

**Livestock grazing impacts to coastal grasslands resources at
Point Reyes National Seashore: Literature review and synthesis**

Prepared by Sasha Gennet
for the National Park Service, Point Reyes National Seashore

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Objective and scope

The objective of this report is to review and synthesize current knowledge about the effects of cattle grazing on biotic resources in California coastal grasslands and embedded riparian habitats, based on available published literature. This report does not consistently include grazing literature for other ecosystems except where no local information is available, and then only includes studies from comparable ecosystems. The effects of grazing on water quality and soil nutrients are outside the scope of this report but are covered elsewhere. For more information refer to the Baseline Water Quality Inventory and Analysis for PRNS, completed in 2004 jointly with the National Park Service Water Resources Division in Fort Collins, Colorado. The effects of livestock grazing on cultural resources are also not included herein.

Additional unpublished materials may be available through agency reports, consulting firms, and research organizations (e.g., Point Reyes Birds Observatory, California Native Plant Society) but are not comprehensively included in this report.

Background

The plant communities at Point Reyes National Seashore (PRNS) dominated by native and introduced low-growing herbaceous and shrub species are defined in modern vegetation classification nomenclature as north, or northern, coastal prairie and northern coastal scrub, respectively (Heady 1988, Stromberg et al. 2002, Ford and Hayes 2007, Keeler-Wolf 2007). These highly human-influenced plant communities are found along much of the California coast where maritime influences (cooler temperatures, salt spray) inhibit trees from establishing; dominant species vary by latitude and distance from the coast (Biswell 1958, Barbour 1973, Heady 1988, Ford and Hayes 2007). Coastal grassland and scrub communities differ markedly from inland communities, and intergrade with each other, influenced by climatic gradients (macro and micro), soil/substrate, and land use/management (Biswell 1958, Bartolome 1994). Northern coastal grassland and scrub are highly heterogeneous and species-rich, comprising

numerous alliances and associations, and provide habitat for a wealth of animals and insects (Heady 1988, Stromberg et al. 2002, Keeler-Wolf 2007). The goal of this report is to synthesize the known effects of livestock grazing on the key biological resources within the coastal ecosystem at PRNS, with an emphasis on the grassland community.

The grasslands throughout California evolved during the Pleistocene with abundant herbivorous mammalian megafauna. Grazing, browsing, and trampling were “important impacts” to those ecosystems (Edwards 1992). Consequently, some components of California’s native flora, including bunchgrasses, co-evolved with intermittent grazing and are tolerant or resistant to it to some degree. The dominance, distribution, and degree of grazing tolerance of these species are still debated, however (Edwards 1996). Climatic shifts that occurred 12,000-10,000 years ago and hunting by recently-arrived humans forced many large vertebrates to extinction; grazing pressure diminished (Edwards 1992). The coast of California was one of the most densely populated regions of North America during the post-glacial Holocene, however, and evidence strongly suggests that Native Americans living near the coast set frequent fires to maintain productive, low-growing plant communities. Although the pre-historic disturbance regimes of native ungulate grazing and, more recently, Native American fire management are not precisely known, the weight of evidence suggests that coastal grasslands evolved with and are sustained by disturbance (Keeley 2002). With Spanish settlement of coastal California domestic livestock became the dominant source of disturbance for coastal ecosystems; many areas experienced very high stocking rates. Seed rain and invasion by non-native species, particularly Mediterranean annual grasses, followed (D’Antonio et al. 2004).

Conservation and restoration goals are best guided by reference sites with the lowest possible levels of anthropogenic influence (Society for Ecological Restoration 2004). Reference sites help managers to quantify a site’s restoration capacity. However, reference sites are difficult or impossible to identify in coastal California for several reasons: 1) the spatially and temporally heterogeneous past disturbance (fire and grazing) regime in coastal California; 2) a lack of botanical records from early Spanish settlement; 3) widespread, ongoing domestic livestock for decades or centuries; and 4) seed rain

and/or invasion by introduced species (D'Antonio et al. 2004, Keeley 2002, Barry 2006). Resource- and site- specific conservation goals are therefore more practical in coastal grasslands.

Mediterranean grasslands such as the ones at PRNS exhibit primarily non-successional, climatically-determined, non-equilibrium system dynamics (Milchunas et al. 1988, Blumler 1992, Callway and Davis 1993, Hobbs and Mooney 1995, Jackson and Bartolome 2007). They are better described as having multiple stable equilibria (Seabloom and Richards 2003), and modeled by state-and-transition catalogues than by the traditional linear “range condition” model developed by Clements and Dyksterhuis in the early 20th century (Westoby et al. 1989,).

The complex vegetation dynamics of the modern coastal grassland community have been well studied in several locales near PRNS. Sites include Bodega Head on the Sonoma coast (Barbour 1973), Sea Ranch in Mendocino County (Hektner and Foin 1977, Peart 1989), Tom's Point in Marin County (Corbin and D'Antonio 2004), Angelo Coast Range Reserve in Mendocino (Thomsen et al. 2006) and Hastings Reserve in Monterey County (Stromberg and Griffin 1996). In addition, many coastal grassland resources in and near PRNS have been thoroughly inventoried, mapped, and monitored over several years or even decades (Elliott and Wehausen 1974, Lathrop and Gogan 1985, Howell and Semenoff-Irving 1998, Fellers and Pratt 2002); some individual components of the California grassland ecosystem, notably *Nassella pulchra* (Purple needlegrass), have been well-studied (e.g., Dyer and Rice 1999, Hamilton et al. 1999, Fehmi and Bartolome 2003). However, replicated, controlled, long-term ecological experiments that test grazing impacts at various intensities and durations are critical to understanding and predicting resource conditions under a range of future climatic conditions and management actions (Biswell 1958, Westoby et al. 1989, Allen and Pitkin 2000, Vesik and Westoby 2001, Johnson 2002, Hayes and Holl 2003, Hayhoe 2004). These experiments are rare for most grassland ecosystems, and are largely absent throughout California (Allen 2000, Bullock et al. 2001, D'Antonio et al. 2004, Hayes and Holl 2003b). The same factors that impede identification of reference sites may partly explain

the relative paucity of spatially- and temporally- replicated grazing comparison studies in this ecosystem.

Data collection methods

Materials were collected for this report through online databases of published literature (BIOSIS and Web of Science) and bibliographies of articles found therein. I searched for articles containing any combination or subset of “coast*”, “California”, “graz*”, and “grassland*”, wherein * represents a wildcard. Where gaps in information occurred for various resources of management concern (e.g. insects, birds), the search was expanded to include research outside California on similar or related resources. Unpublished reports and book chapters were obtained by request from the authors and editors. Additional resources were provided by PRNS. There is far more literature available for California’s inland, or Valley, grasslands than for the coastal grasslands. These two ecosystems are ecologically distinct, with very different abiotic and biotic driving factors. Results from experiments in coastal grasslands often have opposite results to those conducted further inland (see e.g. Hatch et al. 1999 and Bartolome et al. 2004). Therefore, extrapolation from the semi-arid inland grasslands to mesic coastal grasslands should be done with caution; where ecologically relevant and where information is lacking on specific coastal resources this literature was also included.

Because of the low number of replicated experiments testing grazing impacts in coastal California grasslands, statistically-robust meta-analysis was not possible for this report (Gurevitch and Hedges 1999, Hedges et al. 1999); a thorough review and qualitative synthesis follows.

Numerous papers study individual species or ecological issues directly relevant to this report, but are not referenced. Those studies are included in the Bibliographic resources section of this report (page 15) and are summarized individually in Appendix A.

Grazing Ecology

It is likely that all ecosystems contain herbivores and omnivores, and therefore undergo a degree of grazing (Painter 1995). In the California coastal grassland grazers include, at a minimum, insects (e.g., Pickart et al. 1998), small mammals (Barbour 1973, Cockburn and Lidicker 1983, Rice 1987, Fehmi 2002, Fehmi and Bartolome 2002, Fellers and Pratt 2002), large ungulate grazers (Wehausen 1982, Lathrop and Gogan 1985, Fellers and Pratt 2002), and birds (Herkert 1994, Allen and Pitkin 2000).

Surviving native ungulate grazers at PRNS include Tule Elk (*Cervus elaphus nannodes*) and Black-tailed deer (*Odocoileus hemionus columbianus*). Grazing patterns and forage preferences of cattle and elk overlap significantly; both prefer grasses to forbs and avoid browsing on high-protein plant material (Edwards 1996, Jackson and Bartolome 2007). Deer, conversely, are selective browsers, preferring shoots and new growth over grasses.

Livestock grazing is one of few factors that resource managers of wildlands can directly manipulate. The grazing effects of domestic livestock are additional to those of the species listed above, and may interact with them (e.g., Stromberg and Griffin 1996, Eviner and Chapin 2003). One critical factor missing in most grazing studies in California is that livestock grazing is not a binary treatment; the timing, intensity, duration, and frequency of grazing are critical determinants to ecosystem impacts (Heady 1992, Jackson and Bartolome 2007). Livestock have direct and indirect impacts on biological resources through defoliation, trampling, and altered nutrient cycling (Jackson and Bartolome 2007). In addition, their impacts on species composition and forage may be masked or confounded by grazing effects of other species, such as gophers, squirrels, or voles (Cockburn and Lidicker 1983, Rice 1987, Fehmi 2002, Fehmi and Bartolome 2002, Fehmi et al. 2005).

Beef cattle and dairy cows impact grasslands differently. Because they must return to milking and feeding stations daily, dairy cows typically have greater localized impacts

than beef cows. Feeding, compared to grazing, also causes added nutrients to enter the ecosystem.

Research for this report uncovered no local studies of the comparative impacts of livestock grazing and regular mowing. The timing, frequency, and blade height of mowing would undoubtedly determine the impacts to the grassland. Controlled local study would be required before predictions could be made about the impacts to plant, mammal, insect, and bird communities.

For a thorough synthesis of grazing ecology in California grasslands see Jackson and Bartolome (2007).

Grazing Impacts

Grazing impacts to plant communities

Native grasses

Numerous studies document the impacts to native grasses from grazing. However, as discussed above, few have adequate replication or controls, and many focus on a single species. The high diversity, temporal and spatial heterogeneity, and strong historical footprints in this plant community do not allow simple summary of livestock grazing impacts therein.

Consequently, a complete exposition of related literature is not practical here; rather, this report synthesizes key, well-designed studies undertaken in either California coast grasslands or similar plant communities. Conclusions in this report should be tested locally, as responses to grazing may vary according to local climatic and historic conditions, as well as with specific grazing application. Studies from California Valley Grasslands or other inland types, including serpentine, are summarized in Appendix A.

In a spatially-replicated study, Hayes and Holl (2003) found that overall, grazing in coastal grasslands was correlated with higher diversity and abundance of native and non-native forbs, but uncorrelated, overall, with abundance of native grasses as a guild. However, the two most common grasses showed different responses, with *Danthonia californica* responding positively and *Nassella pulchra* inconsistently to grazing. Stromberg and Griffin (1996) showed that at a central California site, relict populations of native grass species were unresponsive to grazing at various intensities; rather, their distribution was determined primarily by history of cultivation and microsite characteristics. Historically cultivated sites contained little or no native species cover. Nutrient-poor, steep soils maintained populations of native grasses. Hatch et al. (1999) found that grazing increased cover of *Danthonia californica*, a key component of the coastal grasslands. *Nassella pulchra*, also an important native bunchgrass, did not respond consistently to any of the treatments of grazing and burning.

