Population Ecology and Ecological Effects of Bison on Santa Catalina Island, California

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EXECUTIVE SUMMARY

The small group of bison first introduced to Santa Catalina Island in 1924 increased over the years and is currently managed by periodic roundups to maintain a herd size of 185-250 animals. The fauna of Santa Catalina Island did not historically include large grazing ungulates, which has led to significant recent concern regarding the potential ecological effects of bison on native and endemic plants and animals on the island. In the intervening years since bison were first brought to the island, however, this large ungulate has taken on important cultural and economic significance to island residents. The challenge for future management of bison on Santa Catalina Island will be balancing conservation interests related to the ecological integrity of the island with cultural and economic values. The focus of this study was to undertake detailed research on the ecological effects on bison on Santa Catalina Island and to provide recommendations on possible management options suitable for minimizing potential ecological damage induced by the activities of bison. In the report we detail and summarize the major findings of this study as they relate to island-based ecological restoration activities and potential future management of the bison on Santa Catalina Island at different levels. In the Executive Summary we briefly highlight the major findings of the study and refer readers to the body of the report for more information and justification for our suggestions on management.

Our research was multifaceted, using a combination of observational, comparative and experimental methods to evaluate many different potential effects of bison on Santa Catalina Island. Related to experimental aspects of the research (bison exclosure experiments), it is important to note that failure to ***detect*** an important ecological effect after a relatively short time frame (2 years for this study) does not mean an effect does not exist. Plant and animal communities are labile, and in ecological studies many years are often required to unequivocally identify important changes resulting from reduced exposure to a disturbance agent (bison grazing and wallowing in the case of this study) that might otherwise be masked by normal climatic or environmental variation. Finally, this study was designed to address the ecological relations that the Santa Catalina Island Conservancy will need to consider when managing bison on the island. As already noted, there are important social, cultural and economic considerations that will be weighed as the Conservancy considers future management directions for bison on Santa Catalina Island, which were not part of our ecological research on the bison on the island. Below we briefly describe the results and implications of the research, including how those results relate to potential changes in bison management. Additional details related to these findings are provided in the **RESULTS** and **DISCUSSION** sections of the report.

Although the introduced bison on Santa Catalina Island appear to be doing well based on long-term population growth and persistence, the animals are significantly smaller than mainland bison, experience relatively low reproductive rates, and appear in relatively poor nutritional condition based on serum chemistry/hematology and frequent observations of open sores (open sores are not typically observed at high frequencies in mainland bison). Taken together these results/observations indicate that the bison on Santa Catalina Island are in general poor health, especially during the relatively frequent drought periods on the island. From a humanitarian perspective, the generally poor body condition of bison on Santa Catalina Island should be considered as the Conservancy discusses management options. For example, bison restricted to a small national monument in Colorado were determined to be in poor nutritional condition based on small body sizes and low reproductive rates relative to bison in other parts of North America. In part, the eventual management decision to remove the bison herd from the Colorado National Monument was a direct result of this finding; officials were concerned that animals suffered from overall poor health.

Bison exclosure experiments indicate that foraging and wallowing is altering plant communities in grassland and riparian habitats more than in island scrub oak woodland/chaparral areas. In bison exposed island scrub oak woodland/chaparral habitats (e.g., Zones 2, 3, 4), however, bison may be altering aboveground canopy structure by rubbing and horning actions. Diets of bison on Santa Catalina Island were composed of a variety of native and non-native grasses and forbs. During dry periods bison altered their diets to include some woody shrubs and cactus, including small amounts of the Channel Island endemic island scrub oak. Santa Catalina Island has a recent history of disturbance by many non-native herbivores (livestock, feral goats, feral pigs, bison) such that island plant communities were already significantly disturbed before substantial numbers of bison were present. Previous research on grazing and herbivory indicates that ecosystems severely damaged by herbivores and grazing (Santa Catalina Island prior to the 1970s) usually require a greater reduction in grazing pressure, or no grazing at all to allow for recovery compared to areas lacking a history of overuse. Once an ecosystem is seriously damaged by herbivores, even low densities of remaining herbivores may prevent recovery. Nevertheless, and based on results from exclosure experiments, one immediate response of plant communities to reduction or removal of bison on the island will be the proliferation of non-native annual grasses currently being grazed by bison.

Importantly, bison are now serving as an important mechanism of dispersal for a variety of non-native grasses and herbaceous forbs, which may undermine ongoing efforts directed at weed management and plant community restoration. Bison hair samples collected from wallows

contained multiple seeds of non-native seeds proportional to the mass of the hair clump. Seeds of non-native plants extracted from hair clumps germinated in both greenhouse and field trials. Thus, bison are actively dispersing seeds of many non-native weedy grasses and forbs across large areas of the island via their wallowing activities. Findings indicated that any future management option that reduces the number of bison below the current 185-250 target will function to reduce dispersal of non-native weedy plants because fewer bison will shed a lower overall mass of hair in fewer wallows across the island.

As part of comparative sampling in Zone 1 (bison absent) and Zone 2 (bison present), we detected no important negative effects of bison on native terrestrial vertebrates (small mammals, amphibians or reptiles. Due to the relatively short duration of our research contract, however, we were unable to perform a true experimental study on the potential effects of bison on small terrestrial vertebrates, which would provide the best method of controlling for site-specific differences that can cause difficulties in drawing inferences from comparative studies. Based on our current results, however, any future reduction in bison numbers on the island would not significantly alter the relative abundance or composition of terrestrial vertebrate communities.

We collected multiple water samples from streams and reservoirs on the island over 12+ months but detected no significant negative effects of bison on any of the measures of water quality evaluated. This part of our study did not include an experimental or comparative approach, however, with samples collected from bison absent areas as a control. Nevertheless, results suggested that any future change in bison management to reduce or remove bison from some or all areas of the island will not result in changes in measures of water quality.

Brown-headed cowbirds and European starlings sometimes occurred among relatively large groups of bison on Santa Catalina Island, but we cannot conclude from our research that the presence of these non-native birds on the island is being positively promoted by the presence of bison. As part of bison group and bison behavioral observations, the presence/absence of brown-headed cowbirds and European starlings was recorded. However, we did not conduct island-wide surveys for either of these species. Because observations of cowbirds and starlings among bison groups were disproportionately distributed near permanent sources of water and/or close to areas of relatively high human use/disturbance, it appears that multiple factors including but not limited to bison are facilitating these species on Santa Catalina Island.

We developed a detailed model to estimate carrying capacities for bison under three different management scenarios (no change from current approach, restricting bison to Zone 2 only, and restricting bison to a smaller area of Zone 2 amenable for maintaining bison viewing opportunities). We also considered the ecological implications of removing all bison from the

island independent of carrying capacity considerations. Our estimates of carrying capacity suggest that *if bison were the only species consuming or otherwise using aboveground plant biomass produced in any given year*, the island area encompassed by Zones 2, 3, and 4 could support absolutely no more than 378 bison. Many species of native vertebrates and invertebrates require forage and plant materials otherwise consumed by bison, however, and when at least as much biomass as that consumed by bison was reserved for use by native organisms, we estimated that only 95 to 189 bison should be allowed to range over Zones 2, 3, and 4. Because there is no reliable information on forage and habitat requirements for the multiple native island organisms in direct or indirect competition with bison for plant materials, however, we recommend that the Conservancy be conservative when reaching decisions on the numbers of bison supportable by different areas of the island. More specifically, we recommend management target numbers of 142 bison under Management Option A, 90 bison under Management Option B, and 13 bison under Management Option C. These recommended target numbers would allow for flexibility in population management because immediate action would not be required when the population is just below or just above a base stocking level. This conservative approach would also reduce risk to island plant communities currently exposed to relatively high numbers of bison, and provide a more acceptable level of protection for the unique natural resources on Santa Catalina. Finally, estimates of biomass production values used in the carrying capacity model were based on the current distribution and extent of grassland habitats on the island. Historically, extensive areas of coastal sage scrub habitat were converted to grassland when livestock were being produced on the island. As restoration of plant communities on Santa Catalina Island proceeds it is likely that the area of grassland habitat on the island will diminish, which will result in reduced grass and forb production and thereby reduce carrying capacities for bison for different regions of the island.

A fourth management option would be the complete removal of bison from Santa Catalina Island. Our results suggest that the complete removal of all bison from the island would significantly improve habitat conditions in grassland and riparian areas. Over the longer term bison removal would also reduce pressure on scrub oak island chaparral habitats, potentially maintaining beneficial habitat conditions for cavity nesting vertebrates. This option would completely eliminate viewing opportunities for island residents and visitors, however, and over the short term would result in the proliferation of exotic grasses and forbs. The buildup of dry plant biomass over several years by reduced grazing pressure would require consideration of a fire management program, potentially including periodic controlled burning to reduce fuel loads in the event of wildfire. A controlled burn schedule would be recommended because unusually

hot fires carried by a heavy understory fuel load would significantly damage island woodland habitats including the island endemic ironwoods and scrub oaks.

From a global conservation and restoration perspective, the ecological integrity of native plant and animal communities on islands is especially important because islands typically include proportionally more unique or endemic species than mainland areas. The Channel Islands of California are estimated to support 26 endemic species and 6 species have so far been identified as occurring only on Santa Catalina Island. Thus, the changes to plant communities on Santa Catalina Island that were identified as being caused by bison in this study should be of important management concern. We therefore recommend that the Santa Catalina Island Conservancy consider a significant reduction in bison numbers on the island and restrict the herd to a smaller area of the island than is currently occupied by the species. Reducing the herd size to around 90 bison and restricting animals to Zone 2 as described under Management Option B would support both of these recommendations. From an ecological perspective, even small numbers of a problematic non-native species occupying an insular ecosystem is cause for concern. Effective conservation often requires balancing multiple conflicting interests, however, and public acceptance of any change in bison management on Santa Catalina Island will be difficult. Nevertheless, the cost of maintaining the status quo on bison management will be significantly reduced ecological integrity of native plant communities on Santa Catalina Island.

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INTRODUCTION

Millions of American bison (*Bison bison*) were once widely distributed across the prairie grasslands and other habitats of North America (Roe 1970). Following indiscriminate slaughter during the 1800s, only a few hundred remained by 1900 (Shaw 1999). The implementation of intensive conservation efforts in the early 1900s averted extinction, however, and bison numbers have since recovered to several hundred thousand. Relatively small populations of free-ranging bison have been reestablished in a number of national and state parks in the United States, and on some private ranches and reserves (Berger and Cunningham 1994). Although bison are usually thought of as a prairie species, they historically occupied a diversity of habitats including montane forests, shrub-steppe rangeland, and desert-like regions (Van Vuren 1987). Associated with their wide ecological tolerances, some bison populations now occur in areas not previously occupied by the species (Lott 1979).

Historically, bison were not native to coastal regions of California nor to the Channel Islands off the coast of southern California (Roe 1970). In the period between 1924 and 1935, 25 bison were introduced to Santa Catalina Island (Lott and Minta 1983), one of four relatively large islands of the Channel Islands group. Attempts to increase the genetic diversity with subsequent introductions started in 1969 (Gingrich 1974), with the most recent acquisition of mainland-raised bison occurring in 1996 (H. Saldaña, pers. comm.). The bison increased in number; between 400 and 500 bison were allowed to roam freely on Santa Catalina Island in the 1960s and 1970s. A yearly cull was initiated in 1969 (Gringrich 1974), partly in response to a report by the U.S. Department of Agriculture suggesting that removal of a large percentage of grazing animals was necessary for the overgrazed landscape of Santa Catalina Island to recover (O'Malley 1994). In 1972, a non-profit organization, the Santa Catalina Island Conservancy (hereafter the Conservancy), was established and now owns and oversees management of around 88% of Santa Catalina Island, including most of the interior of the island. A major mission of the Conservancy is to conserve native biotic and abiotic resources and restore the island to its natural state, including removing introduced species when necessary.

Introduced species are an important conservation problem in general, but they are especially problematic on islands (Savidge 1987, Coblentz 1990, Hobbs and Huennekke 1992, Cree et al. 1995), which have higher proportions of endemic species than mainlands and are more prone to invasion (Lodge 1993, Reid and Miller 1989). Species inhabiting islands are particularly vulnerable to pressures exerted by introduced organisms because they evolved in relative isolation under reduced levels of interspecific competition, grazing, and predation (Simberloff

1994). Because of their size, nutritional requirements, and gregarious nature, bison have the potential to substantially impact habitats and other species that rely on those habitats. To minimize the potential negative effects of bison on native plants and animals, the Conservancy currently maintains the herd between 185 and 250 animals by periodic removals.

Bison are an important cultural icon in the United States. The species has long been a cultural and spiritual symbol to Native Americans, and more recently they are common in modern art, literature, and even as logos of sports teams and government organizations (Berger and Cunningham 1994). Since being introduced to Santa Catalina Island in the 1920s, bison have become increasingly important to island residents both as a symbol of the island's interior and financially as a major draw for tourism (e.g., , Boydston 1998, Duval 2001, Keith 2002, Mecoy 2002). The immense popularity of bison on Santa Catalina Island necessitates that the Conservancy carefully considers its possible management options, including but not limited to: (a) continued maintenance of a free-ranging herd; (b) maintenance of a relatively small fenced herd (< 100 animals); and (c) complete removal of the population. Public interest in maintaining a free-ranging herd is high. If bison are to remain on the island, however, it will be critically important to assess the conservation implications of this management approach. To date there has been no research directed at assessing the potential or real impacts of bison to the Santa Catalina Island ecosystem.

Based on studies of other introduced species and the observations of resource scientists, there are a number of potential concerns related to bison on Santa Catalina Island.
First, unlike plants of the North American prairies, plant communities on Santa Catalina Island did not co-evolve with large, mobile, grazing ungulates and may be seriously damaged by long term and continuing bison grazing (Martin et al. 1951, Minnich 1980). The Channel Islands of California were historically free of most non-native ungulates until the mid- to late-1800s, by which time early European explorers or landowners had introduced domestic livestock to most of the larger islands (Laughrin et al. 1994). Subsequently, a number of negative effects of these introductions on the native vegetation have been documented. For example, the combined effects of pigs, goats, and sheep on Santa Catalina, Santa Rosa, and Santa Cruz Islands have reduced populations of woody perennials (Peart et al. 1994, Wehtje 1994, Lombardo and Faulkner 2000), decreased herbaceous cover, and reduced overall plant species richness and diversity (Van Vuren and Coblentz 1987, Laughrin et al. 1994). Within their native range, bison can significantly influence ecosystems by the combined effects of disturbance and herbivory (Damhoureyeh and Hartnett 1997, Hartnett et al. 1997, Blair et al. 1998, Collins and Steinauer 1998, Knapp et al. 1999). On Santa Catalina Island, however, these same activities may negatively impact plant

communities; herbaceous plants on the island do not recover well from herbivory because the dry summer climate limits plant regrowth and because island-endemic plants in general lack adequate chemical or mechanical defenses against large herbivores (Bowen and Van Vuren 1997). Prolonged exposure to bison grazing may ultimately reduce the fitness of island plants, eventually resulting in reduced native plant species diversity. It had been hypothesized that grazing and disturbance by bison was facilitating the spread of non-native plants on Santa Catalina Island by disrupting succession processes, providing microhabitats suitable for invasion, and dispersal of seeds lodged in hair or hooves (Dyer and Rice 1999, Lombardo and Faulkner 2000).

A second and related concern is that the maintenance by bison of grasslands dominated by exotic annual plant species could have negative consequences for native terrestrial vertebrates, while promoting non-native birds including European starlings (*Sturnus vulgaris*) and brown-headed cowbirds (*Molothrus ater*). Brown-headed cowbirds are native to short-grass prairies of North America, but had spread to California by 1949 (National Audubon Society 2002). Cowbirds have been shown to reduce nesting success of native birds by brood parasitism (Rich 1978, Lowther 1993, Hahn and Hatfield 1995). European starlings were introduced to North America in 1890 (Cabe 1993). These birds were first recorded in California in 1959 (National Audubon Society 2002), and by 1967 they were widespread, although not common, on Santa Catalina Island (Jones 1990). Starlings reduce nesting success of native bird species by competing for nest cavities (Ingold 1994). Both starlings and cowbirds prefer to forage on short, mown, or grazed fields (Goguen and Mathews 2002, Olsson et al. 2002), such as those maintained by bison. Grazing and other activities of bison (wallowing, rubbing, trampling) that change the physical structure of microhabitats may reduce habitat quality and survival of small terrestrial vertebrates by direct trampling-induced mortality and exposing animals to increased risk of predation by reduced cover (Grant et al. 1982, Bock et al. 1990, Heske and Campbell 1991, Matlack et al. 2001). High levels of grazing also may reduce forage for rodents (Jones 1981, Hayward et al. 1997), and alter microhabitat temperature regimes (Jones 1981, Read 2002).

Third, bison consume large quantities of forage year round, but their food intake increases during the spring and summer periods (late gestation and lactation periods; Lott and Galland 1985), which corresponds to the start of the dry season in this part of California. Heavy grazing by bison during this period significantly reduces plant vegetative cover, which may contribute to soil compaction, desertification, and heavy erosion at the onset of the wet season. Moreover, bison consume predominantly grasses in lower latitudes of North America (Reynolds et al. 1982, Shaw and Meagher 1999), but the nutritional quality of exotic annual grasses (i.e., the dominant forage available on the island) is very poor in summer (Sampson et al. 1951, George et al. 2001).

Bison rely heavily on browse in some parts of their native range (Waggoner and Hinkes 1989, Larter and Gates 1991); during periods when succulent herbaceous vegetation is limited on Santa Catalina Island (usually May through December), they may forage on leaves and small twigs of island-endemic shrubs and trees.

Fourth, wallowing and other activities of bison (rubbing, horning) have physically damaged some rare plants and sensitive wetland habitats. Depending on the extent to which bison focus their activities and defecate in and around riparian areas and coastal wetlands, they may seriously degrade habitat and water quality (Coppedge and Shaw 1997, Fritz et al. 1999, Kemp and Dodds 2002). Riparian areas are critical in any habitat, but in xeric regions, they are especially important as a critical source of moisture for plants and wildlife (Belsky et al. 1999), habitat for breeding, wintering, and migration of wildlife (Fleischner 1994), and repositories of biodiversity (Kauffman and Krueger 1984, Fleischner 1994). Livestock grazing has been shown to increase nutrient concentrations, increase sediment loads and turbidity, and reduce dissolved oxygen concentrations of streams in the arid western United States (Kauffman and Krueger 1984, Belsky et al. 1999). Together, the potential effects of bison in wetlands and riparian corridors may have significant implications for the growth, reproduction, and survival of resident riparian, wetland and aquatic organisms (Gary et al. 1983, Cooke et al. 1986, Novotny and Olem 1994, Belsky et al. 1999, Caruso 2001). Finally, the Conservancy is attempting to restore different aspects of the island ecosystem through activities such as mapping and removal of invasive plant species, control of soil erosion, and restoration of native plant communities (Knapp 2002a, Schuyler et al. 2002, Stratton 2002). The presence of bison may jeopardize these conservation efforts, particularly as related to potential impacts of bison on soils and vegetation.

