

Impact of Cattle Grazing on the Smith's Blue Butterfly, Its Host Plant and the Surrounding Plant Community



Final Report – September 2009

*Prepared for The Nature Conservancy and the other Managing Partners of Palo Corona
Regional Park – Monterey Peninsula Regional Park District and Big Sur Land Trust*

J. Hall Cushman, Ph.D.
Department of Biology, Sonoma State University,
Rohnert Park, California 94928

707/664-2142; cushman@sonoma.edu



TABLE OF CONTENTS

Section 1:

<i>Preface</i>	1
----------------	---

Section 2:

<i>Executive Summary</i>	2
--------------------------	---

Section 3:

<i>Influence of Cattle Grazing on Native And Exotic Vegetation</i>	
Abstract	4
Introduction	5
Study System	6
Methods	7
Results	9
Discussion	10
Conclusions & Management Implications	12
Literature Cited	13
Tables	18
Figures	23

Section 4:

<i>Influence of Cattle Grazing on an Endangered Butterfly and its Host Plant</i>	
Abstract	27
Introduction	28
Study System	30
Methods	32
Results	36
Discussion	37
Conclusions & Management Implications	40
Literature Cited	41
Tables	48
Figures	52

SECTION 1

Preface

The research summarized in this report represents a collaborative effort. My two graduate students, Dawn Graydon and Meghan Skaer, were deeply involved in many phases of the research project – study design, data collection, data analysis and presentation as well as writing. Dawn’s primary focus was on the Smith’s blue butterfly and buckwheat host plants whereas as Meghan’s work emphasized the entire plant community. However, each student was heavily involved in both parts of the project.

I have been fortunate to receive invaluable logistical and financial support from the three managing partners at Palo Corona – The Nature Conservancy, Monterey Peninsula Regional Park District and the Big Sur Land Trust. Dr. Scott Butterfield (TNC) has been critical to the project’s success on all fronts and Lynn Overtree and Tim Jensen were essential for enabling the project to run smoothly.

SECTION 2

Executive Summary

Grasslands throughout California are some of the most heavily invaded systems in the world, having undergone a nearly complete transformation from native flora to exotic annual grasses. Such habitats along the coast are less degraded than inland ones, but are still in need of management activities to reduce the dominance of exotic plants and promote the success of natives. Grazing by domestic livestock, such as cattle, may be an effective tool for mitigating these invasions, but results to date have been complex and often come from correlative rather than experimental studies or do not assess the response of all components of the plant community. In addition, very little is known about the extended consequences of grazing for non-target resident animal species, particularly in North America.

This land management challenge is well illustrated by the coastal grasslands at Palo Corona Regional Park, located 1.6 km south of Carmel, California. This landscape is dominated by a wide range of exotic plant species, especially exotic annual grasses, but is also home to a wealth of native plant taxa. Cattle grazing may be an effective management technique for this area but there is a complicating factor – a number of areas in PCRCP are home to the federally endangered Smith's blue butterfly (*Euphilotes enoptes smithi*) and its host plant cliff buckwheat (*Eriogonum parvifolium*). Thus, there is urgent need to determine if cattle grazing can be used to decrease the dominance of exotic plants and increase the success of natives – while at the same time having no or only minimal adverse effects on the Smith's blue.

To address these issues, the Managing Partners (TNC, BSLT and MRPD) and our research team established a cattle-exclosure experiment in January and February of 2007 on the ridge top grasslands of the Panoche Management Unit of PCRCP. These ridge top areas are prime locations for cattle grazing and also support abundance numbers of the Smith's blue and buckwheat. Thus, if there were an effect of cattle on the Smith's blue, it would occur in this area. The experiment consisted of 20 8 x 8 m plots distributed equally across five sites. Half the plots received barbed wire fencing to exclude cattle and the other half were left unmanipulated to serve as controls. For the past three years (2007-09), cattle have grazed the Panoche Unit during the winter and spring, with the number of cow-calf pairs ranging from 53 to 69. Each year, cattle were removed from the area when aboveground plant biomass in the spring reached levels necessary to yield residual dry matter (RDM) values in the fall of approximately 1350-2000 kg/ha (1200-1800 pounds/acre).

Using this three-year exclosure experiment, we have been able to address five research questions: 1) Does cattle grazing have the expected effect of reducing aboveground plant biomass? 2) How does cattle grazing influence the cover and species richness of native and exotic plant taxa from different functional groups? 3) How does cattle grazing impact the growth and fecundity of the most dominant exotic plant species in our study system? 4) Does cattle grazing influence the survival, growth and/or abundance of the Smith's blue butterfly's host plant, *Eriogonum parvifolium*? and 5) Does grazing lead to changes in the abundance of Smith's blue adults and larvae?

After three years, we have found that grazing significantly reduced the cover of exotic annual grasses, while increasing that of exotic annual forbs. However, contrary to our expectations, neither the overall richness nor cover of native forbs and grasses was affected by the grazing manipulations. The effect of grazing on exotic perennial forbs was positive in sites with greater water availability. Additionally, we found that grazing reduced the size and fecundity of the most dominant species, an exotic annual grass (*Bromus diandrus*), which may have long-term implications about the persistence of this competitive dominant in grazed systems. Two hypotheses might explain the lack of response in native species; they may have life history characteristics that prevented a response to grazing within the span of this study, and/or their seed banks may be sufficiently degraded that a response to grazing is not possible. In either case, seed additions of natives may be necessary to augment their species richness and cover.

Our results clearly show that cattle grazing reduced the volume of buckwheat host plants and decreased the average size of adult and juvenile plants. Grazing did not reduce survival of juvenile host plants and had no direct effects on seedling abundance. We also did not detect any effect of cattle on the abundance of male and female butterflies. In contrast, we found that grazing was associated with an increase in the abundance of larvae in one year (2008), but had no effect in another (2009). One possible explanation for the beneficial effects of grazing on larval abundance in some years involves habitat structure. Because grazing substantially decreased the height of invasive annual grasses, we hypothesize that it can increase the apparency of host plant inflorescences in some years and make them more accessible to ovipositing female butterflies. This in turn could lead to the observed increases in larval abundance in one of two years.

If cattle continue to adversely impact host plants in subsequent years, we suspect that any benefits of grazing on butterfly larval abundance may not persist long term and could even switch from positive to negative. However, if such negative effects develop in ridge-top landscapes, we believe that the population-level impacts on this endangered butterfly will be minimal or non-existent, because our research has shown that the Smith's blue is extremely abundant in the adjacent ravine habitats, which are expansive and heavily dominated by its host plant.

In conclusion, although additional years of data will be needed to evaluate the response of native plants, our results clearly show that cattle grazing has been an extremely effective tool for reducing the dominance of the most problematic group of plant invaders at Palo Corona and throughout California – exotic annual grasses. Although there is the *potential* for cattle to have adverse impacts on the endangered Smith's blue on the ridge-top habitats, extensive buckwheat-dominated shrub lands occur on the slopes and ravines at Palo Corona, and these areas support abundant populations of the Smith's blue. Thus, cattle grazing appears to be an important and quite effective approach for managing this invaded coastal grassland.

SECTION 3

INFLUENCE OF CATTLE GRAZING ON NATIVE AND EXOTIC VEGETATION

Abstract. Human-caused introductions of non-native species are occurring at unprecedented rates and spatial scales. These invasions have become so widespread and influential that they are considered one of the major forms of global environmental change. Grasslands throughout California are some of the most heavily invaded systems in the world, having undergone a nearly complete transformation from native flora to exotic annual grasses. Grasslands along the coast are less degraded than inland ones, but are still in need of management activities to reduce the dominance of exotics and to promote the success of natives. Grazing by domestic livestock, such as cattle, may be an effective tool for mitigating these invasions, but results to date have been complex and often come from correlative rather than experimental studies or do not assess the response of the entire plant community. Here, we summarize results from a cattle enclosure experiment that evaluates the effects of grazing on species richness and cover of native and exotic plant groups in a coastal grassland in central California. After three years, we have found that grazing significantly reduced the cover of exotic annual grasses, while increasing that of exotic annual forbs. However, contrary to our expectations, neither the overall richness nor cover of native forbs and grasses was affected by our grazing manipulations. The effect of grazing on exotic perennial forbs was positive in sites with greater water availability. There was also a trend for grazing to have increasingly negative effects on native shrub cover over time. Additionally, we found that grazing reduced the size and fecundity of the most dominant species, an exotic annual grass (*Bromus diandrus*), which may have long-term implications about the persistence of this competitive dominant in grazed systems. Two hypotheses might explain the lack of response in native species; they may have life history characteristics that prevented a response to grazing within the span of this study, and/or their seed banks may be sufficiently degraded that a response to grazing is not possible. In either case, seed additions of natives may be necessary to augment their species richness and cover. Although only part of the management goals were realized, our results indicate that cattle grazing may be an effective tool for the sustainable management of coastal grasslands.

INTRODUCTION

Human-caused introductions of non-native species are occurring at unprecedented rates and spatial scales (Vitousek et al. 1996, Mack et al. 2000). These invaders compete with native species and may lead to the endangerment or extinction of native taxa through their activities as predators, pathogens, herbivores, and competitors (Mooney and Drake 1987, Mack et al. 2000, Levine et al. 2003). Non-native species may also adversely affect the areas they invade by altering fire regimes, nutrient cycling, and hydrology (D'Antonio and Vitousek 1992, D'Antonio and Hobbie 2005), and can even change selective pressures for native communities (Lau 2008). Invasions have become so widespread and influential that they are considered one of the major forms of global environmental change (Vitousek et al. 1996).

Grasslands throughout California are one of the most invaded systems in the world, having undergone a nearly complete transformation from perennial grass-dominated native flora to assemblages dominated by exotic annual grasses (Burcham 1957, D'Antonio et al. 2007). A number of factors have contributed to this dramatic transformation. Over the last two centuries, many exotic, typically Mediterranean, grasses were introduced both actively (by land managers or ranchers) and passively (due to inadvertent dispersal) and because of their grazing tolerance and competitive abilities have since spread rapidly beyond their original sites of introduction (Bartolome et al. 1986, Heady 1988, D'Antonio and Vitousek 1992, Dyer et al. 1996). Additionally, historical droughts, overgrazing, and intensive agriculture have exacerbated the issue (Burcham 1957, 1961, Heady 1988, Heady et al. 1988, Heady et al. 1992, Holstein 2001). This large-scale transformation has dramatically changed the composition and diversity of grassland systems and has altered natural processes (D'Antonio and Vitousek 1992, Vitousek et al. 1996). For example, one consequence of this substantial invasion of annual species is that tremendous amounts of aboveground plant biomass accumulate each year (McNaughton 1968, D'Antonio and Vitousek 1992). This biomass has the potential to greatly influence a number of environmental aspects, including light availability, soil nutrients, and soil temperature (Knapp and Seastedt 1986, Elliot and White 1987), as well as water content and depth (Gordon et al. 1989, Melgoza et al. 1990, D'Antonio and Vitousek 1992). This increased biomass can have a negative effect on plant germination and recruitment and, indirectly, species richness and relative dominance (Bergelson 1990, Facelli and Pickett 1991, Tilman 1993, Foster and Gross 1998). Additionally, research has shown that exotic annual grasses hinder the success of native bunchgrass populations through competition for available resources (Brown and Rice 2000, Maron and Jeffries 2001).

Land managers are now faced with the challenge of simultaneously promoting what native species remain while also attempting to reduce the dominance of invasive exotic species. Mack et al. (2000) suggested that this process requires continuous system-wide efforts, and there are a number of techniques employed to attempt to mitigate these invasions, including herbicide, fire, mowing, and reintroduction of large grazing animals (Luken and Thieret 1997, Griggs 2000). Although it has been implicated in the demise of native grasslands (Fleischner 1994), the use of grazing in particular has been shown to have promise as an effective management tool (Hatch et al. 1999, Griggs 2000, Harrison et al. 2003, Hayes and Holl 2003a, Marty 2005), particularly when focusing on one or a few target species (Dyer and Rice 1997, Dyer 2003, Bartolome et al. 2004).

Although cattle grazing is often put forth as a useful tool for managing invaded grasslands, we are aware of only five papers that have actually evaluated the effects of such grazing on native and exotic vegetation in an entire grassland community (Griggs 2000, Harrison et al. 2003, Hayes and Holl 2003a, Kimball and Schiffman 2003, Bartolome et al. 2004). There are a series of additional studies that focused on the impact of grazing on a few of the dominant exotic or native species in a grassland community (Hatch et al. 1999), or use simulated herbivory (Hayes and Holl 2003b). Unfortunately, whether focusing on the entire community or the dominant species, most of these studies have been non-experimental and many have used coarse measures of community composition, such as species richness. Before cattle grazing can be productively implemented as a management tool, it is important to gain a more detailed understanding of the complex community-level responses to grazing by using rigorously designed field experiments.

The response of plant communities to cattle grazing will be determined in part by the life history characteristics and geographic origins of resident taxa in the system, as well as the changes in competitive dynamics that result from grazing. Plants from different functional groups (based on life history and growth characteristics) may vary greatly in their response to grazing, as might native and exotic species from within the same functional group. Such taxa differ considerably in their responses to disturbances and their colonization and competitive abilities (Grime 1979, Hobbs and Huenneke 1992, McIntyre et al. 1995, Lavorel et al. 1999). In addition, grazing may have large negative effects on plant species in one functional group that in turn alter their competitive interactions with species from other functional groups. For example, a grazing-induced decrease in abundance or cover for members of one functional group may cause an increase in abundance for taxa from other competitively subordinate groups. To develop a holistic understanding of the impacts of cattle grazing on vegetation, and its utility as a management tool, we need to focus on the entire plant community and address the responses of native and exotic species from different functional groups.

Here we summarize a three-year enclosure experiment designed to evaluate the influence of cattle grazing on the plant community in a coastal prairie in central California. Specifically we address the following questions: 1) Does cattle grazing have the expected effect of reducing aboveground plant biomass? 2) How does cattle grazing affect the cover and species richness of native and exotic taxa from different functional groups? And 3) How does cattle grazing affect the growth and fecundity of the most dominant exotic plant species in our study system? Addressing these questions will aid in the development of a framework for understanding the responses of plant communities to grazing and the effectiveness of grazing as a tool for restoring degraded grasslands.

STUDY SYSTEM

This research was conducted in a coastal prairie at Palo Corona Regional Park (PCRP), which is 1.6 km south of Carmel in Monterey County, California (36°29'07.4" N, 121°53'32.7" W). The 4000 ha park is managed by the Monterey Peninsula Regional Park District in association with the Big Sur Land Trust and The Nature Conservancy. PCRP is located along the Santa Lucia Range in the Pacific Coast Range and hosts a variety of vegetation types, including coastal prairie, scrub and chaparral, oak woodland, and redwood forest. The prairie regions of PCRP are

historic ranchlands where grazing occurred for most of the last century, until cattle were removed in 2000. In 2007, cattle grazing was re-introduced to explore its effectiveness as a conservation tool for managing the prairie.

The study region experiences a Mediterranean-type climate, consisting of cool, moist winters and warm, dry summers as well as a strong coastal influence that results in frequent summer fog. The 20-year average annual rainfall preceding this study was 527 mm, which falls predominantly from November through April. The annual rainfall during the three-year study ranged from 346 to 410 mm (California climate data archive).

The study sites were located in the Panoche Management Unit of PCRP, an 81 ha parcel of land 4.8 km inland and between 400 and 450 m in elevation. Soils in the area are primarily of the Cieneba (shallow sandy loam) and Sheridan (granitic sandy loam) series (Web soil survey). The Panoche Unit is comprised of ridgelines dominated by grassland species, which intergrade with shrubland species on the steeper slopes below the ridgelines. The study sites are located at the intersection of these two community types, with an average shrub cover of approximately 20%. The primary shrub species are all native and consist of *Eriogonum parvifolium*, *E. nudum*, and *Lupinus arboreus*. The grassy ridges are dominated by exotic annual grasses (*Bromus diandrus*, *B. hordeaceus*, *Lolium multiflorum*, *Avena barbata*, and *Aira Caryophyllea*), but also support low densities of native perennial grasses (*Nassella pulchra*, *Danthonia Californica*, *Poa secunda*, and *Bromus carinatus*). The two most common forb species are smooth cat's ear (*Hypochaeris glabra*), an exotic annual, and California poppy (*Eschscholzia californica*), a native annual (See Table 1).

METHODS

Cattle-Exclosure Experiment

To address the effectiveness of grazing as a conservation tool, we established a cattle-exclosure experiment in January and February of 2007 on the ridgetop grasslands in the Panoche Management Unit of PCRP. This experiment consisted of 20 8 x 8 m plots distributed across five sites, which each contained four plots (Figure 1). The location of each site was selectively chosen within regions of grassland accessible to cattle, where grassland species and shrubs co-occur. We matched plots within sites visually for similarity in slope, aspect and vegetation composition. We also grouped plots within sites into two blocks based on proximity and randomly assigned one plot in each block to receive fencing that excluded cattle and left the other plot unmanipulated to serve as a control (two controls and two exclosures per site; see Figure 1). All plots were separated by at least 2 m and had four steel t-posts demarking their corners. Exclusion plots had four additional mid-posts, corner bracing, and five strands of barbed wire encircling them. We established four permanent 1 x 1 m quadrats within each quarter of all plots.

Cattle grazed our study area during the winters and springs of this three-year experiment. The site was grazed by 69 cow-calf pairs in 2007 (March 22 to April 16), 63 pairs in 2008 (February 17 to March 30), and 53 pairs and two bulls in 2009 (January 23 to April 11). Each year, cattle were removed from the Panoche Unit when aboveground plant biomass in the spring reached

levels necessary to yield residual dry matter (RDM) values in the fall of approximately 1350-2000 kg/ha (1200-1800 pounds/acre).

Vegetation and Community Response

After cattle were removed in the spring for each of three years, we harvested all aboveground plant biomass from two 25 x 25 cm quadrats placed in the central region of each plot, away from the permanent 1 x 1 m quadrats, and in different locations each year. We pooled the two vegetation samples from each plot, dried them at 60 °C for 48 hr, and weighed. So that the results were more comparable to other studies, we converted biomass data from grams/0.125 m² to grams/m².

To evaluate the influence of cattle grazing on the entire plant community, we sampled the vegetation inside our 20 8 x 8 m plots using standard point-intercept methods. In spring of 2007, 2008, and 2009, we recorded all plant species encountered at 45 points in each of the permanent quadrats. Frequently, multiple taxa were encountered at a single point. We calculated the absolute percent cover of the various species groups by dividing the number of occurrences by the total number of sampled points (45 points). To evaluate species richness, we also conducted whole-plot searches to record all species present in each plot. With these cover and richness data, we grouped species by geographic origin (native and exotic) and functional groups based on life history and growth characteristics (annual and perennial grasses, annual and perennial forbs, and shrubs). These distinctions resulted in seven species groupings (native annual grasses, exotic perennial grasses and exotic shrubs did not occur in our plots). All nomenclature and origin information follows *The Jepson Manual* (Hickman 1993).

To evaluate the effects of cattle grazing on the most dominant exotic annual grass, ripgut brome (*Bromus diandrus*), we found the nearest intact individual grass to 6 standard locations within each of the four permanent quadrats in all plots and measured its height and enumerated the spikelets produced (emergent and non-emergent).

