \frac{(D_p - D_t)}{D_b - D_t} ,$$

where D_p = shoot diameter at point of browsing, D_t = diameter of a representative sample of unbrowsed shoot tips, and D_b = basal diameter of current year's shoot growth. I determined total offtake by multiplying average % leader use by average proportion of twig used.

Cottonwood Production and Browsing

I estimated height, stem distribution and density, and percent leader use of cottonwood saplings (including seedlings and resprouts) and trees. I collected measurements from all cottonwood plants that fell within two 10 m radius (314 m^2) circles at each cottonwood site. Roughly one-third (11 of 32) of the plots were densely vegetated with high homogeneity, so 5 m radius (78.5 m^2) circles were used. I selected plot locations by traveling a random direction and distance from the center of each cottonwood site, ensured they did not overlap other plots, and used a labeled rebar post to mark the center of plots.

For each cottonwood tree (stem with a height greater than 2.5 m) I collected the following measures: the number of trunks, DBH (diameter at breast height [1.4m]), percent dead canopy, number of browsed and unbrowsed current annual growth (CAG) shoots for all branches, and basal sprouts within 200 cm of the ground. For saplings and resprouts (stems less than 2.5 m in height) I measured height, number of stems, canopy diameters, number of browsed and unbrowsed CAG shoots, and percent dead canopy. I determined percent leader use by the same formula for willows.

Statistical Analyses

I analyzed herbaceous production, utilization, and offtake data for between-year and ungulate strata differences using a mixed procedure (PROC MIXED) that is a generalization of the standard linear model designed to analyze data generated from several sources of variation. This method allowed me to account and test for the effects of random sites. I was not able to compare herbaceous or woody production in elk-only versus elk-bison willow communities because they differed in substrate and species composition, but year-to-year comparisons were made within ungulate strata. I analyzed cottonwood and willow browsing (% offtake, % leader use, % twig use) for annual differences between ungulate strata using mixed models. I removed two outliers from willow height analysis, and one from willow canopy analysis and herbaceous offtake analysis. Linear contrast methods were used to test for trends in cottonwood sapling density over time. I transformed percentage data (offtake, leader use, etc) using an arc sine square root transformation to normalize. I log-transformed willow canopy area and volume, and cottonwood sapling density to stabilize the variance. I used SAS statistical analysis software V9.1.3 (SAS Institute, Cary, NC) to analyze data.

RESULTS

Herbaceous Production

Herbaceous production varied greatly by vegetation type (Figure 1.2). Wet meadows in both ungulate strata were the most productive followed by mesic meadows and elk-only willow communities (on the Baca National Wildlife Refuge). The lowest production was in cottonwood understory. Herbaceous production was greater in elk-only than elk-bison wet meadows ($P = 0.007$), and cottonwood communities ($P = 0.028$; Figure 1.2). Production between years was analyzed separately for each ungulate stratum in willow communities and no differences were found. I observed no herbaceous production differences between ungulate strata or year in mesic meadows.

Standing crop at the end of the 2009 growing season indicated that herbaceous production on rabbitbrush and greasewood sites was similar to that observed in cottonwood and elk-bison willow communities (Figure 1.3a). No differences in herbaceous production were found between ungulate strata in either greasewood or rabbitbrush communities.

Herbaceous Utilization and Offtake

Summer herbaceous utilization ranged from -1 g/m2 in willow communities to 297 g/m2 in wet meadow communities (Figure 1.4). Average utilization was greatest in the most productive communities (wet meadows). I found more differences between years in utilization than between ungulate strata; in elk-only willow communities, summer utilization was lower in 2006 than in 2008 ($P = 0.051$), but in cottonwood communities, summer utilization was greater in 2006 than 2008 ($P = 0. 043$, Figure 1.4). Summer utilization (based on a single clipping at the end of the growing season) was higher in elk-bison areas for both greasewood and rabbitbrush communities compared to elk-only, but these differences were not significant ($P \geq 0.1217$); the limited sample size contributed to greater variances likely limiting significant results even with large differences in offtake (Figure 1.3b).

Winter herbaceous utilization was lowest in cottonwood communities and highest in wet meadows (Figure 1.5). Winter herbaceous utilization was greater in elk-bison than elk-only mesic meadows ($P = 0.033$), but in willow communities, winter utilization was greater in elk-only thank elk-bison ($P = 0.007$; Figure 1.5). In wet meadows, winter herbaceous utilization did not differ between ungulate strata, but was significantly greater in winter$_{2005\text{-}2006}$ than the following two winters ($P = 0.005$; Figure 1.5).

I used utilization data to calculate percent offtake of current year's production to compare percent removed by ungulates across vegetation types (Table 1.2). These results indicated elk-bison mesic meadows, and wet meadows in winter, had higher average % herbaceous offtake than comparable areas with just elk. Percent winter herbaceous offtake of end-of-growing-season standing crop was similar (~31-33%) in all communities except cottonwood, which averaged ~21% removal of standing crop (Table 1.2).

Willow Production

Willow canopy volume and canopy area were not different between years in either ungulate stratum (Figure 1.6). In elk-bison willow communities variation in willow heights from 2005 to 2009 was small ($P = 0.090$; Figure 1.6). In elk-only willow communities, I found no differences among years ($P = 0.987$) or trends in height ($P = 0.970$; Figure 1.6). Differences in species of willow precluded comparing willow production between ungulate strata.

Willow Browsing

Summer browsing in elk-only communities resembled levels in elk-bison willow communities (Figure 1.7c). There appeared to be a declining trend in summer willow offtake from 2005 to 2008 in elk-bison willows (Figure 1.7c), but in 2009 summer browsing increased to its highest point during the study, observed at all the study sites in both elk-bison and elk-only willow communities. Summer browsing was significantly lower in 2008 than all other years in elk-bison willows ($P < 0.007$), and lower than 2009 in elk-only willows ($P = 0.013$). I found differences between years in mean percent of twigs browsed (leader use, Figure 1.7a, $P=0.060$) and mean proportion of individual twig biomass removed (Figure 7b, $P=0.004$) in elk-bison willows. In elk-only willows, only percent leader use differed between years (Figure 1.7a)

Table 1.2. Average percent offtake of current year’s herbaceous production, % leader use of cottonwoods, and total willow offtake (%twig use*% willow leader use) in vegetation types grazed by elk and bison or elk-only in the Great Sand Dunes ecosystem. Results represent least squares means and standard errors of data from 2005 to 2008. P-values compare elk-bison to elk-only average offtake.

Vegetation Type	Average % Offtake			
Wet Meadows	Elk-Bison Areas (±SE)	Elk-only Areas (±SE)	P-value	Both Strata Pooled (±SE)
Summer herbaceous	45.0 ± 7.2	31.2 ± 7.2	0.198	38.1 ± 5.1
Winter herbaceous	45.2 ± 6.8	16.9 ± 6.8	0.025	31.1 ± 5.2
Cottonwood Communities				
Summer herbaceous	n.a.	n.a.	n.a.	n.a.
Winter herbaceous	31.0 ± 11.4	11.0 ± 11.4	0.260	21.0 ±5.9
Summer leader use	37.4 ± 4.7	10.1 ± 2.0	0.01	23.8 ± 3.5
Annual leader use	46.7 ± 4.2	21.9 ± 5.1	0.03	34.3 ±6.3
Willow Communities				
Summer herbaceous	46.0 ± 7.4	10.3 ± 9.5	0.014	32.2 ± 7.4
Winter herbaceous	35.3 ± 9.5	33.2 ±10.7	0.890	33.7 ± 5.4
Summer willow offtake	19.6 ± 6.4	18.4*	**	19.2 ±6.2
Annual willow offtake	23.2 ± 8.2	18.8 ± 8.5	**	21.0 ± 5.4
Mesic Meadows				
Summer herbaceous	43.9 ± 10.3	7.4 ± 9.6	0.039	25.2 ± 7.7
Winter herbaceous	63.7 ± 12.2	9.8 ± 10.9	0.016	33.2 ± 10.5
Greasewood				
Summer herbaceous	71.8 ± 25.0	18.3 ±77	0.156	36.2 ±17.2
Rabbitbrush				
Summer herbaceous	38.9 ± 13.5	18.2 ± 10.4	0.247	26.0 ± 8.4

*Only one site; standard error could not be determined

**Comparisons between strata were not made due to lack of several years of data from elk-only sites

Annual browsing (percent of willow production removed over the entire year) was variable among years, but similar in both elk-only and elk-bison areas within individual years (Figure 1.8); no differences were found between ungulate strata (P=0.708). Annual offtake (P=0.003), annual leader use, and proportion of individual twig biomass removed ($P \leq 0.030$) in elk-bison willows was significantly different between years. No significant differences between years were observed in elk-only willows (Figure 1.8). Summer browsing was greater than winter. In summer 2005 through winter 2005/2006 approximately 12% of willow offtake in elk-bison areas occurred during winter (Nov/Dec thru April), and 20% in summer.

Browsing values were negative in winter 2007/2008; that is, greater at the end of the previous summer (Figures 1.7 and 1.8). This may be the result of observer error since different field staff made observations in the spring than fall.

Cottonwood Production

There was no change in cottonwood sapling density at elk-bison grazed sites over the 4-year study period, however sapling density decreased from 2005 to 2009 in elk-only cottonwood communities ($P=0.047$; Figure 1.9). Heights of cottonwood saplings (stems <2.5 m height) were greater in elk-only than elk-bison strata from the outset of the study ($P = 0.020$; Figure 1.10a,b; average sapling heights were 230% taller in elk-only than elk bison) likely due to differences in soil substrate, available water, and site productivity. Mean sapling heights in both strata pooled were greater in 2009 than 2006 or 2005 ($P = 0.044$; Figure 1.10a, b). Mean cottonwood tree heights (stems > 2.5 m height) were not different between years in either elk-bison or elk-only cottonwood communities.

Cottonwood Browsing

Annual percent of cottonwood shoots browsed (% annual leader use) was higher at sites with both elk and bison browsing than elk-only ($P = 0.030$) and summer browsing on cottonwoods was greater in elk-bison than elk-only communities averaged over all years ($P = 0.010$; Figure 1.10c,d). Summer browsing dropped after the first year of the study (51% down to

~32%) on elk-bison cottonwood communities, but remained relatively constant in elk-only areas, ranging between 7% and 13% (Figure 1.10d)

I had data on percent of shoots browsed in winter versus summer in two years, summer 2005 to winter 2005/2006, and summer 2006 to winter 2006/2007. Less than 10% of total leader use in these years occurred in winter, with the exception of elk-only cottonwoods in the first year of the study, which was ~21% (Figure 1.10c). Similar to willow communities, a greater proportion of annual cottonwood browsing occurred in summer than winter.

DISCUSSION

Herbaceous Vegetation

Herbaceous vegetation in willow and cottonwood understory was less productive, senesced earlier, and likely competed with woody species for water and nutrients in these dry communities compared to herbaceous vegetation in wet meadows and even mesic meadows. My finding of lower herbaceous production in elk-bison wet meadows compared to elk-only suggests some impact from 2 grazers. Summer offtake rates in wet meadows did not differ between ungulate strata, but winter offtake was higher in elk-bison than elk-only wet meadows. Przeszlowska (2008) also looked at differences between elk-bison and elk-only wet meadows in this ecosystem; she evaluated soil nutrients and nitrogen (N) mineralization rates for a 3-year period and found no differences between strata in soil N dynamics, C:N ratio, %C, %N, % soil organic matter, or % sand, clay, or silt fraction. Although my study found production differences between strata, differences were not found in these other key ecosystem measures (Przeszlowska 2008). Wet meadows were the most resilient, less water limited, and the most capable of sustaining grazing pressure compared to the other vegetation types evaluated.

Sites with elk and bison did not have significantly higher herbaceous offtake than sites with only elk for most years and in most sites, refuting my first hypothesis that the presence of a second large grazer would substantially increase utilization. Four out of 9 comparisons showed significantly higher utilization in areas with 2 versus 1 large ungulate. Spatial configuration of ungulates on the landscape, as well as ungulate population levels and density, influence the level of utilization. I observed no trends or continuous increases in herbaceous consumption at any site or ungulate strata. Consumption was more variable among years than between ungulate strata, illustrating the spatial heterogeneity of herbivory across the landscape, in which ungulates create as well as respond to heterogeneous resources, partially driven by episodic and patchy rainfall in this arid ecosystem.

A meta-analysis of grazing effects on rangelands worldwide suggested sustainable herbaceous offtake levels for semiarid systems with a short evolutionary history of large herbivore grazing is ~ 35% (Milchunas and Lauenroth 1993). Holechek and Pieper (1992) showed moderate grazing intensity for different semiarid range sites varies from 25 to 50%, with moderate grazing for sagebrush grasslands averaging between 30 and 40% of aboveground net primary production (ANPP). Average summer percent herbaceous offtake in my study was ~44-46%, suggesting herbaceous offtake levels that occurred during my study period are probably within "moderate" grazing intensities for semi-arid rangelands. The exception was greasewood communities that were only measured once (so less comparable statistically to other vegetation types), in which summer offtake was 71%.

Woody Species

Plains bison are not typically browsers and have been shown to select graminoids over shrubs (Hansen and Reid 1975). I found higher browsing in cottonwood communities with both ungulates than just elk, but no browsing difference in willow communities, suggesting that bison may be utilizing cottonwood but not willow. My hypothesis was partially true in that willow browsing did not differ between ungulate strata. More interesting, however, is the result that browsing rates were higher in summer than winter – on both cottonwood and willow. In addition, percent summer herbaceous offtake was higher in elk-bison than elk-only willow communities. These results suggest that behaviorally ungulates are seeking shade and cover in the hot summer, and browsing/grazing while occupying the understory, as opposed to relying primarily on browse in the winter for their primary food source as they do in other more temperate systems such as Yellowstone National Park (Singer and Norland 1994). The comparatively low winter snow cover in this arid system allows elk to continue to utilize herbaceous vegetation, and rely less on winter browse. In addition, the elk population does not remain entirely on the Valley floor in summer; part of the herd migrates to higher elevations in the Sangre de Cristo Mountains, but in winter the core population remains on the Valley bottom (Schoenecker, *unpublished data*). My finding that browsing rates are higher in summer, when the elk population size is actually smaller than winter, is counterintuitive unless the arid climate and summer temperatures are taken into consideration. This finding has important ramifications for management. If ungulates are not relying on browse as a primary food source but seeking protection from heat and sun in summer, herd reductions may not have the desired outcome if behaviorally elk maintain their concentrations in shady, woody areas. Ungulates do not appear to be using these habitats due to limited food resources, but for behavioral reasons that won't be eliminated regardless of herd size. My findings are somewhat contrary to Cook et al. (1998) where authors found no significant effects of forest cover on condition of elk, and concluded that the benefits elk receive in shading from solar radiation in summer were negligible with respect to the thermoregulatory capabilities of elk. I propose that shade may be more important to elk in the hotter, drier climate of my study area in the San Luis Valley (with 28 cm rainfall/yr) than in the cooler forests of the Blue Mountains of Oregon (with 87cm rainfall/yr) where Cook et al. (1998) conducted their research, and that abundance of tree cover/canopy in the Blue Mountains is much greater than the sparse and limited canopy of cottonwood and willow communities in the San Luis Valley.

Willow utilization values have been reported for other study areas in the western Rocky Mountain region. Singer et al. (1998) reported willow utilization in Yellowstone National Park (YNP) and Rocky Mountain National Park (RMNP) was around 30% of current annual growth based on measurements of 30–75% willow leader use and 35–50% removal of twig length. Zeigenfuss et al. (2002) found 33% utilization of current year's willow growth by elk was common in RMNP. Zeigenfuss et al. (1999) estimated that approximately 85% of willow leaders were browsed in RMNP from 1968 to 1993, and Baker et al. (2005) reported that 86–92% of twigs were browsed annually by elk 2 years following simulated beaver cutting in RMNP. Brookshire et al. (2002) estimated utilization at a meadow in northeast Oregon and reported that 90–100% of willow plants were browsed, regardless of whether only wild ungulates or wild ungulates and domestic sheep had access to the area. These authors determined that even relatively light levels of domestic livestock grazing, when coupled with intense wild ungulate browsing, can strongly affect plant structure and limit reproduction of riparian willows (Brookshire et al. 2002). In a study of willows before and after the 1988 wildfires in YNP, Singer et al. (1994) found mean leader use of willows 22 % in the winter of 1987-88, increased to 60% in winter 1988-89 following the drought and fires of 1988, then declined to 44% in 1989-90 and winter 1990-91. Authors felt growth conditions for willows on the northern winter range declined due to a warmer and drier climate this century and locally-reduced water tables, but proximate factors included herbivory by native ungulates (Singer et al. 1998). Woody plants make up only 1% of the landscape in the San Luis Valley, but the importance of riparian ecosystems in regional species diversity is widely recognized (Schulz and Leininger 1990). Annual willow utilization in my study averaged 21% over the study period, across both ungulate strata, but was higher during certain years and/or at specific sites. I don't know why browsing rates jumped so greatly in summer 2009, but it was recorded in both elk-bison and elk-only willow communities, but not in cottonwoods. Continuing to monitor ungulate browsing in woody communities is very important because of the larger role these communities play in supporting species diversity.

Lastly, the role of water in this arid ecosystem cannot be overstated. In a study of the cottonwood community on lower Sand Creek, D. Andersen (USGS, *unpublished data*) conducted tree ring analyses, established wells, measured distance to the stream channel, and used precipitation data to evaluate the role of climate and hydrology in the growth and recruitment of cottonwoods. He concluded that up to 83% of the variation in cottonwood growth and recruitment was attributable to factors related to climate variables such as precipitation and temperature, and stream discharge/hydrology. In semi-arid and arid ecosystems, it is essential to understand the separate and combined role of both herbivory and water.

Overall I found few differences in herbaceous communities with two versus one large herbivore. In woody species, cottonwood leader use was higher on elk-bison than elk-only sites, yet the elk-only sites showed a decrease in sapling density over the study period, and the elk-bison saplings did not. In willow communities browsing did not differ between strata; it could be that bison are browsing cottonwood leaders but do not utilize willows. The tight similarity of browsing levels in elk-only and elk-bison willow communities suggests this is the case, but diet analysis on both species to confirm or refute this hypothesis would be useful.

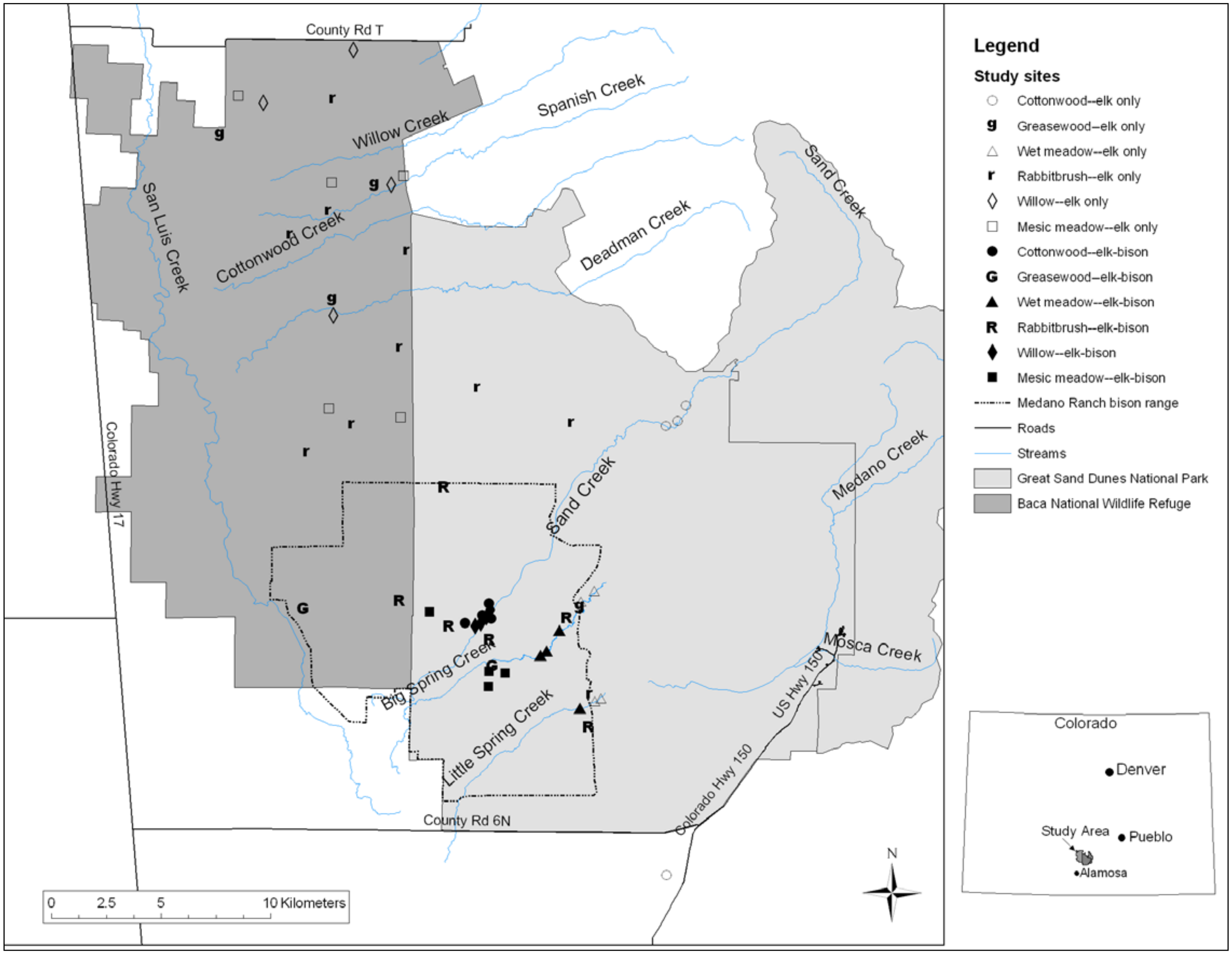

Figure 1.1. Map of study site locations in the Great Sand Dunes ecosystem of the San Luis Valley, Colorado for herbivory research conducted from 2005-2009.