The long-term health of the biotic and abiotic resources making up the Santa Catalina Island ecosystem requires identifying important agents of change impinging on ecosystem function. Without such knowledge, it will not be possible for the Santa Catalina Island Conservancy to achieve its long-term mission of restoring and preserving the island in its natural state. Related to these issues, we initiated a study in January 2001 to assess the multiple potential ecosystem-level consequences of the introduced herd of bison on Santa Catalina Island. Our primary research objectives were to:

(1) Describe the population dynamics of bison.

(2) Assess habitat use, foraging behaviors, and diets of bison.

(3) Evaluate effects of bison on native plant communities, by examining how bison might impact the diversity and structure of herbaceous plant communities, alter the structure of chaparral stands, and facilitate the spread of non-native plants through seed dispersal.
(4) Investigate the possibility that bison would result in changes in the relative abundance and diversity of amphibians, reptiles, and small mammals, particularly because of changes in habitat structure. We also predicted that cowbirds and starlings would be positively associated with bison groups.
(5) Determine whether varying levels of bison use are associated with degradation of water quality (as measured by ammonium-nitrogen, nitrate-nitrogen, dissolved oxygen, pH, and turbidity) in reservoirs, Echo Lake, and streams.
(6) Predict the outcome of managing bison at different population levels.

This report presents the results and analysis from our two-year study, as well as potential options for management of the bison herd on Santa Catalina Island.

STUDY AREA

Santa Catalina Island is a 194-km^2 island located 40 km west of coastal Los Angeles. The elevation ranges from sea level to 640 m (Schuyler et al. 2002). The topography is rugged, with high relief terrain supporting a variety of woody and herbaceous plant communities and habitats (Minnich 1980). There are 6 and 26 extant species of plants endemic to Santa Catalina Island and the Channel Islands, respectively (Thorne 1967, 1969, 1976; Nixon and Muller 1994; Junak et al. 1997), and 5 to 6 subspecies of terrestrial animals endemic to Santa Catalina Island (Collins and George 1990, Schoenherr et al. 1999). The long term mean annual precipitation is 290 mm with most rainfall occurring between November and April (Santa Catalina Island Conservancy 2002).

Historically, no large native grazing animals occurred on Santa Catalina Island. Feral goats (*Capra hircus*) were established on the island sometime in the early 1800's whereas domestic cattle (*Bos taurus*), horses (*Equus caballus*), and sheep (*Ovis aries*) were present in the 1890's. Populations of feral pigs (*Sus scrofa*) were first established in the 1930's (Schuyler et al. 2002). Feral pigs and feral goats have been the focus of a variety of research and more recently an intensive eradication program to reduce their impacts (Coblentz 1978, 1993; Laughrin et al. 1994; Garcelon et al. 1993, Schuyler et al. 2002). Widespread domestic cattle operations had mostly ceased on Santa Catalina Island by the 1950s (Minnich 1980) and the island is considered to be recovering from overgrazing by domestic herbivores (Lott and Minta 1983). Mule deer were

introduced to the island in 1928 and have been controlled by a hunting program since 1990 (Melody and Garcelon 1999). As already noted, bison were introduced to Santa Catalina Island in 1924. As part of the periodic removals to control herd size, predominately young-aged males and some females are removed every one to two years (Lott and Minta 1983).

Three island-wide fences delimiting four hunting zones were constructed between December 1998 and July 1999 in support of efforts directed at eradication of feral pigs (Schuyler et al. 2002; Figure 1). Zone 1, the westernmost area, has been effectively free of pigs since late 1998 (Schuyler et al. 2002) and has been effectively free of bison west of the Isthmus since their introduction (D. Lott, pers. comm.). During our study, Zones 2 and 4 had very low (< 20 and < 40, respectively) numbers of pigs. Although Zone 3 supported high numbers of feral pigs at the outset of the study, the active hunting program beginning in 2001 steadily reduced numbers by July 2002 (Garcelon et al. 2001, Schuyler et al. 2002). Mule deer were present in all four zones. With the exception of three cattle guards and the occasional open gate, the feral animal removal fences limit movement by bison between zones.

For the purposes of this study, we considered four major habitat types most likely to be used by bison for activities such as grazing, wallowing, and loafing: coastal sage scrub, grassland, island chaparral, and riparian. The dominant plant community on Santa Catalina Island is coastal sage scrub, which is characterized by low-growing, drought-deciduous shrubs such as coastal sage (*Artemesia californica*), and succulents such as prickly pear cactus (*Opuntia littoralis*). Grassland is dominated by exotic annual grasses and forbs, such as wild oats (*Avena fatua*) and storksbill (*Erodium* spp.), interspersed with native bunch grasses including purple needle-grass (*Nasella pulchra*) and nodding needle-grass (*N. cernua*). Evergreen and drought-resistant shrubs and low trees such as lemonade berry (*Rhus integrifolia*) and chamise (*Adenostoma fasciculatum*) make up island chaparral habitat. We focused our attention on scrub oak-dominated island chaparral (SOIC) because it is the most common floristic type of chaparral on the island, and because island scrub oak (*Quercus pacifica*) is a Channel Island endemic (Junak et al. 1995). Finally, we used an all-inclusive "riparian" category to include riparian corridors and marshy wetland areas associated with artificial water impoundments and Echo Lake (the only natural lake on the island). The plant communities typical of riparian areas ranged from woodland (including cottonwood, *Populus trichocarpa*), to stream edges dominated by sedges, rushes, and water cress (*Rorippa nasturtium-aquaticum*), to scrubby mixes of shrubs (including mule fat, *Baccharis pilularis*) and various grasses.

METHODS

Climatic Variation

Data on precipitation are critical to understanding interannual variation in primary productivity and concomitant responses of large herbivores such as bison (Van Vuren and Bray 1986). To aid in interpretation of the results of this study, we compiled available data on precipitation for Santa Catalina Island for five different rain gauges (Santa Catalina Island Conservancy 2002). Mean daily precipitation values for the five rain gauges were summed over a 365-day period from 1 July to 30 June to estimate total annual precipitation. Mean daily rainfall values were summed over this period rather than a standard calendar year because of the Mediterranean climate of the area. We calculated the long-term mean annual precipitation for the island by averaging yearly totals from July 1948 to June 1990. The long-term mean was then used to determine the percent deviation from normal for the period from July 1990 to June 2002 (Hayes 2002). Although this technique has limitations when precipitation is not normally distributed, the percent deviation from normal is an easily understood representation of fluctuations in precipitation for a single region (McKee et al. 1993, Hayes 2002), which have profound effects on plant community processes including availability of aboveground biomass for grazing herbivores.

Bison Ecology

a) Population dynamics

To provide estimates of bison distribution, population size, and fecundity for reproductive aged females, we censused the bison population of Santa Catalina Island five times during the course of the study (April, August, and November 2001, and April and August 2002). Censuses were completed by searching the entire island from the ground by systematic road-based surveys, including hiking into areas with poor visibility (dense woodlands, narrow draws, etc.) from vantage points on roads. We had some helicopter support for the April 2002 census. To facilitate searches and avoid double counting, we divided the island into eight areas that were simultaneously searched by teams of 2-3 observers, over 1-2 days (Appendix I). During the censuses, we discriminated among four age and sex classes (calf, yearling, cow, bull) based on size, color, horn shapes, conformation and other traits (Van Vuren and Bray 1986). Sex was assessed for yearlings whenever possible, but we did not attempt to sex calves. We marked the location of each bison group on topographic maps of the island, and later used Geographic

Information System (GIS) software (ArcView GIS 3.2; Environmental Systems Research Institue, Inc. © 1992-1999) to assign an approximate Universal Transverse Mercator (UTM) position to the groups. The final counts for the August and November censuses (completed over two days) were lower than expected when compared to the counts completed in April (done in one day, and augmented by a helicopter for one census). Therefore, in each year we reported the population size as a range, using our final counts (corrected for potential double counting) from summer and fall as the lower limit, and the sum of calves in August and yearlings and adults in April as the upper limit. Annual calving rate was determined by dividing the total number of calves in the fall by the total number of cows $\geq$ 2 years old. Mortality rates of bison on the island were estimated using available data on the number of animals euthanized by the Conservancy, direct observation, and anecdotal reports from Conservancy personnel and volunteers.

In addition to island-wide systematic censuses, we conducted regularly scheduled and ad lib road surveys for "group observations" of bison. Starting in May 2001, we kept a record of the road segments we traveled in search of bison (see *Methods: Effects on Water Quality* for more detail). When bison groups were observed we noted their geographic locations, primary habitat associations, activity, size, and age and sex composition, and the current environmental conditions (temperature, relative humidity, and wind speed). We also recorded the presence or absence of brown-headed cowbirds or European starlings (cf. *Methods: Effects on Terrestrial Vertebrates*, below). To estimate the geographic location of bison groups, we recorded UTM coordinates of the location at which we were standing (using a Garmin GPS III Plus), and then used a laser range finder, compass, and clinometer to measure offset distance, angle, and slope to the approximate center of the bison group. We used Cartesian geometry to estimate the true UTM of the bison group from the offset data (M. Kleinfelter, pers. comm.; Appendix II). Animals within approximately 100 m of one another were considered part of the same group (Lott and Galland 1985). The relationship between individuals in a bison group is essentially random (Lott and Minta 1983); therefore, we considered records separated by 18-24 hrs as independent observations (Komers et al. 1993). We recognized four types of groups: solitary bison (male or female), adult male groups (several males all $\geq$ 2 years old), mixed adult groups (several adults of both sexes $\geq$ 2 years old), and mixed age and sex groups (adult males and females with calves and/or yearlings). ArcView GIS 3.2 was used to (1) assign bison groups to one of 17 habitat classes (Table 1), (2) measure the distance of groups to the nearest semi-permanent water (including horse troughs, Echo Lake, and artificial reservoirs), and (3) calculate slope for each group observation. We used log-linear models (Sokal and Rohlf 1981) to assess seasonal shifts in bison use of habitat, distance from water, and slope.

Table 1. Physiographic/vegetation classes on Santa Catalina Island, California (D. Knapp 2002b).

Habitat	Description
Valley and foothill grassland	Low, herbaceous communities composed of annual and perennial grasses and annual forbs.
Non-native herbaceous	Disturbed areas dominated by non-native herbaceous species such as fennel (*Foeniculum vulgare*).
Coastal sage scrub	Areas dominated by low, drought-tolerant shrubs and forbs; typically found on dry, rocky, south-facing slopes.
Coastal bluff scrub	Low scrub community (< 2 m tall) found at localized sites along coast on bluffs and headlands.
Maritime cactus scrub	Form of coastal sage scrub dominated by rare cactus species such as velvet cactus (*Bergerocactus emoryi*); typically found on arid coastal headlands and bluffs.
Island chaparral	Areas dominated by sclerophyllous shrubs and dwarf trees; best-developed on north- and east-facing shrubs and in protected canyons.
Non-native chaparral/non-native woodland	Areas dominated by non-native, woody species such as Dyer's greenwold (*Genista linifolia*), pines (*Pinus* spp.), and eucalyptus (*Eucalyptus* spp.).
Vernal ponds and reservoirs	Dessicated margins of Echo Lake and manmade reservoirs with unique assemblages of grasses and forbs.
Bare streambed	Drainage bottoms of ephemeral streams.
Riparian herbaceous	Stream corridors dominated by herbaceous plants.
Mule fat scrub	Early seral community along intermittent streams; dominated by mule fat (*Baccharis salicifolia*).
Southern riparian woodland	Permanent stream communities of dense, winter-deciduous tree species.
Island woodland	Dominated by Catalina ironwood (*Lyonothamnus floribundus* ssp. *floribundus*), island oak (*Quercus tomentella*), and Catalina cherry (*Prunus ilicifolia* ssp. *lyonii*).
Coastal marsh	Salt marsh found along sheltered inland margins of bays, lagoons, and estuaries.
Southern beach and dune	Pioneer dune community dominated by prostrate herbs with extensive root systems.
Bare ground	Rocky, eroded, or disturbed areas with < 25% vegetative cover.
Developed	Areas devoid of vegetation or planted with ornamental species.

Associated with bison roundups in October 2000 and 2002, we arranged to have blood drawn from bison by jugular venipuncture to assess pregnancy rates from serum progesterone or pregnancy-specific protein-B (PSPB; Noyes et al. 1997), and to evaluate aspects of body condition/nutritional status by hematology and serum chemistry. Blood used for serum progesterone or PSPB assays was collected in serum-separator tubes, centrifuged for 10 min. at 3,000 rpm, and then frozen or refrigerated until shipped off the island for analyses. Blood collected for hematological analyses was treated with the anticoagulant ethylene diamine tetra-acetic acid (EDTA), and refrigerated for shipment and analyses within four days of collection. Blood drawn for serum chemistry analyses was centrifuged for 10 min. at 3,000 rpm, blood serum was then drawn off, and samples refrigerated and shipped for analyses within four days of collection. Hematological and serum chemistry analyses were done at the IDEXX Veterinary Services laboratories (West Sacramento, California). Two-sample *t*-tests were used to compare the hematological and serum chemistry profiles of bison in 2000 with bison in 2002 (Zar 1999).

Analyses of blood serum for PSPB (samples from 14 ≥ two-year-old females collected in October 2000) were completed by BioTracking in Moscow, Idaho using Enzyme Linked Immunosorbent Assay (ELISA; Sasser et al. 1996). Females were considered pregnant when PSPB values in serum exceeded 0.0195 ng/ml (Sasser et al. 1996). Analyses of blood serum for progesterone (samples from 24 ≥ two-year-old females collected in October 2002) were completed by IDEXX Veterinary Services, using radioimmunoassay (RIA; Munro and Stabenfeldt 1984). Females were considered pregnant when serum progesterone exceeded 1.9 ng/ml based on data for bovids (C. Munro, pers. comm.).

Based on the possibility that Santa Catalina bison are small and experience poor reproductive success compared to herds in other regions, we compared the population structure and reproductive rate of the island population to mainland populations using published values from the native range of bison. We also calculated mean body masses for adult-aged male (6 to 13 years old) and adult-aged female bison (4 to 16 years old; Reynolds et al. 1982, Berger and Cunningham 1994) using data from the 2000 and 2002 Conservancy bison roundups in order to compare body masses of Santa Catalina bison to body masses of bison in multiple mainland locations (statistical comparisons of mean body masses were by *t*-tests with *p*-values corrected by the Dunn-Sidak method for planned comparisons; Sokal and Rohlf 1981). Body masses for adult-aged male and female bison were compiled from agency records on herds of bison in the central and western United States including the National Bison Range, Montana; Theodore Roosevelt National Park, North Dakota; Wind Cave National Park, South Dakota; and Witchita Mountains National Wildlife Refuge, Oklahoma (Halloran 1960).

b) Habitat use

Although group observations provided important data on general patterns of habitat use, this method provided limited insight into habitat use relative to availability because of potential bias associated with visibility from roads, diurnal observations, and unequal sampling effort (Norland et al. 1985). To estimate habitat selection by bison on the island we conducted multiple bison dung belt transects (2 m X 100 m) across areas of the island with a recent history of use by bison (i.e., Zone 1 was not included; Figure 1) and within three focal habitats: grasslands, SOIC, and coastal sage scrub. Activity observations from the bison group data indicated that bison rested and fed in the same proportions in each habitat type (Appendix III), so it was unlikely that fecal deposition rates associated with different activities differed between habitats (Norland et al. 1985, Litvaitis et al. 1994). Furthermore, dung piles represent nocturnal as well as diurnal habitat use (Norland et al. 1985). From group observations we determined that bison focused their

activities in areas with < 25° slope (95% of all bison groups were observed on slopes of < 25°), and we limited dung transects to such areas. ArcView GIS 3.2 was used to superimpose a 100-ha UTM grid (1000 m X 1000 m) on the remaining sampling space (areas with history of bison use and slopes < 25°) and to randomly identify 20 possible dung transect start points within each cell. From the 20 potential dung transect start points within each grid cell, we selected two points that were within the two dominant habitat types in that cell (grassland, SOIC, or coastal sage scrub). In cases where one habitat type contributed > 90% to the cell area, two transect start points within that habitat type were chosen. Along the 2 m X 100 m dung transects, all bison dung piles were counted regardless of age or state of decomposition. For those transects where habitats were a mosaic of multiple plant communities, we noted the major habitat type (> 60% of the transect and immediate area) and the minor habitat type (20-40% of the transect and immediate area). We measured slope and aspect with a clinometer at three points on each transect (0 m, 50 m, and 100 m) and visually ranked density of woody vegetation on a scale of 1 (open) to 5 (extremely dense). During final analyses we collapsed minor habitats into two categories (grassland, shrubby/wooded) and density of vegetation into three categories (open, moderate, dense). Chi-squared tests (Zar 1999) were used to identify habitats used significantly more often than expected relative to availability (primary range), in proportion to availability (secondary range), and less often than expected relative to availability (marginal range) (Norland et al. 1985). Generalized Linear Models (GLM; Systat 8.0, SPSS Inc. © 1998) were used to examine effects of habitat, slope, aspect, distance from water (obtained with ArcView GIS 3.2), and density of vegetation on the amount of bison activity as indexed by number of dung piles.

c) Foraging behaviors and diets

To evaluate activity patterns of bison on Santa Catalina Island, we conducted instantaneous scan sampling (Altman 1974) on randomly selected groups of bison located on different areas of the island. For each scan sampling survey, we drove a pre-determined route and initiated surveys on a randomly chosen group from the first four groups encountered. Over a 14-day period, we attempted to observe groups for three to four hours, three times, in each of three daylight periods (fall/winter: 0700 hr-1100 hr, 1000 hr-1400 hr, 1300 hr-1700 hr; spring/summer: 0600 hr-1100 hr, 1000 hr-1500 hr, 1500 hr-2000 hr). Groups were scanned every two minutes, and we recorded activity for as many animals as we could accommodate in approximately 30 seconds (up to 15 animals). To accommodate shifting group sizes during the scans and occasional unequal hours of observation, we recorded the total number of animals of each sex and age class participating in each activity (Hudson and Frank 1987, Rutley and Hudson 2001). Activity categories were: (1)

resting (included sleeping and ruminating); (2) standing (included ruminating, vigilance, and social interaction); (3) traveling-walking head-up; (4) traveling-running; (5) foraging-walking head-down (i.e. searching for food); (6) foraging-consuming grass; (7) foraging-consuming mixed grass and forbs; (8) foraging-consuming forbs; (9) foraging-consuming shrubs/trees; (10) foraging-consuming cactus; (11) foraging-consuming other; (12) minor-drinking; (13) minor-wallowing; (14) minor-horning/rubbing; (15) minor-sparring; (16) minor-tending/chasing; (17) minor-other (including, for example, nursing and suckling, gamboling, etc.). For the final presentation of activity budgets, the subcategories within foraging, resting, traveling, and minor activity were collapsed, and log-linear models (Sokal and Rohlf 1981) were used to examine the relationship between age/sex and time spent in different behaviors. We predicted that cows would invest more time in foraging during energetically stressful months (i.e., late-stage pregnancy and lactation), and used log-linear models to investigate changes in behavior patterns of cows among seasons.