Studies from Sea Ranch (Hektner and Foin 1977, Peart et al. 1989) and PRNS (Elliott and Wehausen 1974, Lathrop and Gogan 1985) indicate that removal of grazing will lead to conversion of much of the grassland at PRNS to perennial-dominated plant communities, probably scrub dominated by *Baccharis pilularis*.

These studies are contradictory in places, but contain some consistent findings. *Danthonia californica* responded favorably to grazing in two studies, and *Nassella pulchra* did not respond consistently to grazing in any of the studies, indicating that its distribution is dependent on additional, unmeasured ecological factors. Another consistent finding was that succession to denser, perennial-dominated plants due to absence of disturbance is likely in some coastal grasslands.

In summary, grazing appears to be a viable management technique for preventing northern coastal grasslands from type conversion to scrub, but might be met with mixed success over the longterm in conserving and restoring native grasses. A confounding factor is invasion by numerous non-native species of annual and perennial grasses, including Purple velvetgrass (*Holcus lanatus*), now widespread throughout PRNS

grasslands. Many of these species, including *H. lanatus*, are highly tolerant of grazing (Jackson 1985), and may increase with certain grazing applications (Buckland et al. 2001). Accurate local predictions for post-grazing plant composition are difficult based on these few studies. Future research and monitoring should include multiple levels and timing of grazing, because intensity, duration, and timing of grazing may determine its impacts to species composition (Jackson and Bartolome 2007).

Native annual forbs

Few studies have looked directly at the impact of grazing on the native annual forbs of Californian coastal grasslands, despite their tremendous diversity and conservation importance; the majority of species comprised by coast grasslands are annual herbaceous forbs. Most studies have focused on native grasses instead.

One study did look broadly at the effects of grazing on annual forbs, Hayes and Holl (2003). They found that grazed areas throughout the community's distribution contained higher species richness and abundance of both native and non-native forbs.

It is clear that grazing reduces litter and aboveground biomass (Bartolome et al. 2002). Taken together with Hayes and Holl's (2003) study, we can conclude that annual species are better able to compete for light in grazed grasslands.

Native shrubs and oaks

Landscape-level vegetation analyses have shown that native shrubs, notably *Baccharis pilularis* and *Lupinus arboreus*, typically respond negatively to livestock grazing in both grasslands and embedded riparian corridors (McBride and Heady 1968, Elliott and Wehausen 1974, Pickart 1998, Strong 1995, Maron 2001, Lennox 2004).

No studies on the effects of grazing in coastal grasslands on *Quercus agrifolia*, the most common coastal oak, were located for this report. However, a study on *Quercus*

douglasii, an important savannah species in California, showed that trampling and predation negatively impacted seedling success (Borchert et al. 1989). Similar grazing intensities among California's grasslands would suggest that grazing would have a similarly negative impact on oak regeneration at PRNS. Elliott and Wehausen (1974) showed that without grazing, grasslands may convert slowly to oak woodlands in some places.

Although these species are all native to California, shrub and tree encroachment into species-rich, heterogeneous grasslands would likely lead to a significant loss of grassland plant biodiversity in the invaded/converted community, particularly in the guild of annual forbs. Associated small mammal and bird diversity, conversely, might increase overall.

Invasive plants

Grazing impacts on invasive plants are variable, and depend on life-history characteristics and introduction patterns of each species. Non-native invasion biology is a large and evolving field of research in California (see, e.g. Davies 2005, Thomsen 2006), and a thorough explication is not practical in this report. However, a brief discussion of the key ideas and issues merits inclusion.

Although shrub invasion by native plants is a management issue in coastal grasslands (see Native shrubs and oaks section of this report), introduced non-native annual grasses and forbs, and certain species of perennial grasses, are the primary species of concern. Invaders may be disturbance-dependent initially but highly competitive once established (D'Antonio 1993), or may be highly disturbance and grazing tolerant throughout their lives, like the Mediterranean annual grasses that now dominate almost all California grasslands (Jackson 1985). Native species exhibit varying degrees of competitiveness to introduced non-native invasives; Thomsen et al. (2006) showed that *Holcus lanatus*, an invasive perennial grass, was competitive at all densities of competition, while Carlsen et al. (2000) demonstrated that a rare grassland forb could be positively impacted by reduction of competition. Dyer and Rice (1999) found that *Nassella pulchra* was favored

by low interspecific competition. Plant communities contain multiple species of interest, however. Livestock grazing alone is not likely to return type-converted grasslands to native dominance, though it could be part of a strategy that “tips the balance” toward persistent native species dominance (Corbin et al. 2004). More intensive management, including disking or plowing, uniformly appears to cause long-term, irreversible damage to native plant populations, and application of fertilizer is also likely to favor introduced species over natives (Stromberg and Griffin 1996, Weiss 1999, Buckland et al. 2001).

Grazing impacts to non- plant communities

Terrestrial vertebrates

Fifteen studies were found in the published literature that investigated the relationships of livestock grazing and terrestrial vertebrates in California. Few, however, directly compared abundances and diversity in grazed and ungrazed plots. Rather, they investigated the effects of small mammal grazing on plant communities.

While there is evidence from monitoring (Fellers and Pratt 2002, Howell and Semenov-Irving 2005) that small mammal diversity is lower in grazed coastal grasslands than in other near-coastal ecosystems, the relationships between small mammal grazing (especially gophers and voles), plant community diversity and invasion, and livestock grazing are extremely complex (Cockburn and Lidicker 1983, Fehmi 2002, Fehmi and Bartolome 2002, Fehmi et al. 2005, Hobbs and Mooney 1995, Parker et al. 2006, Peart 1989). No studies demonstrated a significant difference between grazed and ungrazed grasslands in small mammal abundances; certain species may depend on grazing to maintain habitat but this conclusion is confounded by current studies. Cattle and mammal impacts to vegetation interact (Fehmi 2002), however, and small mammal activity can impact the plant community to a large degree (Cockburn and Lidicker 1983, Fehmi and Bartolome 2002).

Research by Fehmi et al. (2005) showed no differences in California ground squirrel (*Spermophilus beecheyii*) abundances in a coastal grassland between grazed and ungrazed pastures where ground squirrels were not removed by ranchers.

Large native mammals showed no preference for grazed over ungrazed sites at PRNS and GGNRA (Fellers and Pratt 2002).

Only one study of grazing impacts to reptiles or amphibians in California coastal grasslands was discovered in the published literature search (Fellers et al. 2001); Sullivan (2000) also documents snake populations and distribution in interior California. Because of the high number of reptiles and amphibians that are found in grasslands and are rare in California (e.g., California Red-legged frog, *Rana aurora draytonii*; California tiger salamander, *Ambystoma californiense*), additional studies may exist that were not readily discovered in this literature review. Park researchers have concluded that livestock grazing has different effects on Red-legged frogs in stock ponds versus streams/riparian corridors. Grazing tends to be beneficial for this species in stock-ponds, where trampling and defoliation suppresses tall vegetation, but has negative impacts to frogs in riparian corridors, where stream bank disturbance occurs (Fellers pers. comm. 2006).

Birds

Eleven published sources were directly relevant to understanding the grassland bird community at PRNS (Wirtz 1982, Herkert 1994, Halterman et al. 1999, Holmes et al. 1999, Roth et al. 1999, Johnson M., Allen and Pitkin 2000, Gardali et al. 2001, Goerrissen 2004, Kelly 2004, Roth et al. 2004). Additional unpublished data were available from a study in Alameda and Contra Costa counties of grazing impacts to songbirds (Gennet et al. 2006). Only Herkert (1994) and Wirtz (1982) were undertaken outside coastal California. Allen and Pitkin (2000) is a set of bird management and research guidelines for California grasslands, focused on songbirds, and Rappole (1991) explores the causes of Nearctic neotropical migrant bird declines.

A complex but coherent story emerged from this literature: the impact of ongoing grazing within grasslands likely helps maintain habitat for some species but may negatively impact others. Bird species have different life histories and consequent habitat needs; they can even vary among populations of the same species or within an ecosystem type like California coastal grasslands. There is weak evidence from local studies that grassland specialists' breeding and foraging needs (low-stature grasslands) conflict with those of more abundant, but sensitive, riparian specialists. Populations of brood parasitists and corvids may benefit from grassland habitat but prey on highly threatened shorebird species and nesting neotropical migrants in riparian habitat. The optimum management matrix for avian species will depend on conservation and management priorities and should be highly site-specific, as bird populations' habitat needs may vary even within coastal grassland.

Vegetation structure and food availability vary among plant communities. Species dependant on low- to medium-stature grasslands for nesting and foraging include, among others, several focal species for the Partners in Flight Grassland Bird Conservation Plan: Western Meadowlark (*Sturnella neglecta*), Savannah Sparrow (*Passerculus sandwichensis*), and Grasshopper Sparrows (*Ammodramus savannarum*). Although each of these taxa has somewhat different habitat requirements within the grasslands matrix, a type conversion to taller, dense perennial grassland or coastal scrub could reduce quantity and quality of habitat for Grasshopper Sparrows and Savannah Sparrows, which generally prefer some interstitial spacing within the plant community (Goerrissen 2004). Evidence suggests that Meadowlarks are less sensitive to grassland canopy structure, but are not typically found in scrub. Conversely, species which prefer taller canopies and shrub structure, including riparian specialists, may be negatively impacted by continued grazing if its consequence is maintenance of low-stature grasslands. In addition, there is evidence that two species, Common Ravens (*Corvus corax*) and Brown-headed Cowbirds (*Molothrus ater*), preferentially utilize grazed pastures in the San Francisco Bay Area and benefit from increased food availability at ranches. Ravens prey on shorebirds, herons, and songbirds, and cowbirds parasitize songbird nests, particularly in riparian corridors within grazed lands.

Allen and Pitkin (2000) emphasize the imperative need for a better understanding of grassland birds' habitat requirements and population dynamics in California, and suggest monitoring strategies to obtain better information. Local knowledge is critical; some bird species important to grasslands, such as Grasshopper Sparrows, have shown variable responses to grazing in different types of grasslands. A key point made in Herkert (1994) is that habitat patch size is a critical factor in songbird success. Determining the minimum patch size and additional qualities necessary to each bird species of high management priority is important for conserving them.

Insects: Lepidoptera

Lepidoptera (moths and butterflies) were the only group of insects for which published literature was discovered pertaining to grasslands. Eleven total studies were found, seven in California ecosystems, and two in PRNS.

A study from the Netherlands showed that grazing had no negative impacts on local butterfly species, confirming grazing as an appropriate restoration strategy in restoration projects there (WallisDeVries and Raemakers 2001). Dennis and Eales (1997), Elligsen et al. (1997) and Weiss (1999), in a study at Jasper Ridge Biological Preserve near San Jose, California, show that some butterfly species depend on grazing because it maintains adequately low, open, vegetation structure, or help conserve nectar plants. Kruess and Tscharnke (2002) showed an overall negative effect on butterflies from intensive grazing. In that study, taller vegetation was correlated with butterfly presence and abundance. Blair and Launer (1997), in a study near Palo Alto, CA, showed that butterfly abundance declines even with small amounts of disturbance such as grazing, across all species, though richness peaks with moderate amounts of disturbance.