Statistical Analysis

Unless noted otherwise, all analyses were performed using the general linear model in SAS 9.1.3 (SAS Institute, Inc., Cary, North Carolina, USA). All ANOVA models used grazing treatment (cattle present or absent) as a fixed factor, and site (1-5), and block (A or B) nested in site as random factors. For all repeated-measures analyses, terms containing year were evaluated using Pillai's Trace, which is the most robust to violations of assumptions (Schiener 2001). We log-transformed data when we encountered non-normal data or unequal variances. We analyzed data for aboveground plant biomass (g/m²) using a repeated-measure analysis of variance (ANOVA), with sample year (2007, 2008, and 2009) as the repeated measure.

We analyzed the percent cover and species richness data using two repeated-measure multivariate analysis of variances (MANOVAs), with sample year (2007, 2008, 2009) as the repeated measure. The first MANOVA used the natural log of absolute percent cover of seven plant groupings as response variables (native perennial grasses, exotic annual grasses, native annual forbs, exotic annual forbs, native perennial forbs, exotic perennial forbs, and shrubs).

The second MANOVA used species richness of these plant groupings as the response variables. For all MANOVAs with significant grazing treatment terms, we proceeded with separate ‘protected’ ANOVAs using each of the seven plant functional groups as the response variable. This method addresses possible correlations among the multiple dependent variables (Schiener 2001, Alvarez and Cushman 2002, Cushman et al. 2004).

We analyzed data on *B. diandrus* height and fecundity in 2009 using two linear mixed models with Type III estimation (Littell et al. 2006). This type of analysis was preferable because *B. diandrus* was missing from some quadrats and the mixed model approach is able to handle unbalanced design more appropriately than the general linear model that we used elsewhere. We log-transformed these data to equalize variances.

RESULTS

Our cattle enclosure experiment revealed that grazing caused significant reductions in aboveground plant biomass at our study site ($F_{1,9}=41.44$, $p<0.0001$). As shown in Figure 2, the effects of cattle on biomass varied significantly among years ($F_{2,8}=6.37$, $p=0.0221$), with impacts being greatest in the third year of our experiment. Biomass production also varied significantly among the three years of our study ($F_{2,8}=10.78$, $p=0.0054$), with levels being greatest in the third year.

Although we did not detect a significant effect of cattle grazing on the species richness of the seven plant groupings considered collectively ($F_{1,9}=0.22$, $p=0.6726$), grazing did have an overall significant effect on the percent cover of these groups ($F_{7,59}=1468.36$, $p<0.0001$). Subsequent protected ANOVAs revealed that exotic annual grasses and exotic annual forbs were the major drivers of this MANOVA result. Cover of exotic annual grasses was significantly reduced by grazing (Figure 3A), with there being a trend for grazing impacts to vary among years (Table 2B). This latter interaction resulted from the effects of grazing being less pronounced in 2008 than in the other two years. In addition, we detected a significant three-way interaction among grazing, year, and site. Generally, cattle grazing caused the most dramatic reduction in the cover of exotic annual grasses in the first year of the study in all sites except site 1, which experienced evenly increasing reductions each year.

In contrast to the results for exotic annual grasses, cattle grazing increased the cover of exotic annual forbs (Figure 3C). There was a trend for the effect of grazing on this group to increase in magnitude each year (Table 2D). In addition, there was a trend for grazing impacts to vary among sites, with increases in cover being greater at sites 4 and 5 than at the other sites.

Grazing did not have an effect on the percent cover of native perennial grasses (Table 2A; Figure 3B), native annual forbs (Table 2C; Figure 3D), native perennial forbs (Table 2E; Figure 3F), exotic perennial forbs (Table 2F; Figure 3E), or native shrubs (Table 2G; Figure 3G). However, the effect of grazing on exotic perennial forbs varied significantly among sites (Table 2F), with grazing having a negative effect on cover at sites 2 and 5, no effect at site 4, and a positive effect at sites 1 and 3.

Grazing had substantial effects on the most dominant exotic plant species at our site. The height of *Bromus diandrus* was significantly reduced by grazing ($F_{1,4}=163.86$, $p=0.0002$; Figure 4). Grazing also reduced spikelet production ($F_{1,4}=12.99$, $p=0.0226$; Figure 4), and this effect varied among sites ($F_{4,450}=1.29$, $p=0.0015$), with the most dramatic reduction occurring at site 1.

DISCUSSION

Results from our three-year enclosure experiment have shown that cattle grazing can have large effects on a coastal grassland community through reducing biomass and altering the relative dominance of plant species. Grazing caused a large reduction in the cover of exotic annual grasses (Figure 3B), which are by far the most dominant group in this landscape, comprising over two thirds of the vegetative cover. We hypothesize that cattle are feeding in relation to the abundance of plant species present, and because they are grazers, favor the highly abundant exotic annual grasses. In addition, cattle reduced the size and fecundity of the most dominant of these species, *Bromus diandrus* (Figure 4). In contrast, grazing led to a substantial increase in the cover of exotic annual forbs (Figure 3D) and had no effect on species richness of native and exotic plant taxa, or the cover of native perennial grasses, native annual and perennial forbs, or native shrubs.

Although cattle grazing had a strikingly negative effect on exotic annual grasses, and this response is frequently hypothesized as a critical conservation benefit, few studies have reported such effects. For example, in a non-experimental study comparing grazed and ungrazed plant communities in coastal California, Hayes and Holl (2003a) found the opposite effect at certain times, with cattle grazing associated with higher cover of exotic annual grasses in one of two years. Other studies have also shown that grazing can have a positive effect on some species of exotic annual grasses (White 1967, Fossum 1990). Two explanations for these differences relate to the fact that studies by Hayes, Holl and White were non-experimental and involved comparisons of sites that had been grazed or ungrazed for long periods of time. These studies may have captured the longer-term effects of cattle grazing or their results may reflect initial differences among plots that were unrelated to grazing. In contrast, our experimental study more directly addressed causation, but documented the responses of a plant community to grazing over a shorter time period. In addition, we were studying a system where cattle were being reintroduced after almost a decade absence.

The reduction in cover of exotic annual grasses caused by cattle grazing was associated with an increase in the cover of exotic annual forbs. This response is similar to that found in other studies (Griggs 2000), including those in mesic coastal grasslands (Hayes and Holl 2003a, b). One hypothesis to explain this result is that exotic annual grasses are competitively dominant to exotic annual forbs and, in the absence of cattle grazing, suppress their abundance, biomass and cover. We hypothesize that grazing interrupts this competitive dominance and creates increased availability of space and possibly soil nutrients and/or water that allow exotic annual forbs to thrive and expand in cover.

We were surprised to find that exotic annual forbs were the only group to respond positively to a major decrease in cover of the most dominant group in our system (i.e. exotic annual grasses). Exotic annual forbs are a relatively small part of the plant community (comprising only 20% of

the total vegetative cover) and the observed increase in their cover (15%) due to cattle grazing was not in proportion to the decrease in exotic annual grasses (40%). Thus, cattle grazing has created substantial openings in this grassland ecosystem that have yet to be colonized by other plant groups.

In contrast to our original hypothesis, cattle grazing did not increase the richness or cover of native plant species during our three-year study, even though grazing caused a four-fold decrease in biomass and reduced the cover of exotic annual grasses by over a third. One hypothesis to explain this result is that native species in our system possess life history characteristics that cause them to respond more slowly to grazing than exotic taxa. This seems likely, given that 35% of the native non-shrub species at our site were perennial compared to 6% for exotic taxa. Alternatively, the seed bank of native species may be so depleted – both in number of species and number of seeds – that these taxa are not able to capitalize on (or may be slower at doing so) the less competitive environments created by grazing.

Using community-level sampling methods, we detected a trend for grazing to negatively affect shrub cover over time in our system. Other studies have also shown that grazing has negative effects on shrub cover (Bartholomew 1970, Casasús et al. 2007, Johnson and Cushman 2007). In addition, more detailed shrub-focused sampling in our cattle enclosure experiment by Graydon et al. (*unpublished data*) found that grazing significantly reduced the size and volume of *Eriogonum parvifolium*, which is by far the most dominant shrub species in the system (15% of all vegetation). It is also the primary host plant for an endangered lycaenid butterfly (Arnold 1983). There is no evidence that cattle feed on shrubs in our system (D. J. Graydon and J. H. Cushman, *personal observation*), so cattle herbivory cannot explain the negative impact on shrubs. An alternative explanation is that the reduction in shrub cover is caused by the trampling activity of cattle. Graydon et al. (*unpublished data*) found that grazing caused a significant increase in broken shrub branches, and we suspect that this physical damage is the primary way that cattle negatively affect native shrubs.

Although we did not detect an overall effect of grazing on the cover of exotic perennial forbs, grazing impacts varied significantly among sites. Effects of cattle on these forbs were negative at sites 2 and 5, positive at sites 1 and 3, and absent at site 4. Based on a gravimetric analysis of water content, sites 1 and 3 had the highest water content (M. J. Skaer, *unpublished data*), which may help these species recover from grazing sooner than in sites where water is less available.

We did not detect an effect of grazing on the cover or species richness of native annual or perennial forbs, although other studies have shown that cattle have large impacts on these taxa. For example, Hayes and Holl (2003a) reported that the cover and richness of native annual forbs responded positively to cattle grazing, while the cover and richness of native perennial forbs was negatively impacted. They suggested that the positive response of native annual forbs was caused by decreased light competition and increased bare soil and that the taller native perennial forbs were at a disadvantage when exposed to grazing.

Because they were thought to have dominated pristine California grasslands, native perennial grasses are a common target group for research and management in invaded grasslands, particularly mesic coastal grasslands. However, our research showed that cattle grazing did not

affect – positively or negatively – this group. Their cover was quite low in our system (<1%), and this lack of response is in contrast to Bartolome et al. (2004), who found that, for some species (*Nassella* sp.), native perennial grasses were positively affected by cattle grazing. They suggest, as do others (Dyer and Rice 1997), that this was caused by reduced competition from neighboring annual grasses and forbs. As mentioned earlier, we suspect that depleted seed banks may explain the unresponsiveness of these taxa in our system.

The most dominant plant species in our system, the exotic annual grass *Bromus diandrus*, was negatively impacted not only in cover (M. J. Skaer and J. H. Cushman, *unpublished data*), but also height and fecundity. These reductions could not have been caused by direct grazing activity, because we specifically selected intact, ungrazed individuals for this component of our study. Instead, we hypothesize that cattle influenced the germination and growth phenology of this grass, which subsequently resulted in the observed grazing effects on plant height and fecundity. The vast majority of early germinating individuals were consumed by cattle, so for *Bromus diandrus* individuals to have escaped herbivory while cattle were present, most would have germinated or grown new tillers later in the season, and reached maturity after cattle were removed. These individuals would have experienced more xeric conditions and would therefore be smaller and less fecund than individuals who had germinated earlier in the season and escaped herbivory (those protected from grazing). Thus, for *Bromus* plants to survive and reproduce in our grazed system, they needed to shift their phenologies later in the season, when they experience a harsher climate.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our research has shown that cattle grazing is having part of the desired management effect in this coastal grassland, given that there has been a 40% reduction in the exotic annual grasses, which comprise approximately two thirds of the vegetative cover in this system. Furthermore, the most dominant exotic species in the system, *Bromus diandrus*, is experiencing marked reductions in stature and fecundity, which will likely have long-term effects on their cover through decreased propagule pressure. We had hypothesized that native grass and forb species would respond positively to this reduction, due to competitive release, but thus far they have been unresponsive. Instead, exotic annual forbs have increased in cover, but to a much smaller degree than expected, given the reduction in cover of exotic annual grasses. The key management issue that remains is whether additional years of cattle grazing will allow native grasses and forbs to respond positively to the large decrease in exotic annual grasses. If these native groups remain unresponsive, or if a more rapid response is desired, we suspect that the seed banks are depleted and active restoration through seed supplementation may be necessary to increase the cover of native grasses and forbs.

LITERATURE CITED

- Alvarez, M. E. and J. H. Cushman. 2002. Community-level consequences of a plant invasion: effects on three habitats in coastal California. *Ecological Applications* **12**:1434-1444.
- Arnold, R. A. 1983. Conservation and management of the endangered Smith's Blue Butterfly, *Euphilotes enoptes smithi* (Lepidoptera: Lyceanidae). *Journal of Research on the Lepidoptera*.
- Bartholomew, B. 1970. Bare zone between California shrub and grassland communities: the role of animals. *Science* **170**:1210-1212.
- Bartolome, J. W., J. S. Fehmi, R. D. Jackson, and B. Allen-Diaz. 2004. Response of a native perennial grass stand to disturbance in California's coast range grassland. *Restoration Ecology* **12**:279-289.
- Bartolome, J. W., S. E. Kukkert, and W. J. Barry. 1986. Opal phytoliths as evidence for displacement of native California grassland. *Madrono* **33**:217-222.
- Bergelson, J. 1990. Life after death: site pre-emption by the remains of *Poa annua*. *Ecology* **71**:2157-2165.
- Brown, C. S. and K. J. Rice. 2000. The mark of Zorro: effects of the exotic annual grass *Vulpia myuros* on California native perennial grasses. *Restoration Ecology* **8**:10-17.
- Burcham, L. T. 1957. California range land: an historico-ecological study of the range resource of California. Division of Forestry, Department of Natural Resources, State of California, Sacramento.
- Burcham, L. T. 1961. Cattle and range forage in California 1770-1880. *Agricultural History* **35**:140-149.
- California climate data archive. Western Regional Climate Center. Desert Research Institute.
- Casasús, I., A. Bernués, A. Sanz, D. Villalba, J. L. Riedel, and R. Revilla. 2007. Vegetation dynamics in Mediterranean forest pastures as affected by beef cattle grazing. *Agriculture, Ecosystems and Environment* **121**:365-370.
- Cushman, J. H., T. A. Tierney, and J. M. Hinds. 2004. Variable effects of feral pig disturbances on native and exotic plants in a California grassland. *Ecological Applications* **14**:1746-1756.
- D'Antonio, C. M., C. M. Malmstrom, S. A. Reynolds, and J. D. Gerlach. 2007. Ecology of invasive non-native species in California grassland. Pages 67-83 in M. R. Stromberg, J. D.

Corbin, and C. M. D'Antonio, editors. California grasslands: ecology and management. University of California Press, Berkeley.

D'Antonio, C. M. and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63-87.

D'Antonio, C. M. and S. E. Hobbie. 2005. Plant species effects on ecosystem processes. Pages 65-84 in D. F. Sax, J. J. Stachowicz, and S. D. Gaines, editors. *Species invasions: insights from ecology, evolution and biogeography*. Sinauer Associates, Sunderland, MA.

Dyer, A. R. 2003. Burning and grazing management in a California grassland: growth, mortality, and recruitment of *Nassella pulchra*. *Restoration Ecology* **11**:291-296.

Dyer, A. R., H. C. Fossum, and J. W. Menke. 1996. Emergence and survival of *Nassella pulchra* in a California grassland. *Madrono* **43**:316-333.

Dyer, A. R. and K. J. Rice. 1997. Intraspecific and diffuse competition: the response of *Nassella pulchra* in a California grassland. *Ecological Applications* **7**:484-492.

Elliot, K. J. and A. S. White. 1987. Competitive effects of various grasses and forbs on Ponderosa pine seedlings. *Forest Science* **33**:356-366.

Facelli, J. M. and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* **57**:1-32.

Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* **8**:629-644.

Fossum, H. C. 1990. Effects of prescribed fire and grazing on *Stipa pulchra* (Hitchc.) seedling emergence and survival. University of California, Davis.

Foster, B. L. and K. L. Gross. 1998. Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology* **79**:2593-2602.

Gordon, D. R., J. M. Welker, J. W. Menke, and K. J. Rice. 1989. Competition for soil water between annual plants and blue oak (*Quercus Douglasii*) seedlings. *Oecologia* **60**:149-155.

Griggs, F. T. 2000. Vina Plains Preserve: eighteen years of adaptive management. *Fremontia* **27**:48-51.

Grime, J. P. 1979. *Plant strategies and vegetation processes*. John Wiley and Sons, Chichester, UK.

- Harrison, S., B. D. Inouye, and H. D. Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology* **17**:837-845.
- Hatch, D. A., J. W. Bartolome, J. S. Fehmi, and D. S. Hillyard. 1999. Effects of burning and grazing on a coastal California grassland. *Restoration Ecology* **7**:376-381.
- Hayes, G. F. and K. D. Holl. 2003a. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology* **17**:1694-1702.
- Hayes, G. F. and K. D. Holl. 2003b. Site-specific responses of native and exotic species to disturbances in a mesic grassland community. *Applied Vegetation Science* **6**:235-244.
- Heady, H. F. 1988. Valley grassland. Pages 491-514 *in* M. G. Barbour and J. Major, editors. *Terrestrial vegetation of California*. California Native Plant Society, Sacramento.
- Heady, H. F., J. W. Bartolome, M. D. Pitt, G. D. Savelle, and M. C. Stroud. 1992. California prairie. Pages 313-335 *in* R. T. Coupland, editor. *Natural grasslands*. Elsevier, New York.
- Heady, H. F., T. C. Foin, M. M. Hektner, D. W. Taylor, M. G. Barbour, and W. J. Barry. 1988. Coastal prairie and northern coastal scrub. Pages 733-762 *in* M. G. Barbour and J. Major, editors. *Terrestrial vegetation of California*. California Native Plant Society, Sacramento.
- Hickman, J. C., editor. 1993. *The Jepson manual*. University of California Press, Berkeley.
- Hobbs, R. J. and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* **6**:324-337.
- Holstein, G. 2001. Pre-agricultural grassland in central California. *Madrono* **48**:253-264.
- Johnson, B. E. and J. H. Cushman. 2007. Influence of a large herbivore reintroduction on a plant invasions and community composition in a California grassland. *Conservation Biology* **21**:515-526.
- Kimball, S. and P. M. Schiffman. 2003. Differing effects of cattle grazing on native and alien plants. *Conservation Biology* **17**:1681-1693.
- Knapp, A. K. and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* **36**:662-668.
- Lau, J. A. 2008. Beyond the ecological: Biological invasions alter natural selection on a native plant species. *Ecology* **89**:1023-1031.

- Lavorel, S., C. Rochette, and J. D. Lebreton. 1999. Functional groups for response to disturbance in Mediterranean oil fields. *Oikos* **84**:480-498.
- Levine, J. M., M. Vilà, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B – Biological Sciences* **270**:775-781.
- Littell, R. C., G. A. Milliken, W. W. Stroup, R. D. Wolfinger, and O. Schabenberger. 2006. SAS for mixed models. 2nd edition. SAS Publishing, Cary.
- Luken, J. O. and J. W. Thieret. 1997. Assessment and management of plant invasions. Springer-Verlag, New York.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* **10**:689-710.
- Maron, J. L. and R. Jeffries. 2001. Restoring enriched grasslands: effects of mowing on species richness, productivity, and nitrogen retention. *Ecological Applications* **11**:1088-1100.
- Marty, J. T. 2005. Effects of cattle grazing on diversity in ephemeral wetlands. *Conservation Biology* **19**:1626-1632.
- McIntyre, S., S. Lavorel, and R. M. Tremont. 1995. Plant life-history attributes: their relationship to disturbance in herbaceous vegetation. *Journal of Ecology* **83**:31.
- McNaughton, S. J. 1968. Structure and function in California grasslands. *Ecology* **49**:962-972.
- Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* **83**:7-13.
- Mooney, H. A. and J. A. Drake. 1987. The ecology of biological invasions. *Environment* **29**:10.
- Schiener, S. M. 2001. MANOVA: multiple response variables and multispecies interactions. Pages 94-112 in S. M. Schiener and J. Gurevitch, editors. *Design and analysis of ecological experiments*. Chapman and Hall, New York.
- Tilman, D. 1993. Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology* **74**:2179-2191.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* **84**:468-478.