We assessed bison diets through fecal sampling and bite-count surveys (Litvaitis et al. 1994). During group observations and behavioral surveys, fecal depositions from individual animals were noted. Once animals moved off, small (approximately 20 cc) subsamples of fresh feces were collected and frozen. For all months from March 2001 to August 2002 except April 2002, we collected a minimum of 10 fecal samples from individual adult-aged animals, which were later pooled to create 17 monthly "composite" samples for microhistological analyses of bison diets. Microhistological analysis is a technique that uses plant cell fragments in ungulate fecal samples to determine the relative frequency of individual plant samples consumed (Sparks and Malechek 1968, Reynolds et al. 1978, Van Vuren 1984). Frozen fecal samples were shipped off the island for microhistological analyses at the Diet Analysis Laboratory at Washington State University in Pullman, Washington. As part of microhistological analyses we were interested in the overall contribution of major forage classes to bison diets (annual grasses, perennial grasses, forbs, shrubs, and cactus), as well as identifying rare or endemic species of shrubs and forbs consumed by bison. Thus, two hundred microscope fields (25 views on each of 8 slides) were examined for epidermal fragments of forage plants, which allows for determination of plant tissue fragments to the level of genus and species (Davitt, personal communication). From examination of microscope fields and views of slides, the percent contribution of each plant was estimated for each monthly composite diet. From these data we grouped each species into the major forage classes noted above and used contingency analysis to examine seasonal shifts in diet for the one-year period from March 2001 to February 2002. Although additional data on bison diets from microhistological analyses were available for the period from March 2002 to August 2002, we

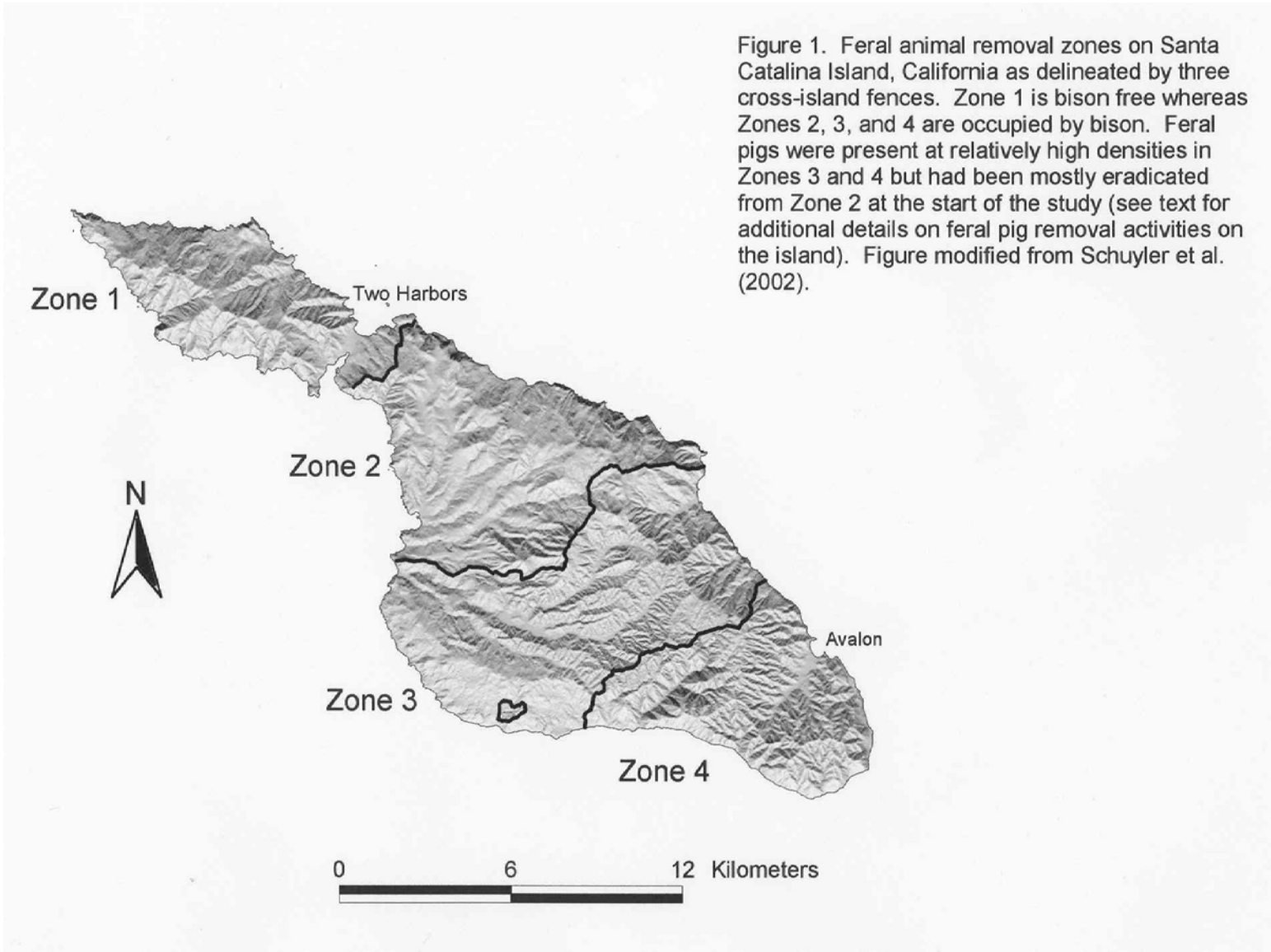

Figure 1. Feral animal removal zones on Santa Catalina Island, California as delineated by three cross-island fences. Zone 1 is bison free whereas Zones 2, 3, and 4 are occupied by bison. Feral pigs were present at relatively high densities in Zones 3 and 4 but had been mostly eradicated from Zone 2 at the start of the study (see text for additional details on feral pig removal activities on the island). Figure modified from Schuyler et al. (2002).

did not include these results in statistical analyses because no samples were collected during April, and because we lacked a second complete year for assessing seasonal variation.

Data on bite-counts were also used to estimate the relative contribution of the major forage classes to bison diets. Bite-count surveys are difficult with untamed animals foraging in brushy, rugged terrain (Sanders et al. 1980). Therefore, rather than using a random sampling procedure for selecting groups to be observed, we opportunistically performed bite-count sampling during group observations, scan sampling, or while en route to research plots elsewhere on the island. Animals up to 50 m away were observed 1 to 10 minutes each through a spotting scope or binoculars. We counted bites of grass, mixed grass-forb, forbs, shrubs, and cactus. We did not attempt to distinguish between annual and perennial grass. It should be noted that both techniques potentially overestimate grasses and underestimate forbs because of differential digestibility of plant species (microhistological analysis; Vavra et al. 1978, Holochek et al. 1982, McInnis et al. 1983), and the wide mouth and sweeping action of bison when they forage (bite counts; Ortega et al. 1995).

Effects on Native Plant Communities

a) Diversity and structure of herbaceous plant communities

In January and February 2001, we constructed four 5-m x 5-m exclosure plots in each of three habitat types (grassland, SOIC, riparian). The plots were bison- and pig-proof but were accessible to birds and small mammals. It was possible, but unlikely, that mule deer entered the bison exclosures. Each bison exclosure plot was paired with a nearby unfenced control plot ($\leq$ 15 m away), matched for slope, aspect, abundant plant species, and disturbance. Within each exclosure and control plot, we staked out four 1-m^2 quadrats for sampling of plant communities. With the exception of one riparian plot (located at Echo Lake, in Zone 3), vegetation plots were located in Zone 2 of the island, in which pig eradication efforts were nearly complete when the study was initiated (Schuyler et al. 2002).

We sampled vegetation within each quadrat using a modified pin-frame method (Higgins et al. 1994). A 10-pin frame was placed systematically at four locations (each 25 cm apart) within each quadrat; at each pin-drop, we measured herbaceous vegetation height (maximum height of vegetation in its natural position), described the substrate (litter, soil, dung, rock) and identified all plant species touching the pin (Hickman 1993). To approach a complete species list for each plot, we also identified and recorded all species of plants not contacted as part of pin-frame sampling. We sampled all plots two times during each growing season to capture a wider range

of plant growth and flowering phenology than possible from one sampling session (Hartnett et al. 1996). In 2001, all plots were sampled in April and May, with the exception of two riparian plots damaged by winter storms. In 2002, all plots were sampled in April, but only riparian plots were sampled again in May. Due to very low annual precipitation in 2002, vegetation in the grassland and SOIC plots had largely senesced by early May and few or no new species germinated in the plots after April.

Species were characterized as native or non-native to Santa Catalina Island based on Hickman (1993) and Knapp (2002b). Absolute canopy cover of native and non-native plant species for each vegetation plot was calculated as the total number of hits of each plant species, divided by the total number of pin placements (160 per vegetation plot), multiplied by 100% (Higgins et al. 1994). In complex or dense communities, absolute cover can exceed 100% because more than one plant species may be contacted at a pin drop position (Higgins et al. 1994). Data on absolute cover were used to compare total canopy cover of native and non-native species in bison exclosure vs. control plots. Additionally, we calculated relative canopy cover of each species (by quadrat and by plot) as the total number of pin-contacts of each species, divided by the total number of pin-contacts of all species. Relative cover values were used to examine shifts in the cover of abundant species and to calculate evenness and spatial heterogeneity. We defined "abundant species" as those making up $\geq$ 2% of the total cover at $\geq$ 3 of the four grassland and coastal sage scrub sites, and $\geq$ 2 of the riparian sites, including either or both of the control or bison exclosure plots at each site. We calculated richness (total number of species; Krebs 1999) for each vegetation plot using composite data from all four quadrats and both sampling periods, and estimated an index of community evenness from relative cover values in the Smith and Wilson evenness equation (E_{var}; Krebs 1999). Diversity (a combination of richness and evenness; Krebs 1999) was calculated with the Shannon-Wiener function (Krebs 1999). Finally, we retained the maximum species relative cover value attained among the two sample periods for the calculation of spatial heterogeneity (Hartnett et al. 1996), which provides a measure of the degree of dissimilarity in species composition from one point to another in a community (Collins 1992). Percent dissimilarity was defined as the complement of the Morissita-Horn Simplified Index (Krebs 1999); mean percent dissimilarity was calculated by averaging the dissimilarity indices for all possible two-way combinations of quadrats at a site (Collins 1992, Hartnett et al. 1996).

To assess aboveground biomass, we clipped herbaceous vegetation of the most recent growing season to ground level in one randomly selected quadrat of each control and bison exclosure plot in October 2001 and August 2002. For August 2002 biomass sampling we

constrained the random plot selection to exclude plots sampled for biomass in October 2001. Samples were sorted by forage class (annual grass, perennial grass, forb, annual rush, perennial rush, and sedge) and oven dried to constant weight at approximately 70^{o}C.

For the purposes of analysis, we considered potential differences in plant community structure for all grassland sites (N = 4) and all SOIC sites (N = 4). We used paired samples *t*-tests (Zar 1999) to compare species richness, total absolute canopy cover, absolute canopy cover of native and non-native plants, relative canopy cover of abundant species, vegetation height, number of soil contacts, spatial heterogeneity, and biomass between the two treatments (Table 2). We used a Wilcoxon Rank Sum test (nonparametric alternative to paired t-test; Zar 1999) to compare evenness and diversity between the control and bison exclosure plots (Table 2). Although we had originally intended to analyze riparian sites together, we felt that the four sites were sufficiently different to warrant individual presentation of results. Within each riparian control and exclosure plot, the percent change of each plant community parameter between 2001 and 2002 was calculated. Assuming that it is desirable to increase richness, diversity, evenness, biomass, vegetative cover, plant height, and to decrease bare soil, we ranked differences between control and bison exclosure riparian plots as positive (+), negative (-), or neutral (0).

b) Structure of scrub oak-dominated island chaparral

To assess the potential effects of bison rubbing and horning behaviors on the structure of SOIC stands, we measured a suite of structural components (Appendix IV) in 30 circular plots. Because feral pigs can have an effect on the structure of wooded areas (Sweitzer and Van Vuren 2002), we situated sampling plots such that disturbance by pigs also could be examined. Ten plots were placed in SOIC patches in each of Zone 1 (bison absent/pigs absent), Zone 2 (bison present/pigs absent), and Zone 3 (bison present/pigs present). We located relatively large, contiguous patches of island chaparral likely to be used by bison (i.e., arborescent canopy, slopes < approximately 25^{o}), then selected a random center point for two independent sampling units: (1) two perpendicular 2-m x 30-m belt transects, and (2) a 706.5 m^2 circular plot, divided in quarters. We counted all shrubs and measured soil disturbance along the transects. Data on canopy closure, vegetation height, and depth and types of litter were collected at the center point and at each end of both transects. The circular plot was used to obtain the number of live tree species and snags (dead, standing trees), mean tree DBH (diameter at breast height), the dispersion of overstory trees, and the amount of coarse woody debris. Slope and aspect were measured at the center point of the sampling plot, and the height of the canopy was measured from one point within each site at which the top and bottom of the overstory were visible.

Finally, we recorded three indices of bison use: the number of dung piles, the number of trees and snags with bison hair on the trunk or branches, and the number of wallows. Averages for each of these variables for each plot were used in analysis.

Table 2. Sampling periods for assessing plant community characteristics in bison exclosure and control vegetation plots in grassland (GL), scrub-oak dominated island chaparral (SOIC), and riparian (RIP) habitats on Santa Catalina Island, California.

Parameter	2001 period	2002 period
Species richness	April and May combined (all habitats)	April (SOIC and GL) or April and May combined (RIP)
Absolute cover of native and non-native plants	May (all habitats)	April (SOIC and GL) or May (RIP)
Relative cover of abundant species	May (all habitats)	April (SOIC and GL) or May (RIP)
Vegetation height	May (all habitats)	April (SOIC and GL) or May (RIP)
Number of soil contacts	May (all habitats)	April (SOIC and GL) or May (RIP)
Spatial heterogeneity	April and May combined (all habitats)	April (SOIC and GL) or April and May combined (RIP)
Biomass	October (all habitats)	August (habitats)
Evenness	May (all habitats)	April (SOIC and GL) or May (RIP)

We examined the hypothesis that bison and feral pigs have an effect on the structure of SOIC patches using permutation tests for mean similarity analysis (ANOSIM; Mac Nally et al. 2001) and nonmetric multidimensional scaling plots (nMDS; Kruskal and Wish 1978). Permutation procedures provide a statistical test of the hypothesis that objects within the same class (e.g., plots in Zone 1) are more similar to each other than they are to objects in different classes (e.g., Zone 1 vs. Zone 2) (Van Sickle 1997). Notably, however, a significant test statistic could result if only one of several classes was compact (objects within a class highly similar to each other) and isolated (objects within a class highly dissimilar to objects in other classes), while the others were diffuse and poorly separated. Therefore, we also used nMDS plots as a pictoral representation of the strength of the classification (Van Sickle 1997, Mac Nally et al. 2001). We used MEANSIM 6.0 (Van Sickle 1998) to perform 10,000 permutations for the ANOSIM and SYSTAT 8.0 for the nMDS.

c) Dispersal of non-native plant species

To investigate the possibility that hair shed during wallowing and rubbing activities acts as a dispersal mechanism for non-native species of plants, we collected shaved clumps of hair from bison processed during a yearly roundup, and clumps of hair dislodged by wallowing at active wallow sites. During the November 2000 roundup, hair was shaved from the forelocks of 39 captive bison. In April and May of 2001, we searched bison wallows for shed hair, and defined a "clump" as the sum total of all pieces of hair at one wallow. We located bison hair clumps at 53 of the 56 active wallows examined in 2001 and 118 of the 132 wallows we searched in 2002. All hair samples were weighed, and then stored in paper bags under cool, dry conditions until analysis. In addition, during wallow searches in 2002 we collected soil from the top 3 to 5 cm of each wallow we searched, and recorded the primary habitat for the wallow.

All hair clumps obtained from the roundup animals, and 19 and 18 randomly selected wallow samples from 2001 and 2002, respectively, were searched for seeds. For each of these hair clumps, the number of seeds was recorded and seeds were identified to species, if possible (Hickman 1993). We did not attempt to identify seeds of annual grasses beyond the level of family; it should be noted, however, that this category likely included *Bromus* spp., *Hordeum* sp., and *Avena* spp. Paired *t*-tests were used to compare the number of non-native seeds in hair clumps with the number of native seeds in hair clumps, regardless of species (Zar 1999). Further, we compared the number of non-native forb seeds against the number of non-native grass seeds. Linear regression (Zar 1999) was used to assess the potential relationship between the log-transformed mass of hair clumps and the log-transformed number of seeds within the clumps. To evaluate seed viability, we randomly selected a subset of the seeds of each species separated from the shaved hair clumps and the 2001 wallow hair clumps for germination trials in a greenhouse at the University of North Dakota in January 2002. With the exception of *Xanthium strumarium*, seeds to be tested were maintained on moistened filter paper in plastic petri dishes (Mian et al. 1995). Burs of *X. strumarium* were wrapped in wet paper towel inside plastic bags, as seeds of this species rarely germinate if left uncovered (Uchytil 1992). We did not use physical or chemical means to break dormancy for any of the species tested (Salisbury and Ross 1992). Seeds that germinated ("viable") or that were decayed, soft, or externally damaged ("not viable", Russi et al. 1992) were removed daily. At the end of 30 days, all remaining seeds with no visible damage and a hard seed coat were considered "dormant"(Salisbury and Ross 1992). We calculated percent viability as the number of seeds that germinated divided by the total number of seeds that were not dormant.