At PRNS, Launer et al. (1992) found that heavy historically grazing likely had negatively impacted populations of Myrtle's Silverspot Butterfly (*Speyeria zerene myrtleae*), a federally-endangered sub-species, but that cessation of grazing across its entire range could threaten populations of host and nectar plants by facilitating non-native species

encroachment. That study suggests a mosaic of grazing intensities across the landscape might be optimum, but would need further study to be conclusive. Adams (2004) found that light to moderate grazing had no significant effect on nectar species richness but was positively correlated with nectar plant density for this taxon.

Other studies documented the critical role caterpillars can play in an ecosystem (Strong et al. 1995, Maron et al. 2001). Intermittent die-back of *Lupinus arboreous*, a native invasive shrub, is caused by caterpillars of the ghost moth or “swift” (*Hepialus californicus*), and impacts populations of other Lepidoptera, as well (Maron et al. 2001). The impacts of grazing on these species were not determined.

In summary, grazing in California coastal grasslands at PRNS could have continued negative effects on some butterfly populations by causing disturbance, particularly at higher stocking rates. However, local research suggests that, overall, light to moderate grazing appears to help maintain habitat and nectar sources for at least one highly-threatened species by moderating invasion of taller perennial species.

Mycorrhizae and soil microbial community

There were six relevant studies on grazing impacts to mycorrhizae and soil microbial community, with inconsistent outcomes (Bethlenfalvay and Dakessian 1984, Allen et al. 1989, Bentivenga and Hetrick 1992, Nelson and Allen 1993, Callaway et al. 2003, Frank et al. 2003). Two of these studies were carried out in California grasslands (Nelson and Allen 1993, Callaway 2003).

Allen et al. (1989) showed no effect of moisture or clipping treatments on vascular-arbuscular mycorrhizae in a study of two tussock grasses in Utah. Bethlenfalvay and Dakessian (1984) obtained results indicating a negative effect on grasses and VAM from grazing by up to 50%. Conversely, Frank et al. (2003) showed a positive effect on *Poa pratensis* and mycorrhizae in Yellowstone grasslands. Fertilizer inputs led to a reduction of mycorrhizal symbiosis in tallgrass prairie, but clipping and mowing showed no

significant effects (Bentivenga and Hetrick 1992). Callway's (2003) study of the competitive interactions mediated by mycorrhizae between *Centaurea melitensis*, *Avena barbata*, and *Nassella pulchra* showed a complex interaction not entirely clarified by the experiment. Nelson and Allen's (1993) test that inoculated invasives would be less competitive with native grasses showed that, though it facilitated growth of *Nassella pulchra* when grown alone, mycorrhizae did not alleviate the negative effects of *Avena barbata* when grown together.

In summary, the role of mycorrhizae in California's coastal grasslands and how it is impacted by livestock grazing are not well illuminated by research done to date.

Litter and Soil Properties

While few studies reported litter and soil characteristics in comparisons of grazed and ungrazed areas in coastal California, the impacts of grazing on these properties are well understood. Grazing directly reduces dead aboveground biomass, also called litter or thatch. Trampling can also cause significant soil compaction and subsequent reduced water infiltration, depending on grazing intensity (Heady 1956, Jackson and Bartolome 2007). A discussion of water quality impacts of beef and dairy cows at PRNS is beyond the scope of this report.

Conclusions

Studies at PRNS have shown that where livestock grazing has been maintained, grassland community types persist at the decadal time scale. Grazing cessation, conversely, facilitates increases in perennial grass and shrub cover in some places, particularly by *Baccharis pilularis* (Lathrop and Gogan 1985). This study, in combination with research from ecologically similar sites in California, suggests that some grasslands at PRNS that are currently grazed by cattle would undergo community-type shifts toward perennial-dominated communities with some shrub component if cattle grazing were halted.

The results of grazing cessation *within* coastal grasslands at PRNS on species composition and distribution are not well predicted by studies published to date. California coastal grasslands are complex and highly heterogeneous in time and space; consequently, post-grazing succession is likely to vary from site to site. The persistence and trajectory of each of its component species is driven by a combination of stochastic weather conditions and micro-climate, edaphic factors (e.g. water and nutrient availability, mulch/litter cover), disturbance, cultivation history, current species distribution and abundance, evolutionary history, grazing by native herbivores, and competitive or facultative interactions with other species. Some components of the ecosystem may be predictable, displaying successional tendencies at identifiable temporal and spatial scales, while others are distinctly non-successional and non-equilibrium, or show multiple stable states. Most studies in the California grassland ecosystem have occurred at small temporal or spatial scales. Many key measurements and studies of important biological components of the ecosystem have not been studied, leaving large knowledge gaps for resource managers. Moreover, several studies are contradictory, likely due to site specific characteristics and confounding factors.

However, several recent studies, taken together, provide evidence that in some California coastal grasslands grazing has a positive correlation with annual species, including native forbs, a neutral or slight positive effects on native grasses, and negative effect on some native perennial forbs. Site conditions and plant responses may vary at PRNS, however, compared to study sites elsewhere, so conclusions should be tested locally. These results present a management conundrum wherein continued grazing in coastal grasslands could negatively impact some populations of native perennial plant species, in order to preserve its diverse community of rare, native, annual forbs, and to prevent a succession to coastal scrub. These studies suggest that a strategy to preserve bunchgrass, annual and perennial forb elements of the native plant community could include a mosaic of lightly, moderately, and ungrazed patches.

The size of the patches within a grazing mosaic may have a strong impact on non-plant components of the ecosystem that are of high management concern, such as small and

large mammals, insects, and grassland-dependent birds. Identifying minimum habitat patch-size requirements and optimal grazing timing and intensity for these species is critical to their persistence.

An additional management conundrum is that certain taxonomic groups, including plants and certain butterflies, are more likely to benefit, overall, from continued light to moderate cattle grazing at PRNS grasslands, while terrestrial vertebrate species' habitat quality and quantity would stay the same or decline.

The trade-off among resource values from continued grazing is true for the avian community, as well: bird species that depend on grasslands would more likely be conserved under continued grazing with certain timing and intensity, but riparian and scrub-dependent species would not increase their habitat availability.

The current state of knowledge in California coastal grasslands suggests that developing a research and management approach like the state-and-transition catalogues described by Westoby et al. (1989) would help prioritize knowledge gaps and maximize current knowledge. Because coastal grasslands appear to behave non-linearly in many cases, with their compositional trajectory directed by multiple biotic and abiotic factors, understanding how stable each known plant community is under a range of climatic and management conditions would be valuable. In such a model, research would be directed toward identifying stable community states and the factors causing transitions between those states. Invasive species treatment and native species conservation and restoration probably must be studied and undertaken on a species-by-species basis, due to the complexity of interactions and variable life-histories of each species. Species are likely to be associated primarily with one or more stable states; management can opportunistically manage toward a mosaic of states containing the most, or most critical, plant and wildlife species of management priority.

References and Bibliographic resources

1. Adams, D. B. 2004. Habitat assessment of the endangered Myrtle's Silverspot Butterfly. M.A. San Francisco State University, San Francisco.
2. Alexander, J. M., and C. M. D'Antonio. 2003. Seed bank dynamics of French broom in coastal California grasslands: Effects of stand age and prescribed burning on control and restoration. *Restoration Ecology* **11**:185-197.
3. Allen, B., and M. Pitkin. 2000. Draft Grassland Bird Conservation Plan: A strategy for protecting and managing grasslands and associated birds in California. Point Reyes Bird Observatory, Partners in Flight.
4. Allen, M. F., J. H. Richards, and C. A. Busso. 1989. Influence of clipping and soil water status on vesicular-arbuscular mycorrhizae of two semi-arid tussock grasses. *Biology and Fertility of Soils* **8**:285-289.
5. Augustine, D. J. 2003. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savannah. *Journal of Applied Ecology* **40**:137-149.
6. Baker, H. G. 1989. Sources of the naturalized grasses and herbs in California grasslands. Pages 29-36 in L. F. Huenneke and H. A. Mooney, editors. *Grassland structure and function: California annual grasslands*. Kluwer Academic Publishers, Boston, Massachusetts.
7. Ballard, G., R. Burnett, D. Burton, A. Chrisney, L. Comrack, G. Elliott, T. Gardali, G. Geupel, S. Heath, D. Humple, B. Kus, M. Lynes, M. Pitkin, L. Pomara, S. Scoggin, S. Small, D. Stralberg, and V. Toniolo. 2004. The riparian bird conservation plan: A strategy for reversing the decline of riparian associated birds in California. *California Partners in Flight*.
8. Barbour, M. G., R. B. Craig, F. Drysdale, and M. T. Ghiselin. 1973. *Coastal ecology of Bodega Head*. University of California Press, Berkeley, CA, USA.
9. Barry, S., S. Larson, and M. George. 2006. California native grasslands: A historical perspective - A guide for developing realistic restoration objectives. *Grasslands* **16**:7-11.
10. Bartolome, J. W. 1993. Application of herbivore optimization theory to rangelands of the western United States. *Ecological Applications* **3**:27-29.
11. Bartolome, J. W. 1994. Coastal prairie. Pages 23-24 in T. N. Shiflet, editor. *Rangeland cover types of the United States*. Society for Range Management, Denver, CO, USA.
12. Bartolome, J. W., W. E. Frost, N. K. McDougald, and M. Connor. 2002. California guidelines for residual dry matter (RDM) management on coastal and foothill annual rangelands. 8092, University of California, Berkeley, Oakland, California, USA.
13. 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.
14. Bartolome, J. W., W. J. Barry, T. Griggs, and P. Hopkinson. 2007. Chapter 14. Valley grassland. in M. G. Barbour, editor. *Terrestrial vegetation of California*. California Native Plant Society, Davis, CA, USA.
15. Bentivenga, S. P., and B. A. D. Hetrick. 1992. The effect of prairie management practices on mycorrhizal symbiosis. *Mycologia* **84**:522-527.