Web soil survey. Natural Resources Conservation Service. United States Department of Agriculture.

White, K. L. 1967. Native bunchgrass (*Stipa pulchra*) on Hastings Reservation, California. Ecology **48**:949-954.

Table 1. List of species present in study plots and absolute percent cover for each, where data is available, in each year of the study. An asterisk (*) indicates the species was present in study sites, but not encountered during quadrat sampling. LH = Life History, FG = Functional Group, N=Native, E=Exotic, A=Annual, P=Perennial, F=Forb, G=Grass, S=Shrub.

<i>Species</i>	<i>Family</i>	<i>Origin</i>	<i>LH/FG</i>	<i>Percent Cover</i>		
				2007	2008	2009
<i>Acaena pinnatifida</i>	Rosaceae	N	PF	*		
<i>Agoseris sp.</i>	Asteraceae	N	AF	0.33	0.08	0.06
<i>Aira caryophyllea</i>	Poaceae	E	AG	2.50	0.06	0.22
<i>Allium sp.</i>	Liliaceae	N	PF	*		*
<i>Amsinckia sp.</i>	Boraginaceae	N	AF	*		
<i>Amsinckia tessellata var. tessellata</i>	Boraginaceae	N	AF			*
<i>Anagallis arvensis</i>	Primulaceae	E	AF	1.22	0.33	1.00
<i>Anaphalis margaritacea</i>	Asteraceae	N	PF	*		
<i>Arabis glabra</i>	Brassicaceae	N	AF	*		
<i>Avena barbata</i>	Poaceae	E	AG	0.47	0.72	3.25
<i>Bromus carinatus var. carinatus</i>	Poaceae	N	PG	*		0.53
<i>Bromus diandrus</i>	Poaceae	E	AG	35.42	42.67	51.03
<i>Bromus hordeaceus</i>	Poaceae	E	AG	19.33	10.19	9.92
<i>Calandrinia ciliata</i>	Portulacaceae	N	AF	0.08	0.11	0.17
<i>Castilleja exserta</i>	Scrophulariaceae	N	AF	*	*	*
<i>Cerastium glomeratum</i>	Caryophyllaceae	E	AF	0.03		
<i>Chlorogalum pomeridianum</i>	Liliaceae	N	PF	0.22	0.14	0.03
<i>Cirsium occidentale var. occidentale</i>	Asteraceae	N	AF		*	*
<i>Clarkia purpurea</i>	Onagraceae	N	AF	0.06	0.19	0.14
<i>Clarkia unguiculata</i>	Onagraceae	N	AF	0.78	0.39	0.58
<i>Crassula conata</i>	Crassulaceae	N	AF	0.03		0.03
<i>Cryptantha clevelandii</i>	Boraginaceae	N	AF	0.11	*	0.08
<i>Danthonia californica</i>	Poaceae	N	PG	0.03		
<i>Daucus pusillus</i>	Apiaceae	N	AF	1.31	0.08	0.03
<i>Dichelostemma capitatum</i>	Liliaceae	N	PF	0.08	0.25	0.11
<i>Eriogonum nudum</i>	Polygonaceae	N	PS	3.03	3.56	2.89
<i>Eriogonum parvifolium</i>	Polygonaceae	N	PS	15.83	16.67	12.56
<i>Eriophyllum confertiflorum</i>	Asteraceae	N	PS		*	*
<i>Erodium botrys</i>	Geraniaceae	E	AF	0.28	0.22	0.89
<i>Erodium cicutarium</i>	Geraniaceae	E	AF	1.58	4.33	9.08
<i>Erodium moschatum</i>	Geraniaceae	E	AF			*
<i>Eschscholzia californica</i>	Papaveraceae	N	AF	5.36	6.94	4.39
<i>Filago gallica</i>	Asteraceae	E	AF		*	*
<i>Galium aparine</i>	Rubiaceae	N	AF	1.17	1.81	1.72
<i>Galium trifidum var. pacificum</i>	Rubiaceae	N	PF	0.25	0.08	*
<i>Geranium dissectum</i>	Geraniaceae	E	AF	*		

Table 1. (Cont.)

<i>Species</i>	<i>Family</i>	<i>Origin</i>	<i>LH/FG</i>	2007	2008	2009
<i>Geranium molle</i>	Geraniaceae	E	AF	1.56	0.08	0.17
<i>Gilia angelensis</i>	Polemoniaceae	N	AF	0.61	0.17	0.08
<i>Gnaphalium californicum</i>	Asteraceae	N	AF	0.06	*	*
<i>Heterotheca sessiliflora</i>	Asteraceae	N	PF	0.06		0.03
<i>Hordeum murinum ssp. leporinum</i>	Poaceae	E	AG	0.06	0.14	0.03
<i>Hypochaeris glabra</i>	Asteraceae	E	AF	4.14	5.08	12.14
<i>Lactuca sp.</i>	Asteraceae	E	AF		0.03	0.44
<i>Lepidium nitidum</i>	Brassicaceae	N	AF	0.19	*	0.08
<i>Lessingia filaginifolia var. californica</i>	Asteraceae	N	PS		*	*
<i>Linanthus grandiflorus</i>	Polemoniaceae	N	AF	0.06	*	0.03
<i>Linum bienne</i>	Linaceae	E	PF	0.03	0.03	*
<i>Lolium multiflorum</i>	Poaceae	E	AG	16.86	2.61	3.72
<i>Lotus purshianus</i>	Fabaceae	N	AF	0.08	*	*
<i>Lotus scoparius</i>	Fabaceae	N	PS	0.58	1.33	3.56
<i>Lotus strigosus</i>	Fabaceae	N	AF	*	*	0.08
<i>Lupinus arboreus</i>	Fabaceae	N	PS	*	0.11	0.64
<i>Lupinus nanus</i>	Fabaceae	N	AF	0.39	0.25	1.94
<i>Madia elegans</i>	Asteraceae	N	AF	4.06	2.58	4.33
<i>Marah fabaceus</i>	Cucurbitaceae	N	PF		*	*
<i>Medicago polymorpha</i>	Fabaceae	E	AF	*	*	
<i>Nassella pulchra</i>	Poaceae	N	PG	0.11	0.39	0.47
<i>Nemophila menziesii</i>	Hydrophyllaceae	N	AF	*		
<i>Phacelia malvifolia</i>	Hydrophyllaceae	N	AF	*	*	*
<i>Phacelia ramosissima</i>	Hydrophyllaceae	N	PF	0.39	0.11	0.08
<i>Phalaris californica</i>	Poaceae	N	PG	*		
<i>Plagiobothrys tenellus</i>	Boraginaceae	N	AF			*
<i>Poa secunda ssp. secunda</i>	Poaceae	N	PG		*	
<i>Pterostegia drymarioides</i>	Polygonaceae	N	AF	0.64	0.11	0.06
<i>Rumex acetosella</i>	Polygonaceae	E	PF	4.22	5.89	5.58
<i>Senecio vulgaris</i>	Asteraceae	E	AF	*	*	
<i>Sidalcea malviflora</i>	Malvaceae	N	PF			*
<i>Silene gallica</i>	Caryophyllaceae	E	AF	1.75	0.33	3.03
<i>Sisyrinchium bellum</i>	Iridaceae	N	PF	*		*
<i>Sonchus asper</i>	Asteraceae	E	AF	*		
<i>Sonchus oleraceus</i>	Asteraceae	E	AF	*	0.06	
<i>Sonchus sp.</i>	Asteraceae	E	AF	0.03		
<i>Stellaria crispa</i>	Caryophyllaceae	N	PF	*		
<i>Stellaria media</i>	Caryophyllaceae	E	AF	5.83	1.31	2.56
<i>Stephanomeria virgata ssp. virgata</i>	Asteraceae	N	AF	0.56	0.33	0.17
<i>Thysanocarpus curvipes</i>	Brassicaceae	N	AF	*	*	*
<i>Thysanocarpus laciniatus</i>	Brassicaceae	N	AF	*		
<i>Torilis nodosa</i>	Apiaceae	E	AF	*		0.44
<i>Trifolium dubium</i>	Fabaceae	E	AF			*
<i>Trifolium gracilentum</i>	Fabaceae	N	AF	1.03	0.08	2.58

Table 1. (Cont.)

<i>Species</i>	<i>Family</i>	<i>Origin</i>	<i>LH/FG</i>	<i>2007</i>	<i>2008</i>	<i>2009</i>
<i>Trifolium microcephalum</i>	Fabaceae	N	AF	0.36	0.17	1.00
<i>Trifolium pratense</i>	Fabaceae	E	PF			0.06
<i>Trifolium subterraneum</i>	Fabaceae	E	AF		*	
<i>Trifolium willdenovii</i>	Fabaceae	N	AF		*	*
<i>Unknown Grass</i>	Poaceae	N	AG			*
<i>Unkown 20</i>	Asteraceae	N	AF		*	
<i>Vicia sativa ssp. nigra</i>	Fabaceae	E	AF	0.06	0.14	0.06
<i>Viola pedunculata ssp. pedunculata</i>	Violaceae	N	AF	0.31	0.33	0.25
<i>Vulpia bromoides</i>	Poaceae	E	AG	1.86	1.06	0.89

Table 2. Results from a series of ‘protected’ repeated-measures ANOVAs evaluating the impact of cattle grazing and numerous other factors on the natural log of absolute percent cover of native and exotic plant taxa from different functional groups. Significant sources of variation are indicated in bold.

<i>Variable and Source</i>	<i>DF</i>	<i>F</i>	<i>P</i>
A. Native Perennial Grasses			
<i>Cattle Treatment (CT)</i>	1,65	0.97	0.3274
<i>Site</i>	4,65	2.05	0.0977
<i>Block(Site)</i>	5,65	0.65	0.6607
<i>Year</i>	2,64	3.19	0.0480
<i>CT x Year</i>	2,64	1.69	0.1921
<i>Year x Site</i>	8,130	0.85	0.5624
<i>Year x Block</i>	10,130	0.69	0.7306
<i>CT x Site</i>	4,65	0.57	0.6839
<i>CT x Site x Year</i>	8,130	0.44	0.8952
B. Exotic Annual Grasses			
<i>Cattle Treatment (CT)</i>	1,65	31.91	<0.0001
<i>Site</i>	4,65	6.78	0.0001
<i>Block(Site)</i>	5,65	2.28	0.0567
<i>Year</i>	2,64	6.33	0.0031
<i>CT x Year</i>	2,64	2.74	0.0719
<i>Year x Site</i>	8,130	0.51	0.8497
<i>Year x Block</i>	10,130	0.50	0.8886
<i>CT x Site</i>	4,65	0.96	0.4356
<i>CT x Site x Year</i>	8,130	1.53	0.0266
C. Native Annual Forbs			
<i>Cattle Treatment (CT)</i>	1,69	0.08	0.7762
<i>Site</i>	4,69	3.30	0.0159
<i>Block(Site)</i>	5,69	2.86	0.0213
<i>Year</i>	2,68	10.45	0.0001
<i>CT x Year</i>	2,68	1.74	0.1842
<i>Year x Site</i>	8,138	2.64	0.0103
<i>Year x Block</i>	10,138	3.03	0.0018
<i>CT x Site</i>	4,65	1.62	0.1802
<i>CT x Site x Year</i>	8,130	0.50	0.8579
D. Exotic Annual Forbs			
<i>Cattle Treatment (CT)</i>	1,65	33.67	<0.0001
<i>Site</i>	4,65	3.84	0.0073
<i>Block(Site)</i>	5,65	0.26	0.9335
<i>Year</i>	2,64	34.37	<0.0001
<i>CT x Year</i>	2,64	2.13	0.1269
<i>Year x Site</i>	8,130	3.71	0.0006
<i>Year x Block</i>	10,130	0.71	0.7104
<i>CT x Site</i>	4,65	1.91	0.1190
<i>CT x Site x Year</i>	8,130	1.00	0.4431

Table 2. (Cont.)

<i>Variable and Source</i>	<i>DF</i>	<i>F</i>	<i>P</i>
<i>E. Native Perennial Forbs</i>			
<i>Cattle Treatment (CT)</i>	1,65	1.21	0.2754
<i>Site</i>	4,65	1.31	0.2765
<i>Block(Site)</i>	5,65	0.78	0.5701
<i>Year</i>	2,64	4.34	0.0170
<i>CT x Year</i>	2,64	1.29	0.2823
<i>Year x Site</i>	8,130	2.54	0.0132
<i>Year x Block</i>	10,130	2.13	0.0267
<i>CT x Site</i>	4,65	1.16	0.3353
<i>CT x Site x Year</i>	8,130	0.50	0.8550
<i>F. Exotic Perennial Forbs</i>			
<i>Cattle Treatment (CT)</i>	1,65	0.59	0.4457
<i>Site</i>	4,65	2.64	0.0418
<i>Block(Site)</i>	5,65	1.48	0.2098
<i>Year</i>	2,64	2.44	0.0956
<i>CT x Year</i>	2,64	1.33	0.2722
<i>Year x Site</i>	8,130	1.80	0.0822
<i>Year x Block</i>	10,130	1.44	0.1708
<i>CT x Site</i>	4,65	3.14	0.0202
<i>CT x Site x Year</i>	8,130	0.88	0.5386
<i>G. Shrubs</i>			
<i>Cattle Treatment (CT)</i>	1,65	0.00	0.9990
<i>Site</i>	4,65	2.07	0.0946
<i>Block(Site)</i>	5,65	0.36	0.8756
<i>Year</i>	2,64	0.63	0.5376
<i>CT x Year</i>	2,64	2.30	0.1088
<i>Year x Site</i>	8,130	0.29	0.9679
<i>Year x Block</i>	10,130	0.42	0.9336
<i>CT x Site</i>	4,65	1.17	0.3305
<i>CT x Site x Year</i>	8,130	0.73	0.6681

Figure 1

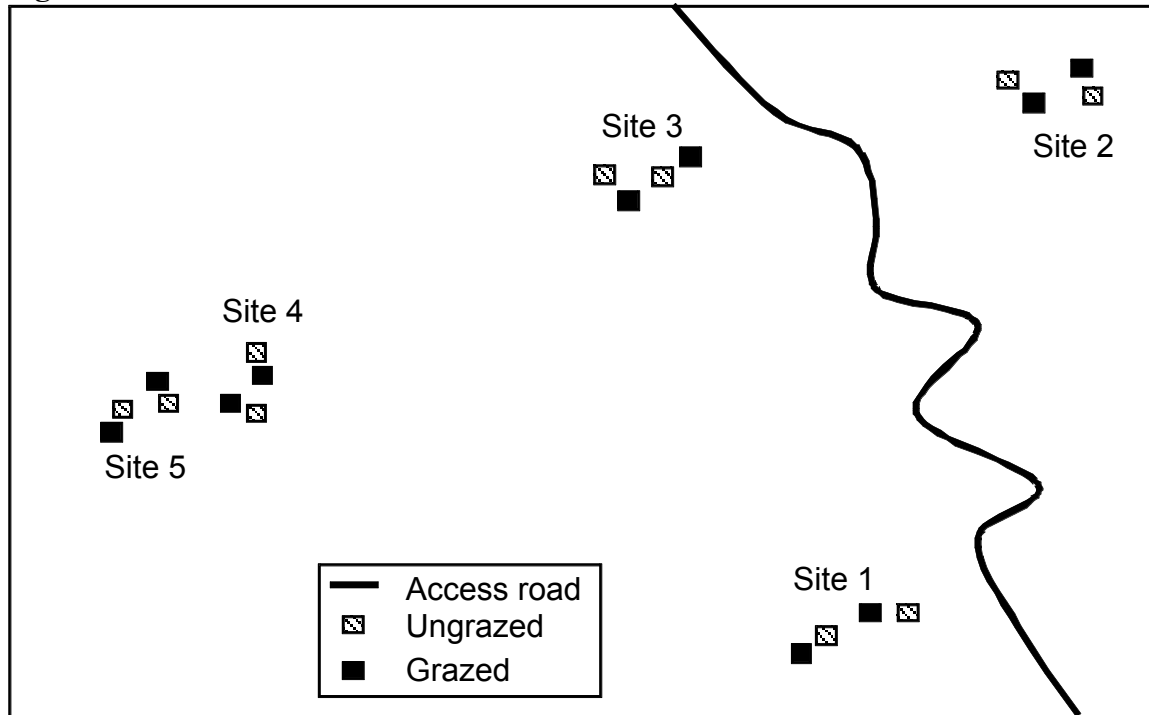


Figure 1. Diagram of the spatial arrangement of plots in a cattle enclosure experiment established in Palo Corona Regional Park. Ungrazed experimental plots are indicated by hatched squares, grazed control plots, by black squares.

Figure 2

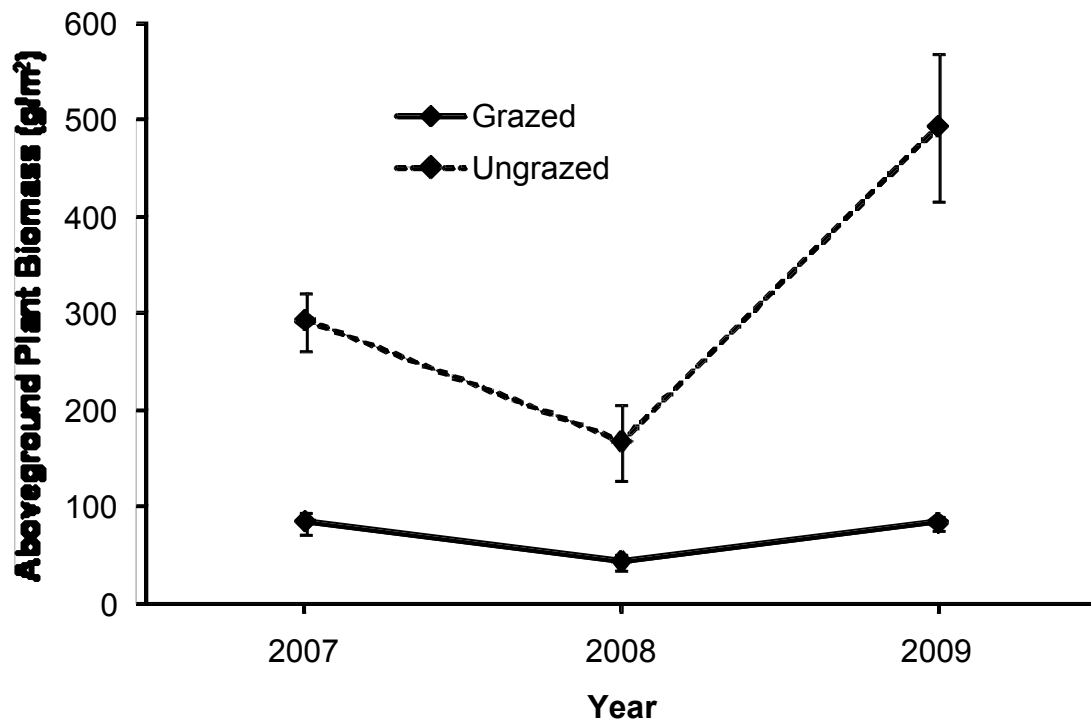


Figure 2. Influence of cattle grazing treatment and year on aboveground dry plant biomass (g/m^2).