In January 2001 and October 2002, the remaining intact wallow samples (34 and 32 samples for each year, respectively) were planted in individual pots in the University of North Dakota greenhouse. Fifty percent of the samples were randomly assigned to be left on the surface of sterilized potting soil, and 50% were buried approximately 2 cm below the surface of 100 ml of potting soil. The pots were kept at approximately 15°C at night and 21°C during a 9.5 hr day, similar to conditions during the growing period in southern California. We also approximated the rain cycle on Santa Catalina Island (Santa Catalina Island Conservancy 2002) by watering the pots every three days with an average of 5.9 $\pm$ 1.6 mm of water delivered by an overhead mister system (as measured with a rain gauge). Hair clumps were "grown" for 24 days in 2001; however, some species require several weeks to germinate (e.g. *Bromus* spp., *Marrubium vulgare*; Clothier 2001), so to maximize germination potential we extended the trials to 48 days in 2002. At the end of the growth period, we counted the number of seedlings, identified them to the lowest taxonomic level possible, and classified each as non-native or native to Santa Catalina Island (Hickman 1993, Knapp 2001).

To estimate persistence of hair clumps in wallows, we cleared five wallows in each of four habitats (grassland, SOIC, coastal sage scrub, and riparian) of all hair in June 2002. Hair clumps chosen at random from clumps $\geq$ 4.5 g (0 = 8.5 + 2.7) were marked with a small amount of white paint and placed in the approximate centers of each wallow beneath a thin layer (< 1 cm) of soil. The minimum hair clump weight was chosen to maximize our chances of recovering pieces of hair broken off from the main clumps. Over the course of this part of the study, many clumps of hair were found caked with mud and/or dung. Therefore, we felt the paint did not significantly alter the probability of hair clumps remaining in the wallows. After hair clumps had been in the wallows for 30 days and 60 days, we sifted through the top 3 to 5 cm of soil at the wallows to locate all persisting clumps of hair. All relocated clumps of hair were weighed, recorded as being found either above or below the soil surface, and returned to wallows at the approximate depth at which they were found.

Seeds may be introduced to wallows by (1) seed rain from nearby plants, (2) human foot or vehicle traffic, (2) birds and other seed predators, (3) falling/dislodging from the pelage of wallowing bison, and (3) clumps of hair shed by wallowing bison (most shedding of hair/pelage occurs in spring). To investigate whether bison hair clumps represent a significant source of seeds relative to the existing seed bank in wallows, we divided 28 randomly selected soil samples from wallows into two pots each, and added a hair clump to one pot of each pair of pots. We germinated the seeds outdoors from 7 June 2002 to 14 August 2002 under a wire cage that prevented entry by vertebrates, but allowed access by invertebrates. Pots received approximately

100 ml of water every three days. At 14-day intervals, we counted and identified seedlings to the lowest taxonomic level possible and classified them as non-native or native. Seedlings with only cotyledons or one pair of true leaves were not included in analyses (J. Takara, pers. comm.). We used paired t*-tests to compare the total number of seedlings between wallow soil with hair and wallow soil with no hair.*

Bison dung may provide another mode of dispersal for non-native species. Therefore, we collected 18 samples (approximately 50 ml each) of fresh bison dung in July and August 2002. Dung samples were air-dried at room temperature (Malo and Suárez 1995) and stored until October, when they were gently crumbled over a bed of sterilized vermiculite (Campbell and Gibson 2001) and transferred to a greenhouse for growth trials. We watered the dung samples on the same schedule and for the same length of time as the hair samples. At the end of the 48-day trial, we enumerated and identified each seedling to the lowest taxonomic level possible.

Effects on Terrestrial Vertebrates

a) Diversity and relative abundance of reptiles and amphibians

In February 2001, we performed 30-minute visual encounter surveys in eight SOIC plots west of the isthmus (Zone 1), where bison have been historically absent, and eight SOIC plots east of the isthmus (Zone 2), where bison are present. During each sampling period, we looked under as many cover objects as possible and scanned the ground surface. When reptiles or amphibians were observed they were identified to species, measured, weighed, and released unmarked. The activity patterns of amphibians and reptiles are strongly associated with ambient weather patterns (Heyer et al. 1994). Thus, at the beginning of each search we recorded temperature, relative humidity, and wind speed.

To assess the potential effect of habitat structure on variation in reptile and amphibian abundance and diversity, we measured a suite of habitat variables in each sampling plot (Appendix V). We characterized topography, tree cover, ground cover, and disturbance by pigs, bison, and rodents. Habitat sampling plots were located in roughly the center of the search area and consisted of two independent sampling units: (1) two perpendicular 2-m x 30-m belt transects; and (2) a 706.5-m^2 circular plot, divided in quarters and centered on the transects (Litvaitis et al. 1994). We measured cover by shrubs and ground disturbance along the transects. Data on canopy closure, vegetation height, and depth and types of litter were collected at the center point and at each end of both transects. The circular plot was used to obtain the number of tree species, the dispersion of overstory trees, and the density of rocks and fallen logs. Slope and

aspect were measured at the center trap. Finally, the height of the canopy was measured from one point within each region at which the top and bottom of the overstory were visible. Variables were averaged to obtain a mean value for each plot. Due to low herptile capture success, we were statistically unable to relate amphibian and reptile abundance directly to habitat structure. Instead, we used ANOSIM and nMDS (Mac Nally 2001) to investigate differences in habitat structure potentially due to the activities of bison (cf. *Methods: Effects on Native Plant Communities*, above).

b) Diversity and relative abundance of small mammals

We estimated the diversity and abundance of small mammals with 60-m x 60-m grids of 49 Sherman live traps. In Zones 1 and 2, we established two grids in each of SOIC, grassland, and coastal sage scrub habitats. Within each habitat type, we attempted to match plots in Zone 1 to plots in Zone 2 with respect to slope and aspect. Traps were baited with a mixture of rolled oats, cracked corn, and black sunflower seeds, and scented with peanut butter. We prebaited $\geq$ 24 hr before trapping and then trapped for five continuous nights. Traps were checked immediately after sunrise every morning. All captured animals were measured, weighed, identified to species, marked with a metal tag in the left ear, and released at the capture site. In 2001, Zones 1 and 2 were trapped simultaneously between 20 August and 9 September. In 2002, we trapped Zone from 3 August to 10 August, then Zone 2 from 11 August to 20 August.

For each night of trapping, we assigned 1 trap night to each trap with a capture or capable of a capture, 0.5 trap nights to closed but empty traps, and 0 trap nights to "unavailable" traps (disturbed by animals or unable to spring shut). An index of relative mammal abundance was calculated as the number of rodent captures per 100 trap nights. To increase our power to detect potential differences in abundance indices, we pooled habitats and simply compared plots from Zone 1 (bison absent) to plots in Zone 2 (bison present) by using *t*-tests (with Welch's adjusted *t*-statistic if necessary) (Zar 1999).

To assess the potential effect of habitat structure on variation in small mammal abundance and diversity, we measured a suite of habitat variables at each small mammal trap grid (Appendix VI). Trap grids were divided into four regions of nine traps each. From each region, one trap was randomly selected as a center point for two independent sampling units: (1) two perpendicular 2-m x 20-m belt transects, and (2) a 314-m^2 circular plot, divided in quarters and centered on the transects (Litvaitis et al. 1994). We measured cover and richness of shrubs, cover by cactus, and ground disturbance along the transects. Data on canopy closure, vegetation height, and depth and types of litter were collected at the center trap and at each end of both transects.

The circular plot was used to obtain the number of tree species, mean tree DBH, the dispersion of overstory trees, density of fallen logs, and an index of bison use, as indicated by the number of dung piles. Slope and aspect were measured at the center trap. Finally, the height of the canopy was measured from one point within each region at which the top and bottom of the overstory were visible. Each variable was averaged by trap location to obtain a mean value for each grid. As with the reptile and amphibian searches, we were statistically unable to relate amphibian and reptile abundance directly to habitat structure because of low capture success. We used ANOSIM and nMDS (Mac Nally et al. 2001) to investigate differences in habitat structure potentially due to the activities of bison (cf. *Methods: Effects on Native Plant Communities*, above).

c) Associations with cowbirds and starlings

During bison group observations (see *Methods: Bison Ecology*, above), we recorded and mapped all associations of bison groups with flocks of cowbirds and starlings. Bison groups for which visibility was too poor to note the presence or absence of birds were censored prior to analyses. Initial graphical displays of cowbird and starling locations suggested that in addition to an association with bison, the two species also might be responding to the presence of human disturbance and standing water. We used logistic regression (Hosmer and Lemeshow 1989) to examine the hypothesis that the presence of flocks of starlings and/or cowbirds was related to bison group size, human activity, and distance to reservoirs. We defined "human use" areas as campgrounds, permanent settlements, summer camps, research stations, and active rock quarries. We constructed a 1-km buffer around such areas using ArcView GIS 3.2 and assessed whether cowbirds and starlings were more likely to occur within the buffer than outside of the buffer. We included all reservoirs on the island except for the Wrigley Reservoir, which is capped to prevent access by birds (D. McDonald, pers. comm.).

Effects on Water Quality

To investigate potential effects of bison on water quality, we measured a suite of parameters in 7 reservoirs (Echo Lake and six man-made reservoirs) and 11 natural stream courses. Areas/sites chosen for sampling for water quality represented a visual range of bison activity as indicated by dung piles, bison tracks, vegetation height, etc. Unfiltered water samples were collected monthly from February to December in 2001 and May to August in 2002 and taken to the laboratory for analysis. The concentration of dissolved oxygen was determined within four hours of collection and ammonia-nitrogen, nitrate-nitrogen, and pH levels were measured within 24 hours of collection (Table 3).

Table 3. Water quality parameters measured in reservoirs and streams from May to December 2001 and May to August 2002 on Santa Catalina Island, CA.

Parameter	Range of detection	Method	LaMotte Test Kit
Dissolved oxygen	> 0.2 ppm	Winkler	# 7414
Ammonia-nitrogen	0.1-4.0 ppm	Colorimetric	# 5864
Nitrate-nitrogen	1-15 ppm	Colorimetric	# 3354
Turbidity	5-200 JTU	Turbidity standard	# 7519
pH	3.0-10.5	Colorimetric	# 5858

We assessed bison activity near (within a radius of 200 m) all water sampling sites using automatic camera systems (camera traps) and time-constrained dung searches. Camera traps were used to estimate the short-term amount of bison activity (i.e. monthly), whereas time-constrained dung searches provided a longer term index of bison activity (several months to over $\geq$ 1 yr of bison activity depending on weather-related variation in persistence of dung piles). During the period from January to December 2001 one TrailMaster automated camera trap (active infrared trail monitor TM1500 with TM35-1 camera kit) was established at each water quality sampling site and programmed to capture 24-hour event records of activity. Camera traps were not operated in 2002 related to logistical constraints imposed by high priority research activities for 2002 and costs for film development, equipment repair and theft. Camera traps were oriented and programmed to be most sensitive to bison activity, but they also recorded activity events associated with mule deer, feral pigs, and humans. We visited camera traps biweekly to change the film and/or batteries, clear events from the data loggers, and repair damage as necessary. Two camera systems were stolen and several sustained irreparable damage from water or animals, so only stations active from May to December (four streams and two ponds) were included in analysis. An index of bison use (BISCAT) was calculated as the monthly mean of (bison pictures)/(camera days) and an index of ungulate use (UNGAT) was calculated as the monthly mean of (bison + deer + pig pictures)/(camera days). For time-constrained dung pile searches in July and October 2001 we conducted 25- to 30- minute searches for bison dung piles within 200 m of the edges of reservoirs and streams near water quality sampling sites. All dung piles encountered were counted regardless of age or state of decay. We attempted to maximize dung counts by focusing our searches on game trails and in areas used by bison for grazing and loafing. Bison use at each site (DUNGCAT) was calculated as the mean of (number of dung piles)/(length of search).

Because of logistical and financial constraints, we initially intended to sample water quality and measure bison activity at reservoirs and streams only for 2001. However, by early spring 2002 it was evident by the lack of significant fall and winter precipitation that 2002 would be a

significant drought year. We anticipated that streams and reservoirs would dry significantly in 2002 compared to 2001 (many reservoirs filled to above capacity and water flow in streams persisted at unusually high volume for longer periods than normal) and decided to continue water quality sampling beginning in May 2002. We considered two implications for water quality related to 2002 being a drought year: (1) bison would have less access to surface water than in 2001, potentially forcing them to invest more time at fewer streams and reservoirs, and (2) water sources would dry more rapidly, thus concentrating nutrients or altering pH. As such, we derived a different, watershed-level index of bison activity in and around water quality sampling sites, based on data from bison group observations and systematic dung transects. Our watershed-level bison activity index provided an estimate of the combination of short-term (i.e. monthly) and long-term (i.e. $\geq$ a yr) bison activity analogous to site-level sampling. As a reminder, while recording bison groups as part of ad lib and scheduled surveys (cf. *Methods: Bison Ecology*, above), we kept a record of the road segments (0 = 1.2 $\pm$ 0.6 km) we traveled in search of bison starting May 2001. Sampling effort in each watershed ($WSHD_i$) was calculated as the sum of (number of times RS_i were driven)*(length of RS_i), where RS_i = road segments from which $WSHD_i$ was visible. An indicator of bison activity (GRPCAT) was calculated as the mean of (monthly number of bison seen in each watershed)/(monthly sampling effort). To estimate bison use on a long-term, watershed scale, we used the results of dung transects to estimate habitat use (cf. *Methods: Bison Ecology* above). An index of bison activity (HBTCAT) was calculated as (sum of dung piles in $WSHD_i$)/(number of transects sampled in $WSHD_i$).

Water quality measurements were collapsed into six sampling periods (2001: May/Jun, Jul/Aug, Sep/Oct, and Nov/Dec; 2002: May/Jun and Jul/Aug) to maximize sample size, but reservoir and stream drying nonetheless resulted in an overall reduction of water sampling sites available for analysis. We used repeated measures ANOVA (Zar 1999) to analyze the bimonthly means of each water quality parameter (Scrimgeour and Kendall 2002) relative to BISCAT (2001), UNGCAT (2001), DUNGCAT (2001), GRPCAT (2001 and 2002), and HBTCAT (both years pooled). Turbidity measurements were log-transformed to stabilize variance (Zar 1999).

In addition to examining the effects bison might have on water quality on Santa Catalina, we noted nitrate concentrations (> 100 ppm) and pH levels (< 5.5 or > 8.5) in reservoirs and streams that could be detrimental to the health of bison. Drinking water standards were based on values recommended for cattle (Grant 1996).

Optimum Stocking Rate

One of the primary aims of this study was to predict the outcome of managing bison on Santa Catalina Island at a variety of population levels. Our objective was to provide approximate stocking rates that would be compatible with the goals of minimizing damage to native plant populations, soils, and riparian systems. We also considered several potential management options that might minimize damage to island plants and animals while also maximizing viewing opportunities for tourists and island residents. To meet this objective, we used information generated by the study on habitat use by bison, diets, and body mass, and published and experimental data on the productivity of different island plant community types. Together these data allowed for estimating bison carrying capacity on Santa Catalina Island under a range of conditions (Norland et al. 1985). Below we provide details on our models of optimum stocking rates and carrying capacity estimates.

a) Management options

We based our models on three potential management options: (1) the bison herd continues to range across the whole island excluding Zone 1 and Avalon (area = approximately 15,908 ha, Management Option A), (2) a small herd of bison is restricted to Zone 2 (area = approximately 5238 ha, Management Option B), and (3) a smaller herd of bison is confined to an approximate 831 ha area within Zone 2, encompassing the Airport-In-The-Sky, El Rancho Escondido, and part of the Inland Motor Tour, a major tour bus route (Management Option C). For the third management scenario a new fence would need to be established to prevent access by bison to several significant ecological areas within Zone 2. Figure 2 provides maps of areas covered by the three management scenarios we evaluated.

b) Habitat classes and range productivity

Production values for forage classes (annual grass, perennial grass, and forbs) were based on a combination of data from this study and published estimates. The suitability of vegetation classes as rangeland depends primarily on the type of soil at the site (Bowman et al. 1973). Therefore, we used the Soil Conservation Service survey of Santa Catalina Island (Cureton 1955) to construct a GIS layer of soil capability class polygons. In general, when clip plot information and detailed soil profiles are available, soil capability classes can be used to indicate and identify rangelands (range sites) with different potentials for forage production (Bowman et al. 1973). The 1955 soil survey of Santa Catalina Island did not include range sites, so we inferred them

from data from the Coastal Plain area around San Diego, California (Bowman et al. 1973). Capability class VIII (typically ridgelines) on Santa Catalina Island represented areas that were steep, moderately to severely eroded, and unsuitable for grazing at the time of the survey (Shipman 1969). We discarded all class VIII polygons from analyses that were described as severely eroded and gullied or for which data on soil types were missing. We assumed that the large-scale removal of feral goats and pigs in recent decades has resulted in some recovery by soils, so we classed moderately eroded class VIII soil polygons as the same range site as surrounding polygons, even though range productivity in the class VIII areas is likely lower than in polygons of other capability classes.

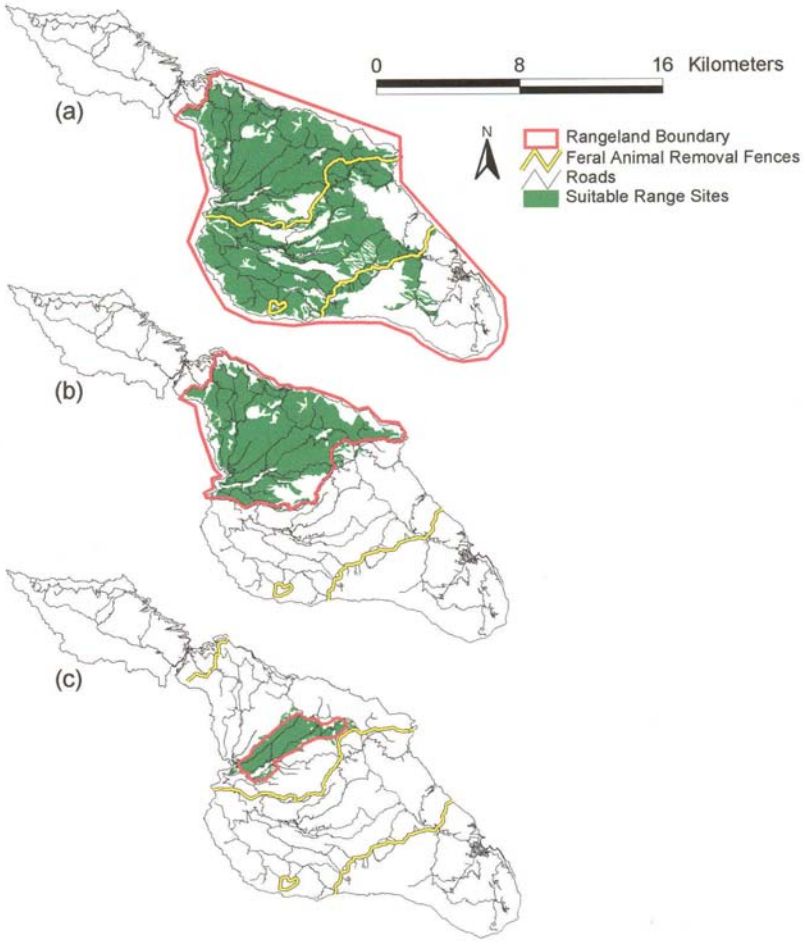

Figure 2. Maps of Santa Catalina Island identifying areas for three potential approaches to future management of bison, including (a) no change from current management (i.e. bison continue to range over Zones 2, 3, and 4); (b) restricting a small number of bison to the area defined as Zone 2; and (c) restricting a small number to a part of Zone 2. Suitable range sites were defined as areas with slope < 25 degrees and moderate to no erosion.