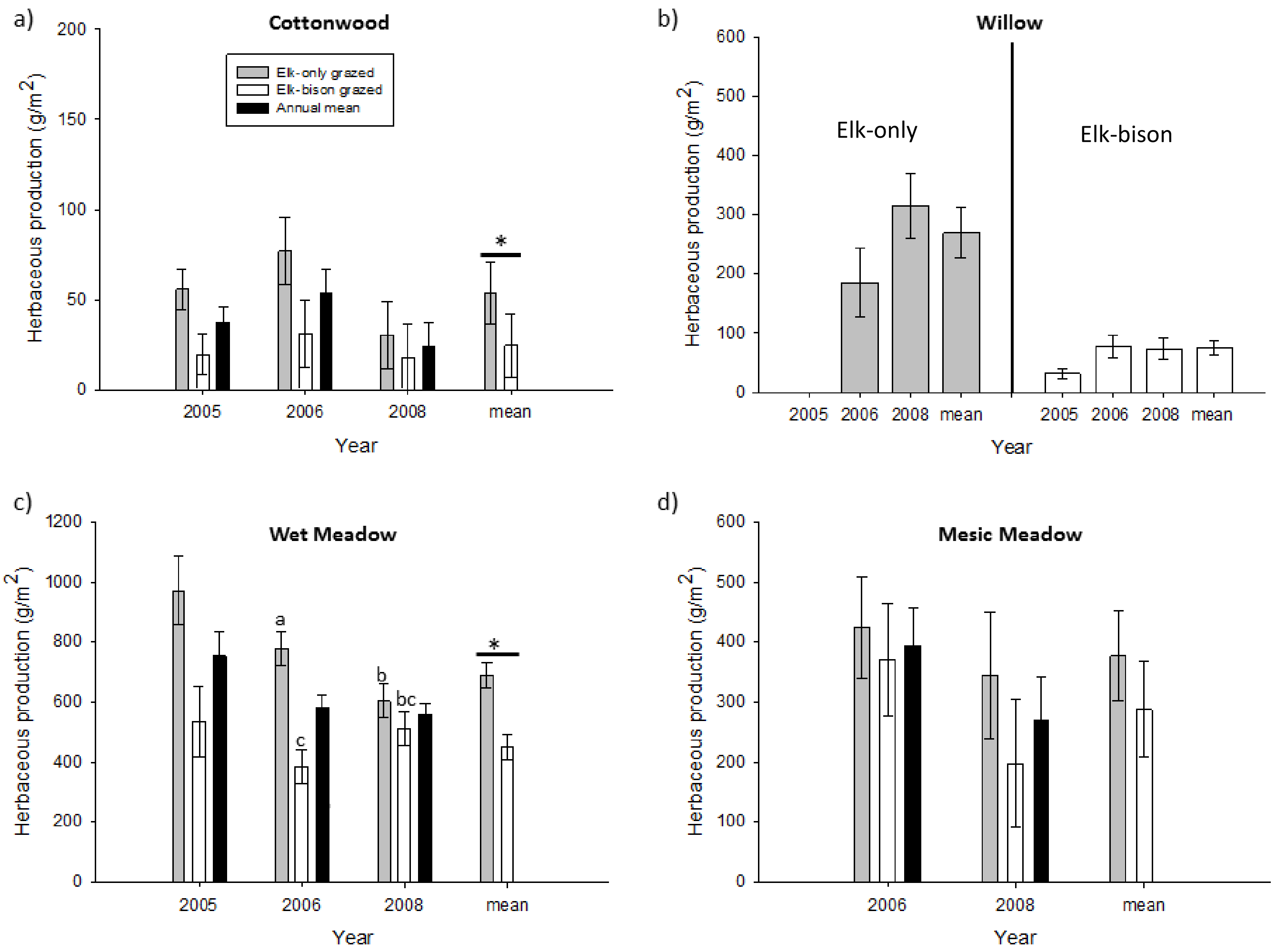

Figure 1.2: Herbaceous production at cottonwood (a), willow (b), wet meadow (c), and mesic meadow (d) sites within different ungulate strata in the Great Sand Dunes ecosystem, 2005-2008. * denotes significant differences ($P \leq 0.05$) between strata; different letters indicate significant differences between years. Site and species differences in willow communities precluded strata comparisons.

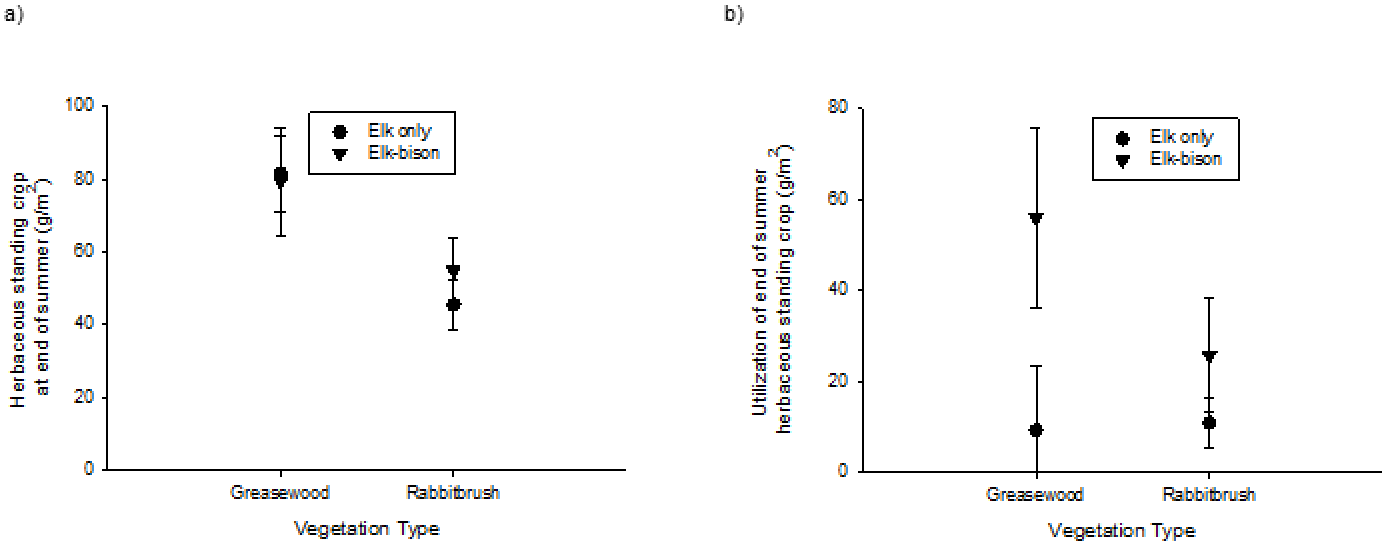

Figure 1.3. Herbaceous standing crop at end of growing season (a) and summer offtake of standing crop (b) in greasewood and rabbitbrush communities of the Great Sand Dunes ecosystem, 2009.

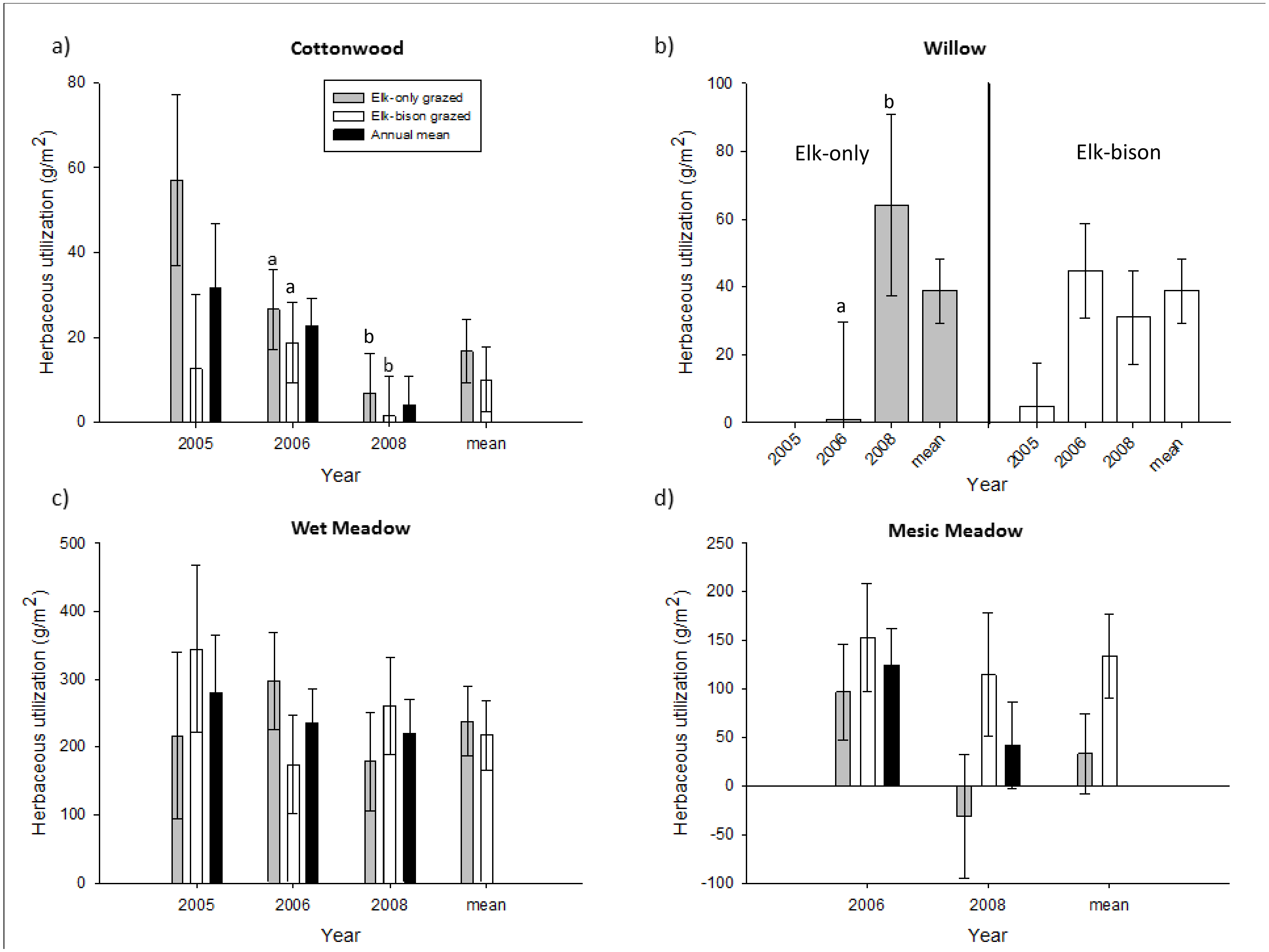

Figure 1.4. Summer herbaceous utilization at (a) cottonwood, (b) willow, (c) wet meadow, and (d) mesic meadow sites within different ungulate strata in the Great Sand Dunes ecosystem, 2005-2008. * denotes significant differences between ungulate strata; different letters denote significant differences between years.

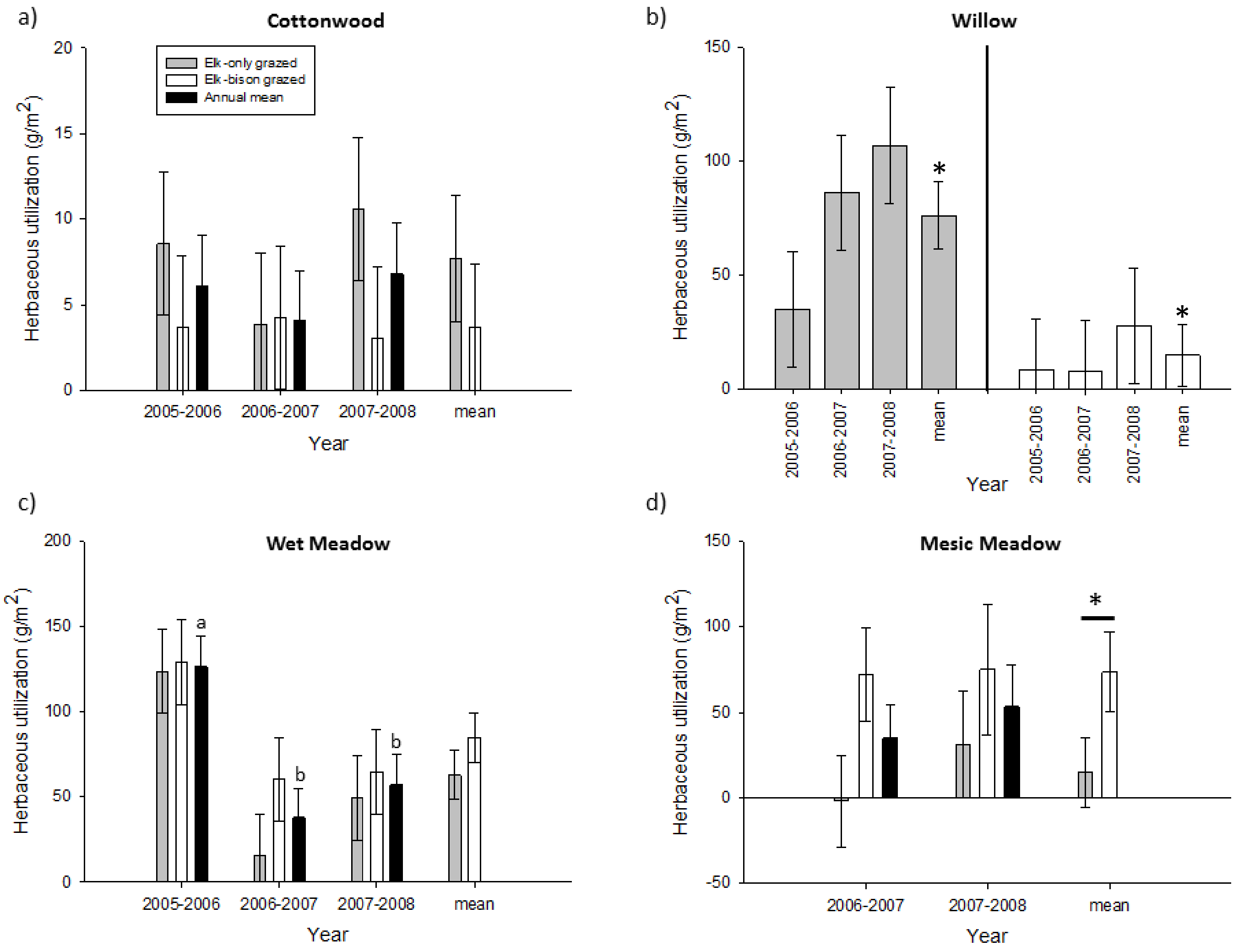

Figure 1.5. Winter herbaceous utilization at (a) cottonwood, (b) willow, (c) wet meadow, and (d) mesic meadow sites within different ungulate strata in the Great Sand Dunes ecosystem, 2005-2008. * denotes significant differences between ungulate strata; different letters denote significant differences between years.

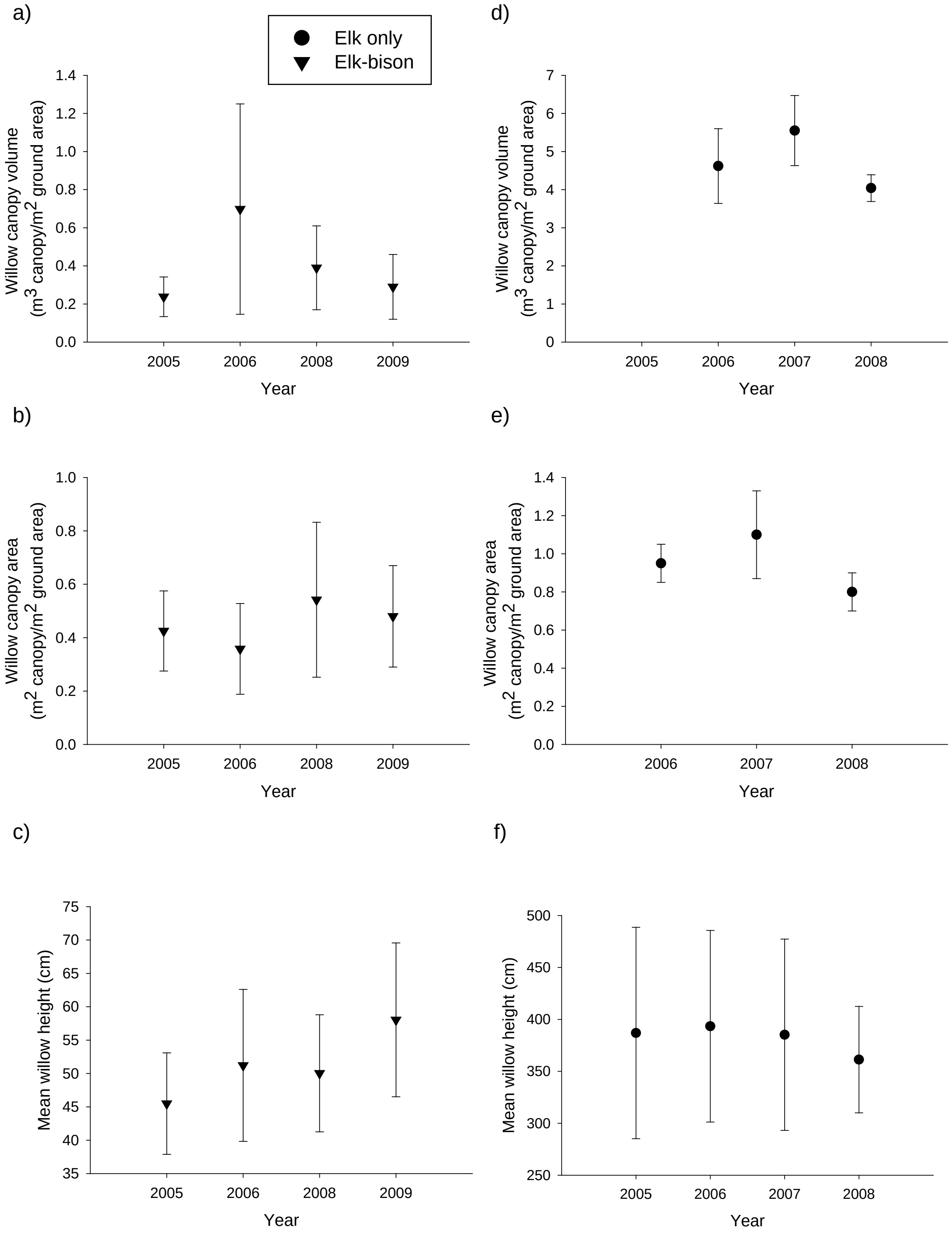

Figure 1.6. Willow production in the San Luis Valley study area, 2005-2009: canopy area (a), canopy volume (b), and height (c) for areas used by elk and bison, and sites used by elk-only (d-f). Different letters denote differences between years. Willow species differences precluded ungulate strata comparisons.

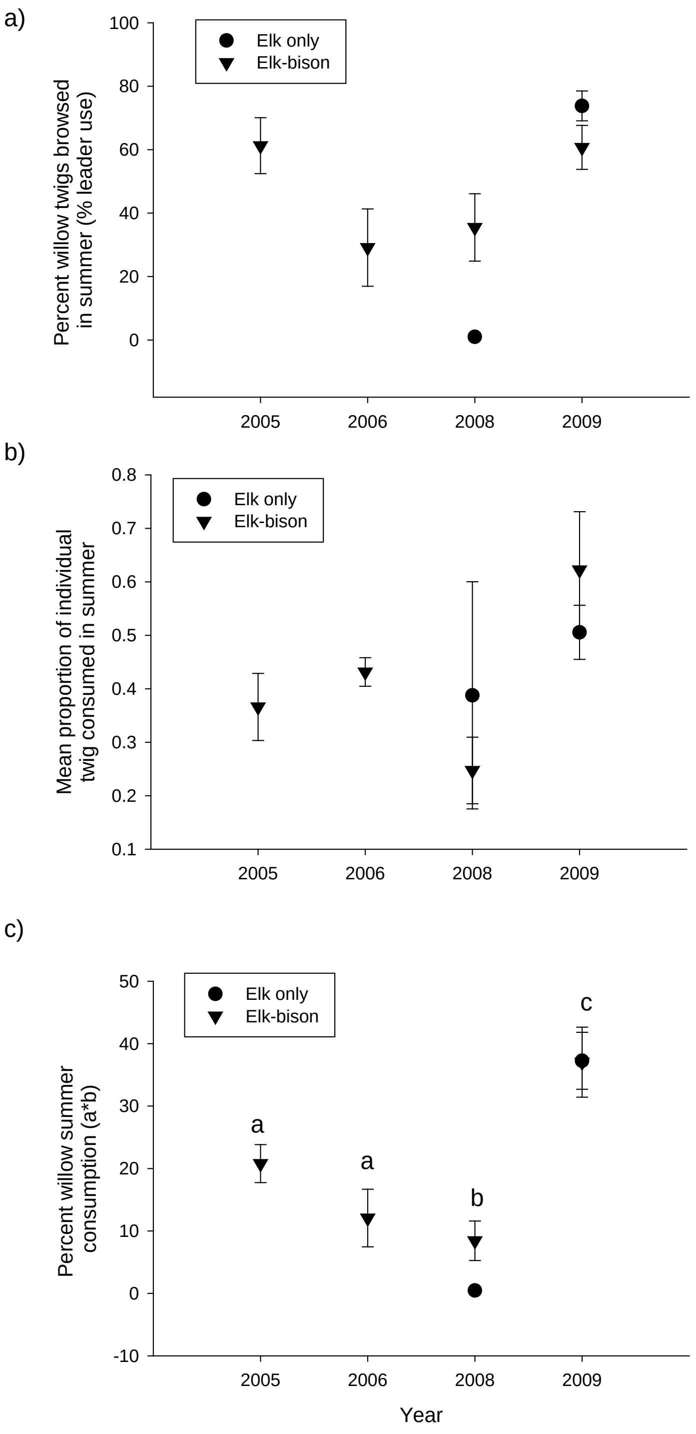

Figure 1.7. Willow summer leader use (a), twig use (b), and total willow offtake (c) for different ungulate strata in the Great Sand Dunes ecosystem, 2005-2008. Total offtake (c) is determined by multiplying (a)*(b). Different letters denote significant difference ($P \leq 0.05$) between years.