Figure 3

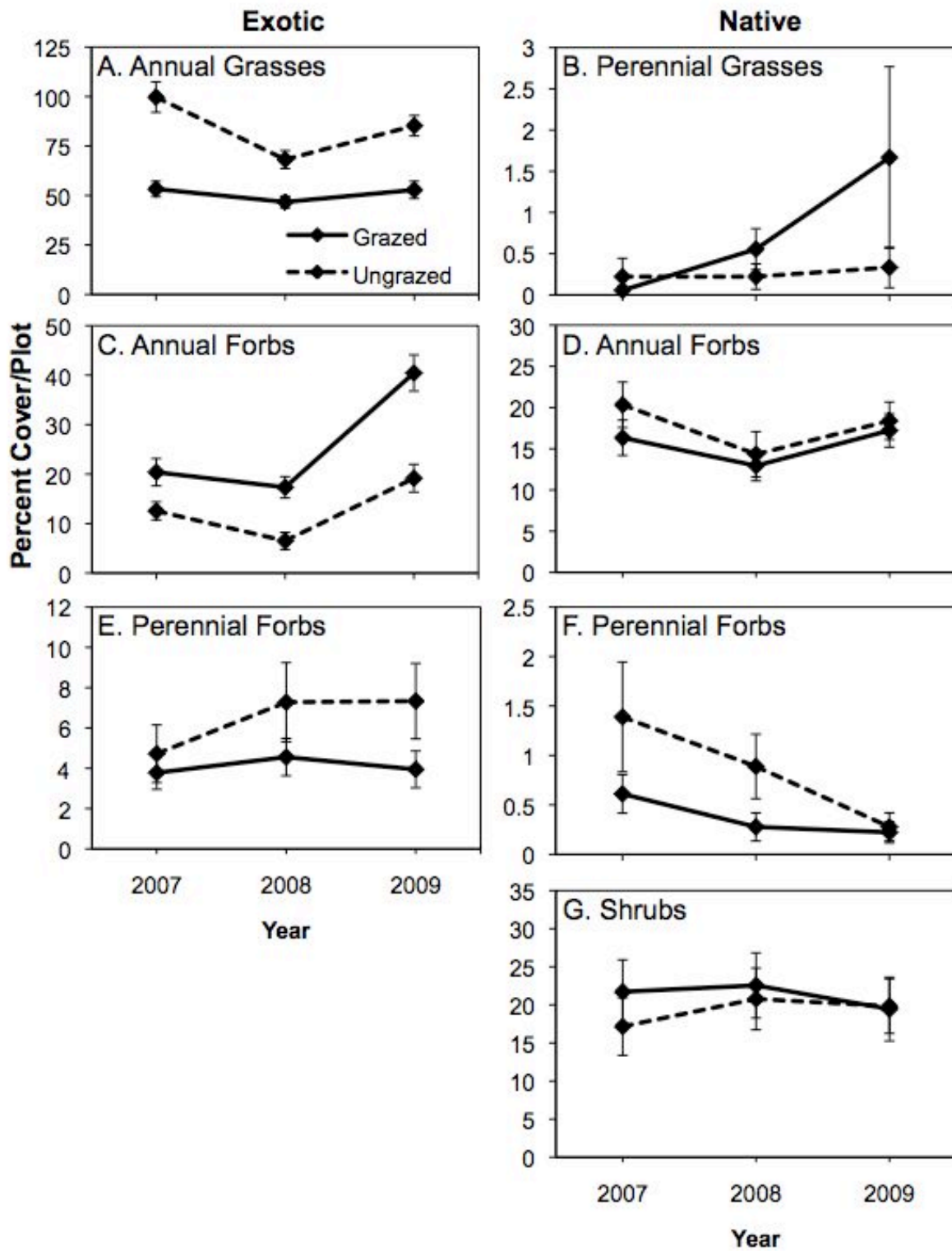


Figure 3. Influence of cattle grazing treatment and year on the absolute percent cover of seven plant functional groups.

Figure 4

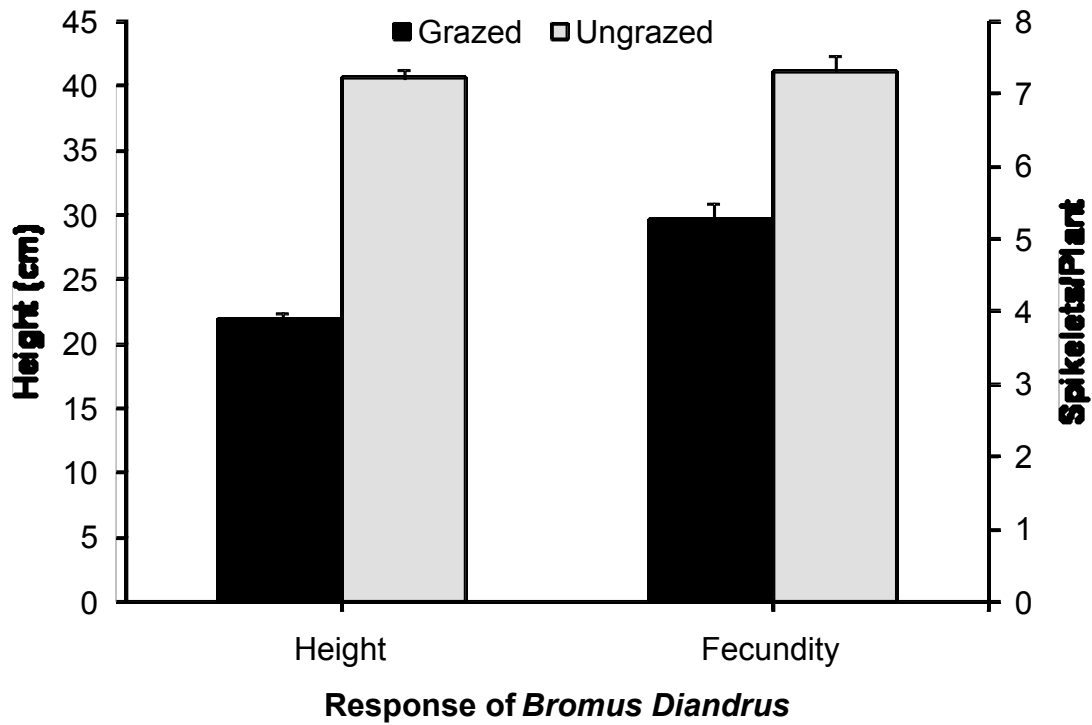


Figure 4. Response of *Bromus diandrus* height (cm) and spikelet production per plant to the presence or absence of grazing treatment in the spring of 2009. Spikelet production (fecundity) is plotted against the secondary vertical axis found on the right of the figure.

SECTION 4

INFLUENCE OF CATTLE GRAZING ON AN ENDANGERED LYCAENID BUTTERFLY AND ITS HOST PLANT

Abstract. Invasion by non-native plant species can cause dramatic changes in plant community composition and is considered to be an important component of global environmental change. In grassland communities, cattle grazing is commonly used as a management tool to control exotic plant invasions and considerable research has focused on evaluating the benefits of this management tool for native plant species. Unfortunately, less attention has been given to understanding the extended consequences of grazing for resident animal species, particularly in North America. Nowhere is this research more urgently needed than in California grasslands, which are one of the most invaded systems worldwide. Here, we summarize research that examines the effects of cattle grazing on an endangered lycaenid butterfly, the Smith's blue butterfly (*Euphilotes enoptes smithi*), in a California coastal grassland. For this research we used an enclosure experiment to address the following questions: 1) How does cattle grazing affect the growth and survival of *Eriogonum* host plants? and 2) How does cattle grazing affect the abundance of adult and larval butterflies? Our results clearly show that cattle grazing reduced the volume of *Eriogonum* host plants and decreased the average size of adult and juvenile plants. Grazing did not reduce survival of juvenile host plants and had no direct effects on seedling abundance. We also did not detect any effect of cattle on the abundance of male and female butterflies. In contrast, we found that grazing was associated with an increase in the abundance of larvae in one year (2007), but had no effect in another (2008). We argue that grazing can benefit larval abundance primarily through changes in habitat structure. Because grazing substantially decreased the height of invasive annual grasses, we hypothesize that it can increase the apparency of host plant inflorescences in some years and make them more accessible to ovipositing female butterflies. This in turn could explain the observed increase in larval abundance in one of two years. If cattle continue to have negative effects on the host plant in subsequent years, we suspect that any benefits of grazing on butterfly larval abundance may not persist long term and could even switch from positive to negative. However, if such negative effects of cattle on butterflies develop in these ridge-top landscapes, we believe that the population-level impacts on this endangered butterfly would be minimal or non-existent, because our research has shown that the Smith's blue is extremely abundant in the adjacent ravine habitats, which are expansive and heavily dominated by its host plant.

INTRODUCTION

As non-native plant species become increasingly prevalent in ecosystems throughout the world (Mooney et al. 1986, Drake et al. 1989, Vitousek et al. 1996, Mack et al. 2000, Mooney and Hobbs 2000, Lockwood et al. 2007), there is an urgent need to develop land management techniques that are effective at reducing the dominance of these invaders. Grasslands in regions experiencing Mediterranean-type climates are particularly vulnerable to plant invasions and are quickly becoming some of the most imperiled ecosystems in temperate zones (Samson and Knopf 1996, Muller et al. 1998, Mack 1989). Grazing by cattle is one tool currently used to manage invaded grassland communities (Knapp et al. 1999, Stohlgren et al. 1999, DiTomaso 2000, Harrison et al. 2003, Hayes and Holl 2003a, Jackson and Bartolome 2007). Although livestock grazing over the past two centuries has been implicated in the initial demise of grassland ecosystems (Waser and Price 1981, Painter and Belsky 1993, Fleischner 1994), an increasing number of studies have shown that, when appropriately managed, cattle grazing can yield positive results for native plant communities (Hayes and Holl 2003b, Marty 2005). Grazing can be used to decrease the dominance of exotic annual grasses, thus effectively reducing the competitive pressure on native taxa and subsequently increasing the survival (Dyer and Rice 1997, Brown and Rice 2000), richness (Harrison 1999, Knapp 1999, Hayes and Holl 2003b, Marty 2005), and abundance (Griggs 2000, Hayes and Holl 2003b, Marty 2005) of native plant species (Howe 1999, Levine 2003).

While there is a growing body of research examining the effects of cattle on native plant communities and the use of grazing as a management tool, much less attention has focused on the extended consequences of grazing for resident animal species (see Gordon and Prins 2007 for a review). Grazing may impact animal taxa by altering the abundance or characteristics of their plant resources and habitats as well as by affecting their ability to move through and perceive the environment. For small mammalian herbivores, reductions in available plant biomass due to high grazing pressure have been attributed to declines in the abundance of field voles, prairie dogs and giant kangaroo rats (Schmidt et al. 2005, Cheng and Richie 2006, Christian et al. 2008). Similar effects have been reported for a number of native insect herbivores, where a decrease in growth or survival of host plants – caused either by direct consumption of the plant by cattle or indirectly by decreasing host plant survival through trampling, soil compaction or altering soil chemistry – can lead to rapid reductions in insect species richness (Kruess and Tschardt 2002, Allen-Diaz et al. 2004, Saarinen et al. 2005).

Cattle grazing has also been shown to benefit a wide range of native animal taxa. For example, grazing had positive impacts on terrestrial invertebrates (Vulliamy et al. 2006, Zahn et al. 2007, Dumont et al. 2009), aquatic invertebrates (Marty 2005, Pyke and Marty 2005), salamanders (Pyke and Marty 2005), lizards (Germano et al. 2001, Newbold and MacMaheon 2006), and kangaroo rats (Germano et al. 2001). More complex results were reported by DeBano (2006), who found that there were wide-ranging responses of insect orders to grazing within the same community. Cattle grazing can also have variable effects on the same animal species. For example, voles and prairie dogs that were negatively affected by high grazing pressure responded positively to moderate grazing (Schmidt et al. 2005, Cheng and Richie 2006).

With only a few exceptions, cattle grazing has been shown to have resoundingly positive effects on native butterflies. Numerous studies have clearly linked cattle grazing with both higher butterfly abundance and species richness (Swengel 1996, Elligsen et al. 1997, Poyry et al. 2004, Saarinen et al. 2005, Dumont et al. 2009). There have been several hypotheses to explain these positive results. First, by reducing exotic plant dominance, cattle can create beneficial environments for native host plants to germinate and become established (Young and Evans 1989, Dyer and Rice 1999), which in turn could support larger butterfly populations. Secondly, cattle grazing may indirectly benefit resident butterflies by reducing grass height and biomass surrounding their host plants, thereby increasing apparency and leading to greater egg deposition on host plants (Severns 2008). Third, foraging by cattle could alter environmental conditions, such as microclimate, changing conditions for immature butterflies or mutualists. For example, in one European grassland, cattle reduced vegetation height and created favorable conditions for an ant mutualist of the large blue butterfly, *Maculinea arion*. When grazing was removed, the ant declined in abundance and the butterfly went extinct at that site (Thomas 1980 in Samways 1994).

A small number of studies have reported negative effects of cattle grazing on butterfly abundance and species richness. However, these negative effects only occurred in systems with very high grazing intensities (Elligsen et al. 1997, Swengel and Swengel 1999, Poyry et al. 2004). While the specific mechanisms underlying these results are not well documented, there is some evidence to suggest that cattle may contribute to declines in butterfly abundance largely through indirect negative effects on larval host plants (Saarinen et al. 2005).

These studies have greatly advanced our understanding of the effects of cattle grazing on native butterfly taxa, but they have a number of limitations. For instance, most of this research has been correlative rather than experimental, which limits our ability to conclude that cattle grazing is causing the observed changes in butterfly abundance and species richness. These studies have also focused primarily on the abundance of adult or immature life stages and very little attention has been paid to the long-term effects of cattle grazing on larval host plants. In addition, almost all of the research examining the effects of grazing on butterflies completed to date has been conducted in Europe and grasslands from this region have had a very long and well-documented evolutionary history of grazing by livestock (Pykala 2000). In comparison, the grazing history, frequency and intensity in other grassland regions is less well studied. For example, large herds of grazing animals have been absent from much of western and southwestern North America for thousands of years (McDonald 1981) and the frequency and intensity of these historical grazing patterns are unknown (Axelrod 1985, Wagner 1989). Therefore, it is reasonable to assume that the responses of extant butterfly populations to cattle grazing in European grasslands may be quite different from butterfly species in other parts of the world.

Here, we summarize results from a three-year exclosure experiment conducted along the central coast of California to evaluate the influence of cattle grazing on the federally endangered Smith's blue butterfly (*Euphilotes enoptes smithi*) and its host plant *Eriogonum parvifolium*. Many populations of this imperiled butterfly occur in coastal grasslands (Arnold 1983a and b; Emmel and Emmel 1993) that, like such habitats throughout California, have become increasingly dominated by exotic grasses from Europe and Asia over the past two hundred years (see Stromberg et al. 2007 and references therein). Cattle grazing has been an integral part of these

landscapes historically and is being used currently in some areas to control the dominance of exotic annual grasses. To address the consequences of this management activity, we explore two research questions: 1) Does cattle grazing influence the survival, growth and/or abundance of the Smith's blue butterfly's host plant, *Eriogonum parvifolium*? and 2) Does grazing lead to changes in the abundance of Smith's blue adults and larvae? Addressing these questions will be critical for efforts to understand the consequences of management actions designed to control plant invasions for non-target animal species such as endangered butterfly species.

STUDY SYSTEM

We conducted this research project at Palo Corona Regional Park (PCRP), a 4000 hectare protected area managed by the Monterey Peninsula Regional Park District in association with the Big Sur Land Trust and The Nature Conservancy. The grassland portions of this landscape were grazed by cattle for decades prior to becoming a park and all grazing stopped as of 2000. In 2007, this research was implemented and grazing was re-introduced to Palo Corona Regional Park.

Study sites were all located within the 81 hectare Panoche Management Unit of PCRP at elevations ranging from 400-450 m. Located 1.6 km south of Carmel in Monterey County, California, and 4.8 km inland, PCRP has a Mediterranean-type climate with a strong coastal influence. The climate is moderate, with rainy winters and warm summers that are typically moderated by frequent coastal fog layer in mornings and evenings. Wind speed and direction varies dramatically, and along exposed ridge tops wind speeds can gust over 32 km/hour.

The Smith's blue butterfly (*Euphilotes enoptes smithi*) occurs in several locations at PCRP and recent surveys have indicated that it is most abundant within the Panoche Management Unit (L. Overtree, personal communication). The vegetation in the Panoche Management Unit consists primarily of open, grassy ridges and steep shrub-covered slopes and ravines. On hilltops and in areas of intermediate slope, the vegetation community is a mix of both grasses and shrubs. Shrubs consist primarily of the sea-cliff buckwheat (*Eriogonum parvifolium*) and to a much lesser degree, the naked-stemmed buckwheat (*Eriogonum nudum*), both members of the Polygonaceae. *Eriogonum parvifolium* is an evergreen woody shrub endemic to California and populations are most abundant within the Panoche Management Unit (L. Overtree, personal communication). At PCRP it grows up to 100 cm in height and width and is typically characterized by an abundant floral display of pink inflorescences. Inflorescences are composed of a dense head of 5-50 small flowers, each approximately 2-3 mm in length. In comparison, *E. nudum* occurs sparsely and in small patches across the Panoche field site; this species is perennial, leaves form basal rosettes, and head-like clusters of 3-20 small white to light-pink flowers grow on leafless pedicels.

Similar to the majority of grasslands in California, the grasslands in the Panoche Unit of PCRP are dominated by a range of exotic annuals from Europe and Asia. The species most frequently encountered are *Bromus diandrus* and *Bromus hordeaceus*, although *Lolium multiflorum*, *Avena barbata*, and *Aira Caryophyllea* are also common (M Skaer, unpublished data). Despite the great abundance of non-native grass species, the grasslands in PCRP also support a variety of

native perennial grasses, *Nassella pulchra* and *Danthonia Californica*, which are found at low densities throughout the study area.

As with many other lycaenid butterflies (Cushman and Murphy 1993a and b, Fiedler 1996), very little is known about the ecology of the Smith's blue, although there are a few publications on its systematics and natural history (see Arnold 1983a and b; Emmel and Emmel 1993). This subspecies is confined to coastal dune, scrub and grassland habitats in Monterey County where it is known to feed and nectar on two species of buckwheat, *Eriogonum parvifolium* and *E. latifolium* (Arnold 1983a).

Some experts consider *Eriogonum nudum* to an inland variety of *Eriogonum latifolium* (G. Hayes, personal communication), and as such, may potentially be a second host plant for the Smith's blue at our study site. In field observations, we only observed Smith's blue butterflies visiting *E. parvifolium* and not *E. nudum* flowers. In addition, at our study area at Palo Corona Regional Park, *E. parvifolium* begins to flower in June and continues to bloom throughout the summer until mid August, at which time most blooms have senesced. In contrast, *E. nudum* was commonly observed with closed buds throughout most of July and a small % of individuals were observed flowering in mid-late July. The observed separation in flowering phenology between the two buckwheat species combined with two years of close observation of butterfly visitation behavior, led us to conclude that in the Panoche unit of Palo Corona Regional Park, only *Eriogonum parvifolium* is a host plant for the Smith's Blue butterfly and hereafter, "*Eriogonum*" will refer to this species only.