From group observations and censuses, we selected a subset of vegetation classes from those available on the island (see Table 1, above; Appendix VII) as potential rangeland. For example, although we occasionally observed bison in bare areas, these polygons were considered unsuitable for foraging by bison because of limited vegetative cover and were therefore excluded from calculations related to stocking rates. Other areas excluded from estimates of rangeland productivity for estimates of bison stocking rates included Avalon, the active rock quarry near the east end of the island, Zone 1, and all areas with slopes > 25^{o}. We used ArcView GIS 3.2 to calculate the contribution of each range site to the productivity of each vegetation class for each of the three management options identified above (Figure 2). Vegetation classes were identified as primary, secondary, or marginal (cf. *Methods: Bison Ecology*, above) based on dung transects and group observations (Appendix VII). It should be noted that the generalized vegetation polygons we used are actually a mosaic of smaller mapping units (Knapp 2002b). Given the nature of the available soil data and our sampling strategy to assess habitat selection (i.e. dung transects; cf. *Methods: Bison Ecology*, above), however, it was inappropriate to attempt the construction of a more detailed carrying capacity model.

To estimate the relative contribution of each major forage class to herbaceous biomass production on the island, we fenced 1-m^2 circular "biomass plots" with hardware cloth. In January 2001, we established five biomass plots in grassland and SOIC habitats and three biomass plots in coastal sage scrub. In October 2002, we removed the original biomass plots and established five new plots in different locations in the each of the three habitat types. Moving the biomass plots between years allowed us to increase coverage and capture a wider range of biomass productivity estimates for each habitat. At the peak of biomass production in May 2001 and 2002 all aboveground vegetation inside biomass plots was clipped to ground level, sorted by forage class, and oven dried to constant weight at approximately 70^{o}C. Biomass values were then used to calculate the mean percent contribution of each forage class to overall biomass production (Appendix VII). Woody plants were not included as a forage class in our model based on conservation issues for island endemic shrubs, and the assumption that shrubs are undesirable to bison as a forage item unless more desirable plants have been eliminated (Bowman et al. 1973),

c) Forage intake by bison

Total annual forage intake per bison was calculated by multiplying daily intake (1.7% of body mass per day; Van Dyne et al. 1981) by average body mass per animal and the number of days in a year. Average body mass per animal on Santa Catalina Island was calculated as a weighted average from the mass of bison captured in the 2000 and 2002 roundups (Santa Catalina

Island Conservancy, unpubl. data), adjusted for the proportion of different age/sex classes in the population as determined by census data (Norland et al. 1985).

d) Calculation of carrying capacity

In general, standard model methods used to predict or estimate carrying capacities typically target one species (usually cattle) with limited consideration of other organisms that may compete with the target species for browse or habitat (Grazing Lands Technology Institute 1997). The initial base or "standard livestock" model we developed to estimate carrying capacities for bison under the three different management options considered (Figure 2) did not explicitly consider forage or habitat needs of island vertebrates and invertebrates. However, because multiple other native species of vertebrates and invertebrates on Santa Catalina Island will consume or use annual grasses for cover/habitat, we varied internal parameters of the model to explicitly reserve some plant biomass for other island species. We therefore produced estimates of "moderate" and "light" bison carrying capacities for each management option as well as the standard livestock carrying capacities. Details of the carrying capacity model follow below.

We adapted the equation in Norland et al. (1985) to derive carrying capacity estimates for each of the three management scenarios listed above. The observed distribution of grazing on a management unit is influenced by a complex array of site characteristics including the location of water, natural barriers, and the kinds and distribution of plants (Grazing Lands Technology Institute 1997). Therefore, rather than prescribing grazing use for every part of a large management unit or the entire plant community, it is more practical to plan grazing use for a "key forage species" within a "key grazing area". In theory, if a key grazing area is properly grazed, the management unit as a whole will not be excessively used (Grazing Lands Technology Institute 1997). In standard livestock grazing systems key grazing areas should provide a significant amount of the available forage in a management unit and be easily grazed due to even topography, accessible water, and other favorable factors influencing grazing distribution. For bison on Santa Catalina Island we defined key grazing areas as all primary and secondary ranges based on analyses of bison group observations and habitat use (see above). This approach was assumed to maximize opportunities for island residents and visitors to view bison because the primary and secondary ranges include relatively open habitats often near main tourism travel routes where bison are commonly viewed. Key forage species are typically preferred by the grazing animal and provide more than 15 percent of the readily available forage in the key grazing area (Grazing Lands Technology Institute 1997). Species-by-species production values for Santa Catalina Island were unavailable, so we were unable to identify a key forage species.

Instead, we identified annual grasses as the "key forage class" for bison on the island based on bite count data and estimated diets from microhistological analyses of fecal samples. It is inherently difficult to precisely estimate rates of forage production, which can vary considerably from year to year based on rainfall and variation in climate (Sneva and Hyder 1962, Murphy 1970, Duncan and Woodmansee 1975, Hufstader 1976). Thus, our estimated stocking rates/carrying capacities should be viewed as conservative (Grazing Lands Technology Institute 1997). To estimate our three different stocking rates (Standard, Moderate, Light), we used forage production estimates for unfavorable years (Grazing Lands Technology Institute 1997; Appendix VII). The bison forage production-utilization model included total annual estimated forage production of annual grasses in unfavorable years (TAP), an allowable use factor for annual grasses (AUF), the proportion of annual grasses in bison spring diets (PD), and annual forage intake rate by bison (YI) (Table 4). The PD for the model was based on spring-summer food habits (as determined by microhistological analysis; Tables 12a,b) to allow for conservative utilization estimates for plants eaten primarily during the growing season, when plants are most vulnerable to overuse (Norland et al. 1985). Unknown grasses and *Poa* spp. (Tables 12a,b) likely contained a mix of annual and perennial grasses; based on the distribution of annual and perennial grasses in bison diets, we assumed that 75% of each group consisted of annual grasses for the purposes of the model. Finally, we calculated the PD as the mean percent of annual grass use by bison over 5 months (March to July 2001; Tables 12a,b). To model for the standard livestock carrying capacity we fixed the AUF for annual grasses within primary and secondary ranges at 0.50. An AUF of 0.50 is considered near the upper limit of plant material that can be removed but still preserve sufficient leaf area after grazing for plant recovery (Norland et al. 1985, Grazing Lands Technology Institute 1997). To model for a moderate bison carrying capacity, the AUF parameter was fixed at 0.25, which can be considered to provide 25% of available annual grass biomass for bison consumption, 25% of plant biomass for other native vertebrates and invertebrates on the island, and leaves 50% of plant leaf area to permit plant recovery from grazing/foraging. To model for a light bison carrying capacity, the AUF parameter was fixed at 0.125, providing 12.5% of annual grass biomass for bison, 37.5% of annual grass biomass for other island species, and leaves 50% of annual grass leaf area for plant recovery from grazing/foraging.

Table 4. Forage production-utilization model used in calculation of bison carrying capacity on Santa Catalina Island, California (adapted from Norland et al. 1985).

$$BY = \frac{(TAP)(AUF)}{(PD)(YI)}$$

Where:

BY = The number of bison that could be supported for 1 year in the key forage area by the key forage class (annual grasses).

TAP = Estimated annual production (kg dry weight) in unfavorable years for the key forage class in the key forage area (Appendix VII).

AUF = Allowable use factor (proportion of available annual forage production that can be consumed without damage to future productivity of a plant.

PD = Proportion of the key forage class in bison spring-summer diets as calculated from fecal analysis.

YI = Average annual forage intake per bison (1719 kg/year).

RESULTS

Climatic Variation

The long-mean precipitation on Santa Catalina Island from 1948 to 1990 was approximately 290 mm. Based on our calculations, 6 of the last 12 years (50%) have experienced below-average conditions (Figure 3). Notably, the positive deviations from normal tended to be greater in magnitude than negative deviations (Figure 3). The periods of 2000 to 2001 (first year of this study) and 2001 to 2002 (second year of this study) deviated +61% and –57% from normal, respectively (Figure 3). Clearly, and based on the long-term average precipitation, 2000 to 2001 was a wet, or favorable year and 2001 to 2002 was an abnormally dry, or unfavorable year. Related to this large interannual difference in rainfall, plant community characteristics (seasonal phenology, primary productivity, etc.) were very different between years.

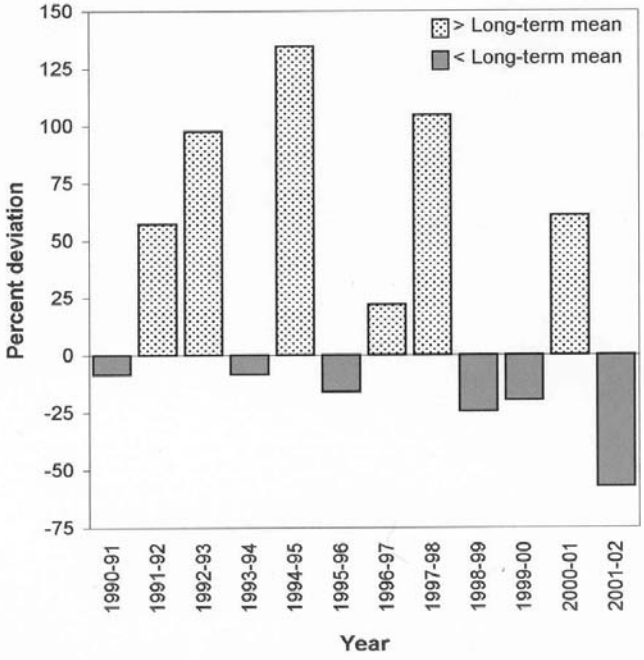

Figure 3. Estimated percent deviation from the long-term mean annual rainfall (approximately 290 mm based on data from 1948 to 1990) for Santa Catalina Island, California during the period from 1990-1991 to 2001-02.

Bison Ecology

a) Population dynamics

Summary information on bison herd sizes, sex ratios, and calving rates was compiled from the five island-wide population censuses completed in 2001 and 2002 (Table 5). Adult sex ratios

Table 5. Estimated parameters describing the population biology of bison on Santa Catalina Island, California during 2001-2002. Estimates were based on data from multiple periodic censuses (see text).

		Herd composition[2]				Sex ratio[3]			
Year	Herd size	Adult females	Adult males	Yearlings	Calves	Adult	Yearling	Calving rate[4]	8
2001	303 - 340	136 (44.9)	57 (18.8)	28 (9.2)	67 (22.1)	0.42	1.14	0.49	
2002	360 - 379	139 (38.9)	76 (21.4)	65 (18.1)	60 (16.7)	0.55	1.03	0.35	1.1 – 1.2

[1] Lower boundary of range represents total count from August census. Upper boundary of range represents sum of calves from August census and adults and yearlings from April census (see text for additional detail).
[2] As determined from the August censuses. Indicates counts, with percentage of total number counted (including unknown age/sex animals) in parentheses. Ad. M = males ≥ 2 yr, Ad. F = females ≥ 2 yr, Yr. = yearlings of both sex, and Cf., = calves of both sex.
[3] As determined from the August censuses. Ad. = number of adult males per number of adult females, and Yr. = number of yearling males per number of yearling females.
[4] As determined from August censuses. Represents number of calves per number of females ≥ 2 yr.

were heavily skewed towards females (0.42 in 2001 and 0.55 in 2002), whereas the yearling male and yearling female sex ratios were nearly 50:50 overall. The mean calving rate for cows ≥ 2 yr was 42%; this is low compared to most captive and free-ranging populations of bison in their native range (Table 6). Estimated pregnancy rates for adult females (≥ 2 years old) based on laboratory analyses of PSPB and progesterone were estimated at 50% in Fall 2000 and 17% in Fall 2002. It is likely that the much lower observed pregnancy rate for Fall 2002 was related to drought-induced nutritional constraints. Additional support for this hypothesis comes from

Table 6. Estimated mean calving rates (% adult females with calves) for adult female bison on Santa Catalina Island, California and from various mainland herds of free-roaming or captive bison.

Location	Calving rate	Female age	Source
Santa Catalina Island	35	≥ 3	Lott & Galland 1987
Santa Catalina Island	42	≥ 2	This study
Captive-raised herds with adequate forage/supplementation	> 95	≥ 3	Lee 1990
Wood Buffalo National Park, NWT	32	≥ 3	Carbyn et al 1998
Theodore Roosevelt National Park, ND	75	≥ 2	Kirkpatrick et al. 1996
Badlands National Park, SD	64	3-7*	Berger & Cunningham 1994
National Bison Range, MT	67	≥ 2	McHugh 1958
National Bison Range, MT	82	≥ 3	Rutberg 1986
Yellowstone National Park			
Hayden Valley	64	≥ 2	McHugh 1958
Northern Range	53	≥ 2	Kirkpatrick et al. 1996
Mary Mountain	43	≥ 2	Kirkpatrick et al. 1996
Konza Prairie, KS	74	≥ 3	Towne 1999
Wichita Mountains, OK	52	≥ 2	Halloran 1968
Wichita Mountains, OK	72	≥ 2	Shaw & Carter 1989
Henry Mountains, UT	52	≥ 2	Van Vuren & Bray 1986
Henry Mountains, UT	62	≥ 3	Van Vuren & Bray 1986

* Most likely an underestimate of calving ratio, as peak fecundity in this population is between 10 and 11 years (Berger and Cunningham 1994).

analysis of the blood data. The comparison of serum chemistry and hematological profiles between 2000 and 2002 indicated multiple differences between years in several key parameters potentially related to nutritional status and dehydration, including glucose, cholesterol, and hematocrit, among others (Table 7). For example, glucose values were approximately 40% lower in blood collected in 2002 (0 ± SE = 81.6 ± 8.0) than in blood collected in 2000 (0 ± SE = 139.0 ± 15.2), and red blood cell counts and percent hematocrit were significantly elevated in 2002 (Table 7). Blood urea nitrogen values, while not significantly different between years, exceeded the normal range for cattle (Table 7). In contrast, cholesterol values were approximately 37 – 52% of the low range for cattle (Table 7).

Table 7. Serum chemistry and hematological profiles of female bison ≥ 2 yr on Santa Catalina Island, California in 2000 (N=13) and 2002 (N=24).

Parameter (units)[1]	2000 Roundup	2002 Roundup	*t* value[2]	Reference range[3]
Serum chemistry				
Alkaline phosphatase (IU/L)	50.6 ± 4.1	53.5 ± 2.2	-0.69	23-96
Aspartate aminotransferase (IU/L)[4]	86.2 ± 5.2	129.0 ± 13.9	-3.18**	53-155
Creatinine kinase (IU/L)[4]	435.9 ± 165.8	912.3 ± 249.5	-1.99	98-913
Gamma-glutamyl transferase (IU/L)	12.4 ± 1.6	29.3 ± 1.6	-6.78**	13-51
Albumin (g/dL)	3.0 ± 0.1	3.2 ± 0.07	-1.43	2.8-3.8
Total protein (g/dL)	8.7 ± 0.2	8.6 ± 0.2	0.11	6.7-8.8
Globulin (g/dL)	5.7 ± 0.2	5.5 ± 0.2	0.67	3.3-6.3
Total bilirubin (mg/dL)	0.1 ± 0.02	0.2 ± 0.01	-4.57**	0.0-0.2
Direct bilirubin (mg/dL)	0.06 ± 0.01	0.10 ± 0.004	-2.34*	0.0-0.1
Blood urea nitrogen (mg/dL)[4]	30.6 ± 0.6	30.0 ± 2.4	1.01	10-23
Creatinine (mg/dL)	1.9 ± 0.1	2.0 ± 0.09	-1.17	0.7-1.2
Cholesterol (mg/dL)	59.6 ± 3.2	82.3 ± 3.6	-4.13**	157-393
Glucose (mg/dL)	139.0 ± 15.2	81.6 ± 8.0	3.69**	41-71
Calcium (mg/dL)	8.3 ± 0.2	9.6 ± 0.2	-5.33**	9.1-11.3
Phosphorus (mg/dL)	6.9 ± 0.3	8.1 ± 0.6	-1.83	5.1-8.7
Bicarbonate (mEq/L)	10.6 ± 0.7	15.7 ± 0.8	-4.42**	19-31
Chloride (mEq/L)	96.2 ± 0.6	94.1 ± 1.3	1.42	93-109
Potassium (mEq/L)	5.8 ± 0.2	7.1 ± 0.3	-4.14**	4.1-5.5
Sodium (mEq/L)	143.8 ± 0.8	142.5 ± 1.1	0.78	136-148
Albumin:globulin ratio	0.5 ± 0.03	0.6 ± 0.03	-1.43	
Blood urea nitrogen:creatinine ratio	17.0 ± 1.0	14.8 ± 0.7	1.79	
Indirect bilirubin (mEq/L)	0.06 ± 0.01	0.11 ± 0.01	-2.39*	
Sodium:potassium ratio	25.1 ± 0.7	20.7 ± 0.7	3.81**	
Anion gap (mEq/L)	42.8 ± 1.7	40.0 ± 1.5	1.21	
Hematology				
White blood cell (10^3/:l)	4.9 ± 0.3	7.7 ± 0.4	-5.33**	5.3-14.9
Red blood cell (10^6/:l)	8.0 ± 0.3	8.8 ± 0.2	-2.53*	5.1-8.5
Hemoglobin (g/dL)	15.5 ± 0.6	16.0 ± 0.3	-0.83	8.5-12.9
Hematocrit (%)	39.8 ± 1.6	43.4 ± 0.9	-2.14*	24-38
Mean corpuscular volume (fL)	50.0 ± 0.6	49.3 ± 0.8	0.62	37-56
Mean corpuscular hemoglobin (pg)	19.5 ± 0.3	18.2 ± 0.3	3.01**	12.9-19.4
MCHC (g/dL)	38.9 ± 0.3	36.9 ± 0.3	4.29**	33.0-36.5
Neutrophil segment (%)	48.5 ± 5.3	43.7 ± 2.5	0.96	22-70
Lymphocytes (%)	40.8 ± 5.1	48.7 ± 2.6	-1.53	23-72
Monocytes (%)	6.6 ± 0.7	2.4 ± 0.4	5.41**	0-9

Eosinophil (%)	4.4 ± 0.9	4.2 ± 0.4	0.23	0-13
Absolute neutrophil (per/:l)	2394.3 ± 295.1	3326.1 ± 231.3	-2.44*	2200-8073
Absolute lymphocyte (per/:l)	1990.8 ± 288.2	3732.3 ± 274.3	-4.05**	1431-8694
Absolute monocyte (per :l)[4]	299.1 ± 25.5	188.8 ± 39.4	4.05**	0-774
Absolute eosinophil (per :l)	193.8 ± 36.8	320.8 ± 41.1	-2.09*	
Fibrinogen (MG/DL)[4]	507.7 ± 70.2	225.0 ± 23.5	4.48**	

[1] MCHC, mean corpuscular hemoglobin concentration.
[2] *p<0.05, **p<0.001
[3] For cattle (IDEXX Veterinary Services).
[4] Analysis performed on log-transformed values.