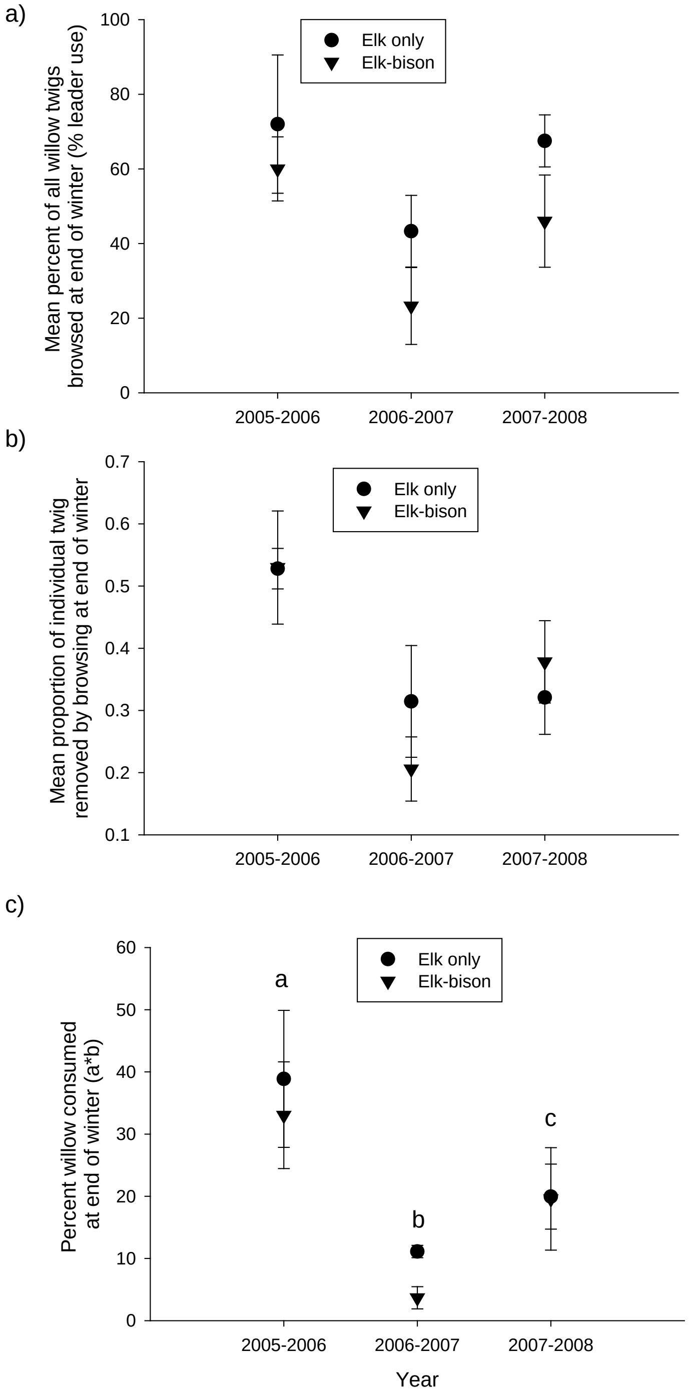

Figure 1.8. Annual willow leader use (a), proportion of individual twig use (b), and total willow offtake (c), for different ungulate strata measured at the end of winter in the Great Sand Dunes study area, for winters 2005/2006, 2006/2007, and 2007/2008. Total offtake (c) is determined by multiplying (a)*(b). Different letters denote significant difference ($P \leq 0.05$) between years.

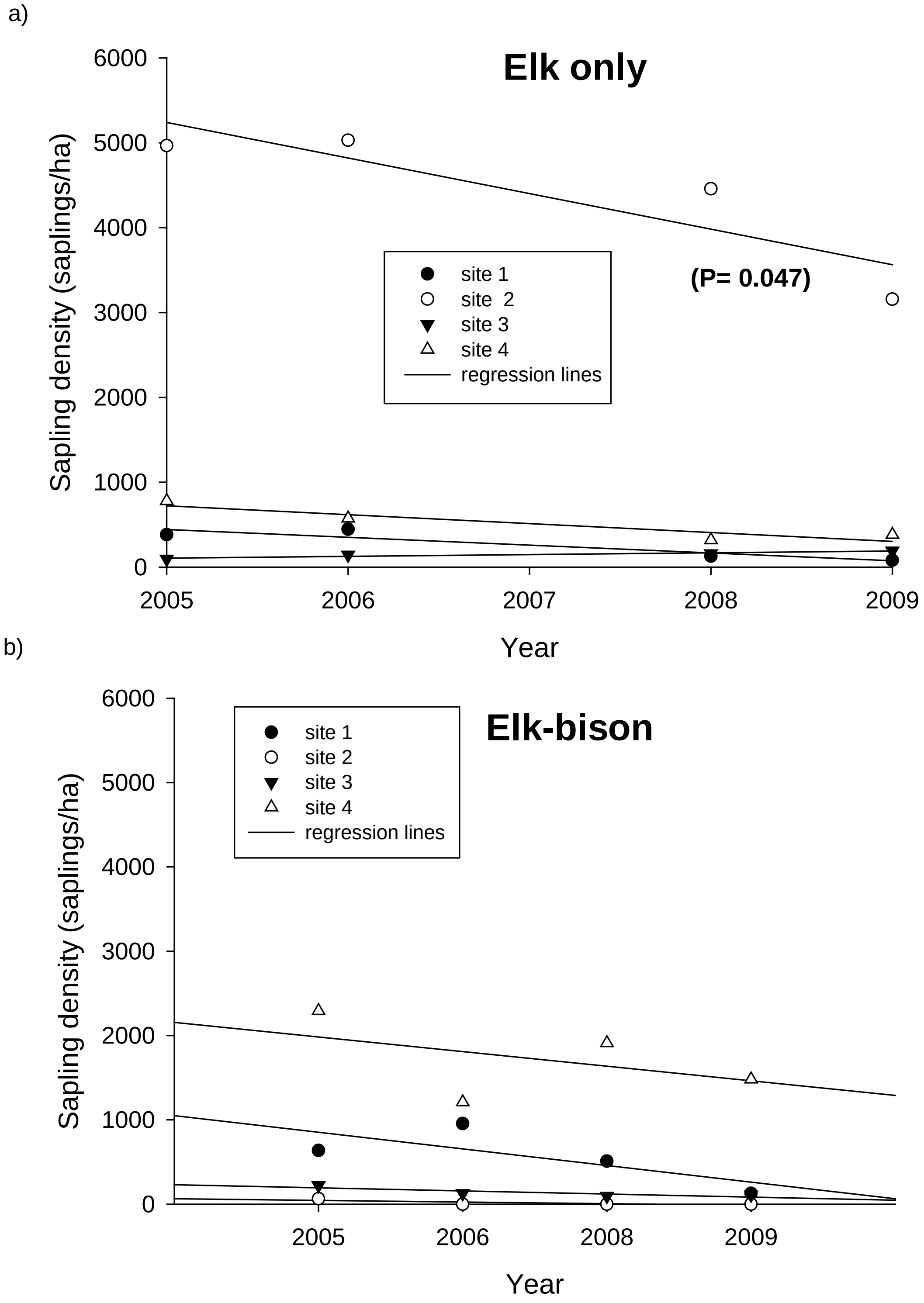

Figure 1.9. Trends in cottonwood sapling density in (a) elk-only, and (b) elk-bison grazed sites in the Great Sand Dunes ecosystem, 2005-2009. Trend line is significant in elk-only cottonwoods.

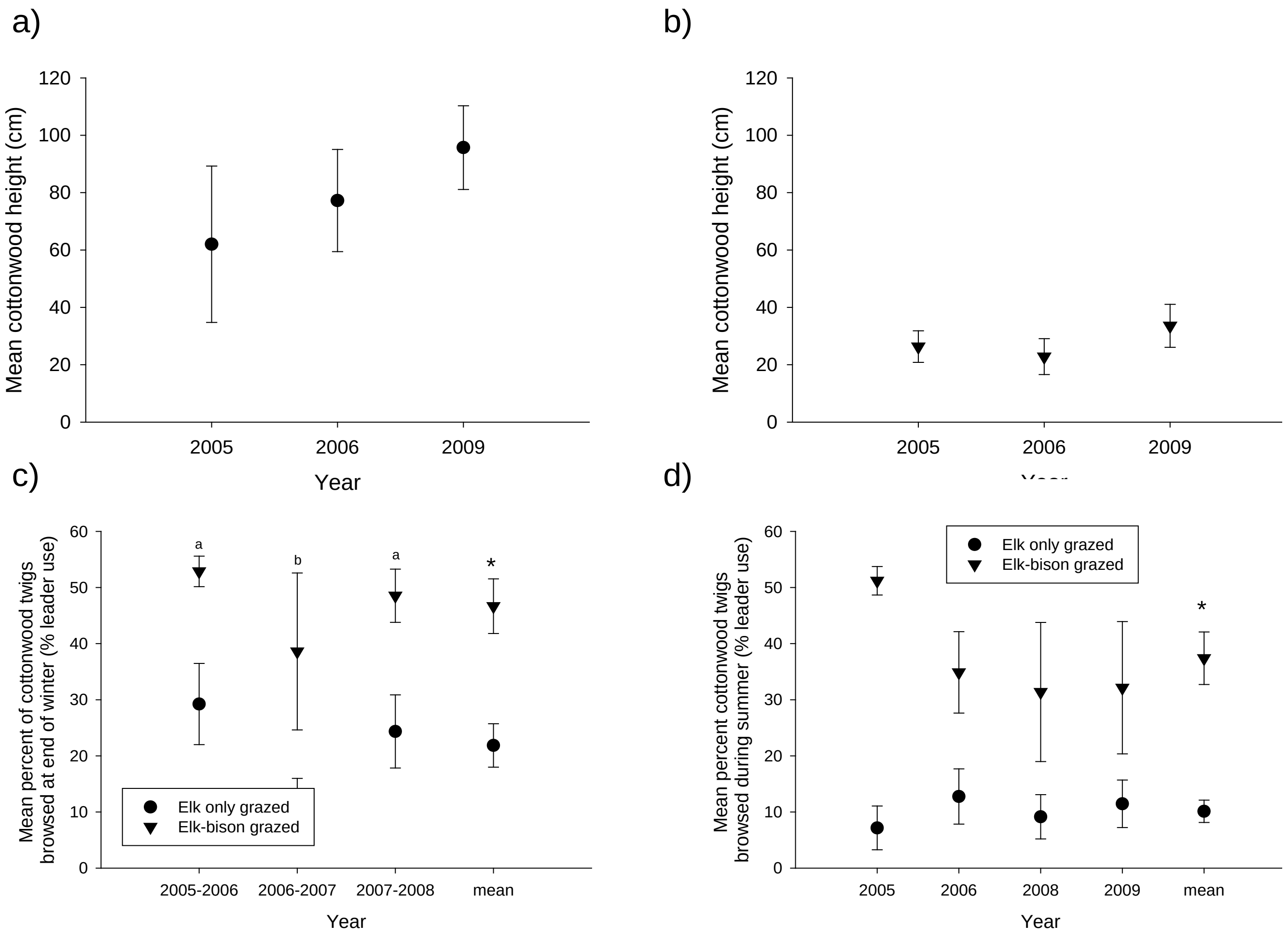

Figure 1.10. Cottonwood height for sites grazed by (a) elk-only, (b) elk and bison, (c) annual leader use, and (d) summer leader use for different ungulate strata in the Great Sand Dunes study area, 2005-2009. *denotes significant difference between ungulate strata; different letters denote significant difference between years.

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CHAPTER 2: HERBACEOUS AND WOODY VEGETATION RESPONSE TO HERBIVORY IN A COLD DESERT ECOSYSTEM

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The concept that grazing may benefit vegetation in some way was first proposed by Ellison (1960) in a botanical review of grazing on rangelands. This potential benefit was later described by the herbivore optimization hypothesis, which predicts an increase in aboveground net primary productivity (ANPP) at moderate grazing intensities up to some optimum, and a decrease with continued grazing (Dyer 1975; McNaughton 1979, Hilbert et al. 1981). The increase in performance has also been defined as plant “tolerance” or “compensation.” Plant overcompensation occurs when grazed plants produced significantly greater ANPP or have higher N-yield than ungrazed plants, equal compensation occurs when ANNP or N-yield do not differ, and under compensation occurs when grazed plants have significantly lower ANPP or N-yield than ungrazed plants (McNaughton 1983, Maschinski and Whitham 1989). Factors that are known to influence the ability of plants to compensate for herbivory include grazing intensity, timing of grazing, water availability, nutrient availability, history of grazing (Painter et al. 1993), and type and age of tissue eaten.

Results of field and laboratory experiments have shown that primary production is stimulated by grazing under some circumstances (Dyer 1975, McNaughton 1979, McNaughton 1983, Nolet 2004, Olejniczak 2011, Pearson 1965, Williamson et al. 1989), while other studies found responses were small or absent (Bergelson et al. 1996, Coughenour et al. 1985, Olson and Richards 1988, Whicker and Detling 1988). Increased nitrogen (N) concentrations have been observed in live tissue of grazed plants compared to ungrazed (Green and Detling 2000, Ouellet et al. 1994), as well as increased nutrient cycling (Coughenour 1984, Ruess et al. 1983) and N mineralization rates (Schoenecker et al. 2004, Singer and Schoenecker 2003). Herbivory can accelerate photosynthetic rate (Houle and Simard 1996, Li et al. 2012, Nowak and Caldwell 1984, Wallace et al. 1984), increase tillering (Coughenour et al. 1984, Painter et al. 1983), and cause a reallocation of plant internal resources (Coughenour 1991).

It was thought that plants could replace tissue lost to herbivory under conditions where environmental resources such as water, light, and nutrients were abundant and readily available, but not under conditions of low resource availability (Chapin and McNaughton 1989). However, further study indicated that plant response to herbivory is plastic and varies depending on multiple environmental conditions. Plants exhibit a wide range in tolerance to herbivory, and how differences in environmental conditions translate into differences in tolerance is still being explored. According to the compensatory continuum hypothesis, overcompensation is most probable in resource rich environments (Maschinski and Whitham 1989) because such conditions provide a higher potential for plant regrowth. The growth rate model predicts lower tolerance in these same conditions (Hilbert et al. 1981), and Wise and Abrahamson’s (2005) limiting resource model predicts conditions under which plants compensate for herbivory by focusing on the specific resources that are limiting plant fitness and the specific tissues that are damaged by herbivory.

Arid systems pose particular challenges to evaluating grazing theory because it is assumed that external factors such as moisture have a more dominant role than internal interactions, such as herbivory (Noy-Meir 1973, 1979/80; Ellis and Swift 1988). Detailed studies that manipulate grazing can reveal whether patterns are caused by herbivore—plant interactions or external factors (Oba et al. 2001) or both. I conducted research to understand the response of plants to herbivory and identify potential constraints on plant compensation in an arid ecosystem.

I used a replicated herbivore exclusion experiment to evaluate herbaceous plant and woody species response to grazing by large ungulates, and to study longer-term trends in ungulate-vegetation dynamics. My general hypothesis is that in areas with both elk and bison (that are presumed to have a higher grazing intensity or even potential overgrazing), plant undercompensation will occur because of the added defoliation of a second large grazer, and in areas with just elk, plants will exhibit equal- or over compensation relative to areas with elk and bison.

STUDY AREA

My study was conducted on the eastern edge of the San Luis Valley of south-central Colorado (Figure 2.1) within Great Sand Dunes National Park, the Baca National Wildlife Refuge, and the Medano Ranch which is owned by The Nature Conservancy. The San Luis Valley is an arid, high altitude (2300 m) intermountain basin just east of the Continental Divide. Streams entering the southern portion form the headwaters of the Rio Grande, while the Closed Basin portion in the north is hydrologically closed. The Sangre de Cristo Mountains along the eastern boundary of the valley extend ~4,000 m in elevation. Precipitation averages 28 cm annually and falls mostly during monsoonal rains in July through September. Summers are warm with average daytime temperatures ranging from 26.5 ^{o}C to 29.5 ^{o}C on the valley floor. Winters are cold and dry with average valley daytime temperatures ranging from -9.5 ^{o}C to 1.5^{o}C. There are eight streams in the study area flowing east to west, all of which have limited flow during the year frequently disappearing underground at their lower reaches.

The San Luis Valley was historically utilized for irrigated agriculture and ranching (Simonds 1995). Bison (*Bison bison*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocapra americana*) were native to the area until about the 1840s when both bison and pronghorn were extirpated. Elk and pronghorn likely moved into the area from surrounding populations to the north and south, and mule deer populations have varied through time. Bison were returned to the landscape by private producers. The former Luis Marie "Baca" Ranch, which makes up the northern part of Great Sand Dunes National Park and all of the Baca National Wildlife Refuge, was actively grazed by cattle (*Bos taurus*) until 2004. A population of bison ranging in size from 1200-1500 range freely within the 20,000 ha Medano Ranch and are managed with annual gathers and removals. A population of 4,500 elk inhabit the entire ~125,000 ha study area.

The primary ecozone is Salt Flats (Chapman et al. 2006), characterized by sparse vegetation where greasewood (*Sarcobatus vermiculatus*) and saltbush (*Atriplex* spp.) predominate with some rabbitbrush (*Chrysothamnus*/*Ericameria* spp.), salt grasses (*Distichlis spicata*), and limited sagebrush (*Artemisia* spp.). Myriad creeks and ephemeral wetlands run through the area, supporting riparian woody vegetation (Figure 2.1). Cottonwood stands are comprised of pure narrowleaf cottonwood (*Populus angustifolia*), while willow stands are made up of *Salix exigua, S. ligulifolia, and S. lucida*. Dominant graminoids include arctic rush (*Juncus balticus*), needle and thread grass (*Hesperostipa comata*), Indian rice grass (*Achnatherum hymenoides*), sand dropseed (*Sporobolus cryptandrus*), saltgrass, slender wheatgrass (*Elymus trachycaulus*), beardless wildrye (*Leymus triticoides*), and sedges (*Carex* spp.). The major forbs include silverweed cinquefoil (*Argentina anserina*), scurfpea (*Psoralidium lanceolatum*), seep monkeyflower (*Mimulus guttatus*), willowherb (*Epilobium* spp.), Rocky Mountain beeplant (*Cleome serrulata*), and Canada thistle (*Cirsium arvense*).

METHODS

I studied herbaceous vegetation and woody species in wet meadows, cottonwood stands, and willow communities of the San Luis Valley. These communities comprise only 2-3% of the landscape but are the most important for native species biodiversity (Schultz and Leininger 1990). I stratified by vegetation type and predominant ungulate species (elk plus bison or elk-only) to evaluate responses to different combinations of herbivores and vegetation type. I used fenced exclosures to create ungrazed treatments from 2005-2009. I defined compensatory ability of plants as overcompensation, equal compensation, or undercompensation following Maschinski and Whitham (1989).

Experimental Design and Treatments

I selected study sites from randomly generated points within target vegetation types in the two ungulate strata. Each potential site was evaluated to ensure there was enough area for a 0.4 ha (1 acre) exclosure and paired grazed plot. Four sites each were located in willow, cottonwood, and wet meadow areas grazed by elk and bison; and four sites each in cottonwood, willow, and wet meadows grazed by elk (Table 2.1). Two plots were selected and a coin flip determined which would be the exclosure versus grazed plot. Exclosures had 2.4 m (8 ft) high fences and were either square or rectangular in shape. Fences were constructed summer-fall 2005.

Some sites were rejected because of potentially confounding influences from legacy effects of disturbance. Areas of cottonwood along Pole and Deadman Creeks had been grazed by cattle for many years (until late 2004), and Medano Creek receives ~90% of the total annual park visitor activity, deterring ungulate presence. Therefore both of these areas were removed from consideration.

Table 2.1. Vegetation type, ungulate strata, sampling location, variables measured, and sampling schedule for herbivore-vegetation research, San Luis Valley, Colorado, USA, 2005-2009. Each vegetation type/ungulate strata/grazing treatment combination had 4 replicate sites with 5 subsamples (clip plots)/replicate for herbaceous measures and 2-3 subsample plots for woody measures.