Like most species in the genus, the Smith's blue butterfly lives in close association with its host plants, using them as a primary nectar source, larvae food source, and to locate, court and copulate with mates (Arnold 1983a). Paralleling the blooming of its host plants, the Smith's blue flight season varies by year and site, but generally spans a period of 40 days over the summer (Arnold 1983a). More coastal populations typically emerge in mid June, while butterflies at inland sites, such as PCRP, often emerge closer to July and can continue into early September. Adult butterflies live for one week, but emergence is staggered over the season. Females lay their eggs singly in *Eriogonum* inflorescences on recently opened flowers or flowers still in bud, and eggs hatch in 4-8 days. The resulting cryptically colored larvae have chewing mouthparts and feed on petals and seeds of their host plant for about three to four weeks. At this study site, we only found larvae on inflorescences that were at least partially in bloom (>3 open flowers per inflorescence) or senescing; no larvae were seen on budding inflorescences. Larvae go through five larval instars before pupating on inflorescences or in the leaf litter at the base of their host plant (Arnold 1983b, D. Graydon, personal observation). Pupation occurs over a period of approximately 12 months from the time larvae pupate in late summer to adult emergence in the summer of the following year.

Arnold (1983a) reports that ants tend late instar larvae of the Smith's blue, but we detected very little evidence for this in the Panoche Unit of PCRP. Additionally, Arnold found that the Smith's blue is attacked heavily (42%– 62% of late in-star larvae) by parasitoids at his coastal study sites (Arnold 1983a), but we found no evidence for a high parasitoid load our sites in Palo Corona. In fact, lab rearings of late in-star Smith's blue larvae yielded only three possible parasitoids from a sample of 43 larvae collected in the field (D. Graydon, personal observation).

METHODS

Design and Establishment of the Cattle-Exclosure Experiment

In January and February of 2007, we established a cattle-exclosure experiment on the ridge tops of the Panoche Management Unit at PCRPP, where grassland vegetation and shrubs co-occur. These ridge top areas are prime locations for cattle grazing and also support an abundance of SBB and its buckwheat host plant. We established 20 8 x 8 meter plots grouped into five sites, consisting of four plots each (Figure 2). Plots within sites were matched visually for similarity in slope, aspect and vegetation composition. In addition, plots within sites were separated from their nearest neighbor by at least 2 meters.

At each site, we grouped plots in pairs based on proximity and then randomly assigned treatment levels within each pair (Figure 2). Plots either received fencing that excluded cattle or remained unmanipulated to serve as controls (two controls and two exclosures per site). All plots had four steel t-posts at their corners and exclosure plots had four additional mid-posts, corner bracing, and four strands of barbed wire encircling them.

Grazing occurred from March 22 to April 16 in 2007 and from February 17 to March 30 in 2008. A rancher placed 69 cow-calf pairs on the Panoche Unit in 2007 and 63 cow-calf pairs in 2008. In both years, cattle were removed from the unit when approximately 544.1 kg/acre (1200 pounds/acre) RDM remained. Grazing was timed to best maximize potential benefits for the native grassland community while simultaneously minimizing any direct negative impacts of cattle on the Smith's blue butterfly by grazing in early spring before adults emerge. By grazing cattle in early spring, only one life stage, pupae, was potentially susceptible to direct impacts of cattle. In addition, the possibility that cattle actually impacted Smith's blue pupae was considered low given the relatively protected location of pupae at the base of host plant shrubs.

Effects of Cattle Grazing on Buckwheat Host Plants

To determine the influence of cattle grazing on host plant density, we located and quantified the size of all *E. parvifolium* shrubs in each of our 20 plots on two dates. Sample one was taken in November 2007 before the 2008 grazing season, and sample two was taken after grazing was completed in May 2008 (Figure 3). For each sample we calculated the size of each buckwheat host plant found in the plots with a minimum height of 5 cm. We determined the center height and four diameters of each shrub and then calculated its volume using the formula for a hemisphere ($\frac{2}{3}\pi r^3$).

To assess the impact of cattle disturbances on individual buckwheat plants, we recorded the number of broken branches found on these host plants in our 20 plots after cattle had been removed in May 2008. We measured the diameter of each broken branch at the base of the break and categorized them as small (diameter ≥ 5 mm and < 10 mm) or large (diameter ≥ 10 mm). Branches with diameters less than 5 mm were not quantified because they may break easily due to wind and are very difficult to count accurately.

To assess the long-term effects of grazing on individual plant survival and growth, we selected and tagged a subset of small plants (< 45 cm in height) within each plot. We randomly selected and labeled three branches on each plant. Our first measurements were taken in February 2008, after the first grazing season in 2007 was complete (Figure 3). We measured the diameter of each branch at the junction with the next woody stem and measured branch length from this junction to the distal tip. To obtain an accurate measure of plant height, we averaged three measurements taken along the line of maximum diameter, the height at each edge and the height at the shrub center. In late April 2008, after the second season of cattle grazing was completed, we searched each plot for our tagged plants and located marked branches. If a plant could not be located, we assumed it had died and, if labeled branches could not be found, we assumed they had broken off.

To determine the effects of cattle grazing on host-plant seedling germination and seedling survival, we sampled the abundance of *E. parvifolium* seedlings two times in 14 of our 20 experimental plots (only one pair was sampled at blocks 3, 4, and 5). The first sample was collected March 1, 2007 just after the second grazing season started and when germination of *Eriogonum* seedlings had begun in our study area. The second sample was collected on April 25, 2007 after grazing was completed (Figure 3). We collected samples using randomly generated coordinates to place four 50 x 50 cm quadrats within each experimental plot. Once a coordinate was reached, we placed quadrats 10cm from the main stem of the nearest reproductive *Eriogonum* host plant. For each sample we carefully searched each quadrat and recorded the number of seedlings and the % cover of bare-ground and herbaceous vegetation.

Flight-Season Phenology and Effects of Grazing on Adult Butterflies

Between early June and early August in both 2007 and 2008, we estimated the relative abundance of adult Smith's blue butterflies in our 20 plots. This was accomplished by walking a V-shaped transect across each plot, going from the North-east corner to the opposite midpoint and then down to the lower-South-east corner. The observer slowly walked this transect over a 45 second period, disturbed herbaceous and woody vegetation with a butterfly net and recorded the total number of male and female Smith's blues observed in each plot. This method was designed to disturb butterflies basking or otherwise hidden from sight and increase the observer's ability to detect adults. Before each survey, we recorded maximum and average wind speed, temperature, and relative humidity using a Kestrel 3000 Pocket Weather Meter. We also estimated aspect, slope, cloud cover and percent of host plant cover in bloom, bud, and senescence. Like many lycaenid butterflies, Smith's blue adults are often much less active during cold and windy weather or low sun radiance (personal observation and see New 1993). Thus, we only conducted butterfly surveys during ideal weather conditions: temperatures over 15°C, average wind speed below 20.9 km/h, and no to minimal cloud cover.

Influence of Cattle Grazing on Larval Abundance

To assess the effects of cattle grazing on Smith's blue larvae, we measured larval abundance in our 20 plots from the exclosure experiment in a detailed sample taken during the 2008 and 2009 flight seasons. In each plot, we recorded larvae abundance, larvae size, number of inflorescences

searched, and the percent of host plant in bloom, in bud, and senescing. We estimated the length of each larva by placing a clear plastic ruler alongside the length of the larva and estimating size to nearest millimeter while taking care not to dislodge or harm the larvae. Sampling was conducted on July 24 and 25 at site 1 (a more phenologically advanced area) and between August 1 and 3 for the remaining four sites. Due to variation among plots in host plant density and the extremely time-intensive nature of searching for the small and cryptically colored Smith's blue larvae, we adjusted search time per plot by two weighting factors. First, we weighted search time by the total volume of buckwheat recorded in May 2008 in each plot. For both years, we searched each plot for 20 minutes per m³ of host plant present. In addition, because larvae are only found on blooming host inflorescences we further adjusted our total search time for each plot by the percentage of buckwheat cover in bloom. In summary, the amount of time spent searching for butterfly larvae was determined by host plant volume and the percentage of that volume available for larvae (blooming).

During larval sampling, we systematically searched all host plants in a plot for the allotted time (described previously) and focused exclusively on inflorescences from the outer surfaces of shrubs, since our results from 2007 showed that this is where the vast majority of larvae are located (D. J. Graydon and J. H. Cushman, unpublished data). We carefully paced ourselves to ensure that samples were taken from the entire area of each plot.

Effects of Cattle on Grass Height

To evaluate differences in vegetation height, we used four permanent 1m x1m quadrats that were placed in the center of each quarter of the experimental plots. In spring of 2007 and 2008 we measured the height of the grass nearest four standard locations in each quadrat.

Statistical Analyses

To assess the influence of cattle grazing on the size of *Eriogonum* shrubs, we performed a repeated-measure mixed model using a linear mixed model in SAS 9.1.3 (SAS Institute, Inc., Cary, North Carolina, USA). For this analysis, we used grazing treatment (grazed, ungrazed), plot (1-20), site (1-5) and block (two per site) nested in site as the grouping factors, sample date (November 2007 and May 2008) as the repeated measure and plot aspect as a covariate. Our response variable for this analysis was total host plant volume per plot. Site and block were treated as random effects whereas all other variables were treated as fixed effects.

For this and all other repeated measure mixed models, we selected the best fitting covariance structure for our analyses by comparing AIC values (Akaike 1973, Littell et al. 1996). We also verified the assumptions of normality and homogeneity of variances for all analyses by comparing model fit using AIC fit statistics and by visually examining residual plots. Except for the grazing treatment term, we removed predictor variables and interaction terms from the model if the initial analysis revealed them to be non-significant.

To evaluate the effects of grazing on size of juvenile *Eriogonum* plants, we used the same model as described above, with the exception of different sample dates (February 10 and April 25 2008)

for the repeated measures. The three response variables were juvenile plant height, branch length, and branch diameter averaged per plot.

To assess the influence of cattle on abundance of *Eriogonum* seedlings and ground cover types, we ran three more repeated-measure analyses. Again, we used the same mixed model as described above for these analyses, with the exception of different repeated measures (March 1 and April 25, 2008) and an additional grouping factor, quadrat (1-4), nested in plot. To assess grazing effects on seedlings, we used the total number of seedlings found per quadrat as the response variable and log-transformed ($\log_{10}[x] + 1$) these data to satisfy model assumptions. Response variables used in the analyses of ground cover types included the mean % cover of bare ground and mean % cover of herbaceous vegetation per quadrat. These response variables were also log transformed to meet model assumptions.

To determine the impact of cattle on adult and larval Smith's blue butterflies, we again performed several mixed models. The models were similar to those described above except for different repeated measures and additional covariates in the analysis of adult abundance. For adult analyses, the repeated measures were sample day (day # since June 1st) nested in sample year (2007 and 2008). We also included % cloud cover, average and maximum wind speed, temperature, % humidity, plot aspect, and % flowering host plant volume (% bloom + % bud) as covariates, and our two response variables were the total abundance of male and female Smith's blues per plot. Plot aspect was the only covariate for the analysis of larval abundance. The response variable used to analyze the effect of grazing on juvenile Smith's blues was the number of larvae found per minute of search time in 2008 and 2009, weighted by the amount of buckwheat in plots and their phenological state. Response variables for all three analyses were log transformed ($\log_{10}[x] + 1$) to satisfy model assumptions of normal distribution and equal variances of data.

We also conducted several non-repeated-measure analyses using linear mixed models to further explore the influence of cattle grazing on *Eriogonum*. Here the basic model was similar to those described previously, except that the repeated measure was omitted. Our response variables for these analyses were the total number of broken *Eriogonum* branches per plot, the abundance of seedlings per quadrat on March 1, 2007 (or 2008) and the percent seedling survival per quadrat (# seedlings/quadrat in April divided by those in March 2007). All three of these response variables were log transformed ($\log_{10}[x] + 1$) to meet assumptions of normality.

To understand the most important variables influencing the survival of juvenile *Eriogonum*, we conducted a backwards elimination stepwise logistic regression using JMP 7.0.1 (SAS Institute, Inc., Cary, North Carolina, USA). The categorical response variable for this analysis was the status of juvenile *Eriogonum* plants (dead, alive) in April 2008 and the predictor variables in the model included grazing treatment, plot aspect, mean juvenile *Eriogonum* height, mean branch length, and mean branch diameter per plant. We tested for differences in percent survival of juvenile plants after one season of grazing using a Wilcoxon/Kruskal Wallis test.

We assessed the relationship between ground cover (% cover of bare-ground and herbaceous vegetation) and *Eriogonum* seedling abundance by performing separate linear regressions using JMP 7.0.1. The dependent variable in these analyses is the total number of *Eriogonum* seedling

found per plot. The predictor variables for these analyses were either mean % cover of bare-ground or herbaceous vegetation per plot. All data were log transformed ($\log_{10}[x] + 1$) to satisfy assumptions of normal distribution and equal variances of data.

We conducted a Wilcoxon/Kruskal-Wallis analysis to determine the impact of cattle grazing treatment on grass height. Means were pooled across years and averaged by plot for this analysis.

RESULTS

Effects of Cattle Grazing on Buckwheat

There was a trend ($P=0.075$) for cattle grazing to reduce the volume of *Eriogonum* shrubs in our exclosure experiment (Figure 4, Table 1a). In addition, we detected a significant grazing x year interaction (Table 1a), with the effect of cattle on shrub volume being greater in 2008 than in 2007. We also found that grazing significantly increased the number of *Eriogonum* branches that were broken, regardless of branch size (Figure 4b, Table 1b).

Cattle grazing had considerable effects on the growth and characteristics of juvenile *Eriogonum*. Although juvenile plant height was not significantly reduced by grazing alone (Figure 5a, Table 2b), we detected a significant grazing x time interaction (Table 2b), with cattle grazing having greater negative effects on plant height later in the season in 2008. Branch length and diameter of juvenile *Eriogonum* were both significantly reduced by cattle grazing (Figure 5b, Table 2b and c). We also detected a significant grazing x time interaction for both branch length and diameter (Table 2b and c), with the effects of cattle on juvenile *Eriogonum* again being greater later in the season. The survival of juvenile *Eriogonum* plants was not directly affected by cattle grazing ($z=1.06$, $P=0.28$, Figure 6). Instead, we found that initial plant height was the best predictor of the survival of juvenile plants from winter (February 10th) to spring (March 25th) in 2008 (Table 2).

Our data indicate that cattle grazing did not have a significant effect on *Eriogonum* seedling abundance (Figure 7, Table 2d). Rather, we found that aspect and sample date were the best predictors of seedling abundance (Figure 7, Table 2d). In addition, cattle had no effect on either the abundance of germinated *Eriogonum* seedlings in winter (Table 2e) or the survival of seedlings from winter to spring (Table 2f).

We found that the abundance of *Eriogonum* seedlings per plot increased significantly with increasing percent cover of bare ground and decreased with increasing percent cover of herbaceous vegetation (Figure 8, Table 4a). Further analysis revealed a trend ($P=0.064$) for grazing to increase the percent cover of bare ground (Figure 9, Table 2g). And although we found no effect of cattle on percent cover of herbaceous vegetation (Figure 9, Table 2h), there was a significant grazing x time interaction (Table 2h), where grazing reduced herbaceous vegetation cover in the winter but had the opposite effect in the spring.

Flight-Season Phenology and Effects of Grazing on the Smith's Blue Butterfly

The flight season for the Smith's blue butterfly at our study site occurred from June 10 through July 25 in 2007 and from June 5 to August 1 in 2008 (Figure 10). Males were more frequently observed along transects than females and emerged earlier in the flight season (Figure 10).

The enclosure experiment showed that cattle grazing did not significantly affect the abundance of female Smith's blue butterflies (Figure 11, Table 3a), but we found that sample day was a significant predictor of female butterfly abundance (Table 3a). In contrast, male butterflies responded significantly to grazing treatment (Figure 11, Table 3b), with more males found in ungrazed plots. In addition, male butterfly abundance increased with increasing wind temperatures and similar to female butterflies, more males were observed as the flight season progressed (Table 6). We also found that the abundance of male Smith's blue butterflies decreased later in the day and decreased with increasing humidity, but that this effect was greatest in ungrazed plots (Table 6).

Our results for larvae were more complex than those for adult butterflies. Although we did not detect an overall effect of cattle grazing on the number of larvae found in plots per minute of search time, there was a significant grazing x year interaction term (Table 5c). As clearly shown in Figure 12, grazing caused an increase in the number of larvae detected in 2008, but this effect was absent in 2009.

Influence of Grazing on Grass Height

Results from the non-parametric Wilcoxon/Kruskal-Wallis test revealed that cattle grazing significantly decreased grass height ($z=4.39$, $P<0.0001$; Figure 13) at our study sites.

DISCUSSION

Lycaenid butterflies are some of the most imperiled fauna in North America (Cushman and Murphy 1993a, 1993b) and commonly occur in grasslands that have been invaded heavily by exotic plants. In this paper, we show that cattle grazing, when used as a management tool for controlling invasive grasses, has complex implications for the long-term persistence of the Smith's blue butterfly, a federally endangered lycaenid. Results from our three-year enclosure experiment showed that the effect of cattle grazing on the abundance of Smith's blue larvae varied between years, being positive in 2008 and neutral in 2009 (Figure 12). During this same period, grazing led to substantial reductions in the abundance and volume of the butterfly's host plant (Figure 4a).

Effects of Cattle Grazing on Buckwheat Host Plants

Cattle grazing substantially reduced the size and volume of adult *Eriogonum* host plants, and this effect increased in magnitude over time (Figure 4a, Table 2a). In addition, cattle reduced the height, branch length and branch diameter of juvenile *Eriogonum* plants after only one season of grazing (Figure 5, Table 2). Several hypotheses may explain these negative effects on adult and juvenile host plants. First, cattle may be consuming host plants in addition to grasses. Although

cattle are not known to be highly selective foragers, several studies have shown that they avoid woody species, instead preferring more palatable and easily digestible resources such as grasses (McInnis and Vavra 1987, Wallis deVries and Daleboudt 1994, Bokdam and Gleichman 2000). Our extensive observations over three years strongly support this view and we are thus confident that cattle herbivory was not responsible for the observed reductions in shrub size and volume.

A second hypothesis to explain the negative impacts of cattle on *Eriogonum* is that these grazers trampled host plants while feeding. Our data offer support for this hypothesis, given that grazing was associated with much higher numbers of broken branches for both adult (Figure 4b) and juvenile *Eriogonum* (Figure 6). Because the majority of broken branches, and large branches especially, were found on the ground near host plants, or scattered nearby, we are confident that branches were not consumed by cattle or other native herbivores such as black-tailed deer. Our findings strongly point to trampling of *Eriogonum* shrubs by cattle as a primary factor causing the observed decreases in host plant size.

Previous research has shown that cattle grazing can provide ‘safe-sites’ for seedling germination and abundance of native plants by disturbing soils (McIntyre and Lavorel 1994), decreasing thatch (Menke 1992), and increasing bare ground (Young and Evans 1989, Milchunas et al. 1992, Meyer and Schiffman 1999). Thus, at the onset of this study, we assumed that disturbances from cattle grazing would be important for *Eriogonum* seedling establishment in our exotic-dominated study sites. This expectation was further encouraged by the finding that cattle greatly reduced aboveground plant biomass (Skaer et al. unpublished data), reduced exotic grass cover (Figure 12), and increased the amount of bare ground (Table 2g) at our study sites. Nevertheless, in contrast to our expectations, we failed to detect an effect of cattle grazing on the abundance or survival of *Eriogonum* seedlings (Table 2). We are fairly perplexed by this result, especially given that our field observations clearly indicated that *Eriogonum* seedlings were most abundant in open patches adjacent to host plants.

One possible explanation for our results is that, at least in the years of our study, seedling abundances were highly variable among plots (see error bars in Figure 7) and this variation swamped any grazing effect. A potential explanation is that seedling mortality was incredibly high during our study, and any grazing effects that might have existed quickly disappeared. An alternative explanation is that *Eriogonum* seedlings do benefit from the “safe-sites” created by grazing, but because seedlings germinate and grow during early spring, they are simultaneously exposed to damage by grazing cattle in this same time period. Thus, the benefits of grazing for buckwheat seedling germination and survival may be offset by the negative impacts of trampling by cattle.