16. Bethlenfalvay, G. J., and S. Dakeasian. 1984. Grazing effects on mycorrhizal colonization and floristic composition of the vegetation on a semiarid range in northern Nevada USA. *Journal of Range Management* **37**:312-316.
17. Biswell, H. H. 1958. Ecology of California grasslands. *Journal of Range Management* **9**:19-24.
18. Blair, R. B., and A. E. Launer. 1997. Butterfly diversity and human land use: Species assemblages along an urban gradient. *Biological Conservation* **80**:113-125.
19. Blumler, M. A. 1992. Some myths about California grasslands and grazers. *Fremontia* **20**:22-27.
20. Bock, C. E., J. H. Bock, and H. M. Smith. 1993. Proposal for a system of federal livestock exclosures on public rangelands in the western United States. *Conservation Biology* **7**:731-733.
21. Borchert, M. I., F. W. Davis, J. Michaelsen, and L. D. Oyler. 1989. Interactions of factors affecting seedling recruitment of Blue oak *Quercus-Douglasii* in California USA. *Ecology* **70**:389-404.
22. Buckland, S. M., K. Thompson, J. G. Hodgson, and J. P. Grime. 2001. Grassland invasions: Effects of manipulations of climate and management. *Journal of Applied Ecology* **38**:301-309.
23. Bullock, J. M., B. C. Hill, J. Silvertown, and M. Sutton. 1995. Gap colonization as a source of grassland community change - effects of gap size and grazing on the rate and mode of colonization by different species. *Oikos* **72**:273-282.
24. Bullock, J. M., J. Franklin, M. J. Stevenson, J. Silvertown, S. J. Coulson, S. J. Gregory, and R. Tofts. 2001. A plant trait analysis of responses to grazing in a long-term experiment. *Journal of Applied Ecology* **38**.
25. Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* **77**:776-790.
26. Callaway, R. M., and F. W. Davis. 1993. Vegetation dynamics, fire, and the physical environment in coastal central California. *Ecology* **74**:1567-1578.
27. Callaway, R. M., B. E. Mahall, C. Wicks, J. Pankey, and C. Zabinski. 2003. Soil fungi and the effects of an invasive forb on grasses: Neighbor identity matters. *Ecology* **84**:129-135.
28. Carlsen, T. M., J. W. Menke, and B. M. Pavlik. 2000. Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands. *Restoration Ecology* **8**:18-29.
29. Clary, W. P., and J. W. Kinney. 2002. Streambank and vegetation response to simulated cattle grazing. *Wetlands* **22**:139-148.
30. Cockburn, A., and W. Z. J. Lidicker. 1983. Microhabitat heterogeneity and population ecology of an herbivorous rodent, *Microtus californicus*. *Oecologia* **59**:167-177.
31. Corbin, J. D., C. M. D'Antonio, and S. J. Bainbridge. 2004. Tipping the balance in the restoration of native plants. Pages 154-179 in M. S. Gordon and S. M. Bartol, editors. *Experimental approaches to conservation biology*. University of California Press, Berkeley.
32. Corbin, J. D., and C. M. D'Antonio. 2004. Competition between native perennial and exotic annual grasses: Implications for an historical invasion. *Ecology*

85:1273-1283.

33. Cremers, B. 2004. Effects of high intensity- short duration and open cattle grazing on oak woodlands/savannah rangeland. M.S. California Polytechnic University, San Luis Obispo.
34. D'Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology* **74**:83-95.
35. D'Antonio, C. M., S. J. Bainbridge, C. Kennedy, J. W. Bartolome, and S. Reynolds. 2004. Ecology and restoration of California grasslands with special emphasis on the influence of fire and grazing on native grassland species. University of California, Berkeley. David and Lucille Packard Foundation, Berkeley, California, USA.
36. Dahlgren, R. A., M. J. Singer, and X. Huang. 1997. Oak tree and grazing impacts on soil properties and nutrients in a California oak woodland. *Biogeochemistry* **39**:45-64.
37. Davies, K. F., P. L. Chesson, S. Harrison, B. D. Inouye, B. A. Melbourne, and K. J. Rice. 2005. Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology* **86**:1602-1610.
38. Dennis, R. L. H., and H. T. Eales. 1997. Patch occupancy in *Coenonympha tullia* (Muller, 1764) (Lepidoptera: Satyrinae): habitat quality matters as much as patch size and isolation. *Journal of Insect Conservation* **1**:167-176.
39. DeSimone, S. A., and P. H. Zedler. 1999. Shrub seedling recruitment in unburned Californian coastal sage scrub and adjacent grassland. *Ecology* **80**:2018-2032.
40. Donovan, T. M., C. J. Beardmore, D. N. Bonter, J. D. Brawn, R. J. Cooper, J. A. Fitzgerald, R. Ford, S. A. Gauthreaux, T. L. George, W. C. Hunter, T. E. Martin, J. Price, K. V. Rosenberg, P. D. Vickery, and T. B. Wigley. 2002. Priority research needs for the conservation of Neotropical migrant landbirds. *Journal of Field Ornithology* **73**:329-339.
41. Dyer, A. R., and K. J. Rice. 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* **80**:2697-2710.
42. Edwards, S. W. 1992. Observations on the prehistory and ecology of grazing in California. *Fremontia* **20**:3-11.
43. Edwards, S. W. 1996. A Rancholabrean-age, latest Pleistocene bestiary for California botanists. *Four Seasons* **10**:5-34.
44. Elligsen, H., B. Beinlich, and 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.
45. Elliott, H. W., III, and J. D. Wehausen. 1974. Vegetational succession on coastal rangeland of Point-Reyes Peninsula. *Madrono* **22**:231-238.
46. Eom, A.-H., G. W. T. Wilson, and D. C. Hartnett. 2001. Effects of ungulate grazers on arbuscular mycorrhizal symbiosis and fungal community structure in tallgrass prairie. *Mycologia* **93**:233-242.
47. Evans, R. A., and J. A. Young. 1989. Characterization and analysis of abiotic factors and their influences on vegetation. Pages 13-28 in L. F. Huenneke and H. A. Mooney, editors. *Grassland structure and function: California annual grassland*. Kluwer Academic Publishers, Dordrecht.
48. Eviner, V. T., and F. S. Chapin, III. 2003. Gopher-plant-fungal interactions affect

- establishment of an invasive grass. *Ecology* **84**:120-128.
49. Eviner, V. T. 2004. Plant traits that influence ecosystem processes vary independently among species. *Ecology* **85**:2215-2229.
 50. Fehmi, J. S. 2002. The context of grassland defoliation. *Conservation ecology* **6**:7.
 51. Fehmi, J. S., and J. W. Bartolome. 2002. Species richness and California voles in an annual and a perennial grassland. *Western North American Naturalist* **62**:73-81.
 52. Fehmi, J. S., and J. W. Bartolome. 2003. Impacts of livestock and burning on the spatial patterns of the grass *Nassella pulchra* (Poaceae). *Madrono* **50**:8-14.
 53. Fehmi, J. S., S. E. Russo, and J. W. Bartolome. 2005. The effects of livestock on California Ground squirrels (*Spermophilus beecheyii*). *Rangeland Ecology & Management* **58**:352-359.
 54. Fellers, G. 2006. Conversation between Fellers (USGS-BRD scientist at PRNS) and John DiGregoria (PRNS Range Manager) regarding cattle grazing impacts to Red-legged frogs. Point Reyes Station, CA, USA.
 55. Fellers, G. M., A. E. Launer, G. Rathbun, S. Bobzien, J. Alvarez, D. Sterner, R. B. Seymour, and M. Westphal. 2001. Overwintering tadpoles in the California red-legged frog (*Rana aurora draytonii*). *Herpetological Review* **32**:156-157.
 56. Fellers, G., and D. Pratt. 2002. Terrestrial vertebrate inventory, Point Reyes National Seashore, 1998-2001. United States Geological Survey, Point Reyes Station, CA, USA.
 57. Fensham, R. J., J. E. Holman, and M. J. Cox. 1999. Plant species responses along a grazing disturbance gradient in Australian grassland. *Journal of Vegetation Science* **10**.
 58. Ford, L. D., and G. Hayes. 2006. Northern coastal scrub and coastal prairie. in M. G. Barbour, editor. *Terrestrial Vegetation of California*. University of California Press.
 59. Frank, D. A., C. A. Gehring, L. Machut, and M. Phillips. 2003. Soil community composition and the regulation of grazed temperate grassland. *Oecologia (Berlin)* **137**:603-609.
 60. Gardali, T., G. R. Geupel, A. L. Holmes, and D. L. Humple. 2001. Landbird response to wildfire in a coastal riparian ecosystem. Pages 57-64 in P. M. Faber, editor. *Riparian habitat and floodplains conference proceedings*, Riparian Habitat Joint Venture, Sacramento, CA, USA.
 61. Gennet, S., J. W. Bartolome, and M. Hammond. Unpublished data from grassland bird monitoring in the East Bay Regional Park District, 2002-2006.
 62. Goerrissen, J. 2005. Grassland birds in California: an investigation into the influence of season, floristic composition, and artificial structures on avian community structure. PhD dissertation. University of California, Davis, Davis, California.
 63. Group, S. f. E. R. I. S. a. P. W. 2004. *The SER international primer on ecological restoration*. Society for Ecological Restoration, Tuscon, Arizona, USA.
 64. Gurevitch, J., and L. V. Hedges. 1999. Statistical issues in ecological meta-analyses. *Ecology* **80**:1142-1149.
 65. Halterman, M. D., S. G. Allen, and S. A. Laymon. 1999. Assessing the impact of Brown-headed Cowbird parasitism in eight National Parks. *Studies in Avian Biology* **18**:153-159.

66. Hamilton, J. G. 1997. Changing perceptions of pre-European grasslands in California. *Madrono* **44**:311-333.
67. Hamilton, J. G., C. Holzapfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* **121**:518-526.
68. 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.
69. 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.
70. Hayes, G. F., and K. D. Holl. 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. *Conservation Biology* **17**:1694-1702.
71. Hayes, G., and K. D. Holl. 2003. Site-specific responses of native and exotic species to disturbances in a mesic grassland community. *Applied Vegetation Science* **6**:235-244.
72. Hayhoe, K., D. Cayan, C. B. Field, P. C. Frumhoff, E. P. Maurer, N. L. Miller, S. C. Moser, S. H. Schneider, K. N. Cahill, E. E. Cleland, L. Dale, R. Drapek, R. M. Hanemann, L. S. Kalkstein, J. Lenihan, C. K. Lunch, R. P. Neilson, S. C. Sheridan, and J. H. Verville. 2004. Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Sciences* **101**:12422-12427.
73. Heady, H. F. 1956. Changes in a California annual plant community induced by manipulation of natural mulch. *Ecology* **37**:798-812.
74. 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 733-759 in M. G. Barbour and J. Major, editors. *Terrestrial Vegetation of California*. California Native Plant Society, Davis, CA, USA.
75. Heady, H. F., J. W. Bartolome, M. D. Pitt, G. D. Savelle, and M. C. Stroud. 1992. Chapter 16. California prairie. Pages 313-335 in R. T. Coupland, editor. *Natural grasslands*. Elsevier Scientific Publication Co., Amsterdam, The Netherlands.
76. Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* **80**:1150-1156.
77. Hektner, M. M., and T. C. Foin. 1977. Vegetation analysis of a northern California coastal prairie, Sea Ranch, Sonoma County, California, USA. *Madrono* **24**:83-103.
78. Herkert, J. R. 1994. The Effects of Habitat Fragmentation on Midwestern Grassland Bird Communities. *Ecological Applications* **4**:461-471.
79. Hobbs, R. J., and H. A. Mooney. 1991. Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology* **72**:59-68.
80. Holmes, A. L., D. L. Humble, T. Gardali, and G. R. Geupel. 1999. Songbird habitat associations and response to disturbance in the Point Reyes National Seashore and Golden Gate National Recreation Area. Point Reyes Bird Observatory, Stinson Beach, CA, USA.
81. Howell, J. A., and M. Semenov-Irving. 1998. Examination of grazing effects on