Vegetation Community	Ungulate Strata	UTM Locations of Study Sites (NAD83)		Variable measured	Year(s) Sampled			
		Exclosed (East/North)	Grazed (East/ North)		2005	2006	2008	2009
Cottonwood	Elk-only	1) 448022/ 4187251 2) 448430/ 4188141 3) 447433/ 4187191 4) 447458/ 4166926	1) 448069/ 4187377 2) 448454/ 4188090 3) 447543/ 4187157 4) 447555/ 4166647	Summer herbaceous production	x	x	x	
				Summer herbaceous N content			x	
				Woody structure (ht, stem density by size class)	x	x	x	x
	Elk-bison	1) 439268/ 4178422 2) 439642/ 4179108 3) 439742/ 4178459 4) 438318/ 4178061	1) 439144/ 4178492 2) 439459/ 4179020 3) 439569/ 4178338 4) 438372/ 4178135	Summer herbaceous production	x	x	x	
				Summer herbaceous N content			x	
				Woody structure (ht, stem density by size class)	x	x	x	x
Wet meadow	Elk-only	1) 444644/ 4174785 2) 444196/ 4174545 3) 444352/ 4179682 4) 443766/ 4179157	1) 444561/ 4174693 2) 444275/ 4174583 3) 444269/ 4179599 4) 443653/ 4179131	Summer herbaceous production	x	x	x	
				Summer herbaceous N content			x	
	Elk-bison	1) 443724/ 4174270 2) 442567/ 4177745 3) 441710/ 4176659 4) 442141/ 4176954	1) 443625/ 4174260 2) 442698/ 4177803 3) 441833/ 4176666 4) 442095/ 4176867	Summer herbaceous production	x	x	x	
				Summer herbaceous N content			x	
Willow	Elk-only	1) 429195/ 4201891 2) 434983/ 4198159 3) 432324/ 4192173 4) 433193/ 4204307	1) 429151/ 4201865 2) 435047/ 4198100 3) 432375/ 4192182 4) 433247/ 4204321	Summer herbaceous production		x	x	
				Summer herbaceous N content			x	
				Woody structure (ht, density, cover)			x	
		Interdunal willows; see Appendix A		Height,offtake, proportion live/dead		x		
	Elk-bison	1) 439333/ 4178361 2) 439485/ 4178721 3) 439065/ 4177961 4) 438896/ 4178053	1) 439321/ 4178406 2) 439511/ 4178752 3) 439080/ 4178137 4) 438813/ 4177997	Summer herbaceous production	x	x	x	
				Summer herbaceous N content			x	
				Woody structure (ht, density, cover)	x	x	x	x

Herbaceous Production

I placed five 1-m^2 cages on grazed controls adjacent to each treatment exclosure starting in spring 2005. The movable cages protected enclosed plants from grazing outside exclosures for short periods. Annual aboveground herbaceous production was sampled by clipping all vegetation within 0.25-m^2 circular plots inside and outside cages, which were then randomly moved for the next sampling. I also randomly placed and clipped 5 circular plots inside exclosures. I was not able to place cages inside exclosures to control for exclosure effects because it would have added 360 additional plots/season. Physical enclosure of plants reduces wind velocity, increases humidity and may lead to increases in dry matter production (Cowlinshaw 1955), so it is possible that ungulate exclosures influenced plant performance but I was not able to measure this potential effect. I conducted herbaceous measurements following McNaughton (1985) and Bonham (1989). All graminoids, forbs, and sub-shrubs within plots were clipped at ground level. Vegetation was oven dried at 55^o C for 48 hours and weighed. A subsample of plots was sorted to separate live and dead plant materials, separating current year from previous year dead.

I conducted sampling twice during the growing season (June and August) in 2005, and three times (mid-late June, late July-early August, and late August-mid-September) in 2006 and 2008 to determine total production (Table 2.1). I estimated total herbaceous production using a modification of the difference method (McNaughton 1985, Bonham 1989):

$$B = P_1 + \sum_{i=1}^{T} (P_{c(i+1)} - P_{ui})$$

where B=total herbaceous biomass produced, $P_{c(i+1)}$ is the average amount of biomass in caged plots at time $i+1$ and P_{ui} is the amount of biomass outside the cage at time . For the first time interval, P_1=P_{ci}. Both positive and negative differences in production for each interval were added to the initial caged biomass to determine production. Inside exclosures production was calculated as the sum of the average biomass clipped at the end of the first time period plus the differences (whether positive or negative) between average biomass between each succeeding time period. Sample sizes for each site were chosen following recommendations in Waddington and Cooke (1971) where authors determined that reduced sample sizes could be used based on 90% confidence intervals rather than power tests. Bonham (1989) recommended 25 cages/site, which was not achievable for my study. I used 5 cages/site (Table 2.1).

Nitrogen Yield

I collected graminoid and forb samples for nitrogen analyses in June, July, and August/September, 2008 from ungrazed treatments and grazed controls. Samples were sorted by plant functional group, vegetation type, ungulate stratum, and grazing treatment. A representative sub-sample of plant material was taken from each sample using all parts of the plant, and combined to form composites with 3 plots/composite. Composites were ground in a Wiley Mill using a 20 gauge mesh screen to form a homogeneous mixture, and run on a LECO C/N analyzer; a 0.10g to 0.11g aliquot of each sub-sample was weighed, recorded, and placed into the auto sampler. The LECO C/N analyzer uses combustion and an inert carrier gas (He) to process samples. Percent N is measured using a Thermal Conductivity Detector. All samples were bracketed in increments of 10 with a blank and a known standard to ensure instrument accuracy. I calculated N-yield by multiplying graminoid and forb production/site by the corresponding %N for that functional group and site.

Willow Production

I randomly located three fixed-radius 10 m^2 circular plots within grazed and exclosed treatments at each willow site and marked the center of circular plots with rebar. I measured all plants that fell completely or greater than 50% within the plot. 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 was measured. For each willow plant I recorded species, shrub canopy diameters (widest and perpendicular to widest diameter), shrub height, number of stems, estimate of percent of canopy dead, a subsample of the number of browsed and unbrowsed current annual growth (CAG) shoots, diameters at shoot base, diameters at shoot tip, diameters at point of browse, and leader lengths.

On lower Sand Creek the willow communities consisted almost exclusively of coyote willow, which tends to have shoots that branch multiple times within a single growing season. In cases of multiple branching shoots, I totaled the length of the longest part of the shoot plus the length of all side shoots from branching point to tip to get 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. I took tip diameters from the apparent main current year's growth shoot, not from branching shoots. For browsed shoot counts on such shoots, I counted browsing on any part of the shoot as one browsed shoot.

Percent leader use was estimated:

$$\%\_leader\_use = \left(\frac{a}{a+b}\right) \times 100 ,$$

where a = number of browsed CAG shoots and b = number of unbrowsed CAG shoots. Average proportion shoot removed was determined following Jensen and Urness (1981) and Pitt and Schwab (1990) using:

$$proportion\_twig\_use = \frac{100(D_p - D_t)}{D_b - D_t} \quad ,$$

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

Cottonwood Production, Regeneration, and Recruitment

I estimated height, and stem density of cottonwood saplings (height $\leq$ 250 cm including seedlings and resprouts) and distribution of stem classes of cottonwood trees (height > 250 cm). I collected measurements from all cottonwood plants that fell within each of two 10 m radius (314 m^2) circles at each site and grazing treatment. Roughly one-third (11 of 32) of the plots were densely vegetated with high homogeneity, so 5 m radius (78.5 m^2) circles were used. I selected plot locations by traveling a random direction and distance from the center of the grazed or exclosed treatment at each site, and marked the center of circular plots with a labeled rebar post. I ensured they did not overlap other plots and were a minimum of 3 meters from exclosure fences to prevent fence effects (shading, trampling, sand and snow deposition).

For each cottonwood tree in a plot I recorded number of trunks, dbh (diameter at breast height [1.4m]), and percent dead canopy. I also recorded the number of browsed and unbrowsed current annual growth (CAG) shoots for all branches and basal sprouts within 200 cm of the ground. For saplings and resprouts I measured: height, number of stems, canopy diameters, number of browsed and unbrowsed CAG shoots, and percent dead canopy. I determined percent leader use using the same formula as for willows.

Interdunal Willow Survey

I collected information on the presence and condition of willows in interdunal wetlands of Great Sand Dunes National Park to record long-term trends. Willow patches were surveyed by walking around them with a handheld global positioning system (GPS) to delineate boundaries of the patch. Patches were defined as a group of willows growing closely together sharing a common willow distribution, willow species diversity, and plant density. If a noticeable change in any patch component occurred, especially density, percent of dead willows, or willow species composition, a new patch was created at the point of transition. Data recorded for each patch included willow species, height, associated vegetation, distance to water, and use by ungulates. I initially located interdunal wetlands from descriptions in Hammond (1998). If other interdunal wetlands were encountered while traveling to these sites, I recorded their location and surveyed them as well.

Statistical Analyses

I analyzed data using SAS statistical analysis software V9.2 (SAS Institute, Cary, NC). Herbaceous production data were analyzed using a mixed linear model procedure (PROC MIXED) that is a generalization of the standard linear model designed to analyze data generated from several sources of variation. I tested for main effects and interaction effects of ungulate stratum, grazing treatment, and year (2006 and 2008) within each vegetation type with the effects of random sites and grazing treatments nested within ungulate stratum. Data collected in 2005 were pre-treatment to ensure sites were similar prior to fencing.

Willow height and canopy data and cottonwood sapling density and height data were analyzed using a mixed model with the effects of random sites, years, and grazing treatments nested within ungulate stratum. Main and interaction effects were tested for the independent variables of year and grazing treatment, and where appropriate, ungulate stratum. Willow canopy area and volume, and cottonwood sapling density were log transformed to stabilize the variance.

I used simple linear regression with contrasts between years to test for trends in density and height over time within each ungulate stratum and grazing treatment. One outlier site was removed from willow height and canopy analysis because the species composition and density did not match any of the other sites. Another outlier was removed from willow height analysis because it was an outlier in box plots and height data were not normal (Shapiro-Wilk *W* statistic). I determined plant response as overcompensation, equal compensation, or undercompensation by comparing production and N-yield of herbaceous and woody vegetation in grazed versus ungrazed treatments

RESULTS

Herbaceous Production

Wet meadows had the highest production of the 3 community types (Figure 2.2). In wet meadows herbaceous production in grazed sites was greater than ungrazed in both ungulate strata (P= 0.016; Figure 2.2). Annual variation in herbaceous production was high. Elk-only wet meadows had higher production in 2006 than 2008, and higher than elk-bison sites in both years (P= 0.008). Cottonwood communities had greater herbaceous production in 2006 than 2008 (P=0.0374). In elk-only willow communities grazed_{2008} herbaceous production was greater than grazed_{2006} production, but was not different from ungrazed in either year (Figure 2.2). In elk-bison willow communities no herbaceous production differences were found between grazed and ungrazed or among years.

Herbaceous Nitrogen Yield

In elk-bison communities, N-yield was mostly similar between grazed and ungrazed treatments. In elk-only areas, N-yield was higher in grazed wet meadow graminoids than ungrazed graminoids ($P= 0.013$), but lower in grazed cottonwood community forbs ($P= 0.035$) and graminoids ($P= 0.072$) than ungrazed forbs and graminoids (Table 2.2).

Willow Heights and Canopy Size

In elk-bison willows, heights at the end of my study were greater in ungrazed than grazed communities ($P= 0.05$; Figure 2.3). I found only annual differences in willow canopy area and volume, but no grazing treatment differences (Figure 2.4). In willow canopy volume, 2005 < 2006, 2008, and 2009; and 2006 < 2009 ($P< 0.001$). Willow canopy area was greater in ungrazed_{2008} and ungrazed_{2009} than ungrazed_{2005} and $\text{ungrazed}_{2006.}$ Grazed_{2009} willow canopy area > grazed_{2006} ($P= 0.036$).

In elk-only willows I had one year (2008) of data from ungrazed treatments, and in this year ungrazed canopy volume ($P= 0.030$) and area ($P= 0.004$) exceeded grazed willows (Figure 2.4), but heights did not differ (Figure 2.3). The year to year variation in willow height was small ($P= 0.95$), likely because willows were already beyond the browse zone of elk in the elk-only willow communities I studied.

Cottonwood Sapling Height and Density

Sapling heights in 2009 were taller in ungrazed than grazed stands in both ungulate strata (ungrazed_{2009} > all other trt-year combinations; $P= 0.004$; Figure 2.5). Heights in elk-bison grazed plots were less than all other treatment-strata combinations ($P =0.042$), although heights of elk-only saplings were greater than elk-bison from the onset of the study ($P = 0.020$).

Table 2.2. Average nitrogen yield (g/m^2) of herbaceous vegetation in 3 vegetation types grazed by elk and bison or elk-only in the San Luis Valley, Colorado. Nitrogen data was collected in 2008 at two different time periods.

	Nitrogen Yield (g/m$_2$)								
Vegetation Type	Elk-Bison (±SE)			Elk-only (±SE)			Both Strata Pooled (±SE)		
	Grazed	Ungrazed	*P*-value	Grazed	Ungrazed	*P*-value	Grazed	Ungrazed	*P*-value
Wet Meadows									
July-Early August									
Forbs	0.51 ± 0.07	0.53 ± 0.22	0.917	0.49 ± 0.33	0.76 ± 0.39	0.628	0.50 ± 0.15	0.63 ± 0.19	0.728
Graminoids	4.52 ± 0.82	3.33 ± 0.31	0.137	5.94 ± 0.56	2.95 ± 0.74	0.049	5.23 ± 0.54	3.14 ± 0.38	0.013
Late August-September									
Forbs	0.24 ± 0.14	0.16 ± 0.11	0.535	2.16 ± 1.55	1.22 ± 0.68	0.429	1.06 ± 0.71	0.62 ± 0.34	0.542
Graminoids	3.55 ± 0.66	3.52 ± 0.78	0.912	4.20 ± 0.77	3.88 ± 0.62	0.418	3.88 ± 0.48	3.70 ± 0.47	0.796
Cottonwood									
July-Early August									
Forbs	nd	nd	nd	0.09 ± 0.04	0.70 ± 0.21	0.035	0.09 ± 0.04	0.70 ± 0.21	0.035
Graminoids	nd	nd	nd	0.56 ± 0.42	0.89 ± 0.45	0.072	0.56 ± 0.42	0.89 ± 0.45	0.072
Late August-September									
Forbs	0.04 ± 0.01	0.48 ± 0.15	0.450	0.09 ± .	0.48 ± 0.15	.	0.05 ± 0.01	0.34 ± 0.12	0.278
Graminoids	0.08 ± 0.01	0.13 ± 0.04	0.257	0.82 ± .	0.81 ± 0.48	.	0.27 ± 0.18	0.52 ± 0.29	0.101
Willow									
July-Early August									
Forbs	0.46 ± .	nd	.	0.94 ± 0.54	0.91 ± 0.54	0.540	0.84 ± 0.43	0.91 ± 0.54	0.547
Graminoids	0.27 ± .	nd	.	3.82 ± 0.91	2.21 ± 0.39	0.153	3.11 ± 1.00	2.21 ± 0.39	0.994
Late August-September									
Forbs	1.30 ± .	0.11 ± 0.05	.	1.23 ± 0.44	0.55 ± 0.26	0.026	1.24 ± 0.34	0.30 ± 0.14	*
Graminoids	0.56 ± 0.08	0.38 ± 0.14	0.002	2.82 ± 0.07	2.20 ± 0.27	0.229	1.85 ± 0.46	1.29 ± 0.37	*

*comparison not made due to site differences between strata

In trend analysis, sapling heights increased over time in both elk-only (*P* =0.022) and elk-bison ungrazed sites (*P* <0.001; Figure 2.6). The density of cottonwood saplings decreased from 2005 to 2009 in elk-only grazed sites (*P* =0.048), but did not increase at ungrazed pairs (*P* = 0.141; Figure 2.7). Sapling density increased at elk-bison ungrazed sites (P=0.021), but did not change at grazed pairs (Figure 2.7).

Cottonwood Tree Density

The density of small diameter cottonwood trees (stems > 250 cm height and < 10 cm dbh) decreased at elk-bison (*P*= 0.017) and elk-only grazed sites (*P*= 0.089), but did not increase at ungrazed pairs (Figure 2.8a). No trends were observed in the density of medium size (10-20 cm dbh) or larger stems (>20 cm dbh; Figure 2.8b, c). The maximum density observed for small diameter cottonwood trees was ~ 350 stems/ha (Figure 2.8a). The maximum density observed for larger stem sizes was > 600 stems/ha (Figure 2.8c).

Interdunal Willows

I located 11 of Hammond’s (1998) interdunal wetland sites and only one site had willows (see Appendix A for locations). An additional 19 interdunal wetland sites were located by field crews, 6 with willows and 13 without. Of the 6 sites with willows, 5 had live willows and 1 had dead willows. Leader use of live willows at these stands averaged 70.9% (± 13.0%), which was much higher than that observed at nearby sites on lower Sand Creek during the same summer. Most willow were *S. exigua*, though one very tall *S. amygdaloides* (>3.5 m high) was recorded. Average height was 44.0 cm. All interdunal wetland sites had signs of ungulate use—mostly elk scat and tracks, but scat of bison, mule deer, and cattle, were also observed. At sites with live willow, half of the patches had moderate sand dune deposition around the willows. Seventy-five percent or more of the willow canopy was dead at sites with moderate dune deposition.

DISCUSSION

Plant Compensation

Herbaceous plants overcompensated for losses of tissue from herbivory in wet meadows of the Great Sand Dunes ecosystem. Grazed wet meadows had consistently higher herbaceous production and N-yield than ungrazed in elk-bison as well as elk-only meadows. In the absence of grazing, wet meadows accumulate senescent plant material, which can lead to increased surface litter and standing material that alters resource availability within microsites, causes self-shading, ties up nitrogen, and can suppress plant production (Coughenour et al. 1984, Knapp and Seastedt 1986, Knapp et al. 1993, Briggs and Knapp 1995). Wet meadows in the San Luis Valley were highly productive, had poorly drained soils, and fairly constant water availability. Grazing removed standing dead material, allowing greater light into microsites and increasing nutrient deposition via feces and urine in readily available forms.

Herbaceous plants in willow and cottonwood communities' responded to herbivory with equal compensation. These results suggest the herbaceous communities I studied are either being enhanced by herbivory or are tolerating herbivory, and can sustain levels of grazing that occurred during my study period. There was one exception in the cottonwood understory vegetation, in which grazed herbaceous vegetation undercompensated in N-yield, likely because cottonwood communities had the lowest herbaceous production of all 3 vegetation types I studied.

Plant overcompensation has been reported in woody species (duToit et al. 1990, Focardi and Tinelli 2005, Stewart et al. 2006, Wolff 1978), but I observed mostly equal- or undercompensation. There was a clear height release in willows and cottonwoods protected from browsing in elk-bison communities, and a canopy release in elk-only willow communities. These results suggest that woody structure of willows is being modified by browsing in both elk-only and elk-bison willow stands.

Grazing Intensity

I observed little differentiation in plant response related to grazing intensity, despite sometimes large differences in offtake (see Table 1.2), refuting my hypothesis. Winter herbaceous offtake in wet meadows that included elk and bison exceeded offtake in wet meadows grazed by elk alone, but both areas showed plants were overcompensating for tissue losses from herbivory. In willow communities, summer herbaceous offtake in elk-bison was significantly greater than elk-only strata, but plants exhibited equal compensation in both areas. Plant response varied more by vegetation community and year than by grazing intensity (ungulate stratum).

Plant Response Relative to Microsite

The structure of woody species responded when browsing was eliminated, but in recruitment, woody plants did not respond to removal of grazing even after 5 years of exclosure. Cottonwood sapling heights increased, but not in all sites, and even grazed cottonwood saplings showed moderate height increases over the study period ($P= 0.06$). More interestingly, cottonwood saplings and small trees protected from browsing did not increase in density at any site. Many factors could influence the ability of adult cottonwood trees to produce new recruits, including soil moisture, parent tree health, light, and soil nutrients. I did not measure these factors at each site, but there were very few differences in soil type and soil drainage between cottonwood sites (see Appendix B). In a study of the cottonwood community on lower sand creek (with both elk and bison) Andersen (2010) found that the potential growth and recruitment of cottonwoods was attributable to climate and hydrology variables. Sixty to 95% of the variation in regression analysis was explained by climate and hydrology, with some unexplained variation potentially attributable to herbivory or other causes. Andersen (2010) concluded that habitat conditions for sexual reproduction of cottonwoods may no longer exist, and the presence of sucker regeneration alone makes cottonwoods more vulnerable to suppression by herbivory, and may increase stressors to the parent tree. I did not observe any increase in sapling density despite removal of ungulate browsing for 5 years, suggesting water and/or nutrients are a stronger influence on cottonwood recruitment than herbivory.

Cottonwood and willow communities in elk-only areas were located closer to the Sangre de Cristo Mountains than elk-bison communities, and differed somewhat in soil type, soil drainage, and potential productivity (Appendix B). I did not measure soil moisture, but anecdotal evidence suggests at least some of these sites had higher annual precipitation due to patchy rainfall patterns that drop more moisture closer to the mountains. In these areas, willow heights were taller, canopy volume and area were larger, cottonwood saplings were taller, and herbaceous production was greater at the start of the study, than areas on lower Sand Creek. Removing herbivory for 5 years did not alter these starting conditions, suggesting microsite characteristics heavily influenced plant performance.

Long Term Trends in Cottonwood Recruitment

The expected pattern of tree stem diameter distribution for healthy cottonwood stands would be an exponential decrease in stem density with increasing stem diameter. All stands measured in my study showed the opposite trend at the beginning of the study, with a greater percentage of total stems in large diameter classes and a lower percentage in small classes. The lack of increase in density of larger dbh classes over the 5 years of the study was not surprising given the relative amount of time it would take for larger stem sizes to move from one DBH class to another. However, it illustrates that larger trees are not dying at such a high rate that tree death could be observed during the study timeframe. More revealing is the low density of small diameter trees compared to medium and large diameter trees. This demonstrates a lack of recruitment from saplings into the smaller tree size class for an extended period of time. I propose that limits to cottonwood recruitment have been in place for quite some time (> 15 years), and environmental conditions are limiting new recruitment even when browsing is removed. This conclusion is supported by anecdotal evidence of substantial manipulation of the stream channel on lower Sand Creek, where there were concrete diversion dams at one time and large equipment was used to flood areas to the north (D. Cooper, CSU, pers. commun.). Alternatively, historic heavy cattle grazing, changes in the stream channel or hydrology, or some combination of these stressors has had lasting effects.