Influence of Grazing on the Smith’s Blue Larvae

Our enclosure experiment produced mixed results for the effects of cattle grazing on Smith’s blue larvae – positive effects in 2008 and no effect in 2009. One hypothesis to explain the positive effects of cattle on larvae in 2008 is that grazing increased the visual apparency of host plants to female butterflies. At our study site, *Eriogonum* shrubs in grazed plots were surrounded by short, cropped grasses and were more visually conspicuous than shrubs growing in ungrazed plots, which grew amidst patches of taller, ungrazed grasses. Greater apparency in

turn could increase egg deposition and subsequently the abundance of larvae on host plants (Courtney 1983 and Wiklund 1984, Severns 2008). Offering support for this hypothesis are studies of another lycaenid butterfly, *Maculinea alcon*, which have shown that taller, more visually apparent host plants received significantly more eggs than shorter, less apparent ones (Nowicki et al. 2005, Arnyas et al. 2006). In addition, Severns (2008) showed that clipping neighboring exotic grasses increased apparency of a host plant and in turn more than doubled egg deposition by the Fender's blue butterfly (*Icaricia icarioides fenderi*). In our system, we hypothesize that tall exotic annual grasses reduced the visual apparency of *Eriogonum* shrubs to ovipositing Smith's blues. By substantially reducing the average height of exotic grasses (Figure 13), grazing cattle may increase host plant apparency, which in turn may increase egg deposition and larval abundance.

We are less clear as to why there was no effect of cattle on Smith's blue larvae in 2009. The result was especially surprising given that cattle reduced plant biomass more in 2009 than in 2008, which would have resulted in buckwheat host plants being even more apparent to ovipositing females and thus led to more larvae on shrubs in 2009. One possible explanation for this result is that, in 2009, the positive effects of grazing (through increased apparency) were canceled out by the negative effects of cattle on buckwheat performance (through trampling). Although we lack data to evaluate this hypothesis, we suspect that the impact of cattle on Smith's blue larvae in any year may be the net effect of these two opposing forces.

Effects of Cattle Grazing on Adult Butterflies

Given that the majority of the literature on grazing report positive effects on adult abundance, and because we found an increase in larvae abundance in grazed plots (Figure 12), we expected that grazing would lead to increased abundance of both female and male adult butterflies. In contrast to this expectation, our exclosure experiment showed that cattle grazing decreased the abundance of male butterflies and had no influence on the abundance of adult female Smith's blue butterflies (Figure 11, Table 5). Here, we propose a number of hypotheses to explain these results. One interpretation of is that adult female butterflies are simply unaffected by grazing, or at least were unaffected at the spatial scale of our exclosure experiment. However, the fact that grazing increased the abundance of larvae (Figure 12) suggests that female Smith's blue butterflies laid more eggs on host plants and probably spent more time in grazed plots.

A second hypothesis to explain our adult abundance results is that the timing and weather conditions of our surveys did not allow us to accurately capture the average conditions experienced by butterflies. Our coastal, ridge-top study sites were frequently subject to high winds and fog during summer months when Smith's blue were active. Since we collected all adult abundance data on low-wind, clear days, it is possible that our data may not be an accurate reflection of adult abundance given the range of environmental variables they experience. In fact, considerable changes in habitat preferences with changing environmental conditions are not uncommon in butterflies (Dennis and Sparks 2006) and the influence of grazing-induced caused in habitat characteristics on adult Smith's blue butterflies may be markedly different during windy conditions.

Finally, our adult abundance results may be an accurate reflection of differential preferences of male and female Smith's blue butterflies. Male butterflies may respond strongly to host plant abundance, which is greatest in ungrazed plots (Figure 4a). In comparison, females may be highly selective, and apparency and accessibility of host plant inflorescences may contribute to a female butterfly's decision about which *Eriogonum* host plants to visit – more abundant patches of host plants in ungrazed plots or the more apparent and accessible plants found in grazed plots. Thus, female abundance may be driven by a more complex series of decisions. Like the males, she may also respond to the abundance of host plant at a site, but she may simultaneously be responding to a number of other variables as well, making her decision between grazed and ungrazed plots less straightforward as the data seem to suggest it is for male butterflies.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Our research has shown that cattle are having negative effects on cliff buckwheat and we suspect that continued grazing each year in the ridge-top areas will, over time, substantially reduce the dominance of shrubs. This prediction is in line with that of McBride and Heady (1968), who suggested that prolonged mechanical damage to native shrubs by cattle was critical in the transformation of shrub-grassland systems to their current grass-dominated state.

The ramifications of these cattle impacts for Smith's blue populations will depend on a number of factors. At a more local scale (i.e. the ridge-tops), we predict that the impact of cattle on this endangered butterfly will be the net effect of two opposing forces – the positive effects of grazing on Smith's blue larvae (through increased host apparency) and the negative effects of cattle on buckwheat performance (through trampling of shrubs). If the latter continues to grow in magnitude over the years, as we predict, then we suspect the net effect of grazing *at this local scale* will become increasingly negative. However, we believe that more landscape-level processes will prevent this from becoming a problem.

If cattle reduce the suitability of ridge-top areas for the Smith's blue, the long-term viability of these populations will depend on the degree to which the butterflies use buckwheat host plants in the adjacent ravines. These areas are dominated by cliff buckwheat and in most cases exceed 80% cover. In August of 2009, we conducted extensive surveys of the Smith's blue at three elevations in five ravines: near the base of the ravines, mid-slope and just below ridge-tops. The result of these timed surveys indicated that Smith's blue adults (both males and females) were extremely abundant in the ravines at all three elevations. While cattle regularly traverse the ravine slopes to reach the grass-dominated ridge-tops, they spend much less time in these areas. Consequentially, buckwheat growing in the ravines will escape serious damage from cattle and should play a critical role in maintaining Smith's blue populations.

LITERATURE CITED

- Akaike H. (1973). Information theory and an extension of the maximum likelihood principle. In B.N. Petrov and B. F. Csaki (Eds.), Second International Symposium on Information Theory, (p. 267-281). Akademiai Kiado: Budapest.
- Allen-Diaz B, RD Jackson, JW Bartolome, KW Tate, LG Oates. 2004. Long-term grazing study in spring-fed wetlands reveals management tradeoffs. *California Agriculture* 58:144-148.
- Arnold RA. 1983a. Ecological studies on six endangered butterflies (Lepidoptera: Lycaenidae): island biogeography, patch dynamics, and the design of habitat preserves. *University of California Publications in Entomology* 99:1-161.
- Arnold RA. 1983b. Conservation and management of the endangered Smith's Blue Butterfly, *Euphilotes enoptes smithi* (Lepidoptera: Lycaenidae). *Journal of Research on the Lepidoptera*.
- Arnyas E, J Bereczki, A Toth, K Pecsénye, Z Varga. 2006. Egg-laying preferences of the xerophilous ecotype of *Maculinea alcon* (Lepidoptera: Lycaenidae) in the Aggtelek National Park. *European Journal of Entomology* 103(3):587-595.
- Axelrod DI. 1985. Rise of the grassland biome, central North America. *Botanical Review* 51:163-201.
- Baughman JF, DD Murphy, PR Ehrlich. 1988. Population structure of a hilltopping butterfly. *Oecologia* (Berlin) 75:593-600.
- Bokdam J and JM Gleichman. 2000. Effects of grazing by free-ranging cattle on vegetation dynamics in a continental north-west European heathland. *Journal of Applied Ecology* 37: 415 – 431.
- Brown CS, and KJ Rice. 2000. The mark of Zorro: effects of the exotic annual grass *Vulpia myuros* on California native perennial grasses. *Restoration Ecology* 8(1):10-17.
- Cheng E and ME Ritchie. 2006. Impacts of simulated livestock grazing on Utah prairie dogs (*Cynomys parvidens*) in a low productivity ecosystem. *Community Ecology* 147:546-55.
- Christian CE, L Saslaw, S Butterfield. 2008. Cattle grazing for grassland management at Carrizo Plain National Monument: one size does not fit all. In: *Desert Report*; CNRCC Desert Committee.
- Courtney SP. 1983. Models of host-plant location by butterflies: The effect of search image and search efficiency. *Oecologia* 59:317-321.
- Courtney SP and S Courtney. 1982. The "edge-effect" in butterfly oviposition: Causality in *Anthocharis cardamines* and related species. *Ecological Entomology* 7(2):131-137.

- Cushman JH, and DD Murphy. 1993a. Conservation of North American Lycaenids - an overview. In Conservation Biology of Lycaenidae (Butterflies) (T.W. New, editor), pages 37-44. International Union for the Conservation of Nature, Gland, Switzerland.
- Cushman JH, and DD Murphy. 1993b. Susceptibility of lycaenid butterflies to endangerment: implications for invertebrate conservation. *Wings* (Xerces Society) 17:16-21.
- Debano SJ. 2006. Effects of livestock grazing on aboveground insect communities in semi-arid grasslands of southeastern Arizona. *Biodiversity and Conservation* 15:2547-2564.
- Dennis LH and TH Sparks. 2006. When is habitat not a habitat? Dramatic resource use changes under differing weather conditions for the butterfly *Plebejus argus*. *Biological Conservation* 129:291-301.
- DiTomaso JM. 2000. Invasive weeds in rangelands: species, impacts, and management. *Weed Science* 48(2):255-265.
- Dover JW. 1990. Butterflies and wildlife corridors. In: Nodder C (editor), *The game conservancy review of 1989*. The Game Conservancy, Fordingbridge p62-64.
- Dover J, and J Settele. 2009. The influences of landscape structure on butterfly distribution and movement: a review. *Journal of Insect Conservation* 13:3-27.
- Drake JA, HA Mooney, F. di Castri, R. H. Groves, FJ Kruger, M Rejmánek, and M Williamson. 1989. Biological invasions – A global perspective. *SCOPE* 37. Wiley, New York, NY.
- Dumont B, A Farruggia, JP Garel, P Bachelard, E Boitier and M Frain. 2009. How does grazing intensity influence the diversity of plants and insects in a species-rich upland grassland on basalt soils? *Grass and Forage Science* 64:92-105.
- Dyer AR, and KJ Rice. 1997. Intraspecific and diffuse competition: the response of *Nassella pulchra* in a California grassland. *Ecological Applications* 7(2):484-492.
- Elligsen H, B Beinlich, H Plachter. 1997. Effects of large-scale cattle grazing on populations of *Coenonympha glycerion* and *Lasiommata megera* (Lepidoptera: Satyridae). *Journal of Insect Conservation* 1:13-23.
- Emmel TG and JF Emmel. 1993. Smith's Blue, *Euphilotes enoptes smith* (Mattoni). In Conservation Biology of Lycaenidae (Butterflies) (T.W. New, editor), pages 131-132. International Union for the Conservation of Nature, Gland, Switzerland.
- Fry G and WJ Robson. 1994. The effects of field margins on butterfly movement. *BCPC Monographs*, 58, 111–116
Schultz, C.B. and Dlugosch, K.M. (1999) Nectar and hostplant

- Fleischner TL. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* 8(3):629-644.
- Germano D, GB Rathbun, LR Saslaw. 2001. Managing exotic species and conserving declining species. *Wildlife Society Bulletin* 29(2):551-559.
- Griggs FT. 2000. Vina Plains Preserve: Eighteen years of adaptive management. *Fremontia* 27(4):48-51.
- Gordon HT, and HHT Prins. 2007. *Ecological studies 195: the ecology of browsing and grazing*. Springer Berlin-Heidelberg.
- Haddad NM. 1999. Corridor use predicted from behaviors at habitat boundaries. *The American Naturalist* 153(2):215-227.
- Hayes GF and KD Holl. 2003a. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology* 17(6):1694-1702.
- Hayes GF and KD Holl. 2003b. Site specific responses of native and exotic species to disturbances in a mesic grassland community. *Applied Vegetation Science* 6:235-244.
- Harrison S. 1999. Native and alien species diversity at the local and regional scales in a grazed Californian grassland. *Oecologia* 121: 99-106.
- Harrison S, BD Inouye, and HD Safford. 2003. Ecological heterogeneity in the effects of grazing and fire on grassland diversity. *Conservation Biology* 17:837-845.
- Howe HF. 1999. Dominance, diversity and grazing in tallgrass restoration. *Ecological Restoration* 17(1):59-66.
- Jackson RD, and JW Bartolome. 2007. Grazing ecology of California grasslands. In: Stromberg M, JD Corbin, CM D'Antonio (editors) *California Grasslands: Ecology and Management*. University of California Press. p197-206.
- Janz N, A Bergstrom and J Johansson. 2005. Frequency dependence of host plant choice within and between patches: a large cage experiment. *Evolutionary Ecology* 19:289-302.
- Knapp AK, JM Blair, JM Briggs, SL Collins, DC Hartnett, LC Johnson, and EG Towne. 1999. The keystone role of bison in North American tallgrass prairie. *Bioscience* 49(1):39-50.
- Kruess A and T Tschardtke. 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation* 106:293-302.
- Levine JM, M Vila, CM D'Antonio, JS Dukes, K Grigulis and S Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B: Biological Sciences* 270(1517):775-781.

- Littell RC, GA Milliken, WW Stroup, and RD Wolfinger. 1996. SAS for Mixed Models, Vol. SAS Publishing, Cary, NC, USA
- Lockwood LJ, MF Hoopes, MP Marchetti. 2007. Editors: Invasion Ecology. Blackwell Publishing, Malden, MA, USA.
- Mack RN. 1989. Temperate grasslands vulnerable to plant invasion: Characteristics and consequences. Biological Invasions: A Global Perspective. John Wiley and sons, New York, NY. Pages 155-179.
- Mack RN, D Simberloff, WM Lonsdale, H Evans, M Clout and FA Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10(3):689-710.
- Marty J. 2005. Effects of cattle grazing on diversity in ephemeral wetlands. Conservation Biology 19(5):1626-1632.
- McBride JR and HF Heady. 1968. Invasion of grassland by *Baccharis pilularis* DC. Journal of Range Management 21:106-108.
- McDonald JN. 1981. North American bison; their classification and evolution. University of California Press, Berkeley.
- McInnis ML and M Vavra. 1987. Dietary relationships among feral horses, cattle, and pronghorn in southeastern Oregon. Journal of Range Management 40(1):60-66.
- McIntyre S and S Lavovel. 1994. Predicting richness of rare, and exotic plants in response to habitat and disturbance across a variegated landscape. Conservation Biology 8(2):521-31.
- Menke JW. 1992. Grazing and fire management for native perennial grass restoration in California grasslands. Fremontia 20(2):22-25.
- Meyer MD, and PM Schiffman. 1999. Fire season and mulch reduction in a California grassland: a comparison of restorations strategies. Madrono 46:25-37.
- Milchunas DG, WK Lauenroth, PI Chapman. 1992. Plant competition, abiotic, and long- and short-term effects of large herbivores on demography of opportunistic species in a semiarid grassland. Oecologia 92:520-531.
- Mooney HA, SP Hamberg, and JA Drake. 1986. The invasions of plants and animals into California. Pg 251-272 in Drake JA, HA Mooney, editors. Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag, New York, NY
- Mooney HA and RJ Hobbs. 2000. Editors: Invasive species in a changing world. Island Press, Washington, DC.

- Muller S, T Dutoit, D Alard, F Grevilliot. 1998. Restoration and rehabilitation of species-rich grassland ecosystems in France. *Restoration Ecology* 6(1):94-101.
- New TR. 1993. Introduction to the biology and conservation of the Lycaenidae. In: *Conservation Biology of Lycaenidae (Butterflies)*. TW New, editor. International Union for the Conservation of Nature; Gland, Switzerland. pp1-21.
- New TR. 1997. *Butterfly Conservation*. Oxford University Press, USA.
- Newbold S and JA MacMahon. 2006. Consequences of cattle introduction in a shrubsteppe ecosystem: indirect effects on desert horned lizards (*Phrynosoma platyrhinos*). *Western North American Naturalist* 68(3):291-302.
- Nowicki P, M Witek, P Skorka, M Woyciechowski. 2005. Oviposition pattern in the myrmecophilous butterfly *Maculinea alcon* (Denis and Schiffermuller) Lepidoptera: Lycaenidae, in relation to characteristics of foodplants and presence of ants. *Polish Journal of Ecology* 53(3):409-417.
- Painter EL and AJ Belsky. 1993. Application of herbivore optimization theory to rangelands of the western United States. *Ecological Applications* 3(1):2-9.
- Pe'er G, D Saltz, HH Thulke. 2004. Response to topography in a hilltopping butterfly and implications for modeling nonrandom dispersal. *Animal Behavior* 68(4):825-839.
- Poyry J, S Lindgren, J Salminen, M Kuussaari. 2004. Restoration of butterfly and moth communities in semi-natural grasslands by cattle grazing. *Ecological Applications* 14(6):1656-1670
- Pykala J. 2000. Mitigating human effects on European biodiversity through traditional animal husbandry. *Conservation Biology* 14(3):705-712.
- Pyke SR, and MJ Samways. 2001. Width of grassland linkages for the conservation of butterflies in South African afforested areas. *Biological Conservation* 101:85-96.
- Pyke CR, and JT Marty. 2005. Cattle grazing mediates climate change impacts on ephemeral wetlands. *Conservation Biology* 19(5):1619-1625.
- Rabasa SG, D Gutierrez, and A Escudero. 2005. Egg laying by a butterfly on a fragmented host plant: a multi-level approach. *Ecography* 28:629-639.
- Saarinen K, J Jantunen, A Valtonen. 2005. Resumed forest grazing restored a population of *Euphydryas aurinia* (Lepidoptera: Nymphalidae) in SE Finland. *European Journal of Entomology* 10:683-690.

- Samson FB, and FL Knopf. 1996. Prairie conservation: preserving North America's most endangered ecosystem. Island Press, Washington DC, USA.
- Samways MJ. 1994. Insect Conservation Biology. Chapman and Hall. New York, NY, USA.
- Schmidt NM, H Olsen, M Bildsoe, V Sluydts, H Leirs. 2005. Effects of grazing intensity on small mammal population ecology in wet meadows. *Basic and Applied Ecology* 6:57-66.
- Schultz CB, and EE Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82(7):1879-1892.
- Severns PM. 2008. Exotic grass invasion impacts fitness of an endangered prairie butterfly, *Icaricia icarioides fenderi*. *Journal of Insect Conservation* 12:651-661.
- Shields O. 1967. Hill topping. An ecological study of summit congregation behavior of butterflies of a southern California hill. *Journal of Research on Lepidoptera* 7:191-204.
- Stohlgren TJ, LD Schell, BV Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications* 9(1):45-64.
- Stromberg M, JD Corbin, CM D'Antonio. 2007. (editors) *California Grasslands: Ecology and Management*. University of California Press.
- Swengel AB. 1996. Observations of *Ineisialia irus* (Lepidoptera: Lycaenidae) in central Wisconsin 1988-1995. *Great Lakes Entomologist* 29:47-62.
- Swengel AB, and SR Swengel. 1999. Factors affecting abundance of adult Karner blues *Lycaeides melissa samuelis* (Lepidoptera: Lycaenidae) in Wisconsin barrens 1987-95. *Great Lakes Entomologist* 29: 93-105
- Thomas JA. 1983. The ecology and conservation of *Lysandra bellargus* (Lepidoptera, Lycaenidae). *Britain Journal of Applied Ecology* 20:59-83.
- Thomas JA, Thomas CD, Simcox DJ, RT Clarke. 1986. The ecology and declining status of the silver-spotted skipper butterfly (*Hesperia comma*). *Britain Journal of Applied Ecology* 23: 365-380.
- Thomas JA, RG Snazell, LK Ward. 2002. Are roads harmful or potentially beneficial to butterflies and other insects? In: Sherwood B, D Cutler, J Burton (editors) *Wildlife and roads: the ecological impact*. Imperial College Press, London p203-222.
- Traveset A and DM Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology and Evolution*. 21(4):208-216.