- vertebrate diversity in a coastal California National Park. United States Geological Survey, Sausalito, CA, USA.
82. Huenneke, L. F., and H. A. Mooney. 1989. Grassland structure and function: California annual grassland. Kluwer Academic, Dordrecht, The Netherlands.
 83. Huntsinger, L., J. W. Bartolome, and C. M. D'Antonio. 2007. Chapter 19. Grazing management on California grasslands. *in* M. R. Stromberg, J. D. Corbin, and C. M. D'Antonio, editors. Ecology and management of California grasslands.
 84. Jackson, L. E. 1985. Ecological origins of California's Mediterranean grasses. *Journal of Biogeography* **12**:349-361.
 85. Jackson, R. D., and J. W. Bartolome. 2007. Chapter 18. Grazing ecology of California grasslands. *in* M. R. Stromberg, J. D. Corbin, and C. M. D'Antonio, editors. Ecology and management of California grasslands.
 86. Johnson, C. 2000. Ordination analysis of grassland types of Santa Cruz Mountains reserves. San Jose State University, San Jose, CA, USA.
 87. Johnson, D. H. 2002. The importance of replication in wildlife research. *Journal of Wildlife Management* **66**:919-932.
 88. Johnson, M. D.? Small mammal and bird responses to a Savory grazing experiment in a coastal California grassland. *in*?
 89. Kauffman, J. B., and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications: a review. *Journal of Range Management* **37**:430-438.
 90. Keeley, J. E. 2002. Native American impacts on fire regimes of the California coastal ranges. *Journal of Biogeography* **29**:303-320.
 91. Keeley, J. E. 2006. Fire Management Impacts on Invasive Plants in the Western United States. *Conservation Biology* **20**:375-384.
 92. Kelly, J. P. 2004. Vague consequences of omnipresence. *The Ardeid: Annual newsletter of the Audubon Canyon Ranch*:1-5.
 93. Kelly, J. P., K. L. Etienne, and J. E. Roth. 2005. Factors influencing the nest predatory behaviors of Common Ravens in heronries. *Condor* **107**:402-415.
 94. Kruess, A., and T. Tschardt. 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation* **106**:293-302.
 95. Lathrop, K. T., and P. J. P. Gogan. 1985. Plant communities of the Tule Elk range, Point Reyes National Seashore. Technical Report 18, Cooperative National Park Resources Unit, University of California, Davis, Davis, CA, USA.
 96. Launer, A. E., D. D. Murphy, J. M. Hoekstra, and H. R. Sparrow. 1992. The endangered Myrtle's silverspot butterfly: Present status and initial conservation planning. *Journal of Research on the Lepidoptera* **31**:132-146.
 97. Lennox, M., D. Lewis, R. D. Jackson, J. Harper, R. Katz, S. Larson, B. Allen-Diaz, and K. Tate. 2004. Riparian ecosystems and buffers: multi-scale structure, function, and management. Pages 1-4 *in* American Water Resources Association, Olympic Valley, CA, USA.
 98. Maron, J. L., S. Harrison, and M. Greaves. 2001. Origin of an insect outbreak: escape in space or time from natural enemies? *Oecologia* **126**:595-602.
 99. Martin, T. G., and H. P. Possingham. 2005. Predicting the impact of livestock grazing on birds using foraging height data. *Journal of Applied Ecology* **42**:400-408.

100. Martin, T. G., S. McIntyre, C. P. Catterall, and H. P. Possingham. 2006. Is landscape context important for riparian conservation? Birds in grassy woodland. *Biological Conservation* **127**:201-214.
101. Marty, J. T. 2005. Effects of Cattle Grazing on Diversity in Ephemeral Wetlands. *Conservation Biology* **19**:1626-1632.
102. Marty, J. T., S. K. Collinge, and K. J. Rice. 2005. Responses of a remnant California native bunchgrass population to grazing, burning and climatic variation. *Plant Ecology* **181**:101-112.
103. McBride, J., and H. F. Heady. 1968. Invasion of grassland by *Baccharis pilularis* D.C. *Journal of Range Management* **21**:106-108.
104. McNaughton, S. J. 1968. Structure and function in California grasslands. *Ecology* **49**:92-972.
105. Menke, J. W. 1989. Management controls on productivity. in L. F. Huenneke and H. A. Mooney, editors. *Grassland structure and function: California annual grassland*. Kluwer Academic Press, Dordrecht, The Netherlands.
106. Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* **132**:87-106.
107. Mills, J. M. 1983. Herbivory and seedling establishment in post-fire southern California chaparral. *Oecologia* **60**:267-270.
108. Nelson, L. L., and E. B. Allen. 1993. Restoration of *Stipa pulchra* grasslands: effects mycorrhizae and competition from *Avena barbata*. *Restoration Ecology* **1**:40-50.
109. O'Connor, T. G. 1991. Local extinction in perennial grasslands: a life-history approach. *American Naturalist* **137**:753-773.
110. Paine, L. K., and C. A. Ribic. 2002. Comparison of riparian plant communities under four land management systems in southwestern Wisconsin. *Agriculture Ecosystems and Environment* **92**:93-105.
111. Painter, E. L., and A. J. Belsky. 1993. Application of herbivore optimization theory to rangelands of the western United States. *Ecological Applications* **3**:2-9.
112. Painter, E. L. 1995. Threats to the California flora: ungulate grazers and browsers. *Madrono* **42**:180-188.
113. Parker, J. D., D. E. Burkepile, and M. E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. *Science* **311**:1459-1461.
114. Peart, D. R. 1989. Species interactions in a successional grassland iii. Effects of canopy gaps, gopher mounds and grazing on colonization. *Journal of Ecology* **77**:267-289.
115. Pickart, A. J., L. M. Miller, and T. E. Duebendorfer. 1998. Yellow bush lupine invasion in northern California coastal dunes I. Ecological impacts and manual restoration techniques. *Restoration Ecology* **6**:59-68.
116. Pyke, C. R., and J. Marty. 2005. Cattle grazing mediates climate change impacts on ephemeral wetlands. *Conservation Biology* **19**:1619-1625.
117. Rappole, J. H., and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. *Auk* **111**:652-660.
118. Reynolds, S. A., J. D. Corbin, and C. M. D'Antonio. 2001. The effects of litter and temperature on the germination of native and exotic grasses in a coastal California

- grassland. *Madrono* **48**:230-235.
119. Rice, K. J. 1987. Interaction of disturbance, patch size, and herbivory in *Erodium* colonization. *Ecology* **68**:1113-1115.
 120. Rich, T. D. 2002. Using breeding land birds in the assessment of western riparian systems. *Wildlife Society Bulletin* **30**:1128-1139.
 121. Robinson, S. K., S. I. Rothstein, M. C. Brittingham, L. J. Petit, and J. A. Grzybowski. 1995. Chapter 15. Ecology and behavior of cowbirds and their impact on host populations. Pages 428-460 in T. E. Martin and D. M. Finch, editors. *Ecology and management of neotropical migratory birds: a synthesis and review of critical issues*. Oxford University Press, New York, NY, USA.
 122. Roth, J. E., J. P. Kelly, W. J. Sydeman, M. W. Parker, and S. G. Allen. 1999. Ecosystem-level management of Common Ravens on the Point Reyes National Seashore. National Park Service, Point Reyes Station, CA, USA.
 123. Roth, J. E., J. P. Kelly, W. J. Sydeman, and M. A. Colwell. 2004. Sex differences in space use of breeding Common Ravens in western Marin County, California. *The Condor* **106**:529-539.
 124. Saab, V. A., C. E. Bock, T. D. Rich, and D. S. Dobkin. 1995. Chapter 12. Livestock grazing effects in Western North America. Pages 311-353 in T. E. Martin and D. M. Finch, editors. *Ecology and management of neotropical migratory birds*. Oxford University Press, New York, NY, USA.
 125. Sarr, D. A. 2002. Riparian livestock exclosure research in the western United States: A critique and some recommendations. *Environmental Management* **30**:516-526.
 126. Seabloom, E. W., and O. J. Reichman. 2001. Simulation models of the interaction between herbivore foraging strategies, social behavior, and plant community dynamics. *American Naturalist* **157**:76-96.
 127. Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grasslands species. *Proceedings of the National Academy of Sciences* **100**:13384-13389.
 128. Seabloom, E. W., and S. A. Richards. 2003. Multiple stable equilibria in grasslands mediated by herbivore population dynamics and foraging behavior. *Ecology* **84**:2891-2904.
 129. Semenoff-Irving, M., and J. A. Howell. 2005. Pilot inventory of mammals, reptiles, and amphibians, Golden Gate National Recreation Area, California, 1990-1997. United States Geological Survey, Sausalito, CA, USA.
 130. Stromberg, M. R., and J. R. Griffin. 1996. Long-term patterns in coastal California grasslands in relation to cultivation, gophers, and grazing. *Ecological Applications* **6**:1189-1211.
 131. Stromberg, M. R., P. Kephart, and V. Yadon. 2001. Composition, invasibility, and diversity in coastal California grasslands. *Madrono* **48**:236-252.
 132. Strong, D. R., J. L. Maron, P. G. Connors, A. Whipple, S. Harrison, and R. L. Jefferies. 1995. High Mortality, Fluctuation in Numbers, and Heavy Subterranean Insect Herbivory in Bush Lupine, *Lupinus arboreus*. *Oecologia* **104**:85-92.
 133. Sullivan, B. K. 2000. Long-term shifts in snake populations: A California site revisited. *Biological Conservation* **94**:321-325.

134. Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* **79**:2890-2903.
135. Tewksbury, J. J., A. E. Black, N. Nur, V. A. Saab, B. D. Logan, and D. S. Dobkin. 2002. Effects of anthropogenic fragmentation and livestock grazing on western riparian bird communities. *Studies in Avian Biology*:158-202.
136. Thomsen, M. A., C. M. D'Antonio, K. B. Suttle, and W. P. Sousa. 2006. Ecological resistance, seed density and their interactions determine patterns of invasion in a California coastal grassland. *Ecology Letters* **9**:160-170.
137. Tisdale-Hein, R. E., and R. L. Knight. 2003. Densities of Brown-headed Cowbirds in riparian and rangeland areas, with and without cattle present, along the middle Rio Grande, New Mexico. *Studies in Avian Biology*:152-156.
138. Vesk, P. A., and M. Westoby. 2001. Predicting plant species' responses to grazing. *Journal of Applied Ecology* **38**:897-909.
139. Vivrette, N. J., and C. H. Muller. 1977. Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum-Crystallinum*. *Ecological Monographs* **47**:301-318.
140. WallisDeVries, M. F., and I. Raemakers. 2001. Does extensive grazing benefit butterflies in coastal dunes? *Restoration Ecology* **9**:179-188.
141. Wehausen, J. D., and H. W. Elliott, III. 1982. Range relationships and demography of Fallow Deer *Dama-Dama-Dama* and Axis Deer *Axis-Axis-Axis* on Point Reyes National Seashore, California, USA. *California Fish and Game* **68**:132-145.
142. Weiss, S. 1999. Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conservation Biology* **13**:1476-1486.
143. Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* **42**:266-274.
144. Winter, M., D. H. Johnson, J. A. Shaffer, T. M. Donovan, and W. D. Svedarsky. 2006. Patch size and landscape effects on density and nesting success of grassland birds. *Journal of Wildlife Management* **70**:158-172.
145. Wirtz, W. O. I. 1982. Postfire community structure of birds and rodents in southern California chaparral. GTR PSW-58, Pacific Southwest Forest and Range Research Station, Berkeley, CA, USA.