Herbaceous plants either compensated or overcompensated for tissue loss from herbivory, suggesting grazing levels observed during my study period are sustainable. Wet meadows, which were the least water limited, overcompensated in both herbaceous production and N-yield; while cottonwood and willow community herbs responded with equal compensation. Woody species mostly undercompensated for herbivory in structure measures, but where water was lacking plants were unresponsive to browsing removal. My results support the idea that external factors such as precipitation and moisture have a more dominant role in this arid ecosystem than internal interactions, like herbivory. However, this is likely to vary across the landscape depending on rainfall patchiness, hydrology, stream flow and other environmental variables. My findings have ramifications for management. Reducing or removing browsing will not likely result in increased production and recruitment of woody species unless water limitation is also managed. Plants have been shown to compensate for woody tissue losses from herbivory when other environmental conditions are not limiting.

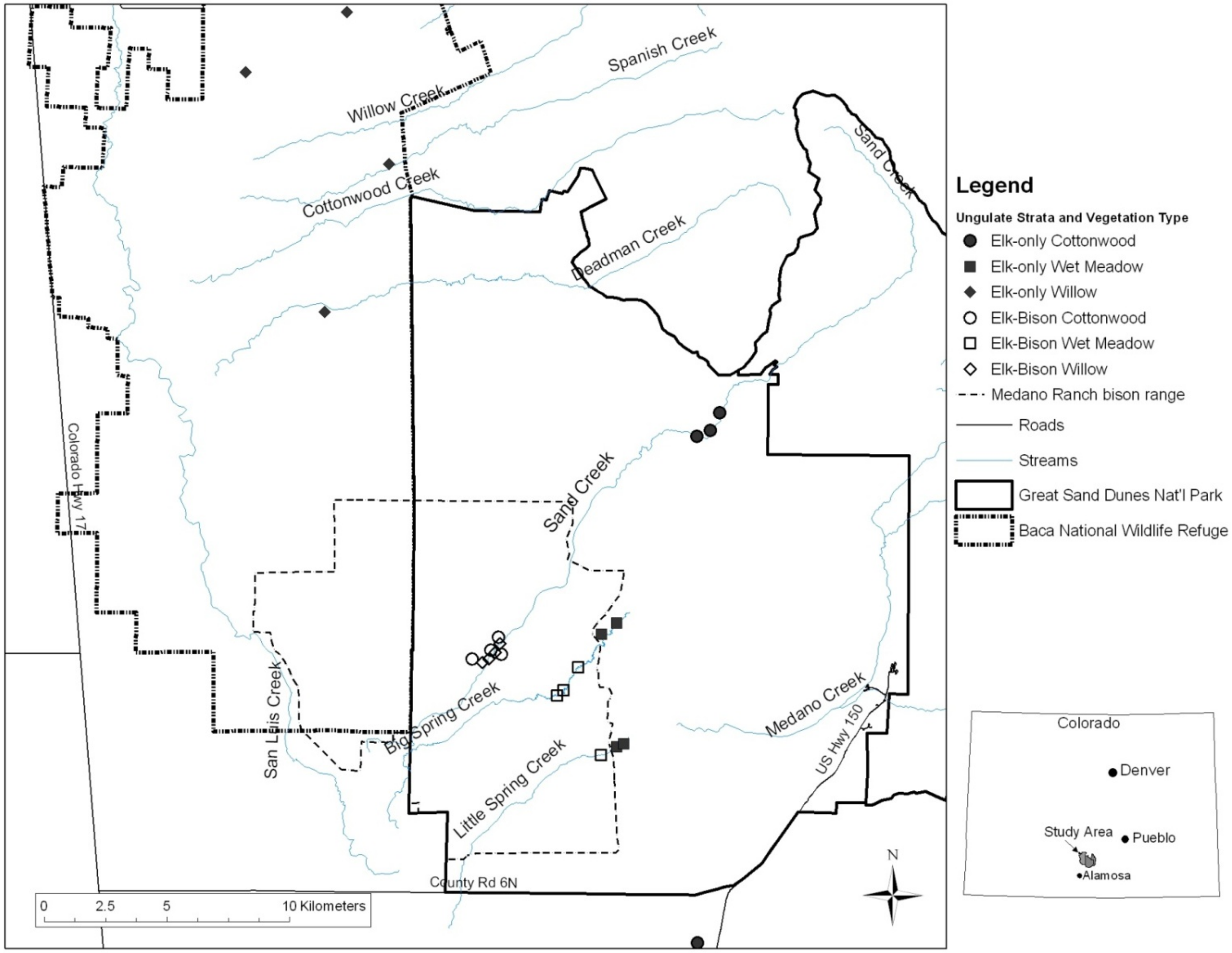


Figure 2.1. Map of exclosure locations and ungulate strata in the San Luis Valley of southern Colorado for herbivore-vegetation research conducted from 2005-2009.

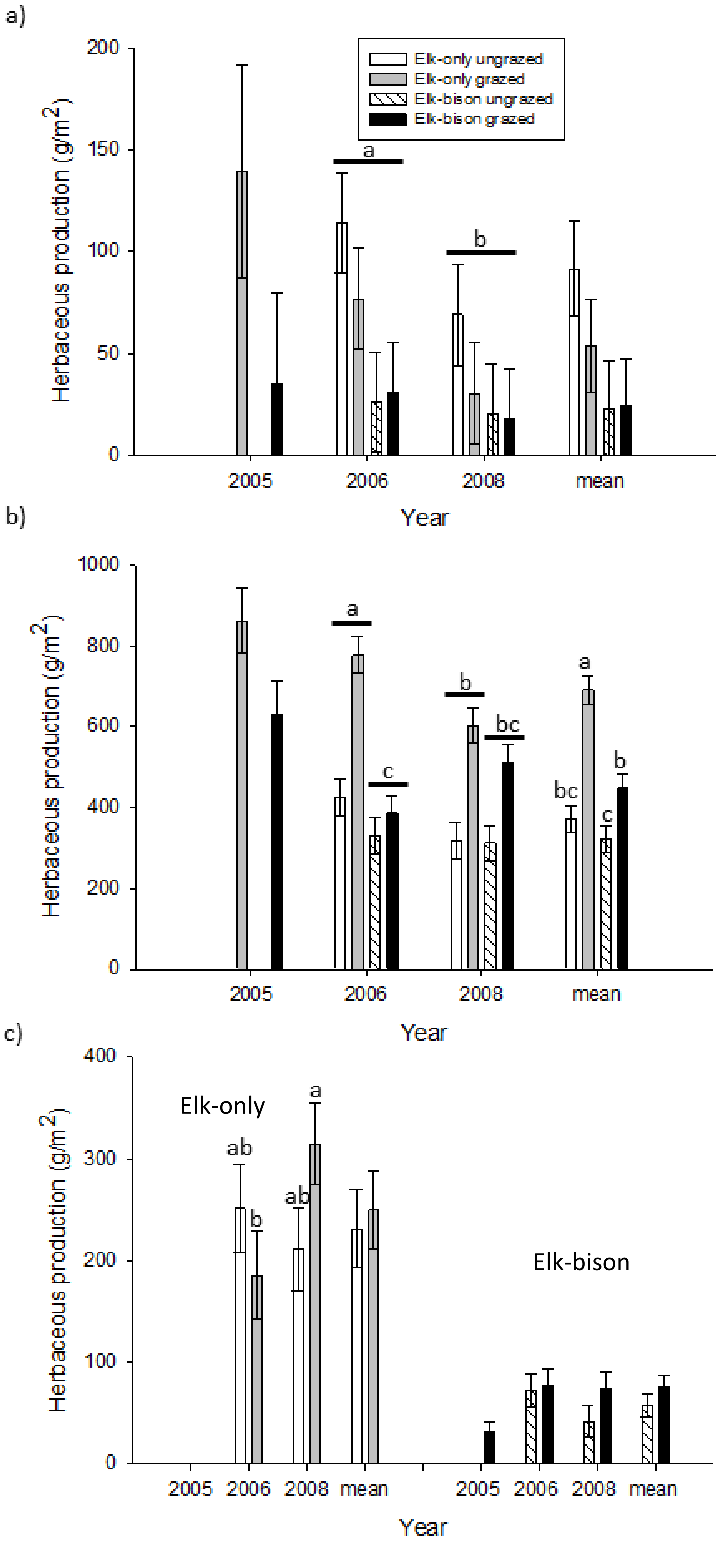


Figure 2.2. Herbaceous production at a) cottonwood, b) wet meadow, and c) willow communities within different grazing treatment and ungulate strata in the San Luis Valley ecosystem, 2005-2008. Different letters indicate significant differences ($P < 0.05$).

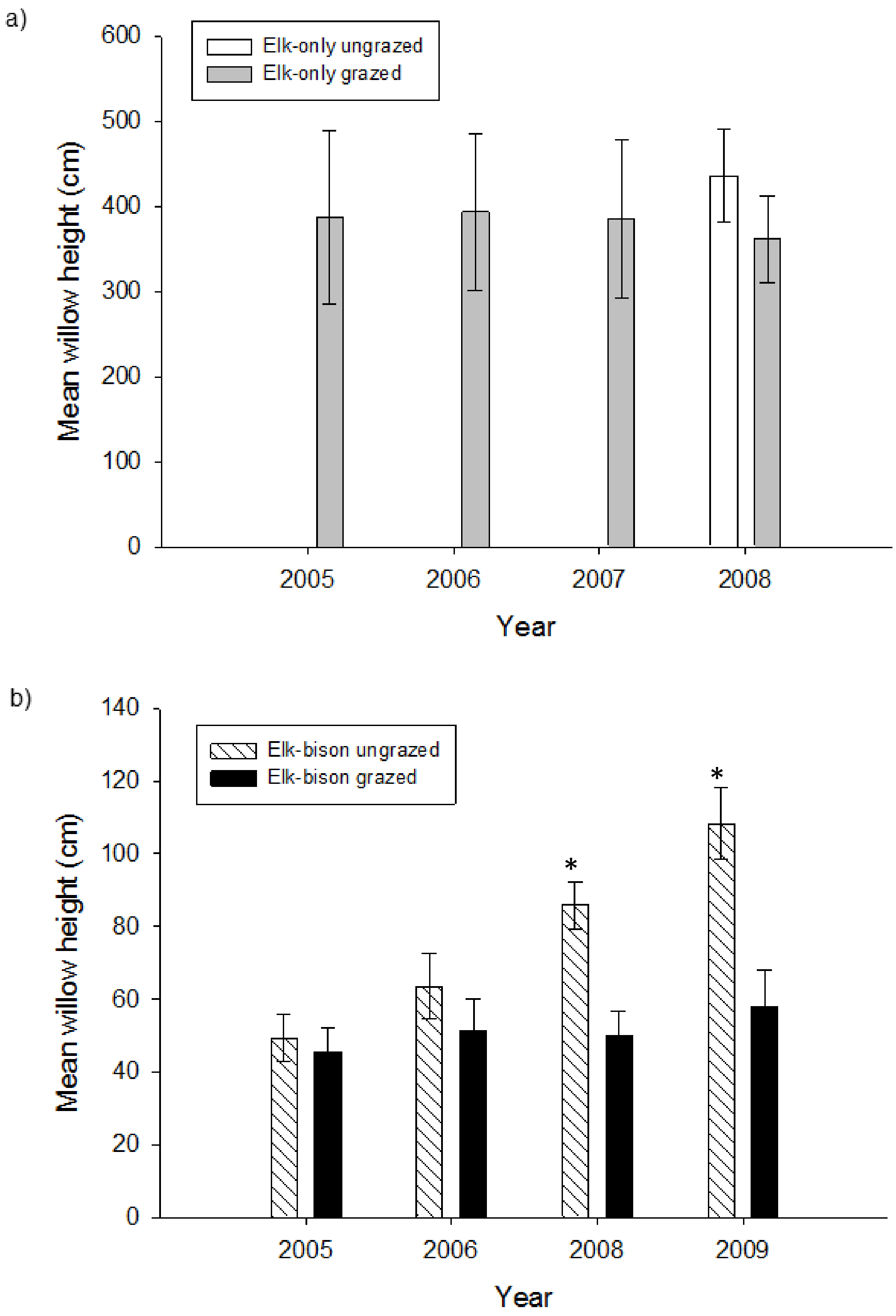


Figure 2.3. Willow heights in a) elk-only and b) elk-bison ungulate strata, and grazed and ungrazed treatments by year in the San Luis Valley ecosystem. *indicates P≤ 0.05.

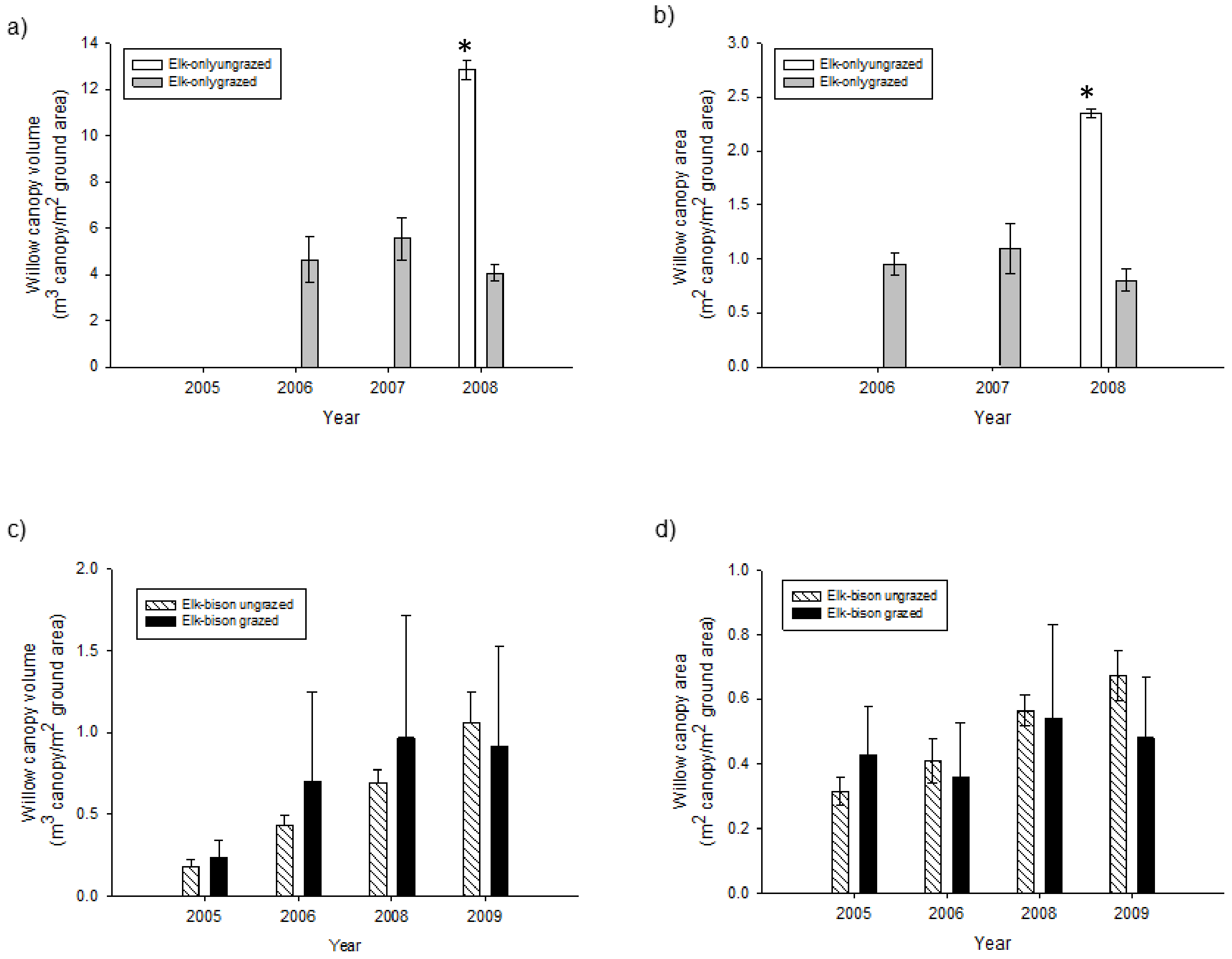


Figure 2.4. Willow canopy volume and area in different grazing treatments of elk-only (a,b) and elk-bison (c,d) willow communities in the San Luis Valley ecosystem, 2005-2009. *indicates $P < 0.05$ for grazing treatment.

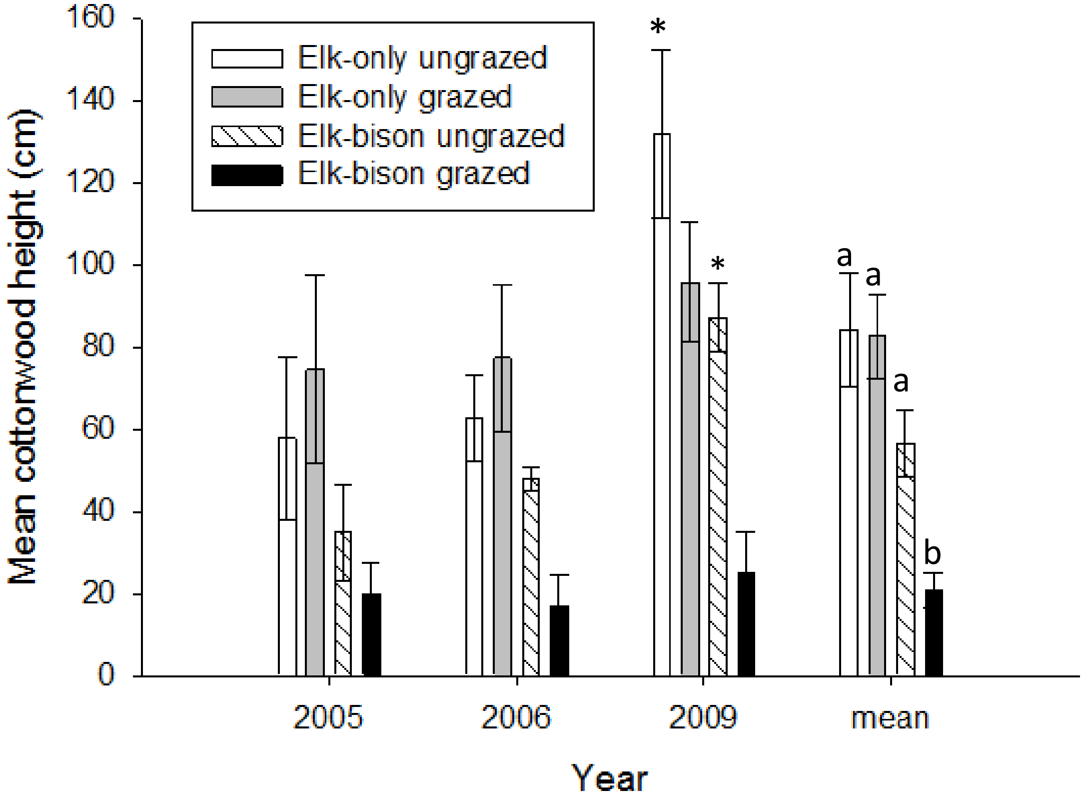


Figure 2.5. Cottonwood sapling heights by year within different ungulate strata and grazing treatment in the San Luis Valley ecosystem, 2005-2009. * indicates P < 0.05 for grazing treatment within each stratum, different letters indicate treatment*stratum differences.

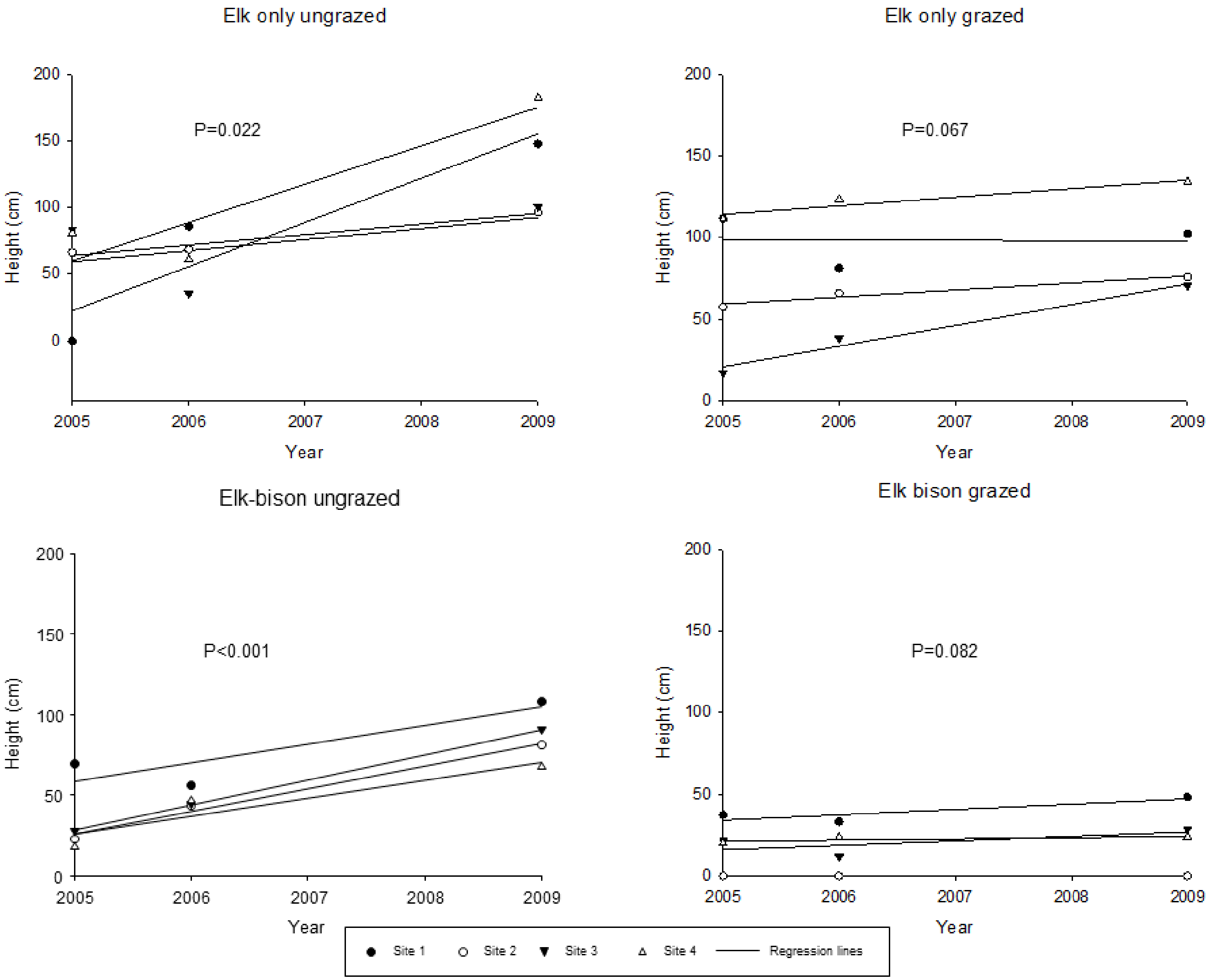


Figure 2.6. Trends in cottonwood sapling height from 2005-2009 within different ungulate strata and grazing treatment in the San Luis Valley ecosystem, Colorado.