- Vitousek PM, CM D'Antonio, LL Loope, M Rejmanek, R Westbrooks. 1996. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* 21(1):1-16.
- Vulliamy B, SG Potts, PG Willmer. 2006. The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. *Oikos* 114:529-543.
- Wagner FH. 1989. Grazers, past and present. In: Huenneke LF, and HA Mooney (editors) *Grassland structure and function*. California annual grassland. Kluwer Academic Publishers, Boston, Massachusetts, USA, p151–162.
- Wallis deVries M, and C Daleboudt. 1994. Foraging strategy of cattle in patchy grassland. *Oecologia* 100:98-106.
- Warren MS. 1987. The ecology and conservation of the heath fritillary butterfly, *Mellicta athalia*. II. Adult population structure and mobility. *Journal of Applied Ecology* 24:483-498.
- Waser NM, and MV Price. 1981. Effects of grazing on diversity of annual plants in the Sonoran Desert. *Oecologia* 50:407-411.
- Wiklund C. 1984. Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. *Oecologia* 63:23-29.
- Young JA and RA Evans. 1989. Dispersal and Germination of Big Sagebrush (*Artemisia tridentata*) Seeds. *Weed Science* 37:201-206.
- Zahn A, A Juen, M Traugott, and A Lang. 2007. Low density cattle grazing enhances arthropod diversity of abandoned wetland. *Applied Ecology and Environmental Research*, 5(1):73-86.

Table 1. Results from linear mixed model analyses evaluating the effects of cattle grazing on reproductive adult *Eriogonum parvifolium* host plants. All non-significant terms, except main effects of cattle treatment, were removed from the final model. Significant effects ($p < 0.05$) are in bold. Covariance structure used for repeated measures was unstructured (*). Z statistics are presented for random variables (***).CT = Cattle Treatment

<i>Variable and Source</i>	<i>df (num,denom)</i>	<i>F / Z</i>	<i>P</i>
A. Volume (m^3)*			
Cattle Treatment	1, 9.04	4.04	0.075
Sample Date	1, 17.5	173.4	<0.0001
Date x CT	1, 17.5	4.60	0.046
B. Mean # Broken Branches			
Cattle Treatment	1, 5.4	8.09	0.008

Table 2. Results from linear mixed model analyses evaluating the effects of cattle grazing on seedling and juvenile *Eriogonum parvifolium*, as well as percent cover of bare ground and herbaceous vegetation. All non-significant terms, except main effects of cattle treatment, were removed from the final model. Covariance structures used for repeated-measures were unstructured (*), compound symmetry (**), and variance components (***). Significant effects ($p < 0.05$) are in bold and Z statistics are presented for random variables (****).

<i>Variable and Source</i>	<i>df(num,denom)</i>	<i>F / Z</i>	<i>P</i>
A. Juvenile Plant Height**			
Cattle Treatment	1, 9	3.47	0.095
Sample Date	1, 18	40.4	<0.0001
Date x CT	1, 18	47.9	<0.0001
B. Juvenile Branch Length**			
Cattle Treatment	1, 18	22.9	<0.0001
Sample Date	1, 18	50.5	<0.0001
Date x CT	1, 18	46.9	<0.0001
C. Juvenile Branch Diameter*			
Cattle Treatment	1, 17.5	22.5	0.0002
Sample Date	1, 18	12.6	0.0023
Date x CT	1, 18	48.7	<0.0001
D. Seedling Abundance***			
Cattle Treatment	1, 103	0.23	0.63
Sample Date	1, 103	52.7	<0.0001
Aspect	1, 5	16.3	0.009
E. Seedling Germination			
Cattle Treatment	1, 50	0.15	0.70
F. % Seedling Survival			
Cattle Treatment	1, 42	1.17	0.28
G. % Cover Bare Ground*			
Cattle Treatment	1, 4.5	5.94	0.064
Sample Date	1, 55	22.76	<0.0001
H. % Cover Vegetation***			
Cattle Treatment	1, 102	0.18	0.68
Sample Date	1, 102	94.6	<0.0001
Date x CT	1, 102	5.51	0.021

Table 3. Results from a backwards stepwise logistical regression on the effects of cattle grazing, plot aspect, mean plant height, mean branch length, and mean branch diameter on the status (dead or alive) of juvenile *Eriogonum parvifolium* in spring, after the second season of grazing. The main effect of cattle treatment was locked into the model; significant effects ($p < 0.05$) are in bold.

<i>Variable and Source</i>	χ^2	P
<i>Spring Plant Status</i>		
Cattle Treatment	0.90	0.34
Plant Height	6.33	0.012

Table 4. Results of linear regressions conducted to determine relative importance of cover variables in explaining variation in seedling abundance (mean # seedlings/plot). Significant effects ($p < 0.05$) are in bold.

<i>Variable and Source</i>	adjusted r^2	P
<i>Spring Seedling Abundance</i>		
Bare Ground	0.29	0.0271
Herbaceous Vegetation	0.72	<0.0001

Table 5. Results from linear mixed model analyses evaluating the effects of cattle grazing on adult and larval Smith's blue butterfly abundance. All non-significant terms, except main effects of cattle treatment, were removed from the final model. Covariance structure used for repeated measures was spatial power (*). Significant effects ($p < 0.05$) are in bold and Z statistics are presented for random variables (***)).

<i>Variable and Source</i>	<i>df(num,denom)</i>	F / Z	P
<i>A. # Female Butterflies*</i>			
Cattle Treatment	1, 143	0.004	0.85
Sample Day ***	–	1.83	0.034
<i>B. # Male Butterflies*</i>			
Cattle Treatment	1, 71.7	5.94	0.02
Time of Day	1, 153	15.6	<0.0001
Wind Max	1, 152	3.92	0.049
Humidity x CT	2, 177	4.03	0.019
Sample Day ***	–	2.01	0.022
<i>C. Larvae/Minute</i>			
Cattle Treatment	1, 27	1.14	0.30
Year	1, 27	48.86	<0.0001
Year x CT	1, 27	8.09	0.0084

Table 6. Covariance parameter estimates and least-square means. Random variables are designated with an asterisk (*).

<i>Variable and Source estimate</i>	estimate	LS-means	SE
<i>A. # Female Butterflies</i>			
Cattle Treatment			
Grazed	0.0054	0.1761	0.0481
Ungrazed	0	0.1707	0.0481
Sample Day *	0.0092	–	–
<i>B. # Male Butterflies</i>			
Cattle Treatment			
Grazed	- 0.272	0.264	0.065
Ungrazed	0	0.308	0.065
Time of Day	- 0.00041	–	–
Wind Max	0.0147	–	–
Humidity x CT			
Grazed	- 0.00018	–	–
Ungrazed	- 0.00491	–	–
Sample Day *	0.02578	–	–

Figure 1.

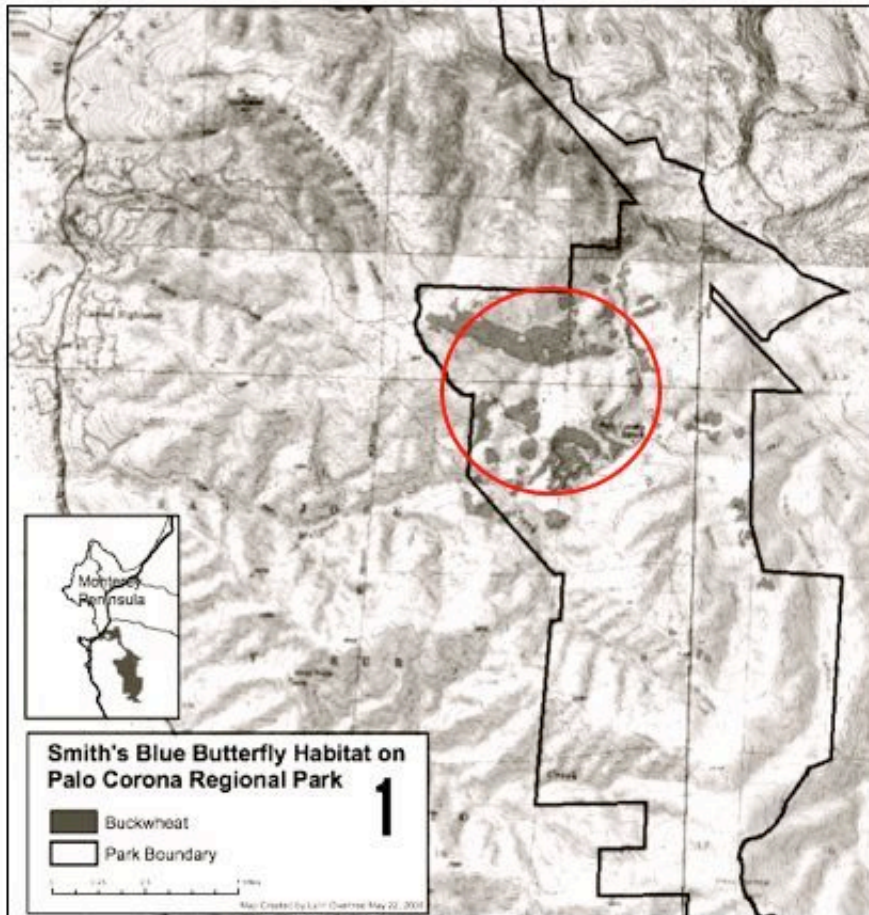


Figure 1. Location of Palo Corona Regional Park in Monterey County, California. The red circle identifies the region of the Panoche Management unit where research sites are located.

Figure 2

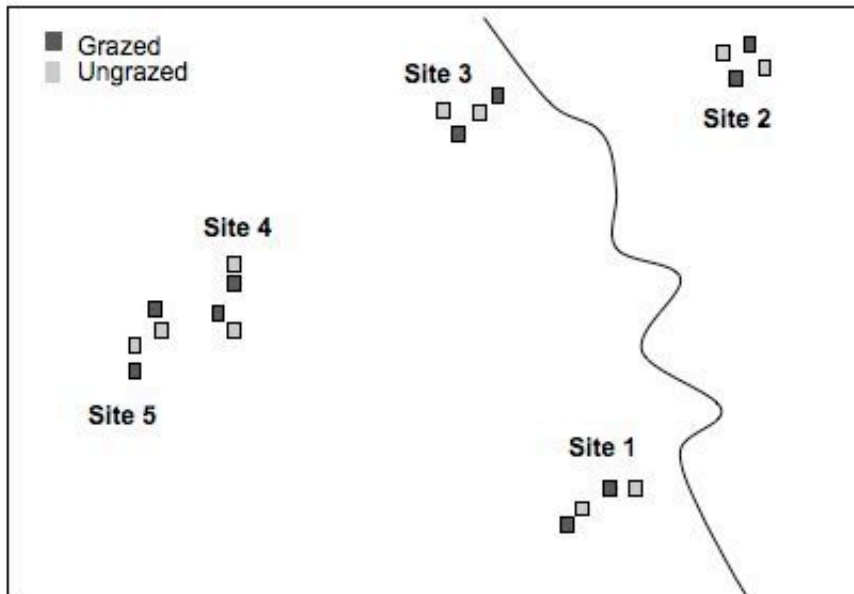


Figure 2. Schematic diagram illustrating the spatial arrangement of study plots in a cattle enclosure experiment within the Panoche management unit of Palo Corona Regional Park. The location of ungrazed, fenced plots, are indicated by light grey squares and grazed control plots are represented by dark grey squares.

Figure 3

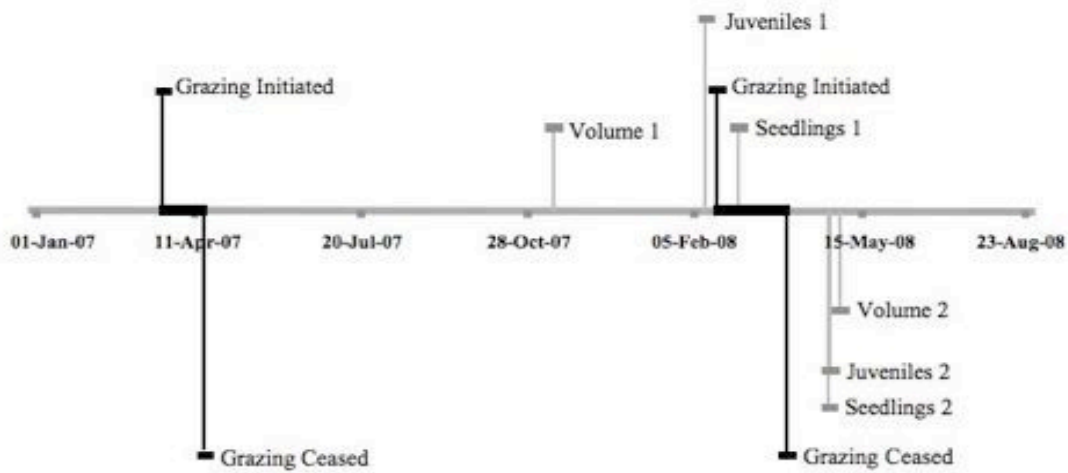


Figure 3. Time-line depicting the order and dates of data collection for *Eriogonum parivifolium* host plants. Grazing was conducted on two separate dates, from March 22 – April 16, 2007 and again from February 17 – March 30, 2008. Host plant volume data were collected first on November 11, 2007 and again on May 1, 2008. The first sample taken on juvenile *Eriogonum* shrubs was February 10, 2008 and the second sample was conducted on April 25, 2008. Seedling data were collected first on March 1, 2008 and then again on April 24, 2008.

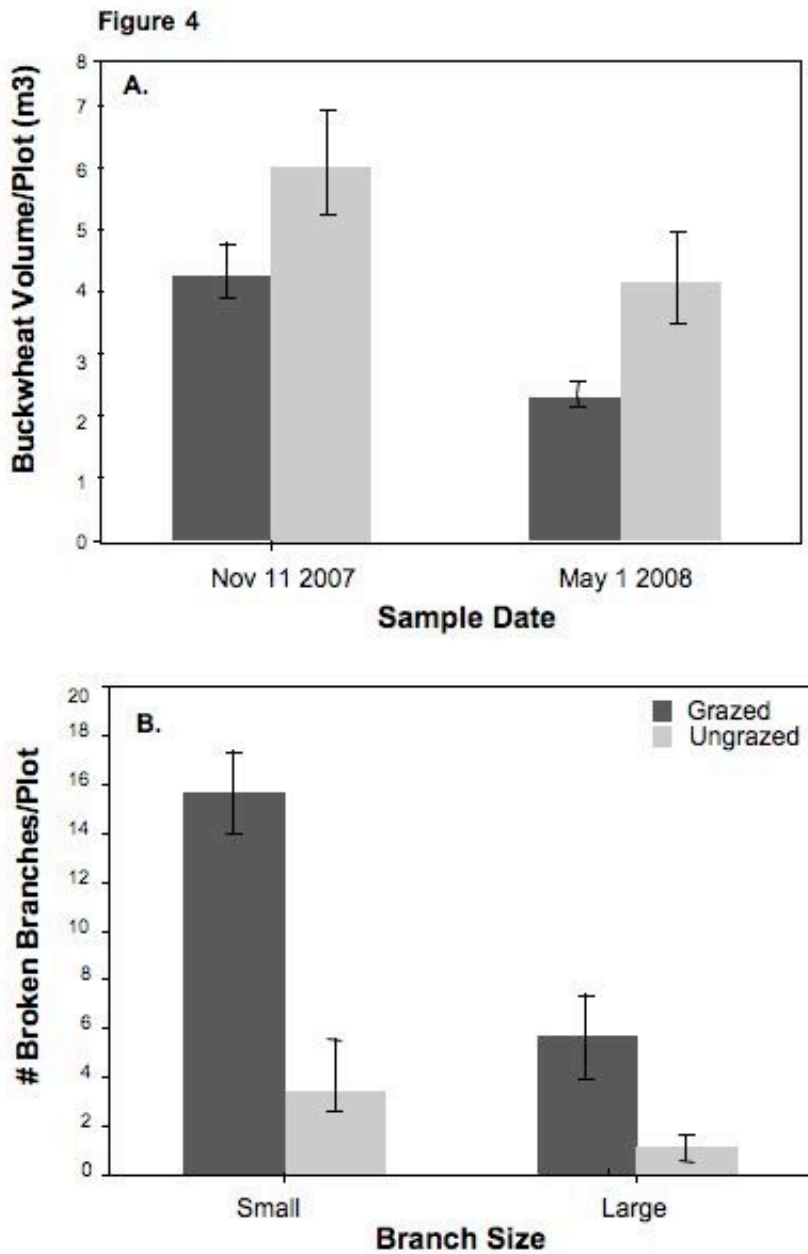


Figure 4. Response of reproductive *Eriogonum* host plants to the presence or absence of cattle grazing. (a) Mean (\pm 1 S.E.) *Eriogonum* volume per plot as a function of sample date and treatment, and (b) mean (\pm 1 S.E.) number of broken branches on host plants as a function of branch size and grazing treatment.

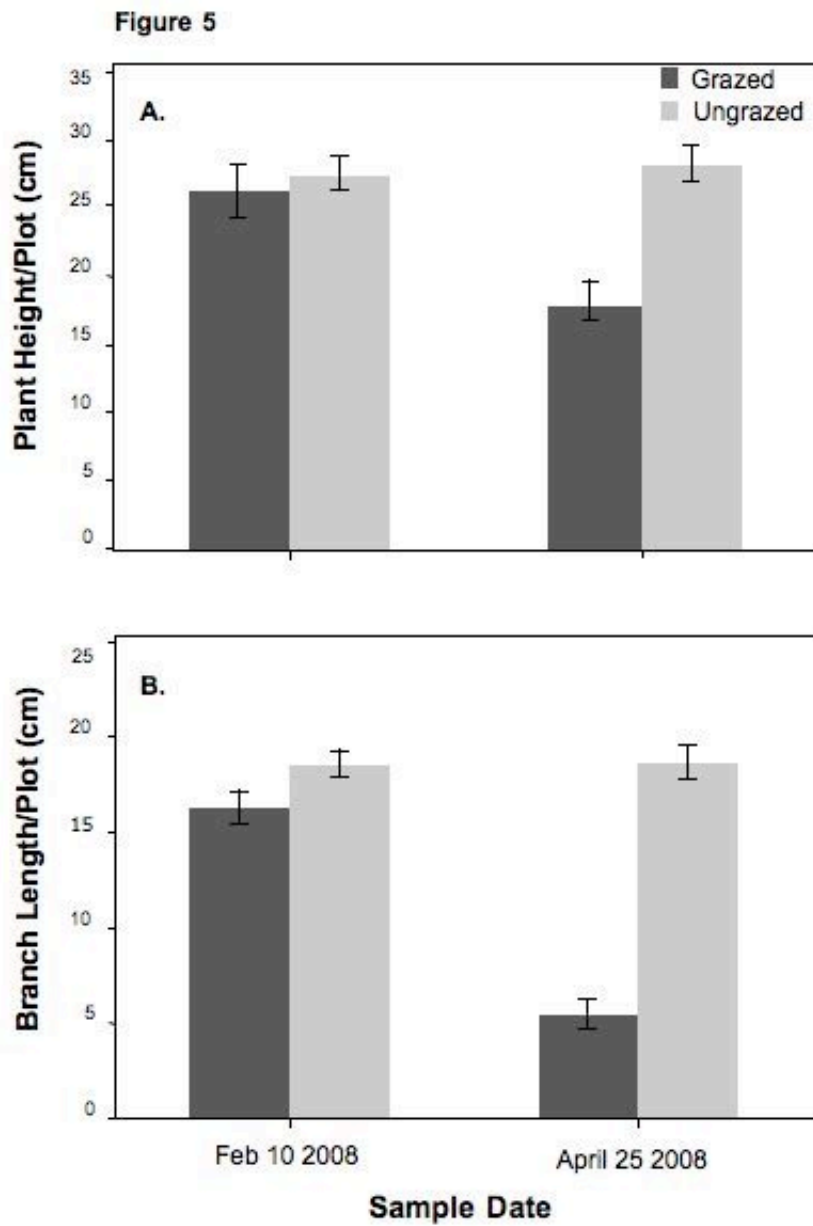


Figure 5. Influence of cattle grazing and sample date on mean (+ 1 S.E.) (a) plant height and (b) branch length of juvenile *Eriogonum parvifolium* shrubs.