Natural bison mortality appeared relatively low on Santa Catalina Island. During the period from 1995 to 2002 there was an average of 6 known/reported bison mortalities per year (Table 8; Santa Catalina Island Conservancy, unpubl. data). Most mortalities were the result of natural causes (36%) and euthanasia due primarily to broken legs/injuries (32%). At least 4 broken legs/injuries were known to be incurred when animals attempted to navigate cattle guard partitions separating Zones 2, 3 and 4.

Table 8. Known bison mortalities on Santa Catalina Island, California during the period from 1995 to 2002.

	Cause of death					
Sex	*Natural*	*Euthanized*	*Roundup*	*Hunted*	*Unknown*	*Total*
Male	2	3	1	2	0	8
Female	16	12	3	0	7	38
Unknown sex	0	1	0	0	3	4

Male and female adult bison on Santa Catalina Island were significantly smaller than animals in Theodore Roosevelt National Park, North Dakota; the National Bison Range, Montana; Wind Cave National Park, South Dakota; and the Wichita Mountains National Wildlife Refuge, Oklahoma (all comparisons $t \geq -9.21$, df ≥ 24, $P < 0.0005$, at Dunn-Sidak adjusted $\forall = 0.013$). Notably, there appears to be a north-south gradient in mean body mass for both sexes of adult bison, with animals becoming progressively larger with increasing latitude (Figure 4).

Bison group sizes observed during the period of the study were relatively small (Figure 5). Eighty-nine percent, or 1,925 of 2,153 bison groups observed, included fewer than 20 individual animals (Figure 5a). We detected minimal variation in bison group sizes during different seasons of the year (Log-ratio Chi-Square = 13.6, df = 9, $P = 0.13$). When assessed by month, however, mean sizes of mixed age/sex groups were largest in late spring/early summer (breeding period or rut) and smaller in September and January (Figure 5b). All adult and all male groups were similar in size across all months (Figure 5b).

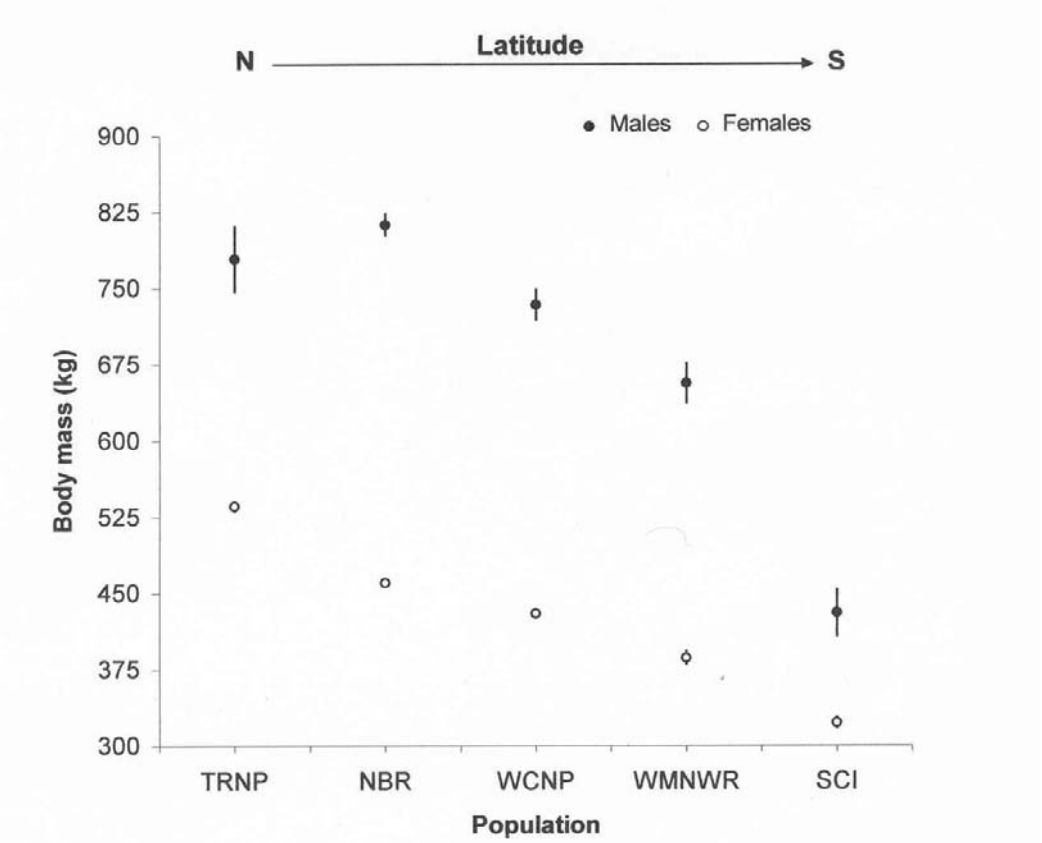

Figure 4. Mean body masses (± SE) of young to prime-aged adult male bison (6-13 years old) and adult female bison (4-16 years old) from Theodore Roosevelt National Park, North Dakota (TRNP; N = 11 males and 82 females); Wind Cave National Park, South Dakota (WCNP; N = 22 males and 277 females); Wichita Mountains National Wildlife Refuge, Oklahoma (WMNWR; N = 13 males and 32 females); National Bison Range, Montana (NBR; N = 41 males and 98 females); and Santa Catalina Island, California (SCI; N = 15 males and 61 females). Estimated standard errors for mean body masses for adult females were negligible for most bison populations and are not apparent in the figure.

A comparison of group sizes from our study with data on bison group sizes on Santa Catalina Island in the 1970s (Lott and Minta 1983, Galland 1989) suggested that feral animal removal fences may currently be limiting group size during the rut. The maximum group size observed during this study was 73 animals, whereas Galland (1989) reported a group of 191 animals during the spring/early summer breeding period (Table 9). Further, Lott and Minta (1983) and Galland (1989) reported larger median and mean bison group sizes for all periods of year compared to our group information (Table 9). We were unable to access the original data from these studies for more detailed comparisons or statistical comparisons, however.

Table 9. Comparison of bison group sizes on Santa Catalina Island, California before cross-island fencing was installed for feral animal removal in 1998-99. Data on group sizes during "pre-fence" years were from the 1970s based on Lott and Minta (1983) and Galland (1989). Data on group sizes during "post-fence" years are from this study during 2001 and 2002.

Attribute	Pre-fence	Post-fence
Approx. size of population	400	360-379
Range of group sizes[1]	1-191	1-73
Median group size – entire year[1]	7	5
Mean group size (+ SD, if available)[2]		
Entire year	13.0	8.5 ± 9.9
During rut[3]	17.4	10.4 + 12.7
Non-rut	10.2	8.1 + 9.2

[1] From Galland (1989).
[2] From Lott and Minta (1983).
[3] Defined as 5/30 to 7/24 of each year (sensu Lott and Minta 1983).

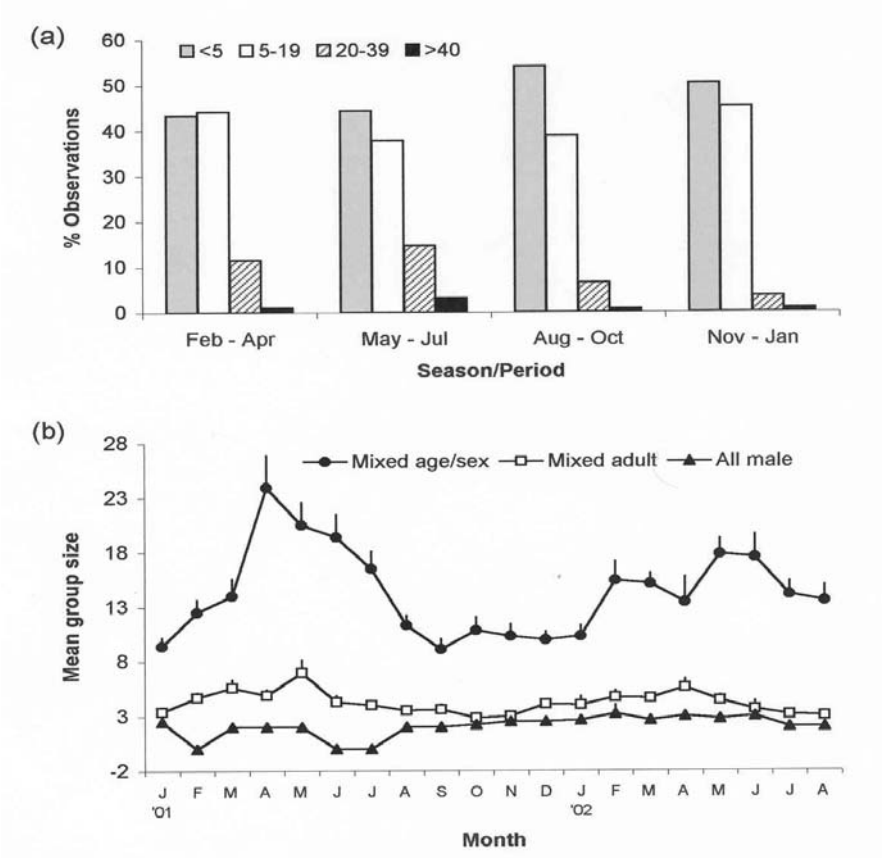

Figure 5. Estimated seasonal variation in (a) bison group sizes and (b) sizes of different types of bison groups (plotted as monthly mean ± SE) on Santa Catalina Island, California from January 2001 to August 2002. Mixed age/sex groups included adult females (≥ 2 years old), yearlings and calves, and subadult and adult males (≥ 2 years old). Mixed adult groups included some combination of adult females, adult males, or both. All male groups included males ≥ 2 years old.

b) Habitat use

Data on locations of 2,145 groups of bison collected from January 2001 to August 2002 indicated an uneven distribution of bison activity across the island (Figure 6). The majority of the bison groups (98.3%) were observed in Zones 2 and 3, with a heavy concentration of bison activity in and around the centers of these Zones (Figure 6). No bison were observed on the extreme east end of the island. Approximately 87% of all of these bison groups were recorded in grassland, coastal sage scrub, or island chaparral habitat (Table 10). We did not observe bison groups in bare streambeds, or in patches of maritime cactus, coastal bluff scrub, or southern beach and dune habitat. We detected no evidence for seasonal shifts in patterns of habitat use (Figure 7; Log-ratio Chi-square = 8.8, df = 15, $P = 0.89$) or differing slopes (Figure 7; Log-ratio Chi-square = 5.9, df = 6, $P = 0.43$). Similarly, there was no detectable evidence for bison focusing their activities near water sources (Figure 7; Log-ratio Chi-square = 2.2, df = 12, $P = 1.0$); bison were commonly observed relatively near and far from water throughout the year including during very dry summer and early fall periods.

Table 10. Distribution of bison groups (%) in 17 different physiographic/vegetation types on Santa Catalina Island, California.

Habitat type	% Area of Zones 2 - 4	% Group observations
Valley and foothill grassland	18.3	43.6
Coastal sage scrub	38.5	24.9
Island chaparral	30.2	18.6
Bare ground	9.0	4.8
Non-native herbaceous	0.5	4.8
Developed	1.1	1.0
Non-native chaparral/non-native woodland	0.6	0.6
Southern riparian woodland	0.5	0.6
Riparian herbaceous	0.06	0.3
Vernal ponds and reservoirs	0.1	0.3
Mule fat scrub	< 0.01	0.3
Island woodland	0.4	0.1
Coastal marsh	< 0.01	0.1
Bare streambed	0.13	0
Maritime cactus scrub	0.01	0
Coastal bluff scrub	0.26	0
Southern beach and dune	0.27	0

Analyses of data from 213 dung transects indicated that grassland habitats were strongly preferred by bison on the island, whereas SOIC and coastal sage scrub were used less than expected relative to availability (Figure 8). An overall General Linear Model analysis suggested bison activity in any given area was related to the major (≥ 60%) and minor habitat (20-40%) types present, slope, and vegetation density (Table 11). Scheffé multiple contrast tests indicated that bison were more likely to use open areas dominated by grassland or with a significant grassland component and avoided homogeneous areas of dense woodland or shrub land.

Table 11. Results of a General Linear Model analysis used to assess factors influencing bison activity (indexed by bison dung transects) on Santa Catalina Island, California. Overall, the model explained approximately 60% of the variation in bison activity ($R^2 = 0.59$).

	SS	df	MS	F-ratio
Major habitat[1]	14.1	2	7.0	29.4**
Minor habitat	2.6	1	2.6	10.7*
Slope	3.2	1	3.2	13.5**
Aspect	1.9	8	0.2	1.0
Distance from nearest water	0.2	1	0.2	1.0
Density of vegetation	13.7	2	6.9	28.7**
Error	47.1	197	0.2	

[1] See methods for definitions of major and minor habitats.
*p<0.05, **p<0.001

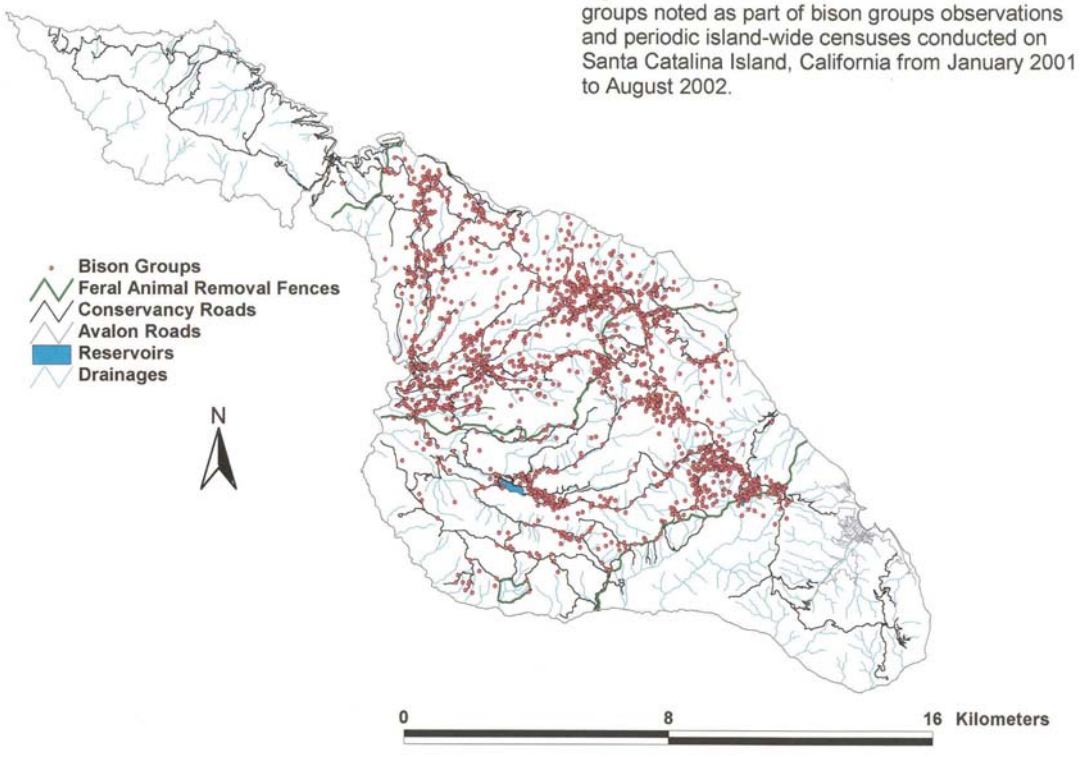

Figure 6. Estimated or measured locations of bison groups noted as part of bison groups observations and periodic island-wide censuses conducted on Santa Catalina Island, California from January 2001 to August 2002.

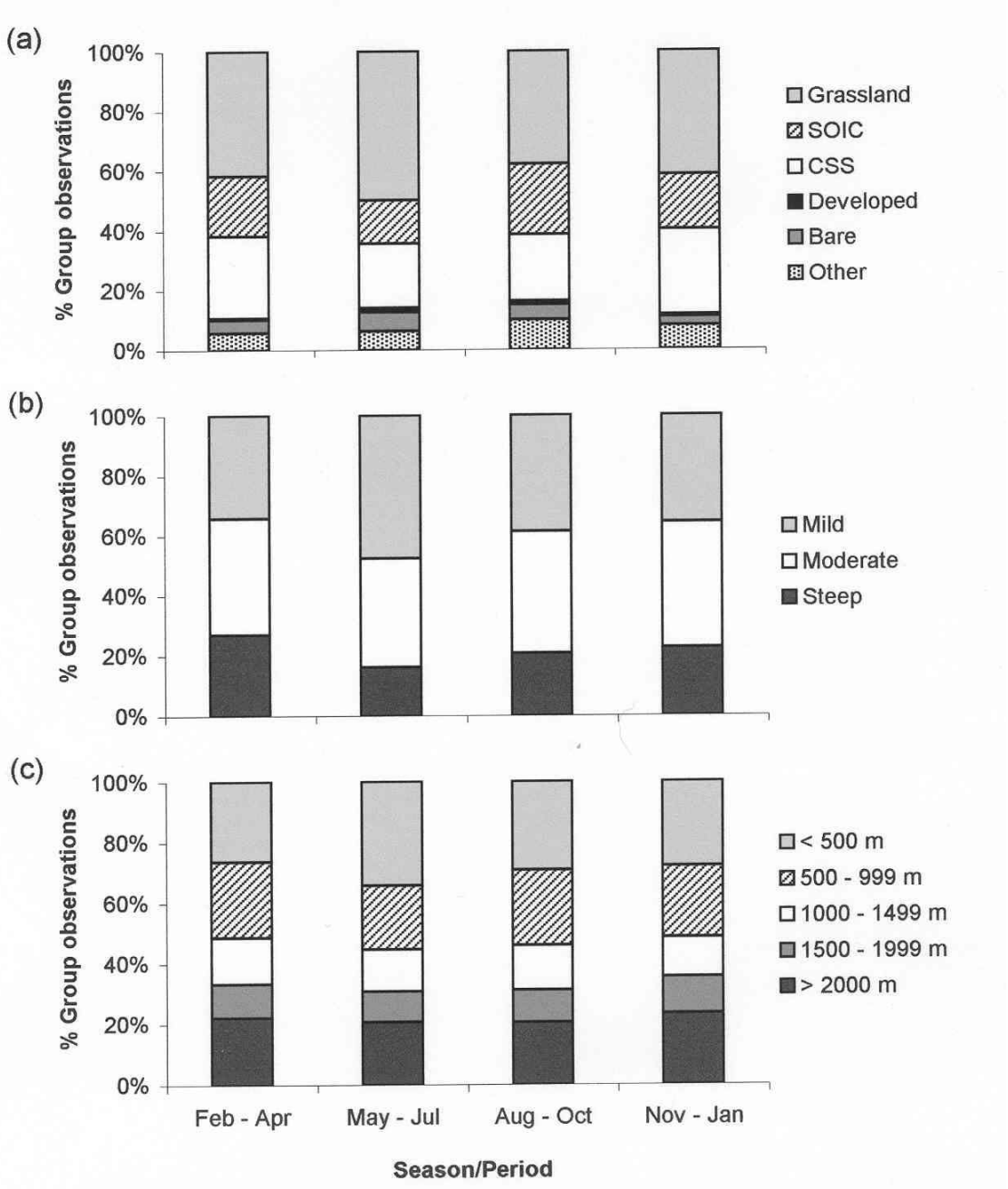

Figure 7. Seasonal variation in different aspects of habitat use by bison on Santa Catalina Island, California illustrated by (a) bison group observations in multiple different physiographic/vegetation classes for the island, (b) bison group observations on island terrains of different slopes, and (c) bison group observations at different distances from reservoirs, streams, or other water sources. Sesaons were defined by four different three month periods with Nov-Jan and Feb-Apr encompassing the wet season and May-Jul and Aug-Oct encompassing the warm and dry period.