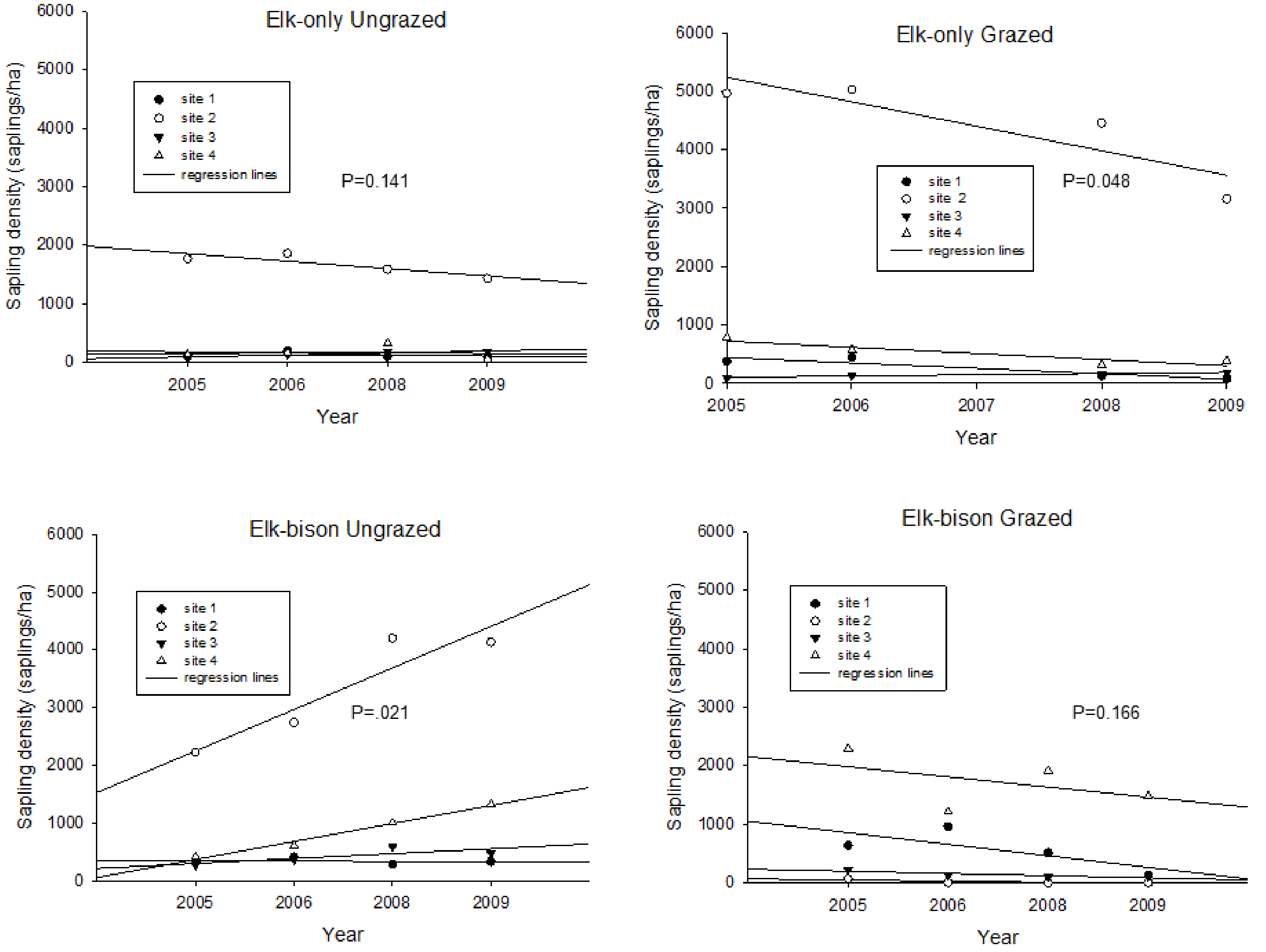
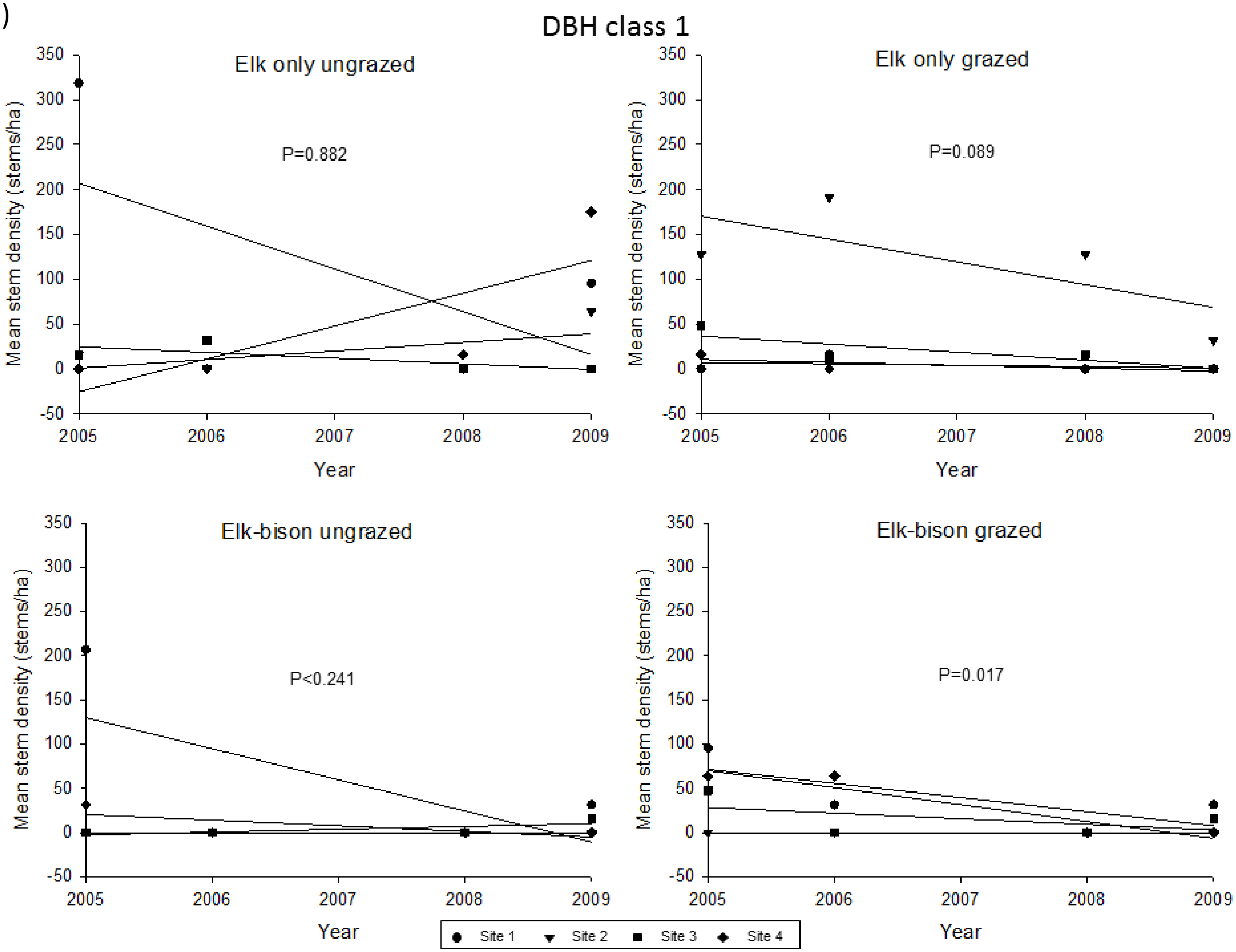


Figure 2.7. Trends in cottonwood sapling density from 2005 to 2009 within different ungulate strata and grazing treatment in the San Luis Valley ecosystem.

a)



DBH class 1

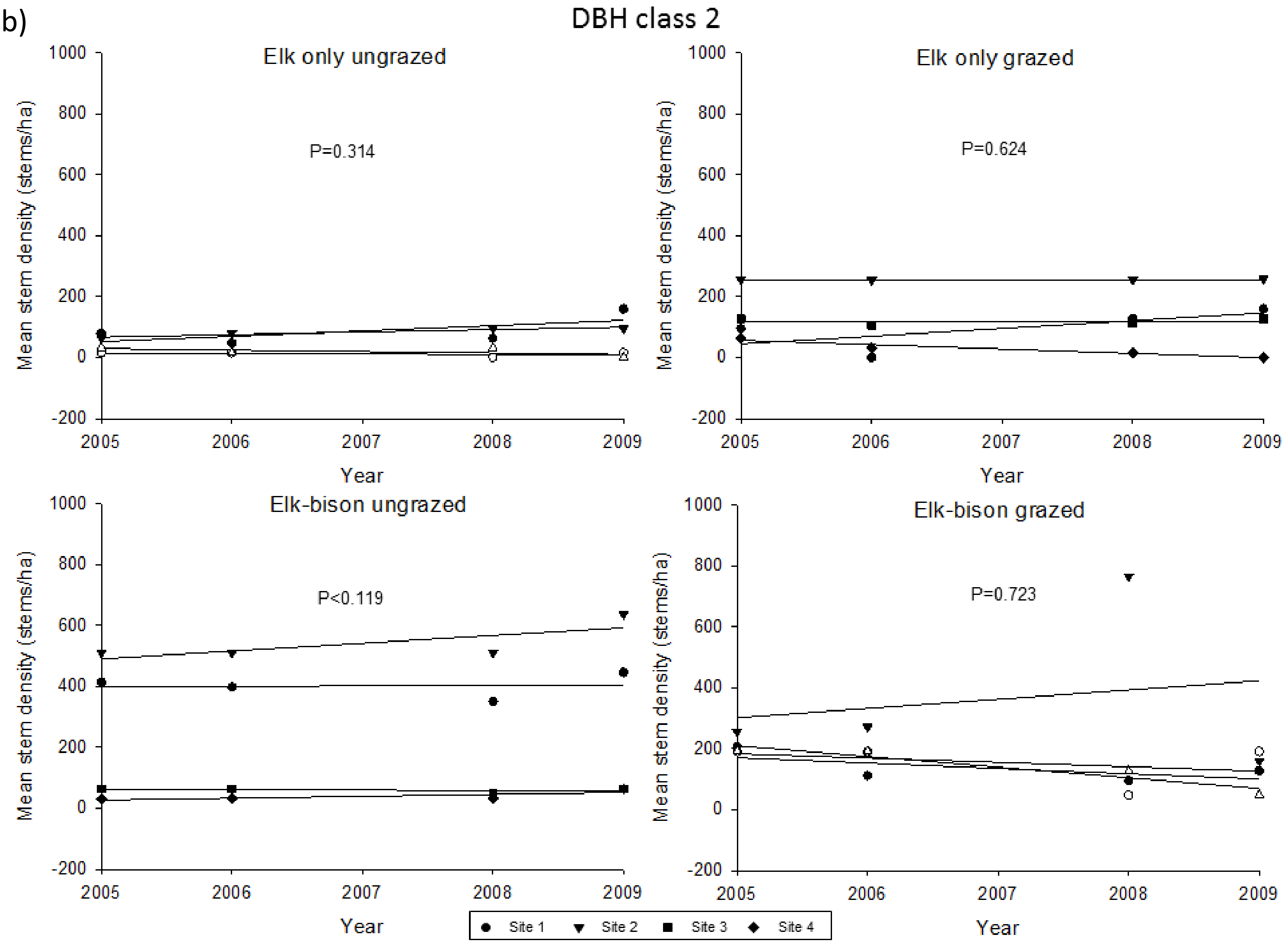
Elk only ungrazed

Elk only grazed

Elk-bison ungrazed

Elk-bison grazed

b)


DBH class 2
Elk only ungrazed
P=0.314
Elk only grazed
P=0.624
Elk-bison ungrazed
P<0.119
Elk-bison grazed
P=0.723
Mean stem density (stems/ha)
1000
800
600
400
200
0
-200
2005
2006
2007
2008
2009
Year
● Site 1
▼ Site 2
■ Site 3
◆ Site 4

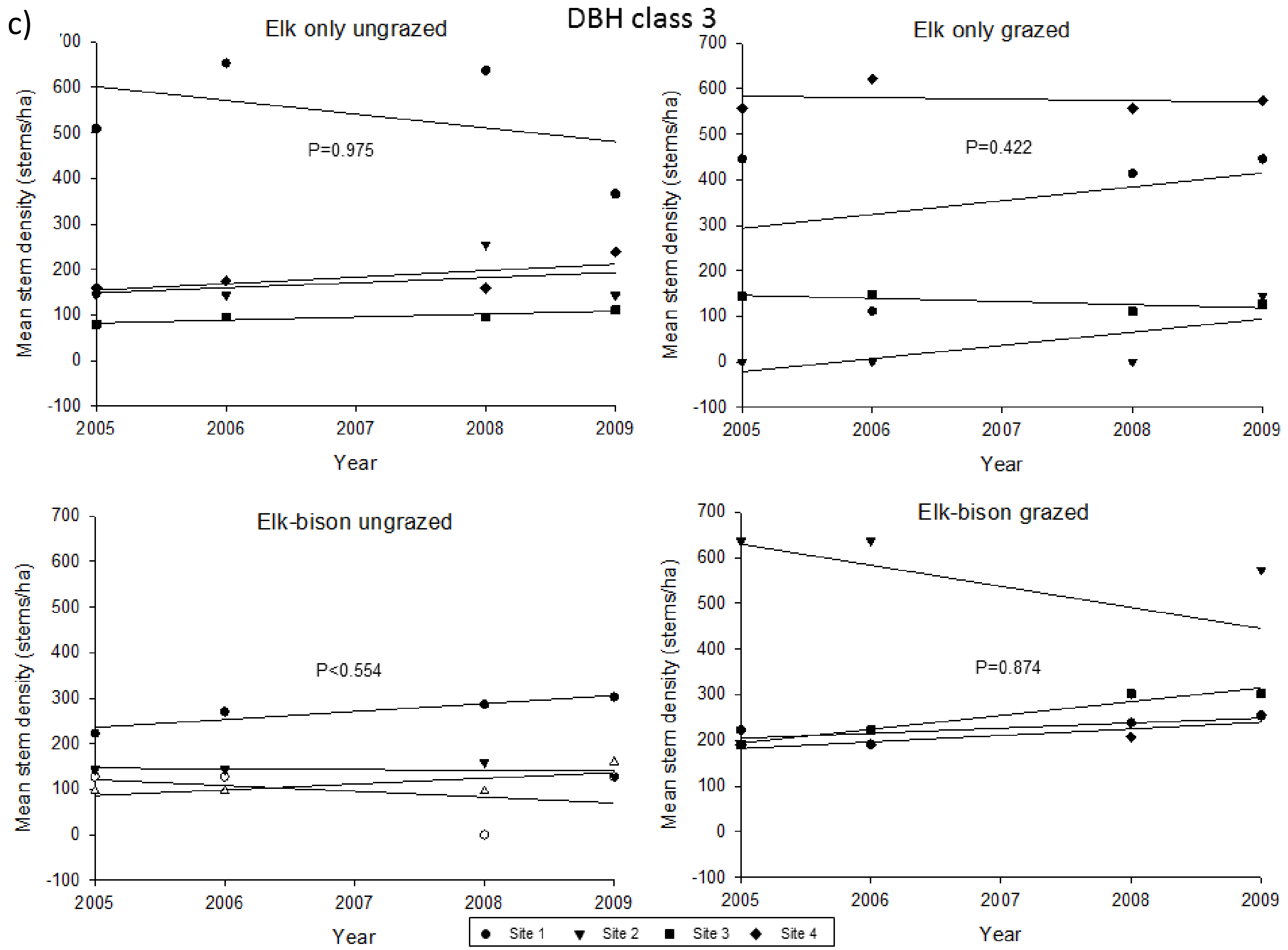


Figure 2.8. Trends in density of a) small (DBH class 1), b) medium (DBH class 2), and c) large (DBH class 3) diameter cottonwood trees from 2005 to 2009 within different ungulate stratum and grazing treatments in the San Luis Valley ecosystem.

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CHAPTER 3: A STOCHASTIC POPULATION DYNAMICS MODEL FOR PLAINS BISON (*BISON BISON*) IN AN ARID ECOSYSTEM, 1993-2011

Historically the highest densities of plains bison (*Bison bison*) occurred on the Great Plains, but their full range included intermountain areas of the western USA (Wilson and Ruff 1999). In Colorado, bison remains have been found throughout the mountains and inter-mountain shrub-steppe nearly statewide and at all elevations, with the exception of the Uncompahgre Plateau and the San Juan Mountains (Meany and Van Vuren 1994). Little is known about the ecology and habitat interactions of bison in areas outside the Great Plains, especially arid habitats. Desert ecosystems cover 20-30% of the terrestrial surface of the earth (Hadley and Szarek 1981) and another 25% is semi-desert (Pearson 1965). Understanding species-habitat interactions in arid ecosystems is relevant to >50% of the global terrestrial landscape, and important locally for land managers tasked with managing wildlife. In general, population dynamics of bison are poorly understood and quantitative data are scarce. I conducted a study to determine the population demographics of bison inhabiting one of their historic habitats, the cold desert.

Information from other bison populations indicates calving rates are correlated with precipitation (Williams 1977). Body weights of bison have been shown to vary based on timing of precipitation, where June precipitation resulted in higher body weights than July and August (Craine et al. 2011), and body weights of female ungulates are known to influence weight and survivorship of calves (Parker et al. 2009, Thorne et al. 1976). Maternal nutritional condition affects bison parturition date and synchrony of calving (Gogan et al. 2005) which has been shown to affect fecundity of female calves later in life. Fecundity is the number of calves born/female. Green and Rothstein (1993) reported increased fecundity in adult female bison that had early birth dates as calves compared to late born females, lasting up to 9 years of life. In the arid ecosystem that I studied, precipitation is typically a late summer “monsoon” occurring August-September. For these reasons, I hypothesized that fecundity would be lower than fecundity of bison inhabiting grassland landscapes. I hypothesized that calf survival rates will differ from published studies on bison inhabiting prairie habitats, but may resemble herds that contain at least some arid habitat types, such as the Henry Mountains in Utah. To test these hypotheses, I evaluated the interaction of climate variables and demographics of bison using state-space modeling.

The state-space modeling framework (Calder et al. 2003, Newman et al. 2006) provides a structure for including both observation error and process variance in time-series models. An important component of modeling is accounting for sources of stochasticity or uncertainty, which can operate independently to affect model predictions. Classical statistical models have difficulty incorporating multiple sources of uncertainty (Clark 2003b), and typically lump all sources into a single variance term (e.g., regression, ANOVA and GLM). Advances in optimization and computing such as Markov chain Monte Carlo (MCMC) have allowed the development of approaches that handle multiple uncertainties from differing sources.

Making robust statistical inferences requires correct handling of two types of stochasticity – variability and uncertainty (Clark 2003a). Variability is an inherent property of most natural systems; many ecological processes vary in space and time. Variability does not decrease with increasing sample size, it merely becomes better quantified -- estimates of the process become more precise (Biggs et al. 2009). Uncertainty relates to our ability to capture ‘truth’ with experimental techniques; most ecological experiments involve a degree of error when observations of a state or process are made. This occurs either because measurements are imprecise, or because a surrogate measure must be used. As sample size increases, uncertainty about parameter values tends to decline (Biggs et al. 2009). I define variability as ‘process variance’, and uncertainty as ‘observation error’. Process variance includes all of the influences on the true state of the population that are not included in the deterministic model.

State-space modeling is ideally suited for situations where there is uncertainty about the processes that affect population dynamics, and when observations of population size contain error. The use of a hierarchical model structure allows for the organization of individuals comprising the population in ways which permit inter-individual variation in vital rates, such as survival and recruitment. By explicitly incorporating variability associated with space, time and individual variation, we can make more realistic parameter estimates and future predictions for population trends (Clark 2003a). A failure to separate observation error from process variance can lead to erroneous conclusions, such as the detection of strongly density-dependent dynamics when in fact density dependence may be weak or even absent (Freckleton et al. 2006). Hierarchical Bayesian methods (e.g., state-space models) can provide direct links between deterministic population models (for instance describing age and sex classes, recruitment, survival and density-dependent effects) and the noisy and often limited data available for model parameterization and evaluation (Clark 2003b). They provide a coherent and consistent framework for breaking down complex problems into computable sub-models (Biggs et al. 2009).