Table of summary findings. *Relationship between livestock grazing and biological resources.* Bold type face indicates California coastal grassland-specific study. N/A indicates that the study relates to grazing impacts but did not conclude whether livestock grazing has positive, negative, or no effect. Each study is complex; the summary effect shown here is the interpretation of the report author and may not be authoritative.

	Studies showing positive effect	Studies showing negative effect	Studies showing no effect/ equal	N/A
Large mammals		141*	56	
Small mammals	30, 53, 97	56, 81, 129	131	50, 51, 79, 95 113, 114
Birds	61, 80	80, 88, 122	61	3, 60 78, 145
Lepidoptera	38, 44, 140, 142	18, 96		95, 132
Native grasses	69, 70		69, 70, 130	
Native forbs	28, 70			
Native shrubs/oak		21, 45, 70, 97		
Mycorrhizae	59, 108	15, 16	4	27

*Positive effects were to non-native ungulates *Dama Dama* (Fallow Deer) and *Axis axis* (Axis Deer).

Appendix A.

Reference and bibliographic materials summaries

Code:

A= agency study or other report

C= California study

G= explicit grazing or clipping study

I= single-species study

M= experimental/manipulative, with control plots

N= introduced/non-native species study

O= observational study, inventory, or monitoring study

P= northern coastal grassland study

R= replication across multiple sites

S= shrub/scrub

T= theory or management recommendations

W= non-vascular plant study, wildlife (mammals, birds, insects, mycorrhizae)

Alexander and D'Antonio 2003

C, I, P, R, S

Fire reduces seed bank of French broom (*Genista monspessulana*), but repeated burning doesn't continue to reduce seeds. Young stands have as large a seed bank, or larger, than old stands. Non-broom grassland species seed banks decline under broom cover, more so as the stands age.

Allen, Richards, and Busso 1989

G, M, W

Near Logan, Utah, two tussock grasses (grazing tolerant *Agropyron desertorum*, and grazing-sensitive *A. spicatum* studied for impacts of soil water and grazing on vascular-arbuscular mycorrhizae over a 4-year period. Neither moisture, clipping, nor moisture*clipping had a significant on VAM infection. Interannual differences were significant, however. Results suggest that VAM are highly plastic and respond to environmental pressures we do not yet understand.

Allen and Pitkin, Partners in Flight 2000

C, G, A, W

Partners in Flight California grassland bird conservation plan explicitly call out Ferruginous Hawk, Grasshopper Sparrow, Mountain Plover, Northern Harrier, White-tailed Kite, Western Meadowlark, and Savannah Sparrow as focal species (high management and research priority in CA grasslands). Five primary problems for birds in CA today:

- Replacement of native species with introduced species
- Loss of grassland habitat
- Decreased/decreasing patch size of remaining grasslands
- Private landownership
- Paucity of critical information

Imperative to develop monitoring program throughout CA grasslands to assess effects of habitat type, fragmentation/edge, and other management questions on birds.

Grazing critical: Midwest research shows species response complex and often studies are contradictory (studies show 50% of species show positive, 50% negative response to grazing; GRSP respond well to light/moderate grazing in tallgrass, but negatively in shortgrass, semidesert, and mixed grass areas).

Patch size critical; too small patches are effectively worthless for most grassland spp.

Recommendations: avoid disking or mowing during breeding season, avoid burning during breeding season.

Amme 1986.

A, C, T

Recommendations for seed mixes and restoration practices at Point Reyes National Seashore.

Seeding and planting should occur in the fall; introducing native perennial grasses early after disturbance can stabilize soils and provide resistance to invasion by introduced species.

Species descriptions included.

Augustine 2003

G, M

Effects of livestock on African rangelands. Study indicates that movement of livestock impacts soil fertility by enriching (P, Ca, N) areas where cattle are penned, and lowered fertility in less-utilized areas. This enrichment can last four decades.

(note: impacts on species distribution and competitive interactions between native and non-native species in California coast rangelands)

Barbour et al. 1973

C, O, P, W

Bodega Head is ungrazed preserve on coast of Sonoma County.

Coastal climate is much cooler and fluctuations moderated compared to inland. Much reduced incoming radiation through fog cover in summer and longer, more frequent storms/clouds in winter.

6 identifiable plant communities within a few hundred meters from coast. Grassland only covers lower half of Head.

Temperature, soil moisture/texture, salt spray/salinity (distance gradient, seasonal pattern) effect plant distributions, e.g. California poppy. pH pretty neutral.

Salinity up to 800 ppm in soil.

Short and long-distance gradients, as well as temporal gradients (*note: non-equilibrium system)

Wildlife include: deer mice, house mouse, skunk, raccoon, voles, brush rabbit, grey fox, black-tailed deer etc.

Insect community includes lined snail and swift moth (*Hepialus behrensi*), thought to be responsible for the intermittent die-backs in bush lupine (*Lupinus arboreus*) populations.

Average primary productivity= 527 g/m²/year

Barry et al. 2006

C, G, T

California grasslands = 25% of state, include 90% of species listed in Inventory of Rare and Endangered Species of California (Skinner and Pavlik 1994).

Provide essential hydrologic functions, wildlife habitat, and native flora.

Many conservation lands have been protected from grazing; invasion by woody and introduced species often occurs on these lands.

Coastal restoration may have better success than inland because they are more mesic. Avoid restoration on shallow soils.

Frequent burning may decrease woody plants and increase weedy annuals.

Increasing native grass cover on sites that have been cultivated may require re-seeding or plug planting as well as vegetation management (depleted native species seed bank)

Bartolome et al. 2002 (RDM guidelines)

A, C, G, T

Residual dry matter (RDM), also called natural mulch.

Maximum productivity for sites with 15-40 inches of rain (Point Reyes) is around 750 lb/acre (or kg/ha) in fall, depending on slope and woody cover (shrubs and trees).

Bartolome et al. 2004

C, G, M, P

Sather Canyon study. Experimental manipulation of seasonal presence and timing of grazing for 3 years and autumn burning for 2 years. No treatment effects on diversity. Initial starting condition (species composition) and stochastic environmental variation were important parameters.

Grazing removal led to a shift from annual-dominated to more perennial-dominated community. *Nassella pulchra* increased over time regardless of grazing treatment, with greatest increase under spring grazing. *N. lepida* was greatest increase with grazing removal. Under mesic conditions grazing removal can increase native perennial grasses cover if already established there; if *N. pulchra* is the only native grass present, spring grazing would be effective.

Follows from Dyer and Rice that *N. pulchra* increases when released from diffuse competition with neighboring annuals and forbs.
Danthonia did not show an increase.

Bartolome and Gemill (1981) had rejected the idea of *N. pulchra* as a relictual dominant, hypothesizing rather that it is a disturbance adapted species thriving where light is less limiting than belowground resources (*note: confirmed by Gea-Izquierda et al.)

Variable, non-equilibrium system

Bentivenga and Hetrick 1992

G, M, R, W

Effects of tallgrass prairie management (mowing, burning, and fertilizing) on mycorrhizal symbiosis: little consistent effect on species composition or abundance in winter, but fertilizer inhibited symbiosis in spring and summer (the growing season). P and P+N fertilization showed greatest effects; N effects probably offset by large increase in biomass production consequent to N addition. Mycorrhizae.

Bethlenfalvay and Dakessian 1984

G, M, R, W

Northern Nevada study. Density of forage grasses and their colonization by VAM was significantly reduces as a result of grazing, by as much as 50%. No difference shown between grazed and ungrazed broadleaf plants.

Blair and Launer 1997

C, O, R, W

Coast range grasslands near Palo Alto, CA. Species richness of butterflies peaked at moderately disturbed sites while abundance decreased with disturbance.

Even small perturbations such as grazing in the open-space recreation area prior to 1989 and current use by hikers lead to a loss of species.

Blumler 1992

C, G, O, T

CNPS goal: maximum native diversity. Myths about the California grasslands: successional (disturbance is critical), annuals need disturbance to persist, bunchgrass prairie, introduced species are less well adapted than natives, bunchgrasses vs. sodgrasses (bunches can do fine with grazing), grasses require grazing (they tolerate it), uniform adaptation of natives (they're diverse).

Don't trade off native grasses for forbs, because forbs are the most diverse component. Established native grasses are competitive with annuals.

Bock et al. 1993

A, G, T

Suggestion to experimentally exclude cattle from 20% of federal lands. Grasslands are controlled by weather, fire, and grazing, operating on long temporal and large geographic scales.

Livestock can function as a keystone species; repercussions of grazing can be significant for entire ecosystem.

Borchert et al. 1989

C, M, R

Blue oak (*Quercus douglasii*) seedling recruitment. Buried and surface acorns tested for predation by gophers, birds, mice, deer, and cattle. Buried acorns had much higher recruitment rates and were mainly predated by gophers. Surface acorns desiccated and were eaten by cattle, mice, and gophers. Seedling recruitment correlated with canopy cover and mesic conditions at low elevations, but negatively at high elevations. Livestock had strong negative impact on seedling recruitment through predation and trampling.

Bullock et al. 1995

G, M, R

Grazers (here sheep) impact vegetation through creation and maintenance of small gaps. Study in England (Park grass). Gap size effects colonization and species composition, favoring common species. Magnitude of difference between gap and closed sward composition depends on gap size.

Bullock et al. 2001

G, M, R

Long-term experimental study of plant community responses to changes in grazing intensity (rare type of study!). Lowland UK grassland sheep study. Mechanisms differed strongly among seasonal treatments. Summer grazing responses linked to gap colonization ability; responses to winter and spring grazing positively related to grazer selectivity.

Strong need for long-term experimental analyses of community responses to grazing as vegetation responses may develop over a long time. Traits analysis recommended for research to understand/manage any grassland for diversity, weed control, etc.

Burke and Grime 1996

G, M, R

Long-term field experiment in UK to identify plant attributes and vegetation characteristics conducive to successful invasion. Fertilizer and disturbance gradients subject to single seed inoculum. Susceptibility of invasion strongly related to availability of bare ground created; most heavily invasible were sites with high disturbance and eutrophication. (*note- in keeping with California literature)

Callaway et al. 2003

C, M, R, N, W

Mycorrhizal fungi can alter interactions among plants through direct effects (providing resources to plants) and indirect effects. In this experiment *Centaurea melitensis*, an introduced weedy thistle, *Avena barbata*, and *Nassella pulchra* were tested with and without anti-fungal treatment. Grown alone, untreated *C. melitensis* was less robust than treated; with *N. pulchra* the effects were reversed. This effect was not shown with *A. barbata*. Complex interactions, mechanisms not entirely clear.

Callaway and Davis 1993

C, G, M, O, P, R, S

Using aerial photographs from 1947 to 1989, measured rates of directional change in coastal California grasslands. Communities dynamic. Less directional change in grazed or burned than in ungrazed or unburned. Fire, grazing, and physical environment interacted to determine rate of directional change.