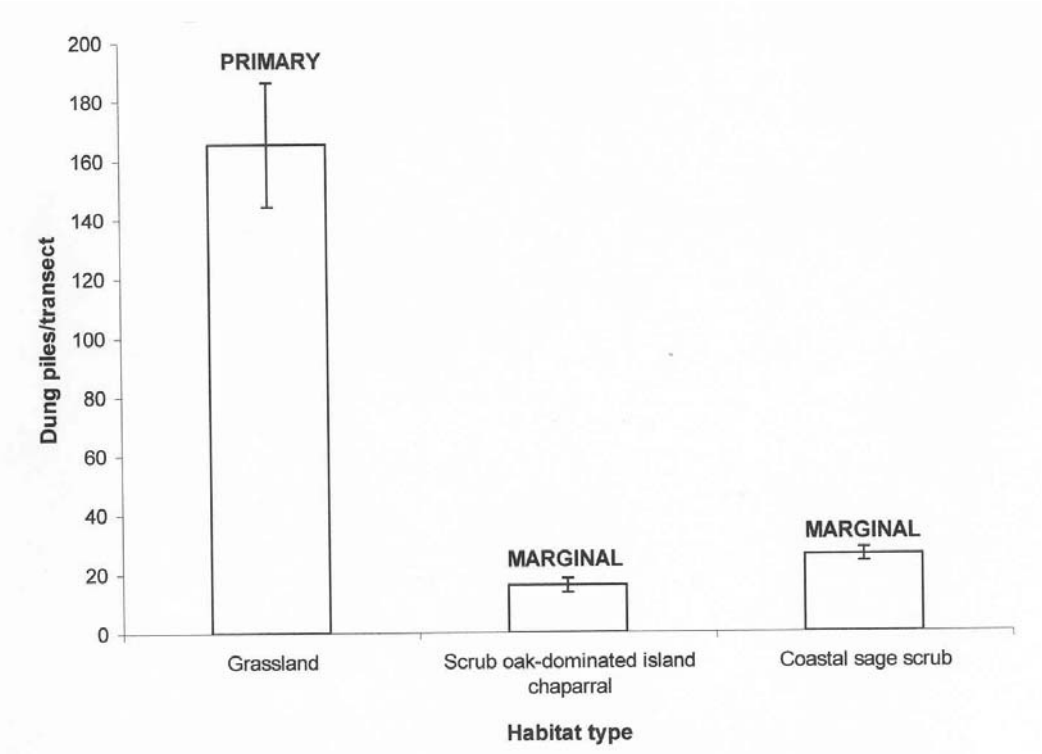

Figure 8. Mean (± SE) numbers of dung piles/transect enumerated along multiple systematic 100 m X 2 m belt transects in three different habitats on Santa Catalina Island, California in May and June 2002. Habitats were designated as "Primary" or "Marginal" based on the results of significant Chi-squared tests comparing use to availability ($P < 0.05$).

c) Foraging behavior and diets from bite counts

Bison behaviors and activity budgets were assessed from data on 286.6 hours of observations during 11 different 14 day sampling periods. On average, bison spent most of the daylight hours resting (45.2%), foraging (27.6%), or standing (18.8%), with less time devoted to traveling (6.5%) and other minor activities (2%). Behaviors and activities of adult and yearling bison of both sexes were similar across all seasons (Figure 9a; Log-ratio Chi-square = 9.7, df = 16, $P = 0.88$). Contrary to expectations related to energetics of reproduction/lactation, adult female bison did not significantly alter activity budgets among seasons (Figure 9b; Log-ratio Chi-square = 12.4, df = 8, $P = 0.13$). As part of group and behavioral observations, details on plant material consumed and bite counts of individual bison were available for a combined 16.7 hours. When foraging, bison appeared to consume predominately grass (86.1%) or a mix of grasses and forbs (13.2%) (Figure 10). Bite count data suggested that forbs (0.6%), shrubs (0.02%), and cactus (0.04%) made up a very small proportion of bison diets on Santa Catalina Island. Notably,

observations of bison consuming cactus were recorded only in October, November, and December 2001, potentially due to water stress.

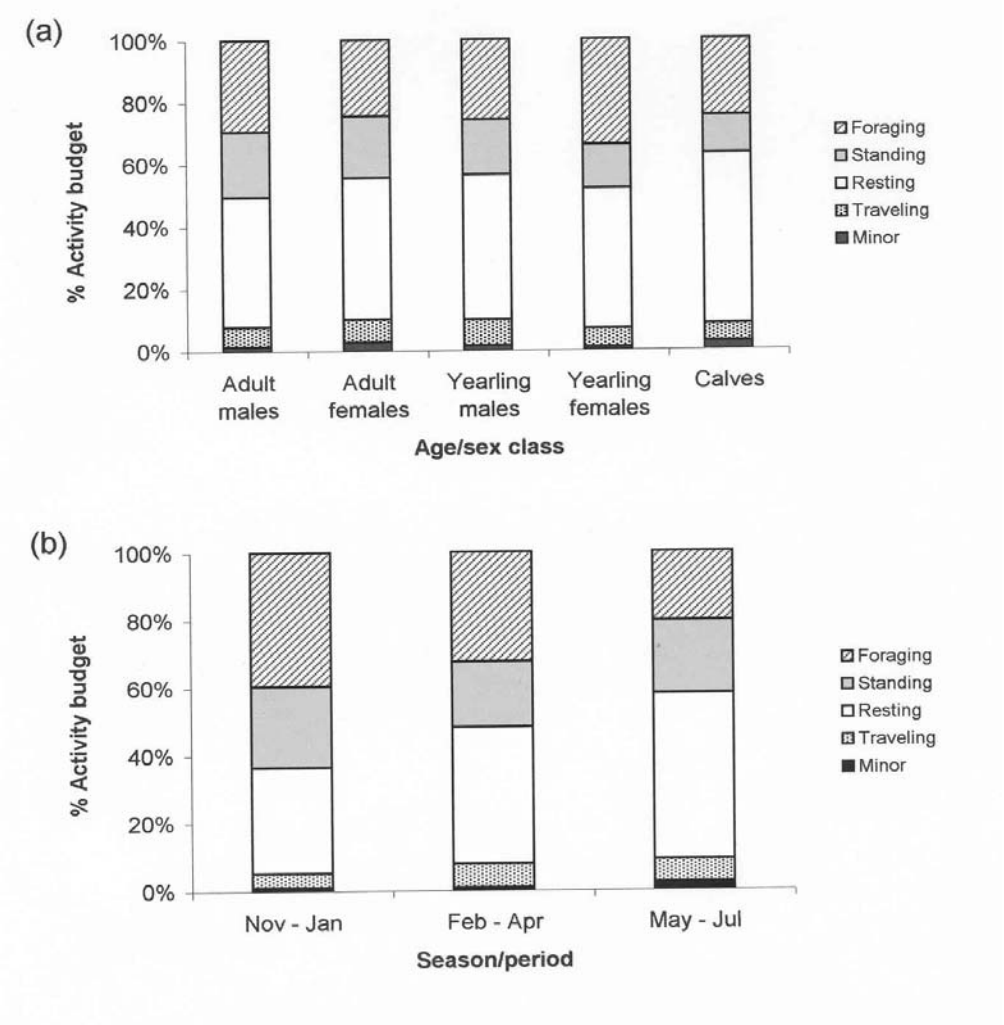

Figure 9. Estimated activity budgets for (a) all age and sex classes of bison over all seasons of the year combined and (b) adult female bison (≥ 2 years old) during three different four month time periods. Data are from scan samples during bison group behavioral observations on Santa Catalina Island, California from February 2001 to July 2002. Definitions for different types of activities/behaviors are provided in the text.

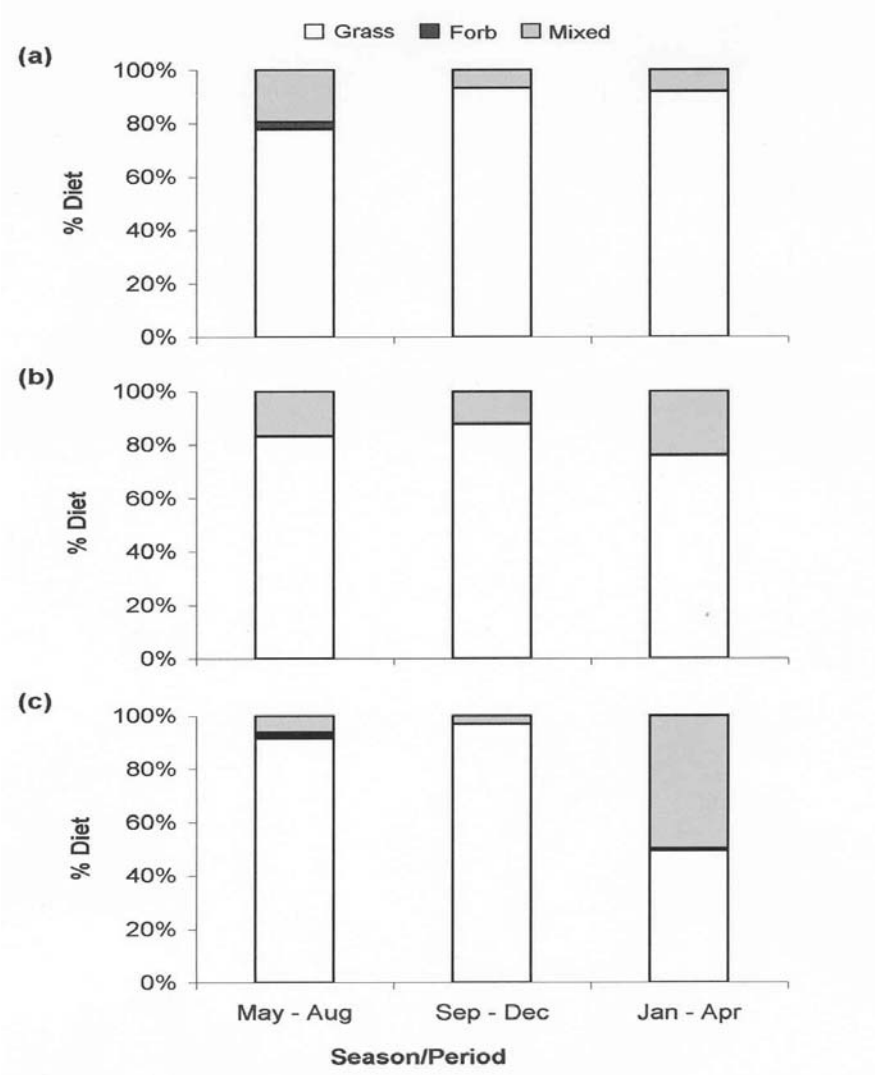

Figure 10. Proportions of different types of plants observed ingested by (a) adult female bison (≥ 2 years old), (b) ≥ 2 year-old male bison (e.g., spikes and bulls), and (c) yearling males and female bison based on bite-counts recorded as part of bison group behavioral observations on Santa Catalina Island, California, from May 2001 to April 2002.

d) Diets from microhistological analyses of dung samples

Results from microhistological analyses revealed that grasses were the dominant dietary item consumed by bison for all months assessed; grasses composed ≥ 80% of bison diets in all months except October 2001 (Table 12). The forb component of bison diets was also important but more variable among months. Forbs represented from 2.3% (May 2001) to 16% (October 2001) of bison diets (Table 12a). Although woody shrubs were nearly absent from bison diets during the wet season (March to May) they were increasingly eaten over the course of the dry season (Table 12). Similar to woody shrubs, cactus (Opuntia littoralis) was eaten primarily

Table 12a. Plant species and percentages of different plant species identified as part of the diets of bison on Santa Catalina Island in 2001. Estimates of monthly diets were by microhistological analyses of composite fecal samples collected from March 2001 to December 2001. For composite samples, 4 to 10 samples from different animals were collected each month and combined for analyses.

	Month (2001)									
Plant type/species	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep***	**Oct**	**Nov**	**Dec**
Grasses										
Agrostis pallens[a]	8.0	8.1	8.3	10.1	11.4	7.1	3.7	4.3	2.7	7.0
Avena spp[b]	1.9	0.4		3.1	4.8	2.4	2.9	2.3	2.5	3.2
Brachypodium distachyon[b]	8.3	17.5	34.5	7.8	4.2	9.0	13.4	22.3	17.0	11.6
Bromus spp.[b]	12.4	15.4	24.3	27.2	24.6	16.1	24.9	12.2	15.3	22.1
Digitaria sanguinalis[b]					1.5	1.6	0.4			
Festuca arundinacea[b]	9.7	5.8	1.1	1.8	5.9	4.9	7.0	3.4	7.4	3.4
Hainardia cylindrica[b]	7.2	8.4	6.3	7.2	7.0	2.4	1.8	2.0	0.2	2.1
Hordeum murinum[b]	4.2	7.9	2.4	5.2	6.7	5.7	8.8	4.3	6.7	6.3
Leymus spp[a]	4.4	1.2		0.2	1.1	3.3	3.7	1.4	4.5	4.0
Lolium spp[b]	2.6	4.4		1.0	0.8	4.0	1.4		1.1	3.4
Nassella spp[a]	15.2	11.6	15.8	11.1	7.6	9.7	9.9	9.7	11.9	10.5
Poa spp[c]	11.7	7.5	3.9	4.3	3.6	4.9	6.0	9.9	9.9	10.5
Vulpia bromoides[b]				5.4	6.7	6.6	2.3		3.4	3.4
Unknown grasses	5.3	4.4	0.7	1.9	2.1	5.3	2.7	4.5	2.0	3.8
Total grasses:	*90.9*	*92.6*	*97.3*	*86.3*	*88.0*	*83.0*	*88.9*	*76.3*	*84.6*	*91.3*
Sedges/Rushes										
Carex spp.[a]			0.4		0.6	0.7	0.4	2.6		0.9
Eleocharis macrostachys[a]					1.1	3.5	2.5			
Juncus spp.[a]						0.7			0.5	0.8
Total sedges/rushes:	*0.0*	*0.0*	*0.4*	*0.0*	*1.7*	*4.9*	*2.9*	*2.6*	*0.5*	*1.7*
Forbs										
Achillea millefolium[a]					0.4				1.1	
Bloomeria crocea[a]										0.4
Calystegia macrostegia[a]	0.1									
Chenopodium spp.[a]						0.4				
Erodium spp.[b]	4.3	3.3			0.6					
Foeniculum vulgare[b]	0.4								0.5	
Galium spp.[a,d]	0.6	1.2								
Jepsonia malvifolia[a]	0.5									
Lathyrus vestitus[a]				1.7	0.1		0.5	0.7		0.1
Lotus spp.[a,e]	0.4	0.7				0.1				
Rumex spp.[c]	0.4									
Trifolium spp./*Melilotus* spp.[c]		0.3	0.1	1.6	1.3			7.0		
Unknown forb/forb parts	2.4	1.3	2.2	6.2	4.9	9.7	2.7	8.3	6.4	3.2
Total forbs:	*9.1*	*6.8*	*2.3*	*9.5*	*7.3*	*10.2*	*3.2*	*16.0*	*8.0*	*3.7*
Shrubs/Cactus										
Artemisia californica[a]					1.8	1.1	1.9	1.4	1.8	0.3
Baccharis spp.[a]								0.6	0.7	
Malacothamnus fasciculatus[a]				2.3				0.3	0.7	
Opuntia littoralis[a]							2.3	2.8	2.9	1.9
Quercus pacifica[a,f]				1.9		0.4				
Rhus integrifolia[a]		0.6			0.8					
Salix spp.[a]										1.1
Unknown shrubs/shrub parts					0.4	0.4	0.4		0.8	
Total shrubs:	*0.0*	*0.6*	*0.0*	*4.2*	*3.0*	*1.9*	*4.6*	*5.1*	*6.9*	*3.3*

*Mosses were present as 0.4% of the diets of bison during this month (mosses were not detected in any other month).

[a] Native to Santa Catalina Island

[b] Not native to Santa Catalina Island.

[c] Island vegetation includes native and non-native representatives within the genus.

[d] May include *G. catalinense* ssp. *catalinense*, a Santa Catalina Island endemic and/or *G. nuttallii* ssp. i*nsulare*, a Channel Island endemic.

[e] May include *L. argophyllus* var. *argenteus*, a Channel Island endemic.

[f] Endemic to the Channel Islands.

during the later part of the dry season (Tables 12a,b). Based on data from Tables 12a and 12b, we calculated that native plants comprised an average of 25.8 ± 1.1% (range 17.4 to 34.8%) of the diets of bison from March 2001 to August 2002. Non-native plants comprised an average of 58.2 ± 1.8% (range 46.5 to 71.0%) of the diets of bison from March 2001 to August 2002 (Table 12).