State-space models have two main components; a process model and a data model. Observations of time-series data (e.g., census estimates of total population size) are assumed to arise from some ‘true’ unobserved state that represents the true dynamics of the population

(Calder et al. 2003). The data model describes this relationship between the observed data and this true state by incorporating observation error. The dynamics of the true state of the population through time are described by the process model, which explicitly incorporates process variance.

STUDY AREA

The San Luis Valley in south-central Colorado is a cold desert ecosystem receiving 28 cm of rainfall annually, mostly in the form of summer monsoonal rains in July-September. It is a high elevation valley bordered by the Sangre de Cristo Mountains to the east and the San Juan Mountains to the west. The bison range lies at the lowest point in the valley, 2255-2347 meters, adjacent to San Luis Lakes State Park. There are 3 major ecoregions, described by Omerik (1987). In the San Luis Shrublands and Hills, big sagebrush (*Artemesia tridentate*), rabbitbrush (*Chrysothamnus*/*Ericameria* spp.), and winterfat (*Krascheninnikovia lanata*) occur, as well as grasslands of slender wheatgrass (*Elymus trachycaulus*), green needlegrass *(Stipa viridula),* blue grama (*Bouteloua gracilis*), and needle-and-thread (*Hesperostipa comata*). The Salt Flats include an alkaline basin surrounding San Luis Lakes; vegetation is sparse, with greasewood (*Sarcobatus vermiculatus*) and shadscale (*Atriplex confertifolia*) dominating, with scattered areas of horsebrush (*Tetradymia spinosa*), spiny hopsage (*Grayia spinosa*), rabbitbrush, saltgrass (*Distichlis spicata*), alkali sacaton (*Sporobolus airoides*), and small areas of sagebrush. The Sand Sheet consists of longitudinal dunes stabilized by scrubby vegetation. Sand sheet plants include rabbitbrush, sand dropseed (*Sporobolus cryptandrus*), spiny hopsage, sand verbena (*Abronia* spp.), and prairie sunflower (*Helianthus petiolaris*; Omelik 1987). In the San Luis Valley desert and wetlands exist side by side. Bison primarily utilize a mix of mesic grassland habitat, and rush (*Juncus* spp.)/sedge (*Carex* spp.) meadows occurring along perennial creeks.

The history of bison in the San Luis Valley is somewhat cryptic. Spencer's (1975) history of the San Luis Valley references bison in the northern part of the valley, and Meaney and Van Vuren (1994) reported bison remains located in the same northern area. Over 500 bison were seen in the San Luis Valley by the Vargas expedition in 1694 (Espinosa 1939), but surprisingly there are only 2 localities on the valley bottom where bison remains have been documented (Meany and Van Vuren 1994). Zebulon Pike described bison to the east and north of the San Luis Valley, but this was according to memory; his original notes were confiscated by the Spaniards and may have held further mention of bison in the area. Access points for bison moving into the San Luis Valley would have been Poncha Pass and LeVeta Pass in the north and east, respectively. Hunting by Native Americans may have restricted bison distribution in the southern part of the state. Humans directly impacted the movement of bison, as evidenced by bison seeking refuge west of the Front Range in later years when the slaughter on the plains was greatest (Fryxell 1926, Figgins 1933). The Ute Indians are known to have hunted bison in the Rocky Mountains (Hughes 1977), and bison remains have been found as high as 424 meters (Fryxell 1928) illustrating their ability to disperse with little geographic limit. The presence of bison in Colorado ended in 1897 when the remaining 4 extant individuals were poached in South Park (Meany and Van Vuren 1994). Bison were returned to the state in modern times via ranching. The bison population I studied was established in 1986 for production. In 1999 The Nature Conservancy (TNC) purchased the ranch and established it as a conservation herd, and eventually subcontracted management to a private rancher in 2005. The bison are free-roaming within the ~20,000 ha, fenced Medano Ranch and are managed with annual gathers and removals. There are no predators that can significantly impact adult bison but calves are somewhat vulnerable to coyotes (*Canis latrans*).

METHODS

Data

I observed age, sex, and number of bison during annual gathers from 2004 through 2011. Age was determined by tooth eruption (Fuller 1959). Prior to 2004 I used inventory records from TNC (1999-2003) which provided reliable data on number of adults, yearlings, and calves on the ranch, as well as number removed. Data from 1993-1998 came from production and inventory records of Rocky Mountain Bison, which were solely from adult females and removal data were scant. I obtained average spring/summer precipitation data from the National Oceanic and Atmospheric Administration (NOAA; Station GHCND: USC00053541, GREAT SAND DUNES NAT).

The Model

I developed a state-space model for the bison population to estimate posterior distributions of past states including age structure, sex ratios, and population size before TNC ownership, and population parameters such as survivorship and recruitment. I used a discrete time, stage-structured model to describe the dynamics of 4 age and sex classes of bison: calves (class 1), female yearlings (class 2), adult females (class 3), and males ≥ 1.5 years old (class 4; Figure 3.1). Age and sex classes were determined by pooling groups with similar vital rates, or grouping where needed due to data gaps.

The process model

The process model describes the evolution of counts $N_{i,j}$ over time as a function of recruitment and survival rates. Model equations were developed to account for the birth pulse occurring in April to early May and census occurring in November. Recruitment is defined as the number of calves produced per adult cow (age > 2.5 years) that survived to their first census at approximately 6 months of age. Survival is defined as the proportion of each age and sex class that survives to the next census. I had no data on survivorship from age 0 to 6 months (N_0 to N_1) because census occurs 6 months after the birth pulse (Noon and Sauer 1992). My model assumes that the majority of mortality occurs after census and before the next birth pulse.

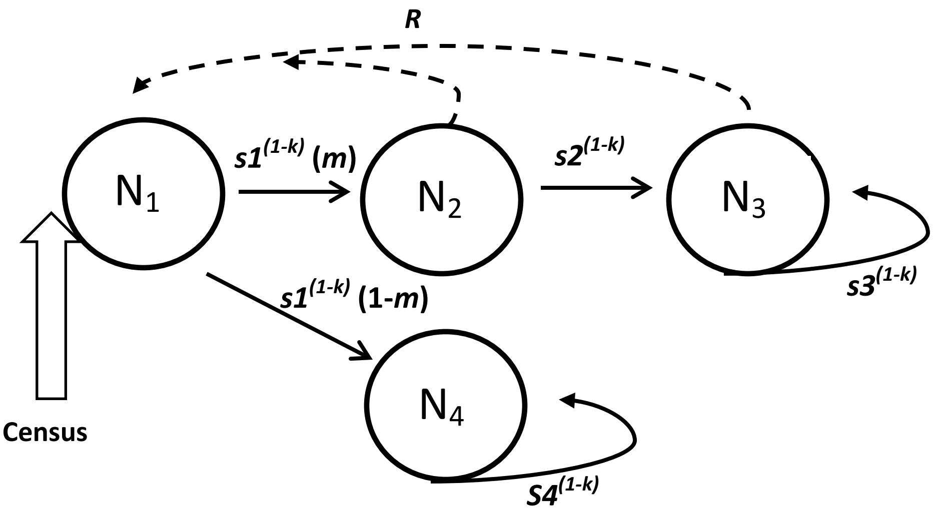

Figure 3.1. Diagram of state-space population model for the San Luis Valley bison population from 1993-2011 depicting 4 age and sex classes, where N_1 is the population size of 6 month old calves, N_2 is 1.5 year old females, N_3 is adult females age > 2.5 years, and N_4 is age > 1.5 year males; *s* is the survival rate from one age class to the next; *k* is the proportion of time between the birth pulse and the next census in each time interval (Noon and Sauer 2001); *m* is the proportion of offspring that are female; and R is the recruitment to age ~6 months.

I defined a four element column vector $\mathbf{N_{i,\,t}} = [(N_{1,t}, N_{2,t}, N_{3,t}, N_{4,t})]^T$ that includes the number of animals in each age class at time *t*, indexed by *i* = 1: calves, *i* = 2: female yearlings, *i* = 3: adult females, and *i* = 4: males 1.5 year and older. Thus, $N_{1,t}$ would be the number of calves at time *t*. The estimate of total population size at time *t* is given by $N_{total,t} = \sum_{i=1}^{4} N_{i,t}$

I defined four time-invariant survival rates:

s1: the probability of survival of calves from their first census at approximately 6 months to their second census at 1.5 years,

s2: the probability of survival of female yearlings from age 1.5 years to age 2.5 years,

s3: the probability of survival of adult females from a minimum age of 2.5 years onwards,

s4: the probability of survival of males from a minimum age of 1.5 years onwards.

I included a density-dependent effect of total population size on recruitment that assumed recruitment was an inverse logit function of the total population size, i.e., $R_t = \frac{e^{b0+b1\cdot N_t}}{1+e^{b0+b1\cdot N_t}}$. I assumed that the true population size for the *i*th age/sex class at time *t* can be represented as a lognormal distribution with median $\mu_{i,t}$ and standard deviation σ_i , where σ_i represents the process standard deviation on the log scale for age/sex class *i* (i.e., the process variance). I defined *m* as the proportion of offspring that are female surviving to the yearling age class. I included the raw count of bison removed during years data were available, from 2001-2011, but prior to 2001 data were sparse and unreliable. Hence removals were incorporated into estimated stochastic 'survival' parameters in years 1993 to 2001 (one for each age/sex class: *sr1* to *sr4*). The model essentially involves two separate set of 'survival' parameters: from 2002 to 2011 they are true survival probabilities for each age/sex class (*s1*, *s2*, *s3*, *s4*). However, from 1993 to 2001 these 'survivals' are in fact the probability of surviving and not being removed from the population at census time (*sr1*, *sr2*, *sr3*, *sr4*).

The resulting process model is given by:

$$N_{i,t+1} \sim \text{lognormal}(\log(\mu_{i,t+1}), \sigma_i)$$

for i =1...4, where for years 1993-2001:

$\mu_{1,t+1} = \mathrm{s3} \cdot \mathrm{N}_{3,t} \cdot \mathrm{R}$

$$\mu_{2,t+1} = \text{s1} \cdot \text{m} \cdot \text{N}_{1,t}$$

$$\mu_{3,t+1} = (\text{s2} \cdot \text{N}_{2,t}) + (\text{s3} \cdot \text{N}_{3,t})$$

$$\mu_{4,t+1} = (\text{s1} \cdot \text{(1-m)} \cdot \text{N}_{1,t}) + (\text{s4} \cdot \text{N}_{4,t}),$$

and for years 2002-2011:

$$\mu_{1,t+1} = \text{s3} \cdot (\text{N}_{3,t}\text{-rem}_{3,t}) \cdot \text{R}$$

$$\mu_{2,t+1} = \text{s1} \cdot \text{m} \cdot (\text{N}_{1,t}\text{-rem}_{1,t})$$

$$\mu_{3,t+1} = (\text{s2} \cdot (\text{N}_{2,t}\text{-rem}_{2,t})) + (\text{s3} \cdot (\text{N}_{3,t}\text{-rem}_{3,t}))$$

$$\mu_{4,t+1} = (\text{s1} \cdot \text{(1-m)} \cdot (\text{N}_{1,t}\text{-rem}_{1,t})) + (\text{s4} \cdot (\text{N}_{4,t}\text{-rem}_{4,t}))$$

I selected a lognormal distribution because it is appropriate for data that are continuously distributed with positive values only, where the logs are normally distributed.

I calculated average spring/summer precipitation over March to August and included this as an effect on recruitment. For each year, the departure from the long-term average precipitation (1950 to 2008) was calculated as the observation of precipitation for a given year minus the long-term mean precipitation across all years, divided by the long-term mean. I denoted this quantity Pt_t, where:

$$R_t = \frac{e^{b0+b1\cdot N_t+b3\cdot Pt_t}}{1+e^{b0+b1\cdot N_t+b3\cdot Pt_t}}.$$

I included an effect of precipitation on recruitment because the San Luis Valley is an arid ecosystem, and habitat conditions (hence female body condition) are largely determined by annual precipitation. Winter temperatures are not severe or enduring; mean winter temperature during the study period was -3.9ºC (25ºF), mean max temperature was 2.6ºC (37ºF), and mean minimum temperature was -10ºC (14ºF; SNOTEL site 914, Medano Pass). The inferences I make are based on the model described above.

The Data Model

The data model describes the relationship between the observed data (the number of animals counted during the gather in each age class, y_i) and the underlying 'true' state of the population (the total number of animals in the population including those animals that were not gathered, N_t) by explicitly incorporating observation error. I had two categories of count data for bison in SLV: adult females only from 1993 to 2000 (y_3 only), and all 4 age/sex classes from 2001 to 2011. I represented y_3 with a data model that assumes a Poisson distribution. However, because the mean and variance of the counts for adult females during the period 1993 to 2000 were not equal, I used a Poisson-gamma mixture to represent the data:

$$y_{3,t} \sim \text{ Poisson}(\lambda_t)$$

and

$$\lambda_t \sim \text{ gamma}\left(\frac{N_{3,t}^2}{\sigma_{o.2}^2}, \frac{N_{3,t}}{\sigma_{o.2}^2}\right),$$

where $N_{3,t}$ is the model's estimate of the posterior distribution of the true number of adult females, and $\sigma_{o.2}$ is the estimate of the observation error on the counts of the number of adult females. The Poisson distribution represents count data of things that occur randomly over time and space, and the gamma distribution is appropriate for continuous data that are strictly positive.

From 2001 to 2011 I had data on raw counts of total population size, and used a Poisson-gamma mixture to represent the total population size:

$$y_{total,t} \sim \text{ Poisson}(\lambda_t)$$

and

$$\lambda_t \sim \text{ gamma}\left(\frac{N_{total,t}^2}{\sigma_o^2}, \frac{N_{total,t}}{\sigma_o^2} \right),$$

where $N_{total,t}$ is the model’s estimate of the posterior distribution of the true total population size at time t $\left(N_{total,t} = \sum_{i=1}^{4} N_{i,t} \right)$, and σ_o is the estimate of the observation error on the total number of animals in the population. In the years I had complete age/sex data (2001 to 2011) I used a multinomial distribution to form the model’s estimate of the posterior distribution of the number of animals in each age/sex class at time t:

$$y_{.n_t} \sim \text{ multinomial}(p_t, \sum_{i=1}^{4} y_{.n_{i,t}}),$$

where $p_{i,t}$ is the model’s estimate of the proportion of sex/age class i at time t. The multinomial distribution is appropriate for count data that fall into >2 categories, such as the number of individuals in age classes.

The Hierarchical State-Space Model

Let $\boldsymbol{\theta}$ be a vector of the parameters in the process model, excluding process variance. Let σ be the vector of process standard deviations for process variance, such that $\sigma = (\sigma_1, \sigma_2, \sigma_3, \sigma_4)$. Let η be a vector containing the estimates of the initial conditions for each age/sex class. Given the assumptions on the distributions above, the fully stochastic, Bayesian model is specified by:

$$
\begin{aligned}
p(\theta,\sigma,\sigma_o,\sigma_{o.2},\mathrm{N} \mid y_3, y_{total}) \;\propto\; & \prod_{t=2}^{n}\prod_{i=1}^{4} \text{lognormal}(\log(N_{i,t} \mid \mu_{i,t}),\sigma i) \;\times \\
& \prod_{t=1}^{8} \text{Poisson}(y_{3,t} \mid \lambda_t) \text{ gamma}\left(\lambda_t \mid \frac{N_{3,t}^2}{\sigma_{o.2}^2}, \frac{N_{3,t}}{\sigma_{o.2}^2}\right) \;\times \\
& \prod_{t=9}^{16} \text{Poisson}(y_{total,t} \mid \lambda_t) \text{ gamma}\left(\lambda_t \mid \frac{\left(\sum_{i=1}^{4} N_{i,\,t}\right)^2}{\sigma_o^2}, \frac{\left(\sum_{i=1}^{4} N_{i,\,t}\right)}{\sigma_o^2}\right) \;\times \\
& \prod_{t=9}^{16} \text{multinomial}(y_{.n_t} \mid p_t, \sum_{i-1}^{4} y_{.n_{i,t}}) \;\times \\
& p(\theta)\,p(\sigma)
\end{aligned}
$$

The prior distributions $p(\theta)\,p(\sigma)$ were chosen as conjugates whenever possible and made appropriately informative where data existed. Prior distributions and their parameters are presented in Table 3.1.

Model implementation

I simulated a dataset using known distributions, processes, and parameter values and used this dataset to assure estimation procedures were accurate. The model above was able to recover estimates of parameters generating the simulated data. I then used the population data to estimate the posterior distribution for each parameter using MCMC methods implemented in OpenBUGS (Lunn et al. 2000) and R (R-Development_Core_Team 2009). MCMC chains were initialized with 3 different sets of starting parameter values. After discarding the first 200,000 iterations, 30,000 samples were accumulated from each chain. Convergence was assured by visual inspection of trace plots and Raftery diagnostics (Raftery and Lewis 1992, 1995) to assure stationarity and that plots were non-directional. Average autocorrelation for model variables was 14.5 across the 3 chains. The minimum chain length recommended by Raftery diagnostics was 3746; I used a chain length of 300,000 with burn-in of 200,000. I used diagnostics of Gelman

Table 3.1. Prior distributions for model parameters for a bison population model in the San Luis Valley, Colorado, 1993-2011.

Parameter	Prior distribution and parameters	Notes
s1, calf survival	uniform(0.8,0.98)	Informative[1]
s2, female yearling survival	uniform (0.6,0.98)	Informative[1]
s3, female adult survival	uniform (0.8,0.98)	Informative[1]
s4, male 1 yr+ survival	uniform (0.7,0.98)	Informative[1]
sr1, calf survival and not removed	uniform(0,1)	Uninformative
sr2, female yearling survival and not removed	uniform(0,1)	Uninformative
sr3, female adult survival and not removed	uniform(0,1)	Uninformative
sr4, male 1 yr+ survival and not removed	uniform(0,1)	Uninformative
b0, intercept of logit relationship for density dependent effect on recruitment	uniform (0,1)	Uninformative
b1, slope of logit relationship for density dependent effect on recruitment	uniform (0,1)	Uninformative
b3, slope of the relationship for precipitation effects on recruitment	norm (0,0.0001)	Uninformative
m, proportion of offspring that are female	beta(77.82,78.95)	Informative[2]
σ_o, the standard deviation for observation error on total population counts	uniform (0,500)	Uninformative
$\sigma_{o.2}$, the standard deviation for observation error on counts of adult females	uniform (0,500)	Uninformative
$\sigma_{p.1}$, the standard deviation for process variance of age/sex class N_1 on the log scale	uniform (0,2)	Uninformative
$\sigma_{p.2}$, the standard deviation for process variance of age/sex class N_2 on the log scale	uniform (0,2)	Uninformative
$\sigma_{p.3}$, the standard deviation for process variance of age/sex class N_3 on the log scale	uniform (0,2)	Uninformative
$\sigma_{p.4}$, the standard deviation for process variance of age/sex class N_4 on the log scale	uniform (0,2)	Uninformative

[1] Based on data from Fuller et al. (2007b), Gaillard et al. (2000), Udevitz and Gogan (2012), and van Vuren and Bray (1986)

[2] Based on data from San Luis Valley bison herd (1997 to 2008) for counts of female and male calves during gathers.

(Brooks and Gelman 1988, 1997) and Heidelberger (Heidelberger and Welch 1981, 1983; Schruben 1982) implemented in the coda package (Plummer et al. 2010) in R. I obtained several derived quantities: model predictions for total population size and removals per age/sex class.

RESULTS

Survival rates of all age/sex classes during study years exceeded 70% (Table 3.2). The highest survival occurred in adult females and the lowest in yearling females. Calf and adult female survival probabilities were both greater than 89%, and yearling plus adult male survival was 0.87 (0.72 - 0.98; Table 3.2). Female yearling survival was the most variable (credible intervals 0.61 - 0.96) of the 4 age/sex classes modeled. Sex ratio at birth slightly favored females (m = 0.52), and recruitment averaged 0.63± 0.05 (credible interval 0.52-0.69).

The model estimates for population size are shown in Figure 3.2, depicting the growth and decline of the herd over time. Note that credible intervals are wider during years when data on total population size were not available, accurately representing the uncertainty. During the period from 1993-1999 the herd was managed for production, and total population size was maintained at ~2,000 bison. After TNC obtained the ranch, conservation and restoring a natural age-structure was the primary objective for the herd, so overall numbers were reduced to provide a greater buffer for drought, and to promote other uses on the landscape. In 2005, production became the primary use again and the herd size was increased again to support economic goals (Figure 3.2).

Number of bison per age/sex class also varied over the study period, reflecting differences in the number and age/sex classes selected for removal and differences in management goals described above (Figure 3.3). In particular, number of adult and yearling

Table 3.2. Parameter estimates for the model predicting population size of the San Luis Valley bison herd from 1993-2011. Model includes removals and a spring/summer precipitation effect on recruitment.