Carlsen, Menke, and Pavlik 2000

C, I, M, N, R

Rare annual forb *Amsinckia grandiflora* is declining due to competitive suppression by exotic annual grasses, and may perform better in native perennial bunchgrass matrix. Outplanted *Poa secunda* in three densities and compared to exotic composition plots in three densities. Both *Poa* and exotic plots showed reduced soil moisture at increasing densities in same linear fashion. Exotics reduced *Amsinckia* more at low and medium

densities than *Poa*; at high densities suppression was same for both. Low to medium density native grass restoration would be good for *Amsinckia*.

Cockburn and Lidicker 1983

C, G, I, M, W

Voies (*Microtus californicus*) exhibited seasonal fluctuations in numbers along with two extreme peaks in abundance. Floristic richness changed with heavy vole grazing but spatial pattern remained the same. Parameters of female survival and reproduction were correlated with floristic micropattern. Voies perform better in vegetation dominated by native grass *Elymus (Leymus) triticoides*.

Corbin and D'Antonio 2004

C, M, N, P, R

Tested relative competitiveness of native perennial and exotic annual grasses of coastal California grassland at Tom's Point in Marin County by seed rain experiment. Competitive interactions in the first season favored exotics but natives became more competitive over time, as they limited light and space available for seedlings to germinate. If this is true elsewhere, seed rain from exotics was probably not sufficient to cause type-conversion to annual grassland regionally.

Cremers 2004

C, G, M

In an annual grassland short duration rotational grazing was associated with declines in native plant species cover.

D'Antonio 1993

C, I, M, R

Experiment on *Carpobrotus edulis* on coastal grassland, backdunes and coastal scrub. Interference by established plants limited invasion in grasslands; requires soil disturbance (e.g. gopher mounds) to invade there. When disturbance occurs, however, rapid establishment through clonal growth is great and not affected by herbivory.

Herbivory counteracted invasion potential.

DeSimone and Zedler 1999

C, M, R, S

Coastal sage scrub recruits after fire but also under mature canopy in gaps. Small mammals positively affected shrub establishment in grasslands (germination on gopher mounds) but not in the scrub and ecotone. Late spring rains did not affect recruitment (seed coat helps?).

Donovan et al. 2002

A, T

Research working group from Partners in Flight establishes research priorities for Neotropical migrant landbirds. California coast protection is a priority because of development and habitat change. Understanding grazing relationship a priority in sub-steppe and riparian areas.

Dennis and Eales 1997

O, R, W

Habitat quality, patch size, and isolation account for 61% of variation in occupancy of *Coenonympha tullia* (Lepidoptera: Satyrinae). Restoration potential important since it's both quality and quantity of habitat that matter.

Dahlgren et al. 1997

C, G, I, M, R

Oak and grazing study on soil properties. Showed that oaks help maintain soil nutrients and moisture. Light to moderate grazing had no effect on soil properties (bulk density, P availability), though heavier grazing might. Forage increases after oak removal are short-term.

Dyer and Rice 1999

C, M, I, R

Effects of competition on resource availability and growth of *Nassella pulchra*: bunchgrass grew larger and had more culms without interspecific competitors. Also impacted by intraspecific competition when no interspecific competition. Competition for light in spring when annuals growth is most rapid suppresses bunchgrass; annuals reduce access to belowground resources by competitive interference; dominance of annual species in California grasslands results in underutilization of deeper soil resources.

Ellingsen et al. 1997

G, M, W

Cattle grazing by herdsmen in Ukraine impacts *Coenonympha glycerion* and *Lasiommata megera* (Lepidoptera: Satyridae). Both species require habitats formed by cattle; moderate, infrequent grazing preferred. Patchy habitat mosaics preferred, would be lost by intensification or cessation of grazing.

Elliott and Wehausen 1974

C, G, O, P

Land clearing and sustained cattle grazing have forced coastal scrub and prairie to early successional states/seres. Comparison between heavily grazed, moderately grazed, and 6

years ungrazed. Removal of grazing caused a change toward “climax community” over six years; 78.5% native species compared with 65% native species in heavily grazed plot. Perennial introduced species are well adapted and would be expected to remain in “climax community”.

Eom et al. 2001

G, M, R

Complex interactions among mycorrhizal fungi, plants, and herbivores in tallgrass prairie. Direct and indirect effects. Moderate and intense grazing positively impacted root colonization by fungi in both years, but diversity of fungi decreased.

Fehmi 2002

C, G, T, W

Interacting effects of cattle and voles might explain the inconsistent results from grazing experiments and their derived management practices. Livestock management may not be the only determinant of vegetation structure and composition.

Fehmi and Bartolome 2002

C, G, M, P, W

Plant species richness and composition respond variably to grazing. Vole activity may play a major role in species richness and distribution. Ungrazed coastal grasslands had higher species richness where more vole burrows. Perennial site compared to annual site; perennial site contained species of annual site, also contained more voles.

A possible tradeoff exists between livestock and rodent herbivory in California annual grasslands.

Fehmi and Bartolome 2003

C, I, M, P

Burning and grazing in California coastal grassland impacts on *Nassella pulchra*, which responded well to burning and grazing exclusion.

Fehmi et al. 2005

C, G, M, W

Effects of moderate grazing in Coast Range grasslands on California ground squirrels (*Spermophilus beecheyii*). Densities did not differ between grazed or ungrazed areas, or habitat types, though declines occurred throughout study. No negative effects on ground squirrels. Standing biomass in grazed plots was lower than in exclosures.

Fellers and Pratt 2002

A, C, O, W

Fewer species of small vertebrates were found in grazed pasture and iceplant/dune than any other site. Larger mammals showed less habitat preference. Grazing is not positively correlated with abundance or diversity of terrestrial vertebrates at Point Reyes.

Frank et al. 2003

G, M, R, W

Soil microbes in Yellowstone grasslands grazed and ungrazed; microbe community was different; dominant plant density consequently different. AMF affected *Poa pratensis*, AMF spore communities differed in grazed and ungrazed, no evidence of pathogenic fungi. Need to better examine role that soil microbial community plays in regulating terrestrial ecosystems.

Gardali et al. 2003

C, O, S, W

In burned riparian corridors habitat changes resulted in increases of Song Sparrows, Orange-crowned Warblers, but reduction in Chestnut-backed Chickadee and Pacific-slope Flycatcher. Variable responses to fire, useful if fire is to be used as management tool.

Gurevitch and Hedges 1999

T

Statistical issues in meta-analysis described, recommendations made.

Hamilton 1997

C, G, T

For central and southern California the relict theory of bunchgrass dominance is probably incorrect. Many areas dominated today by annual grasses may formerly have been dominated by different vegetation types such as oak woodland, chaparral, or coastal scrub.

Hamilton et al. 1999

C, M, R

Coexistence and interference between a *Nassella pulchra* and introduced annual grasses in Santa Ynez Valley, central Coast Range. Recruitment by *Nassella* was seed-limited, presence of annuals decreased growth and seed production of *Nassella* at all ages. Water competition seems to be the reason. *Nassella* does better in drought years than annuals, and may persist because it can survive drought.

*note these results could be different along coast where moisture less limiting.

Harrison et al. 2002

C, G, M, R

Grazing and fire in Coast Range grassland affected total species richness positively in both serpentine and non-serpentine soils. Burning increased enhanced native species more on serpentine soils. Grazing increased native species richness on serpentine but not non-serpentine soils.

Soil information and ecological heterogeneity important considerations in grassland restoration.

Hatch et al. 1999

C, G, M, P, R

Danthonia californica responded favorably to grazing. *Nassella pulchra* did not respond consistently to grazing treatments.

Hayes and Holl 2003.

C, G, M, P, R

Grassland communities are disturbance-dependent but few studies documenting complex disturbance responses. Factorial experiment with clipping, litter removal, and soil disturbance in coastal grassland. More frequent clipping reduced cover of exotic grasses and favored exotic forbs, whereas native species were unaffected by clipping frequency. Litter and soil treatments did not affect vegetation composition. Treatments varied within guilds among sites, highlighting importance of replicating experiments at several sites before recommending conservation practices.

Hayes and Holl 2003b

C, G, O, P, R

Impacts of grazing on California coastal grasslands. Native annual forb species richness and cover were higher in grazed sites, concomitant with reduced litter and decreased vegetation height. Native perennial forbs suffered. Soil properties explained little variation. Complex management ramifications: mosaic grazing management recommended.

Hayhoe et al. 2004

T

Under all of the IPCC projected scenarios significant changes are expected to occur in California's climate by 2100. Predictions: hotter, slightly drier, with more extreme heat events and changes to water supply (runoff).

Heady et al. 1988 Natural grasslands book.

C, O, T

Some parts of coastal grassland may be successional to scrub. Successional relationships may have resulted from heavy grazing by Roosevelt Elk.

Hedges et al. 1999

T

Meta-analysis method using response ratios.

Hektner and Foin 1977

C, O, P

Sea Ranch vegetation analysis. 10 years without grazing. Succession towards perennial grasses occurring. Small scale patchiness. They expected annuals to disappear as recovery from grazing proceeds.

Herkert 1994

M, R, W

Patch size critical for Dickcissels in tallgrass prairie. Area-sensitive birds may not be able to colonize at all below a certain patch size. Fragmentation leads to decline.

Heady 1956

C, M, R

Hopland study, inland Mendocino. Mulch has variable effects on species, direct effect on species composition. Mulch reduces runoff and erosion. *Nassella* colonized under mulch.

Hobbs and Mooney 1995

C, M, R, W

Jasper Ridge preserve, near San Jose, California.

Changing species importances, complex disturbance regime, and importance of disturbance history make modeling this system very difficult. Gopher exclusion led to increasing then decreasing perennial species cover.

Many practical problems with maintaining long-term field experiments and analyzing complex time series data which suffer from inadvertent deviations from the original experimental design.

Holmes et al. 1999

C, G, O, P, R, W

Songbird habitat associations and effects of grazing at PRNS and GGNRA. Riparian areas are critical. Shrub reduction from grazing results in reduction or loss of several

species associated with that habitat type. Conversely, grassland-specialists respond positively to grazing.

Howell and Semenov-Irving 2005

A, C, O, P, W

At GGNRA and PRNS vertebrate diversity and abundance in grazed areas is less than ungrazed.

Hunt 1992

C, O, W

San Diego valley pocket gophers eat shoots primarily; forb shoots in late autumn through spring, grass shoots from summer into autumn. Forb shoots are the preferred food.

Jackson 1985

C, N, T

Annual Mediterranean grasses that have been introduced and invaded California grasslands are primarily ruderal species in early successional grasslands or open degraded maquis in their home ranges. They do not form stable communities like in California. Ruderal life history characteristics and suitable periods of heavy grazing and drought may have combined to allow spread in California. Introduced and native perennials have slower winter growth rates and lower reproductive outputs during their first year than annuals.

Jackson and Bartolome 2007

C, G, T

Grazing affects grasslands by defoliation, compaction, and altering biogeochemical cycles (nutrient cycling). Phenomena are manifest at different scales of ecological organization, and are influenced by site and time specific variables. Grazing effects on climatically different California grasslands may be more disparate than between coastal prairie and tallgrass, say, both of which are dominated by perennials.

Grassland management must be based on scientifically produced information that is applicable to appropriate sites and scales.

Range managers control type, intensity, frequency, and duration of grazing; it's not on or off.