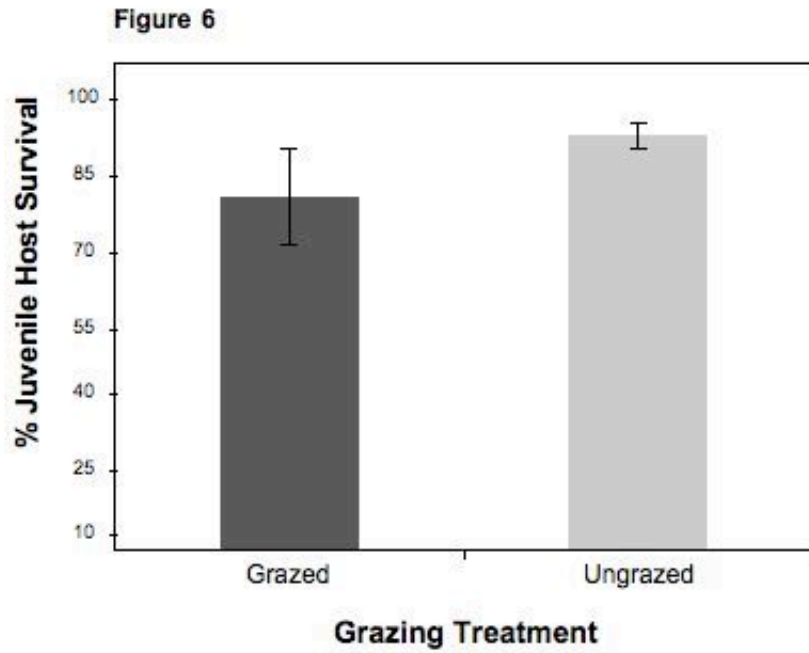


Figure 6. Average (+ 1 S.E.) percent survival of juvenile host plants as a function of grazing treatment; difference is not significant.

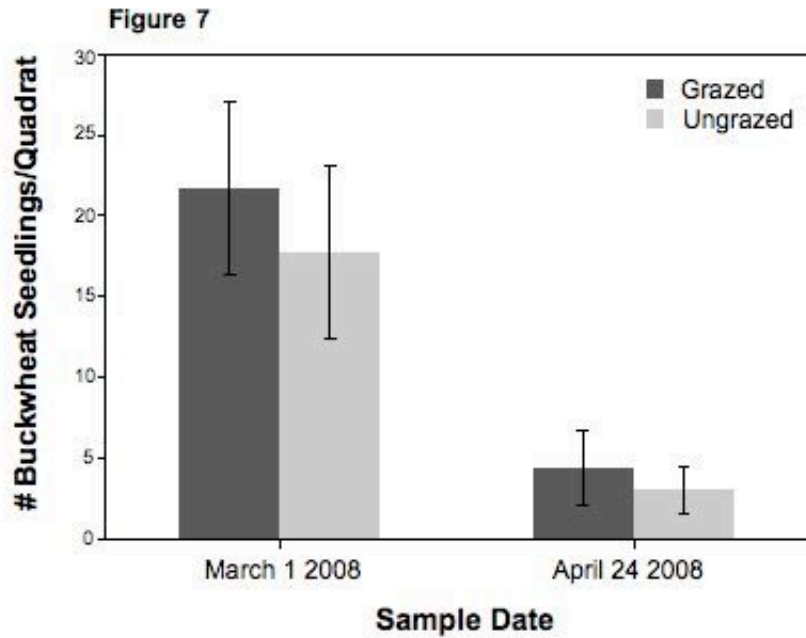


Figure 7. Mean (+ 1 S.E.) number of *Eriogonum* host plant seedlings per quadrat as a function of sample date and cattle grazing treatment.

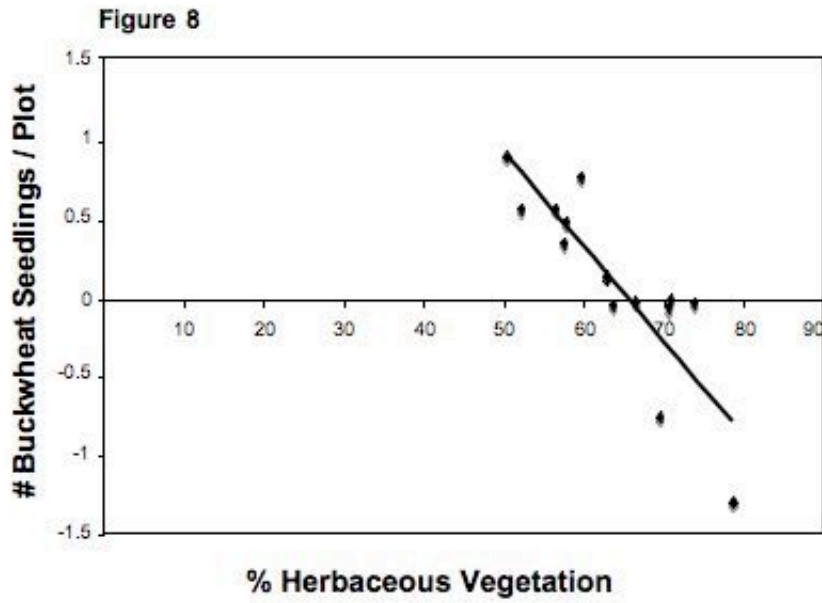


Figure 8. Influence of cattle grazing treatment on the mean (+ 1 S.E.) percent cover of herbaceous vegetation and bare ground.

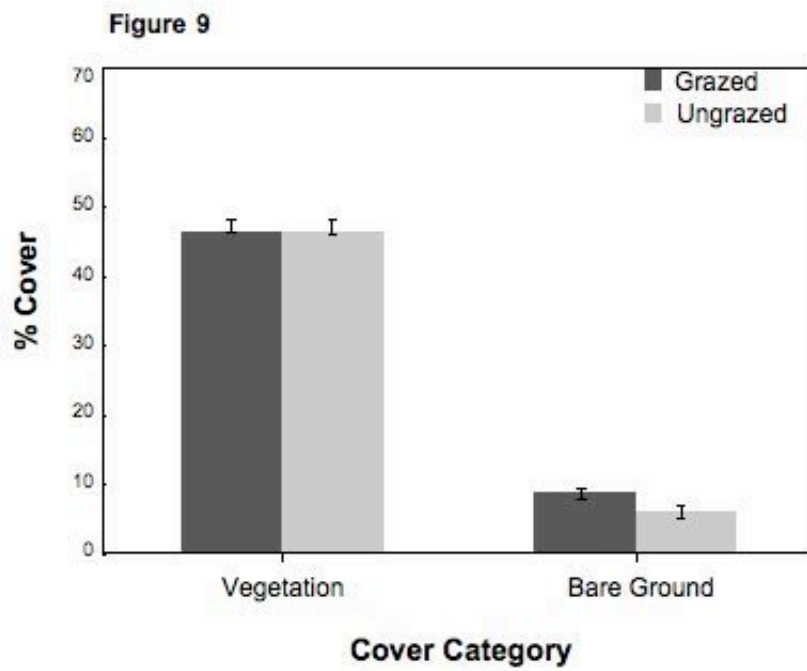


Figure 9. Relationship between percent cover of herbaceous vegetation and the abundance of *Eriogonum parvifolium* seedlings. Both variables were log-transformed to meet model assumptions of normality.

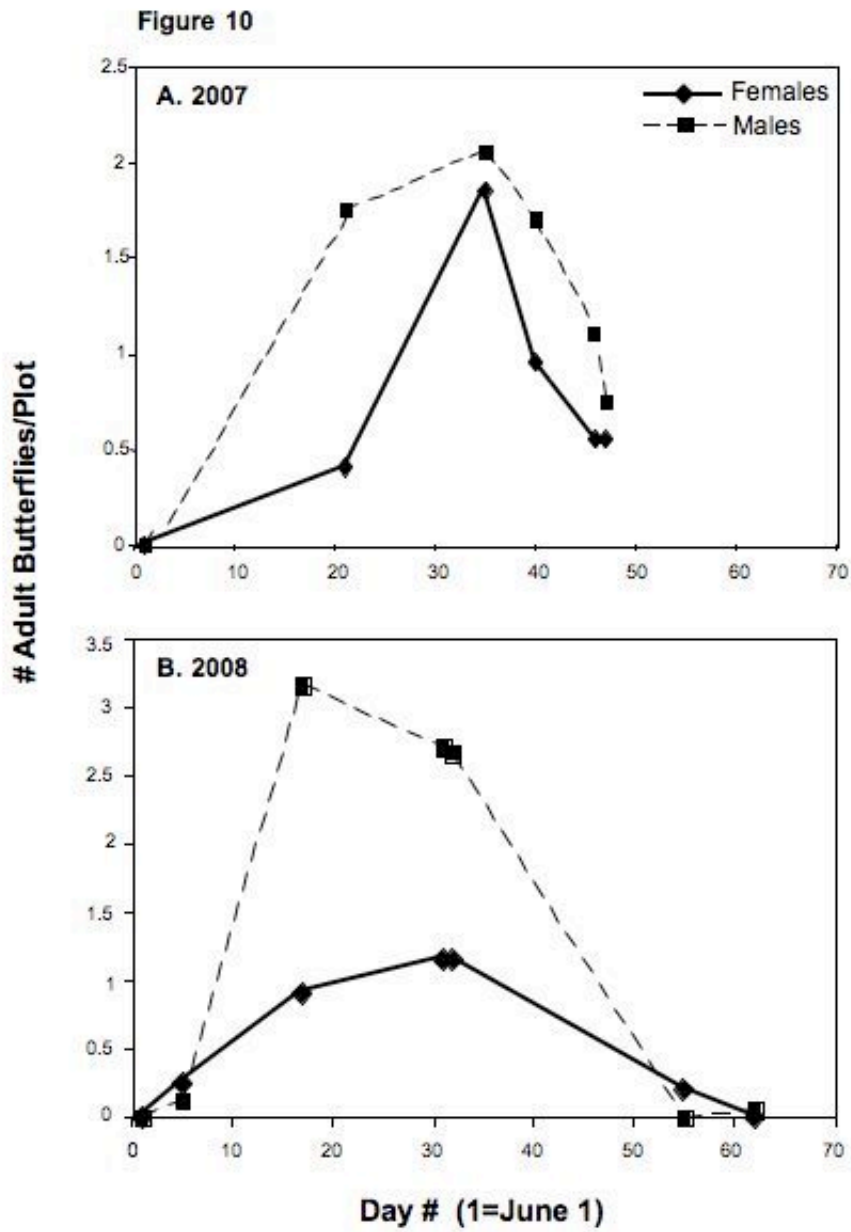


Figure 10. Distribution and abundance of adult Smith's blue butterflies observed in grazed and ungrazed experimental plots over the (a) 2007 and (b) 2008 flight seasons. Dashed lines indicate abundance of female butterflies and solid lines represent abundance of males.

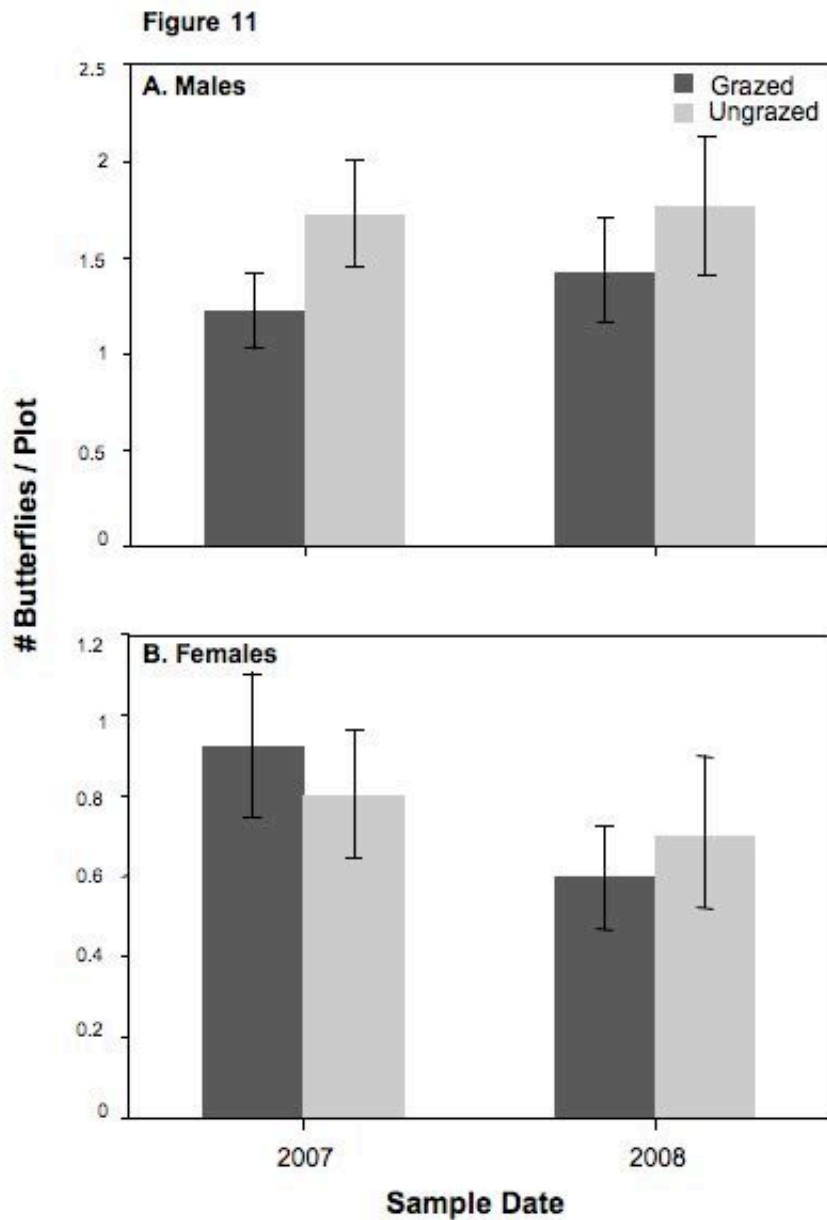


Figure 11. Mean (\pm 1 S.E.) number of adult (a) male and (b) female Smith's blue butterflies as a function of presence or absence of cattle grazing and sample year.

Figure 12

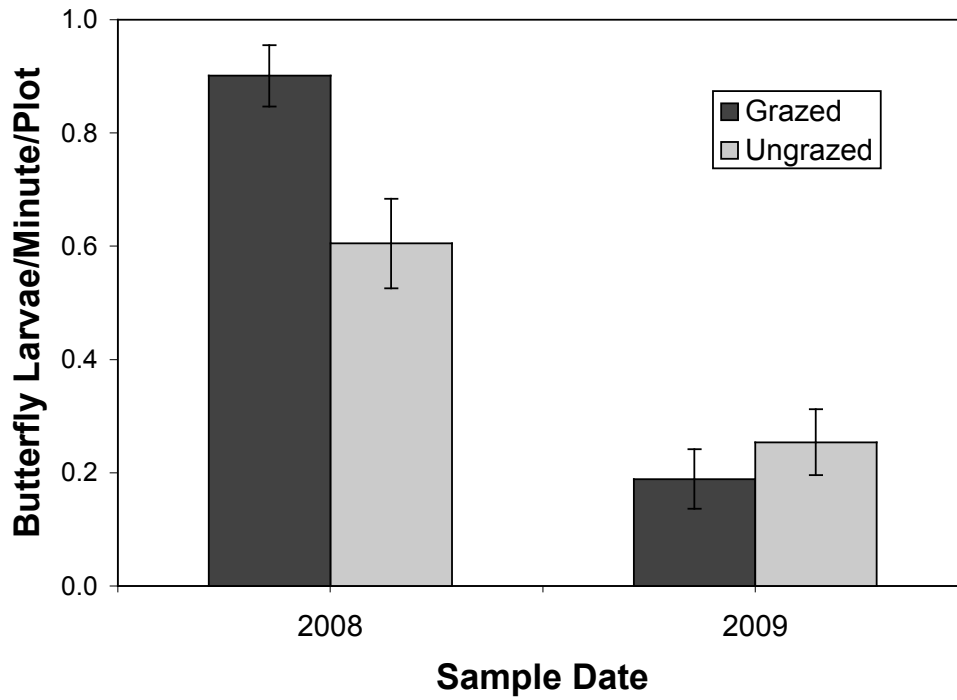


Figure 12. Mean (+ 1 S.E.) number of Smith's blue butterfly larvae found per minute of search time shown as a function of cattle grazing treatment and sample year.

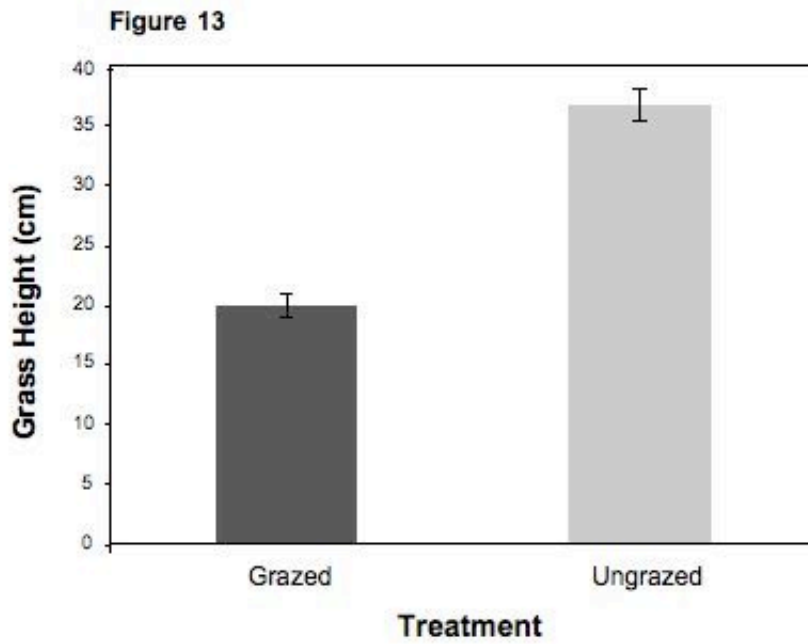


Figure 13. Influence of cattle grazing grass height (mean + 1 S.E.) averaged over two sample years.