Parameter	Mean	Stdev	95% credible interval
s1, calf survival (2002–2011)	0.89	0.04	0.81 - 0.97
s2, female yearling survival (2002–2011)	0.75	0.10	0.61 - 0.96
s3, female adult survival (2002–2011)	0.94	0.03	0.85 - 0.98
s4, male 1 yr+ survival (2002–2011)	0.87	0.07	0.72 - 0.98
sr1, calf survival/non-removal (1993–2001)	0.59	0.19	0.24 – 0.96
sr2, female yearling survival/non-removal (1993–2001)	0.54	0.27	0.04 – 0.98
sr3, female adult survival/non-removal (1993–2001)	0.90	0.06	0.74 – 0.99
sr4, male 1 yr+ survival/non-removal (1993–2001)	0.15	0.12	0.004 – 0.46
b0, regression constant for logit relationship of density dependent and precipitation effects on recruitment	0.87	0.12	0.55 - 0.99
b1, partial correlation coefficient of logit relationship for density dependent effect on recruitment	0.0002	0.00007	0.0001 – 0.0004
b3, partial correlation coefficient of logit relationship for precipitation effect on recruitment	0.45	0.27	0.02 - 0.96
m, proportion of offspring that are female	0.52	0.03	0.46-0.57
σ_o, the standard deviation for observation error on total population counts (2001–2011)	70	65.71	2 - 248
$\sigma_{o.2}$, the standard deviation for observation error on counts of adult females (1993–2000)	97	72.41	4 - 275
$\sigma_{p.1}$, the process standard deviation of N_1 on the log scale	0.36	0.11	0.21-0.63
$\sigma_{p.2}$, the process standard deviation of N_2 on the log scale	0.32	0.11	0.16-0.59
$\sigma_{p.3}$, the process standard deviation of N_3 on the log scale	0.19	0.04	0.12-0.29
$\sigma_{p.4}$, the process standard deviation of N_4 on the log scale	0.19	0.07	0.09-0.38
Recruitment (mean *R* from 1994–2011)	0.63	0.05	0.52-0.69

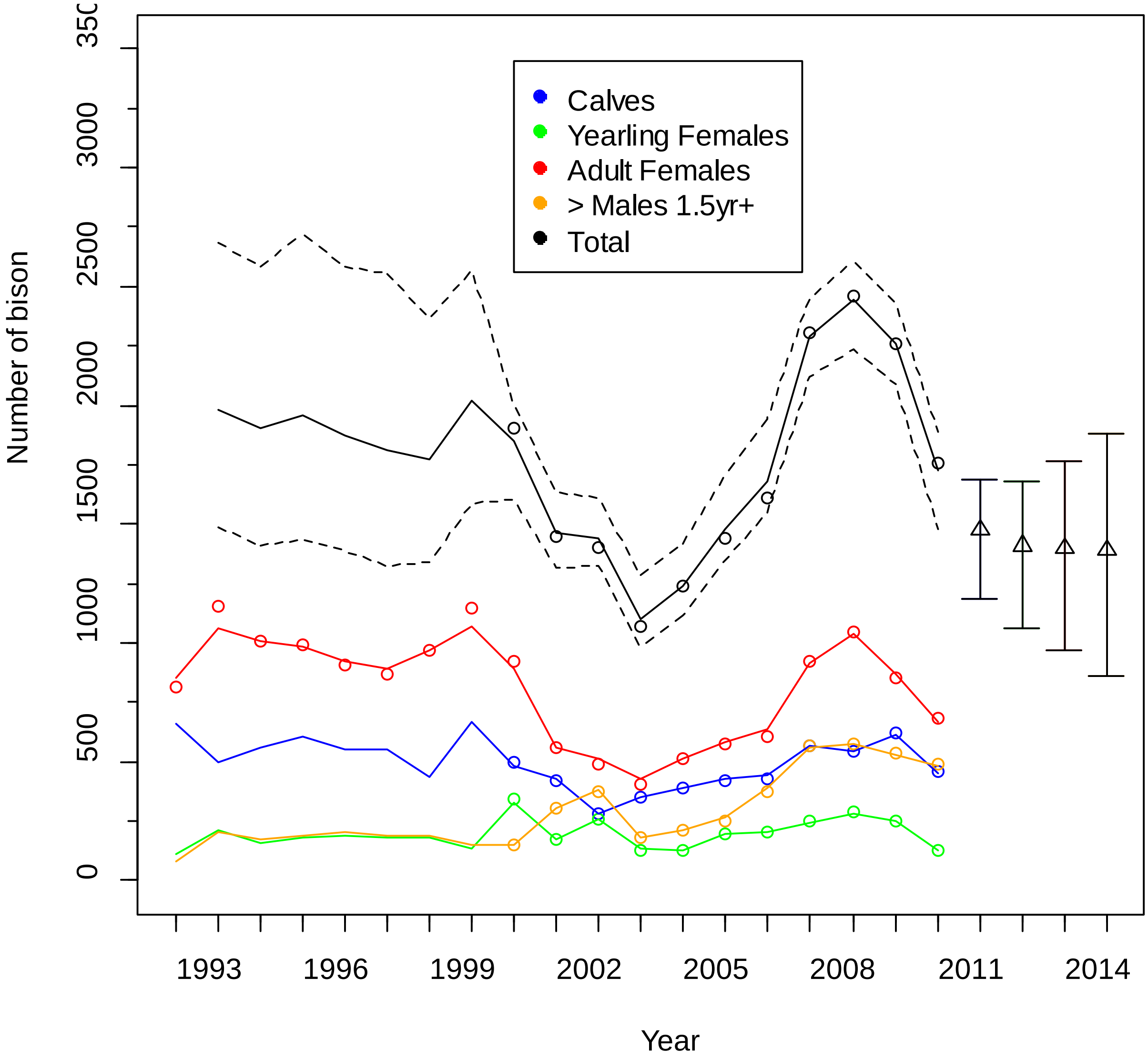

Figure 3.2**.** Model estimates for population size of the San Luis Valley bison population from 1993 to 2011. Open circles are census data, solid lines are the mean of the posterior distributions for each age/sex class and total population size, and dotted lines are the 95% credible interval around the posterior mean for total population size. Triangles are predictions to 2015 with annual credible interval bars. Predictions were based on a management scenario using the same culling regime in 2012 that was used in 2011, and henceforth removing 75 adult females plus 150 males annually to maintain the population at ~1400 bison.

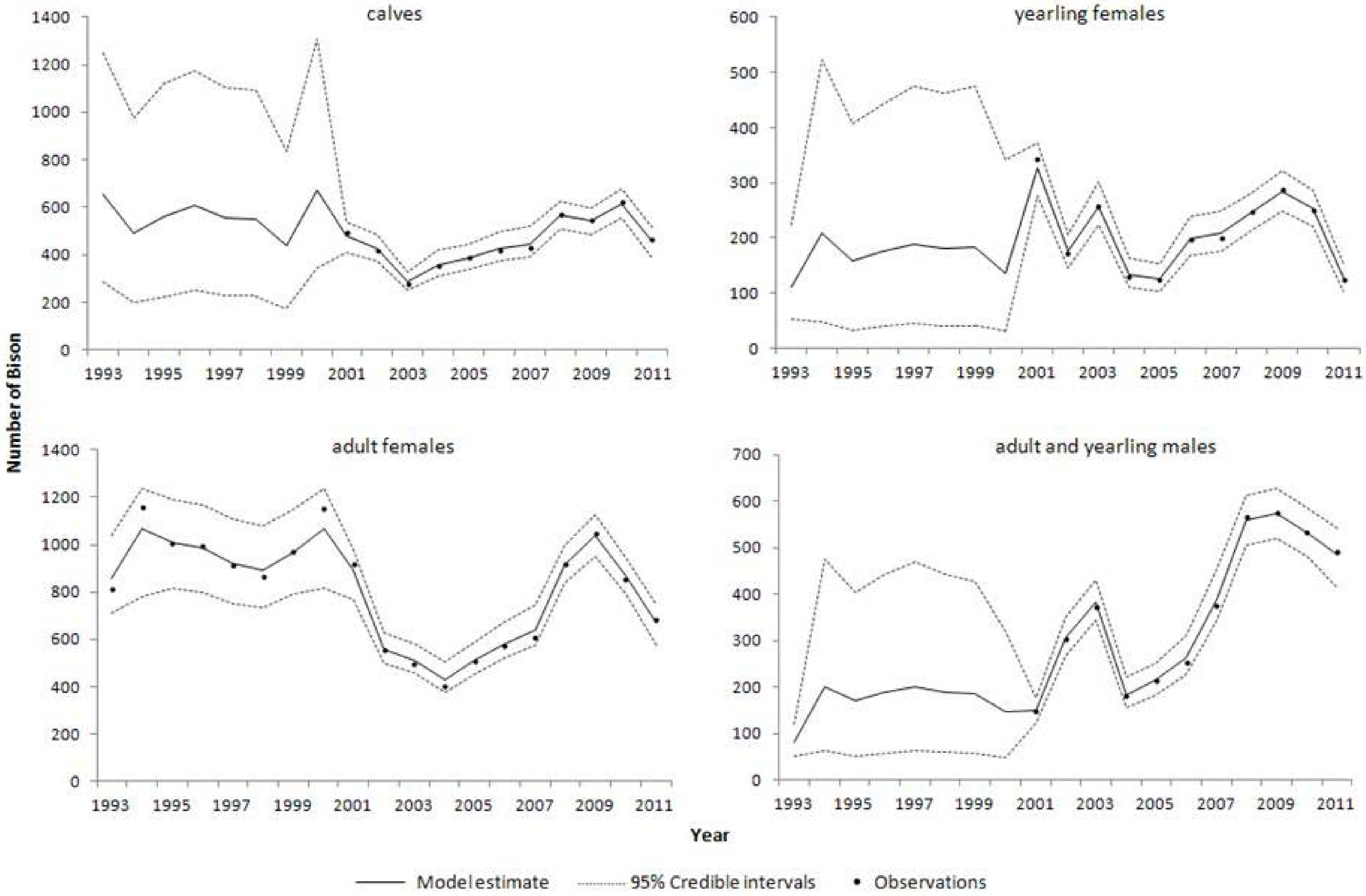

Figure 3.3. Model estimates for each age/sex class from 1993 to 2011. Symbols are census data, solid lines are the mean of the posterior distributions for each age/sex class, and dotted lines are 95% credible intervals.

males increased after 2005, supporting TNC's goals to establish a natural age-structure in the population. Number of males also increased as the overall herd size increased from 2005 onward.

Current management goals for the population are to reduce it to 1400–1500 bison and maintain population size at that level (P. Robertson, TNC, pers. commun. 2012). One example of a culling scenario to achieve this management goal is shown in Figure 3.2. By using the same culling regime for 2012 as was used in 2011, and henceforeth culling 75 adult females plus 150 males annually, a herd size of ~1400 bison can be maintained to 2015. By 2015, credible intervals are too wide to be predictive, and modeling should be conducted to calibrate population growth with an updated culling program.

DISCUSSION

I provide the first estimates of vital rates for bison inhabiting an arid ecosystem. Estimates were consistent with current knowledge of bison life history, and did differ somewhat but not greatly from bison populations inhabiting different habitat types, supporting Fuller (1961) who compared 4 bison populations with broadly varying climate and vegetation, and found few differences in the ecology of bison. The survival of all age/sex classes of bison in the San Luis Valley was high and probably facilitated by the near absence of predators, except coyotes, and the maintenance of the population below ecological carrying capacity.

Survival rates of bison have been reported for other herds. Wood bison in northern Canada had average calf survival rates of 0.57 over a 14-year period (Larter et al. 2000), compared to 0.89 in San Luis Valley bison. Calf survival was 0.94 in the Henry Mountains of Utah, and in a review of *Bovidae* species that included buffalo (*Syncerus caffer*), bison (*Bison bison*), Chillingham cattle (*Bos primigenius*), musk ox (*Ovibos moschatus*), Greater kudu

(*Tragelaphus strepsiceros*), Nyala (*Tragelaphus angasii)*, and waterbuck (*Kobus ellipsiprymnus*), mean calf survival was 0.55 (Gaillard et al. 2000).

My modeled estimate for San Luis Valley female yearling survival was lower than *Bovidae* spp. in general (0.83 in Gaillard et al. 2000, compared to 0.75 in my study), and lower than Badlands National Park, where modeled juvenile survival ranged from 0.93−0.96 (Pyne et al. 2010).

Estimated adult female bison survival in the San Luis Valley was 0.94, very similar to bison from Yellowstone National Park, Wood Buffalo National Park, and the Henry Mountains which all ranged from 0.92–0.96 (Fuller et al. 2006, Larter et al. 2000, Van Vuren and Bray 1986). Gaillard et al. (2000) reported average adult female survival for *Bovidae* spp. of 0.89. Udevitz and Gogan (2012) reported all female survival (calf+yearling+adult) in Yellowstone from 2002–2003 of 0.85. This is almost identical to my finding of 0.86 for the same cohort in the San Luis Valley population. Adult plus yearling male survival in the Henry Mountains was 0.95 (Van Vuren and Bray 1986), contrasted with 0.87 in the San Luis Valley bison herd.

Female juvenile survival was most variable (0.61–0.96) of all 4 age/sex classifications I estimated, consistent with Fuller et al. (2007b) and Larter et al. (2000), and process variance was greatest for calves and yearling females, and lowest for adult males and females in my study. For juveniles, this is expected because typically, juvenile ungulates are strongly affected by multiple environmental and biotic processes including predation, weather, maternal state and qualities, timing of parturition, and habitat resources (Gaillard et al. 1998). Survival of adult females in ungulate populations is generally buffered against temporal variation, regardless of the causes of mortality (Gaillard et al. 1998, 2000). Changes in the number of adult females from year to year was influenced by survival and recruitment of yearling females to the next age class, as well as removals of yearling and adult females, which sometimes varied widely. Growth rate of Yellowstone bison was also shown to be highly elastic to adult survival (Fuller et al. 2007a).

Sex ratio of calves slightly favored females (*m*= 0.52) in my model, but credible intervals were within the range of studies in other habitat types that have indicated equal sex ratios at birth in bison (Fuller 1960, Green and Rothstein 1991, Shaw and Carter 1989). The juvenile sex ratio of bison in the Henry Mountains slightly favored females as well (0.53; Van Vuren and Bray 1986), and also at the Konza Prairie Research National Area, Kansas (0.53; Towne 1999). The Trivers-Willard hypothesis predicts females in good body condition will produce more male than female offspring, and females in lower body condition are biased toward female offspring (Trivers and Willard, 1973). In one test of the hypothesis, non-lactating bison cows at the National Bison Range, Montana, carried more male fetuses than lactating bison cows (Rutberg 1986). Fetal sex ratios in bison are consistently male-biased (Fuller 1961, Meagher 1973, Palmer 1916), so the female bias in San Luis Valley calves was either the result of lower survival of male calves from age 0 to 6 months before the first census, or greater loss of male calves in utero, or lower body condition of female bison consistent with the Trivers-Willard hypothesis.

Recruitment in the San Luis Valley bison herd was 0.63 (0.52–0.69) calves per adult female during my study period, similar to that reported for Yellowstone bison (Fuller et al. 2007b). Recruitment averaged 0.67 in the Wichita Mountains bison population in southwestern Oklahoma (Halloran 1968), 0.88 in the National Bison Range, Montana herd (Rutberg 1986), 0.74 at the Konza Prairie (Towne 1999), and 0.78 for bison at Fort Niobrara National Wildlife Refuge, Nebraska, and Wind Cave National Park (Haugen 1974). Recruitment in the Henry Mountains bison herd varied widely by year, but averaged 0.52 in adult females (but 0.62 for females ≥3 years of age; Van Vuren and Bray 1986). In the San Luis Valley, precipitation is typically monsoonal, occurring in August−September annually. Late season precipitation has been shown to reduce body weights of bison compared to weights of bison in areas with early season precipitation (Craine et al. 2009). Thus the normal precipitation pattern in the San Luis Valley may regularly limit body condition of cows, ultimately influencing calf weights and juvenile survival. Calf recruitment in the San Luis Valley was at the low end of the scale of herds listed above; only one other population had lower recruitment – the Henry Mountains.

Density dependence has been reported in bison (Fowler 1981), but my model suggested a very weak density dependent effect of total population size on recruitment in San Luis Valley bison (Table 2, *b1*= 0.0002, credible interval does not overlap zero). Though this estimate for *b1* seems small, using the average total population size over the study period (~1500 bison) and increasing the value of parameter *b1* from 0 to 0.0002 results in a 0.05 decrease in recruitment, or a decline of 72 calves recruited into the population. This is considerably less than the strength of density dependence reported for Yellowstone bison which was ~0.004 (Fuller et al. 2007a).

I detected an effect of precipitation on recruitment in the population (Table 2, *b3*; 95% credible interval does not overlap zero). My results indicate than in years of low spring and summer precipitation recruitment of calves into the population per adult female can be expected to decrease. The effects of climatic variability on large ungulates are typically most pronounced on neonatal survival (Fuller et al. 2007b), which I was not able to estimate in my model because the time of first census (the annual roundup) occurs in the fall when calves are already ~6 months of age. Climate change is likely to increase this precipitation effect on recruitment. Some climate projection models indicate a warming climate in future decades for this particular region of Colorado (Ray et al. 2008). Information on neonatal survival would be useful to better understand how survival and population growth in the San Luis Valley bison herd is influenced and fluctuates in this arid ecosystem.

My hypothesis was only partially true. I did not find that bison inhabiting an arid ecosystem had lower overall survival than bison in other habitat types, but I did find that San Luis Valley bison recruitment was lower than other herds and comparably low to the Henry Mountains herd. Calf sex ratios slightly favored females in both of these herds as well. The lower male to female calf ratio in San Luis Valley bison could be related to habitat conditions with high interannual variability in precipitation and hence nutrition coupled with a pattern of late season precipitation, potentially maintaining females in lower body condition. In my model, the highest bison population size was in 2009, exceeding all previous years, and occurred during a time of prolonged drought. The San Luis Valley has had below average precipitation since 2001 according to the Palmer Drought Severity Index. Koons et al. (2012) emphasizes the stronger effect of drought on recruitment during high relative to low population density.

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Appendix A. Interdunal willow survey site locations and characteristics, including status of willows (alive, dead, absent), dune deposition, soil type, potential productivity, and percent leader use of willows in the Great Sand Dunes ecosystem, 2006.

Willow Status	Site	Dune Deposition	Site Location UTME_NAD83	UTMN_NAD83	Soil Type[1]	Site Productivity[2]	Percent leader use
Absent	Hammond_55	low	444409	4181649	Cotopaxi sand	Low	na
Absent	Hammond_51	low	444640	4181716	Cotopaxi sand	Low	na
Absent	Hammond_47	low	444412	4181749	Cotopaxi sand	Low	na
Absent	Hammond_34	low	444615	4182047	Dunefield	Low	na
Absent	Hammond_48	moderate	445122	4181737	Dunefield	Low	na
Absent	Hammond_56	none	443873	4181631	Cotopaxi sand	Low	na
Absent	Hammond_110	none	444168	4181652	Cotopaxi sand	Low	na
Absent	Hammond_108	none	444047	4181730	Cotopaxi sand	Low	na
Absent	Hammond_106	none	444267	4181769	Cotopaxi sand	Low	na
Absent	Hammond_42	none	444271	4181918	Cotopaxi sand	Low	na
Alive	28_JUN_06	low	444897	4180084	Space City loamy sand	Low	57
Alive	Hammond_102	Low	444755	4182138	Dunefield	Low	54
Alive	7_31_06(2	low	444200	4182342	Cotopaxi sand	Low	80
Alive	7_31_06	low	444200	4182342	Cotopaxi sand	Low	80
Alive	28_JUN_06	moderate	446994	4176394	Cotopaxi sand	Low	38
Alive	Patch_2_o	moderate	446992	4176434	Cotopaxi sand	Low	100
Alive	28_JUN_06	moderate	446976	4176581	Cotopaxi sand	Low	89
Alive	Hammond_102a	moderate	444755	4182138	Dunefield	Low	76
Dead	7_31_06	moderate	444995	4181663	Dunefield	Low	na

[1] Soil Survey Staff, Natural Resources Conservation Service, United State Department of Agriculture. Soil Survey Geographic (SSURGO) Database for Alamosa and Saguache counties, Colorado. Available online at http://soildatamart.nrcs.usda.gov. Accessed March 22, 2012.

[2] United States Department of Agriculture, Natural Resources Conservation Service. National range and pasture handbook. [http://www.glti.nrcs.usda.gov/]

Appendix B. Soil type, soil drainage and productivity potential for vegetation sampling sites the Great Sand Dunes ecosystem, Colorado, 2005-2009.

Vegetation Community	Ungulate Strata	Site	Soil type[1]	Soil drainage[1]	Site productivity[2]
Cottonwood	Elk-only	1	Cotopaxi sand	Excessively drained	Low
		2	Cotopaxi sand	Excessively drained	Low
		3	Cotopaxi sand	Excessively drained	Low
		4	Zinzer loam	Well drained	Low
	Elk-bison	1	Space City loamy fine sand/ Cotopaxi sand	Excessively drained	Low
		2	Cotopaxi sand	Excessively drained	Low
		3	Cotopaxi sand	Excessively drained	Low
		4	Space City loamy fine sand	Excessively drained	Low
Wet meadow	Elk-only	1	Medano fine sandy loam	Poorly drained	Med
		2	Medano fine sandy loam	Poorly drained	Med
		3	Medano fine sandy loam	Poorly drained	Med
		4	Medano fine sandy loam	Poorly drained	Med
	Elk-bison	1	Medano fine sandy loam	Poorly drained	Med
		2	Medano fine sandy loam	Poorly drained	Med
		3	Medano fine sandy loam	Poorly drained	Med
		4	Medano fine sandy loam	Poorly drained	Med
Willow	Elk-only	1	Medano fine sandy loam	Poorly drained	Med
		2	Schrader sandy loam	Poorly drained	High
		3	Vastine loam--alkali	Poorly drained	High
		4	Vastine loam	Poorly drained	High
	Elk-bison	1	Space City loamy fine sand/ Cotopaxi sand	Excessively drained	Low
		2	Space City loamy fine sand/ Cotopaxi sand	Excessively drained	Low
		3	Cotopaxi sand	Excessively drained	Low
		4	Cotopaxi sand	Excessively drained	Low

[1] Soil Survey Staff, Natural Resources Conservation Service, United State Department of Agriculture. Soil Survey Geographic (SSURGO) Database for Alamosa and Saguache counties, Colorado. Available online at http://soildatamart.nrcs.usda.gov. Accessed March 22, 2012.

[2] United States Department of Agriculture, Natural Resources Conservation Service. National range and pasture handbook. [http://www.glti.nrcs.usda.gov/]