Johnson 2002

T

Replication is critical in wildlife studies within studies, and over time.

Johnson ? Humboldt State.

C, G, O, P, W

Onset of grazing negatively impacted rodents and birds in coastal grassland.

Kauffman and Krueger 1984

G, T

Riparian areas are well-defined habitat zones within drier surrounding areas, make up minor proportion of entire area, more productive than surrounding area, and critical source of biodiversity within rangelands.

Understanding their role in the landscape and ecosystem critical to good management. Variable depending on ecosystem.

Keeley 2006

O

Fire impacts on invasive plants in Western U.S. Prescription burning has had questionable success when applied to disturbance-dependent annuals. Success is most likely when coupled with ecosystem restoration that alters the competitive balance between introduced species and natives.

Keeley 2002

C, P, T

Lightning fire frequency here is lowest in U.S., highest pre-Columbian population of people. Ecological studies in coastal CA have failed to uncover clear soil or climate factors explaining grassland and shrubland distribution patterns. Landscape was type converted by Native Americans for grassland by frequent fire; otherwise coastal prairie turns to scrub. Grasslands are disturbance dependant.

Kruess and Tschardt 2002

G, M, W

Grazing intensity effects on plant and insect diversity examined in North Germany at low and high grazing, short term and long-term ungrazed grasslands. Vegetation complexity was higher on ungrazed than grazed plots. Insect diversity increased in following order: intensively grazed, extensively grazed, short-term ungrazed, long-term ungrazed. Vegetation height was significant predictor of insect diversity

Maron et al. 2001

C, M, O, P, S, W

Bodega Marine Reserve. Tussock moth caterpillars (*Orgyia vetusta*) outbreak on bush lupine (*Lupinus arboreus*). Spatial escape from parasitoids facilitated the growth of incipient local outbreak. Moth causes dieback of lupine.

Marty et al. 2005

C, G, M, R

At Beale Airforce base, Sierra foothills annual grasslands. Bunchgrass densities did not differ among treatments, though they did decline over time. Above average rainfall and below average temperatures favored native bunchgrasses.

*what? This study isn't clear to me.

Marty 2005

C, G, M, R, W

Removal of grazing caused decline in vernal pool plant species and aquatic fauna by releasing annual species and drying down.

McBride and Heady 1968

C, G, O, P

Grazing removal in Berkeley hills caused succession to scrub (*Baccharis pilularis* dominated).

McNaughton 1968

C, M, O

Productivity at Jasper Ridge inversely related to diversity and positively related to dominance. Stability was related neither to productivity, diversity, or dominance. Productivity could be optimized without jeopardizing stability? The annual grassland vegetation is a mosaic of floristic composition and ecological properties, shifting in response to habitat patterns but without abrupt discontinuities.

McNeill et al. 2003

A, G, O, P

Morro Bay monitoring program testing best management practices. Grazing intensities were reduced, fencing erected, roads improved, etc. Specific data not included here, but overall increases in water quality occurred though little quantifiable change in species composition. Aboveground biomass tended to increase, especially within fenced-out riparian corridors.

Michunas et al. 1988

T

Current models relate predation, competition, and disturbance to community structure with mixed results; this paper includes environmental moisture, pre-existing community, and evolutionary history of grazing, as well.

Mills 1983

G, C, S, W

Insect herbivory did not affect shrub seedlings post-fire. Herbivory was due to small mammals.

Nelson and Allen 1993

C, G, M, W

Mycorrhizae did not alleviate negative effects of competition of *Avena barbata* on native bunchgrass *Nassella pulchra*. Once annual grassland has been revegetated with *Nassella* the original fungal species composition will return quickly. Where *Avena* dominates inoculation will not suffice for establishing *Nassella*; usual practices for weed control need to be employed.

O'Connor 1991

T

Perennial obligate seed-producers can become extirpated/locally extinct through heavy grazing due to decreased seed input, competition from grazing-resistant/resilient annuals and invasives.

Painter 1995

C, G, T

Livestock herbivory not natural part of California grassland ecosystems, does not mimic Pleistocene or modern native mammals. Ungulates can have negative impacts.

Painter and Belsky 1993

G, T

Authors contend that available evidence indicates that whole-plant overcompensation and optimization of productivity rare occur and may have little or no evolutionary significance, these concepts are being used to justify heavy grazing on Western lands.

*also see Bartolome 1993 in Ecological Applications for response, in which compensatory growth has been well linked to ecosystem processes in highly productive and managed lands, but not semi-arid systems.

Parker et al. 2006

N, G, W

Meta-analysis of manipulative field studies showed that native herbivores suppressed exotic plants, whereas exotic herbivores facilitated abundance and richness of exotic plants.

Peart 1989
C, G, O, P, W

Sea Ranch (a successional grassland released from grazing). Remaining disturbances include canopy gaps from death of individual bunchgrasses, soil disturbance by gophers, and grazing by native animals.

Canopy gaps from death of bunchgrasses and gopher disturbances strongly affected colonization success. Best colonizers were *Anthoxanthum* and *Holcus lanatus*. Native bunchgrass species did not colonize well as a guild. Species with highest density of seed rain did best, seed size correlated with colonization success.

Canopy gaps favored same species that colonized in undisturbed sites. Both types of disturbance increased colonizations by perennials in annual-dominated vegetation, and canopy gaps were required for changes in species dominance in perennial vegetation.

Dominant species at Sea Ranch are *Holcus*, *Anthoxanthum*, *Deschampsia*, *Vulpia bromoides*.

Pickart et al. 1998
C, M, P, S

Nitrate and ammonium increase with *Lupinus arboreus* cover. Bush lupine invasion results in direct soil enrichment and indirect enrichment through encroachment of other invasives, particularly grasses. Treatment reduces establishment of introduced grasses and recruitment of new lupine seedlings. In areas with low native propagules and high lupine cover revegetation is required.

Pyke and Marty 2005
C, G, M, R

Grazing can confound hydrologic changes concomitant with climate change, playing a critical role in maintaining suitability of vernal pools for endangered aquatic invertebrates and amphibians.

Reynolds et al. 2001
C, M, N, P, R

Litter and temperature may play a role in invasion by exotic annual and perennial grasses. Species react independently, not as part of guild. Using guild analysis masks responses. Germination of *Festuca arundinacea* was higher than all other species. *Holcus lanatus* showed no advantage over native species under heavy litter. *Avena barbata* and *Vulpia myuros* were first to germinate.

Rice 1987

C, G, I, M, N, R

Colonization of *Erodium* depends on gap patch size and differential environmental conditions within the patch. Sheep have negative impact on vole population by eliminating litter, and voles eat *Erodium* seeds. Thus, sheep grazing indirectly facilitates *Erodium*.

Lathrop and Gogan 1985.

C, A, G, O, P, S, W

Relatively little vegetation community distribution change over period from 1952 to 1985. *Lupinus arboreus* has dynamic continuous process of establishment and mortality.

Grazing maintains grasslands at Point Reyes; absence of grazing will lead to encroachment of shrubs.

Seabloom et al. 2003

C, N, M

Santa Ynez valley, Sedgwick Preserve. Native bunchgrasses are good competitors for light and water once initial recruitment limitations have been overcome.

Semenoff-Irving and Howell 2005

A, C, O, P, W

Report on species abundances across all traps in GGNRA and PRNS from 1990-1997. Analysis of grazing effects not clear.

SER Primer 2004

T

Describes ecological restoration, attributes of restored systems, best planning practices, and how to incorporate restoration into other management activities.

Stromberg and Griffin 1996

C, G, M, O, W

Hastings Reserve, Monterey County. Species composition patterns reflect past cultivation. Relict stands of natives are on uncultivated, steep, clay sites, with a range of current grazing conditions.

Gophers graze, reduce biomass.

Stromberg et al. 2002

C, G, E, P

Coastal prairies are defined by grasses *Danthonia californica*, *Nassella pulchra*, *Festuca rubra*, and shrubs and forbs *Baccharis pilularis*, *Viola* sp., *Sidalcea* sp., *Cammissonia* sp., and *Acaena* sp. Coastal grasslands should be protected as species hotspots.

Strong et al. 1995

C, G, O, P, S, W

Intermittent *Lupinus arboreus* die-off is a result of root damage by caterpillars of the ghost moth or “swift” (*Hepialus californicus*). Not results of folivory by western tussock moth.

Sullivan 2000

C, W

No snake studies in coastal grassland published. Inland, snakes maintained abundances across two decades, despite widespread development

Thomsen et al. 2006

C, M, N, P

Angelo Coast Range reserve. Ecological resistance and propagule density interact in their effects on invasive species establishment. Studied *Holcus lanatus* in coastal grassland dominated by exotic annuals. Decreased competition from exotic annuals had no effect. Late-season water availability facilitated invasion, as did spring watering, because they reduced resistance.

Vesk and Westoby 2001

G, R

Plant species do not show consistent responses to livestock grazing across experiments based on plant traits. The more experiments one does the more likely one of them will show a directly opposite response to grazing.

Vivrette and Muller 1977

C, I, M, N, R

Mesembryanthemum crystallinum invaded coastal grassland in central coastal California. It accumulates salt throughout its life, then released it through fog and rain leaching after it dies. The soil beneath it becomes saline, preventing growth of nontolerant grassland species through osmotic interference.

WallisDeVries and Raemakers 2001

G, W, M

Grazing at low stocking rates in Netherlands is common in restoration projects. This study found that butterflies, critical indicators of habitat quality for many plant and

animal species, related to structure and composition of vegetation. Species richness was not affected by management. Butterflies were more abundant in grazed and ungrazed areas over cut (mowed) areas. Individual species responded variably to treatments; open grassland species benefited from grazing especially. None responded significantly negatively to grazing.

Wehausen and Elliott 1982

A, C, G, O, P, W

Axis and fallow deer, both introduced species, benefited from grazing at Point Reyes. Both prefer grassland species as forage.

Large areas of scrub at PRNS have been converted to grasslands through bulldozing, burning, plowing, and seeding.

Weiss 1999

C, I, M, W

Jasper Ridge Preserve near San Jose, California. Nutrient-poor serpentinitic soils support many rare species of plants and wildlife, including the Bay checkerspot butterfly (*Euphydryas editha bayensis*). Nitrogen deposition from pollution (smog dry deposition) facilitates invasion of introduced species, and grazing keeps them in check. Butterfly populations have crashed following cessation of grazing.

Proximate causes of crash were invasion by introduced grasses, particularly *Lolium multiflorum*. *note *Lolium* does better in more mesic sites like those along coast

Westoby et al. 1989

G, T

State-and-transition models, based on a catalogue of alternative plant community states and catalogue of potential transitions between states, describe rangeland ecosystems better than successional models (e.g. range condition model) based on equilibrium assumptions. This would enable managers to act opportunistically when conditions favoring a positive transition occur. Research under state-and-transition models would aim to improve the catalogues. Non-linear model.

Grassland respond to weather; this model accounts for this and the interaction between weather and livestock stocking rates and timing.

Wirtz 1982

C, O, W

Changes to rodent and avian community after fire in chaparral in southern California documented. Rodents rebounded quickly to pre-fire abundances. Avian species increased in species richness due to more and new food sources. Avian repopulation rapid.