Table 12b. Plant species and percentages of different plant species identified as part of the diets of bison on Santa Catalina Island in 2002. Estimates of monthly diets were by microhistological analyses of composite fecal samples collected from January 2002 to August 2002 (no samples were collected in April). For composite samples, 3 to 11 samples from different animals were collected each month and combined for analyses.

	Month (2002)						
Plant type/species	**Jan**	**Feb**	**Mar**	**May**	**Jun**	**Jul**	**Aug**
Grasses							
Agrostis pallens[a]	2.1	7.2	6.6	1.9	4.7	8.2	9.2
Avena spp.[b]	2.8	4.9	3.7	4.1	4.4	1.1	3.1
Brachypodium distachyon[b]	12.9	11.9	8.5	22.2	10.2	10.7	11.8
Bromus spp.[b]	9.4	9.6	10.7	19.3	21.2	15.4	19.4
Digitaria sanguinalis[b]	0.7			2.1	0.9	0.7	
Festuca arundinacea[b]	9.9	8.6	6.4	4.8	10.0	6.9	5.2
Hainardia cylindrica[b]	1.4	2.7	1.4	1.7	1.8	1.4	0.5
Hordeum murinum[b]	8.2	15.6	10.1	8.7	12.9	9.4	14.8
Leymus spp.[a]	0.7	4.9	4.3	1.7	1.8	4.8	1.1
Lolium spp.[b]	2.8	3.3	2.3	1.9	0.7	1.1	3.9
Nassella spp.[a]	14.3	14.6	10.3	12.4	8.9	10.5	11.4
Poa spp.[c]	11.5	7.0	17.8	4.1	3.8	7.1	7.0
Vulpia bromoides[b]	0.5	1.8	7.1	5.8	6.0	4.8	3.3
Unknown grasses	2.8	2.9	4.1	3.1	5.3	1.6	2.4
Total grasses:	*80.0*	*95.0*	*93.3*	*93.8*	*92.6*	*83.7*	*93.1*
Sedges/Rushes							
Carex spp.[a]						2.1	
Eleocharis macrostachya[a]		0.4	0.4				
Juncus spp.[a]			0.7	0.8	0.7	1.4	
Total sedge/rush:	*0.0*	*0.4*	*1.1*	*0.8*	*0.7*	*3.5*	*0.0*
Forbs							
Erodium spp.[b]			0.9	0.4		2.1	0.6
Lathyrus vestitus[a]	0.5						0.6
Lotus spp.[a,e]			0.4				0.4
Lupinus spp[a]					0.2	0.2	0.2
Pholistoma racemosum[a]		0.2					
Trifolium spp./*Melilotus* spp.[c]			1.8				
Unknown forb/forb parts	2.1	2.8	2.1	4.4	4.0	3.4	2.6
Total forbs:	*2.6*	*3.0*	*5.2*	*4.8*	*4.2*	*5.7*	*4.4*
Shrubs/Cactus							
Artemisia californica[a]	1.2				0.9	0.9	1.6
Atriplex semibaccata[b]	0.2					0.2	
Opuntia littoralis[a]	15.3	0.8	0.4		0.9	4.6	0.4
Quercus pacifica[a,f]	0.7						
Salix spp.[a]				0.6		1.4	
Unknown shrub/shrub part		0.8			0.7		0.5
Total shrubs/cactus:	*17.4*	*1.6*	*0.4*	*0.6*	*2.5*	*7.1*	*2.5*

[a] Native to Santa Catalina Island

[b] Not native to Santa Catalina Island.

[c] Island vegetation includes native and non-native representatives within the genus.

[e] May include *L. argophyllus* var. *argenteus*, a Channel Island endemic.

[f] Endemic to the Channel Islands.

There was some apparent seasonal variation in the diets of bison on Santa Catalina Island from March 2001 to August 2002 (Table 12a,b). During the wet season bison consumed primarily grasses and forbs whereas during the dry season their diets increasingly diversified to include proportionally more sedges, shrubs and cactus (Figure 11; Table 12a,b). Increased consumption of sedges and rushes during warm, dry summer months (Table 12a,b) suggested bison shifted some of their foraging to wetland or riparian habitats during these periods. One of our hypotheses/predictions was that bison would alter their diets to include more riparian vegetation (sedges/rushes) and woody shrubs (shrubs/cactus) during the extended dry period typical of the Mediterranean climate of Santa Catalina Island. On average, monthly bison diets included 0.9% (SE = 0.29) riparian vegetation and woody shrubs during the wet season (Mar 2001 to May 2001 and Feb 2002 to April 2002) compared to 7.2% (SE = 1.4) during the dry season (Jun 2001 to Jan 2002 and May 2002 to Aug 2002; unequal variances t = -4.21, df = 11, P = 0.0007). Although these results indicate a seasonal shift in bison diets in support of our hypothesis, when we grouped data for the 12 month period from March 2001 to February 2002 into 3 month seasons, we detected a trend but no significant variation in proportions of the different forage types eaten by bison (Figure 11; Log-ratio Chi-Square = 18.0, df = 12, P = ***0.12).***

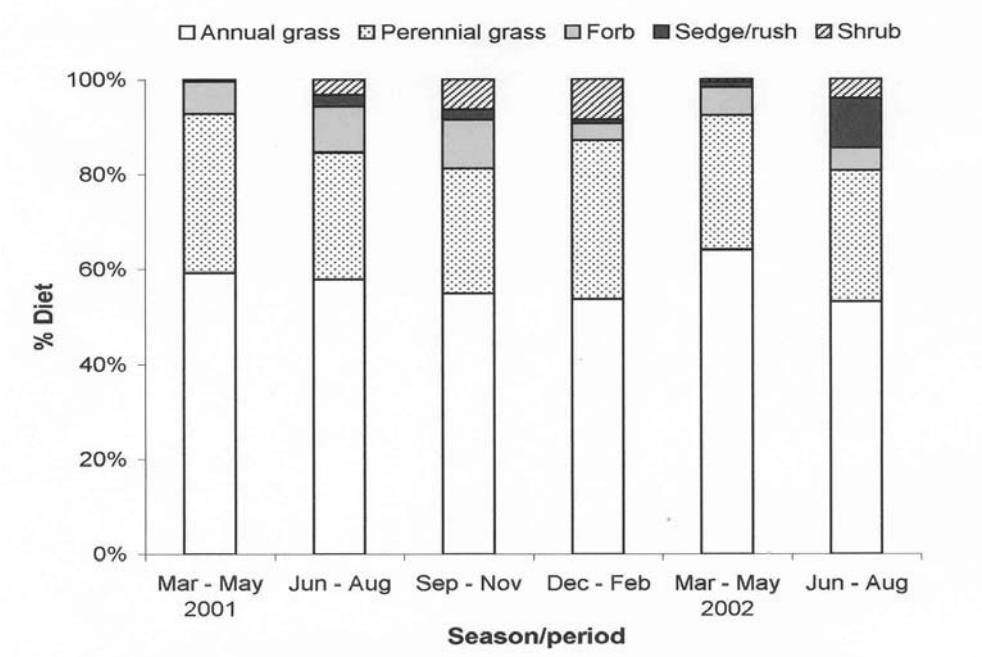

Figure 11. Proportions of different types of plants consumed by bison on Santa Catalina Island, California based on microhistological analysis of composite fecal samples collected from May 2001 to August 2002 (excluding April 2002).

Effects on Native Plant Communities

a) Diversity and structure of herbaceous plant communities

Bison exclosure and control vegetation plots were first established in winter 2001 with analyses of plant community attributes first assessed in spring 2001 and then again in spring 2002. Appendix VIII provides a summary list of the 90 different plants species identified in bison exclosure and control vegetation plots. Among these 90 species of plants, nearly 59% were non-native to Santa Catalina Island; 13% of the non-native species were common to all habitat types sampled (Appendix VIII). Summaries and analyses of plant community attributes in grasslands and SOIC habitat areas will focus on data collected during spring 2002, which represents information on developing differences between bison exclosure and control vegetation plots after two growing seasons of removal of the activities of bison from exclosure plots. Data on plant community attributes for bison exclosure and control vegetation plots in riparian habitat areas are presented differently because of wide variation among riparian areas with respect to plant communities and underlying hydrological patterns that influence vegetation communities.

Plant communities in bison exclosure plots in grassland habitats were characterized by higher species richness, a trend for higher species diversity, greater absolute cover, higher absolute cover for non-native plants, higher forb biomass, and higher overall plant height than plant communities in control plots after two years of protection from bison activities (Table 13).

Table 13. Plant community attributes for bison exclosure and control vegetation plots in four different grassland areas of Santa Catalina Island, California in spring 2002. Data are expressed as means ± 1 SE.

Parameter	Control	Bison exclosure	*t* statistic	P
Richness	8.2 ± 1.1	12.2 ± 1.2	-3.27	0.047
Evenness (E_{var})	0.52 ± 0.04	0.31 ± 0.06	-1.46[1]	0.144
Diversity (*H'*)	2.13 ± 0.18	2.53 ± 0.20	1.83[1]	0.068
Spatial heterogeneity	0.41 ± 0.11	0.33 ± 0.04	0.87	0.450
Total absolute cover (%)	54.4 ± 22.3	100.8 ± 23.7	-4.94	0.016
Native plants	9.1 ± 8.1	18.6 ± 13.3	-1.67	0.193
Non-native plants	41.7 ± 13.4	99.8 ± 12.1	-4.44	0.021
Total biomass (g)[2]	1.4 ± 0.4	1.7 ± 0.2	-1.05	0.372
Annual grass[2]	1.3 ± 0.4	1.6 ± 0.2	-0.84	0.463
Perennial grass[2]	0.2 ± 0.2	0.2 ± 0.2	-1.00	0.391
Forbs[2]	0.5 ± 0.4	0.9 ± 0.4	-10.03	0.002
Plant height (cm)	3.6 ± 1.2	10.3 ± 1.1	-5.32	0.013
Soil contacts	53.0 ± 19.8	41.8 ± 18.0	0.94	0.416

[1] Z-statistic
[2] Log-transformed

In contrast, for SOIC habitats we detected no differences in plant community attributes between bison exclosure and control vegetation plots (Table 14). There was a strong trend, however, for increased vegetation cover in exclosures based on more soil substrate contacts in control plots (Table 14).

Table 14. Plant community attributes for bison exclosure and control vegetation plots in four SOIC areas of Santa Catalina Island, California in spring 2002. Data are expressed as means ± 1 SE.

Parameter	Control	Bison exclosure	*t* statistic	P
Richness	6.2 ± 1.2	7.8 ± 0.95	-0.91	0.432
Evenness (E_{var})	0.43 ± 0.15	0.43 ± 0.17	-0.36[1]	0.715
Diversity (*H'*)	1.86 ± 0.38	1.65 ± 0.12	-0.73[1]	0.465
Spatial heterogeneity	0.16 ± 0.09	0.13 ± 0.06	0.83	0.468
Absolute cover (%)	54.4 ± 23.0	100.8 ± 23.7	-1.14	0.338
Native plants	3.9 ± 2.5	8.3 ± 4.7	-0.67	0.551
Non-native plants	49.4 ± 21.1	90.5 ± 19.0	-1.19	0.319
Total biomass (g)[2]	0.6 ± 0.3	1.3 ± 0.2	-2.19	0.116
Annual grass[2]	0.5 ± 0.2	1.1 ± 0.1	-1.48	0.236
Perennial grass[2]	0.3 ± 0.3	0.6 ± 0.4	-1.70	0.187
Plant height (cm)	5.6 ± 2.4	10.6 ± 1.2	-1.47	0.238
Soil contacts[2]	1.5 ± 0.3	0.2 ± 0.2	2.82	0.066

[1] *Z*-statistic
[2] Log-transformed

Plant community attributes for bison exclosure and control plots in riparian habitat areas were summarized separately by habitat plot because of their distinct differences (Table 15). Plant communities in both bison exclosure and control vegetation plots appear in flux, related to the combination of variation in climate between 2001 and 2002 and differences in bison activity in control plots.

Among a total of 32 qualitative comparisons of the plant community attributes between bison exclosure and control habitat plots in riparian areas, 22 indicated an improvement in exclosures compared to control plots after two years of restricted bison access (Table 16). One comparison was neutral and 9 suggested the plant community attribute had changed for the worse in the bison exclosure (Table 16).

Table 15. Percent change in plant community attributes in bison exclosure and control vegetation plots between spring 2001 and spring 2002 for four different riparian areas on Santa Catalina Island, California. NOTE: Echo Lake and Picnic Tree were not sampled in 2001 due to flooding and/or flood damage to plots.

	Control			Bison exclosure		
Plot/parameter	**2001**	**2002**	**% Change**	**2001**	**2002**	**% Change**
Middle Cottonwood						
Richness	16	14	0.88	11	16	1.45
Evenness (E_{var})	0.15	0.21	1.40	0.18	0.27	1.50
Diversity (H')	1.77	1.94	1.10	1.68	2.22	1.32
Spatial heterogeneity	0.09	0.09	1.00	0.02	0.29	14.5
Total absolute cover (%)	181	86	0.48	226	154	0.67
Total biomass (g)	2.0	16.3	8.15	131.1	200.4	1.53
Plant height (cm)	15.7	6.7	0.43	37.5	16.0	0.43
Soil contacts	156	150	0.96	160	159	0.99
Black Jack Reservoir						
Richness	11	22	2.00	8	18	2.25
Evenness (E_{var})	0.25	0.26	1.04	0.24	0.22	0.92
Diversity (H')	1.36	2.00	1.47	2.04	2.42	1.19
Spatial heterogeneity	0.04	0.08	2.00	0.33	0.35	1.06
Total absolute cover (%)	124	154	1.24	173	228	1.32
Total biomass (g)	528.5	567.4	1.07	485.22	503.2	1.04
Plant height (cm)	22.5	52.2	2.32	33.6	52.7	1.57
Soil contacts	156	131	0.84	152	46	0.30
Echo Lake						
Richness	---	32	---	---	42	---
Evenness (E_{var})	---	0.36	---	---	0.25	---
Diversity (H')	---	2.89	---	---	3.33	---
Spatial heterogeneity	---	0.15	---	---	0.09	---
Total absolute cover (%)	---	108	---	---	397	---
Total biomass (g)	---	17.5	---	---	289.5	---
Plant height (cm)	---	5.0	---	---	49.9	---
Soil contacts	---	145	---	---	105	---
Picnic Tree						
Richness	---	23	---	---	12	---
Evenness (E_{var})	---	0.35	---	---	0.58	---
Diversity (H')	---	2.90	---	---	2.70	---
Spatial heterogeneity	---	0.66	---	---	0.46	---
Total absolute cover (%)	---	115	---	---	86	---
Total biomass (g)	---	147.1	---	---	382.6	---
Plant height (cm)	---	31.8	---	---	24.5	---
Soil contacts	---	96	---	---	35	---

Table 16. Comparison of plant community attributes for each riparian habitat plot at the end of the last sampling period in spring 2002. Plus/minus signs indicate that the mean estimate for a particular plant community attribute was better/worse in the bison exclosure plot compared to the control plot based on current understanding of plant community ecology, structure, and function (Barbour et al. 1999).

Plot/parameter	Control	Bison exclosure	Direction
Middle Cottonwood			
Richness	14	16	+
Evenness (E_{var})	0.21	0.27	+
Diversity (*H'*)	1.94	2.22	+
Spatial heterogeneity	0.09	0.29	+
Total absolute cover (%)	86	154	+
Total biomass (g)	16.3	200.4	+
Plant height (cm)	6.7	16.0	+
Soil contacts	150	159	-
Black Jack Reservoir			
Richness	22	18	-
Evenness (E_{var})	0.26	0.22	+
Diversity (*H'*)	2.00	2.42	+
Spatial heterogeneity	0.08	0.35	+
Total absolute cover (%)	154	228	+
Total biomass (g)	567.4	503.2	-
Plant height (cm)	52.2	52.7	0
Soil contacts	131	46	+
Echo Lake			
Richness	32	42	+
Evenness (E_{var})	0.36	0.25	-
Diversity (*H'*)	2.89	3.33	+
Spatial heterogeneity	0.15	0.09	-
Total absolute cover (%)	108	397	+
Total biomass (g)	17.5	289.5	+
Plant height (cm)	5.0	49.9	+
Soil contacts	145	105	+
Picnic Tree			
Richness	23	12	-
Evenness (E_{var})	0.35	0.58	+
Diversity (*H'*)	2.90	2.70	-
Spatial heterogeneity	0.66	0.46	-
Total absolute cover (%)	115	86	-
Total biomass (g)	147.1	382.6	+
Plant height (cm)	31.8	24.5	+
Soil contacts	96	35	+

After two years of protection from bison, relative canopy covers of common species of plants did not differ between bison exclosure and control plots in any habitat except for *Stelleria media,* (a non-native herbaceous forb), which was more than twice as abundant in bison exclosures in SOIC habitats than in adjacent control areas (Table 17).

Table 17. Relative canopy cover (mean + 1 SE) of abundant plant species (relative cover of ≥ 2% at ≥ 3 sites) in grassland, SOIC, and riparian vegetation plots on Santa Catalina Island, California.

Habitat plot/species	Spring 2001 Bison exclosure	Spring 2001 Control	Spring 2001 *t* statistic[1]	Spring 2002 Bison exclosure	Spring 2002 Control	Spring 2002 *t* statistic[1]
Grassland habitat plots						
Atriplex semibaccata	--	--	--	16.8 ± 7.8	15.9 ± 4.8	0.21
Brachypodium distachyon	16.3 ± 10.0	15.6 ± 12.0	0.29	--	--	--
Bromus hordeaceus	11.3 ± 2.1	8.6 ± 1.8	1.37	8.4 ± 3.0	14.8 ± 1.3	-2.45
Hordeum intercedens	17.0 ± 4.0	7.8 ± 2.6	--	2.5 ± 0.5	7.5 ± 5.4	--
Hordeum murinum	--	--	--	12.9 ± 4.0	24.2 ± 9.6	-0.84
Lolium multiflorum	19.3 ± 9.3	16.0 ± 4.4	0.64	4.2 ± 1.6	9.4 ± 8.5	--
Medicago polymorpha	7.4 ± 2.1	3.1 ± 2.3	0.98	--	--	--
Vulpia bromoides	5.4 ± 1.9	5.2 ± 1.9	1.94	--	--	--
SOIC habitat plots						
Brachypodium distachyon	22.4 ± 6.3	17.0 ± 7.3	0.74	24.4 ± 8.8	24.2 ± 9.9	0.02
Bromus diandrus	21.5 ± 7.4	25.8 ± 2.1	-0.72	43.3 ± 12.5	48.2 ± 9.6	-1.05
Chenopodium californicum	--	--	--	7.1 ± 4.8	5.4 ± 0.6	--
Claytonia perfoliata	22.6 ± 7.8	11.4 ± 4.0	0.98	--	--	--
Hordeum murinum	--	--	--	10.4 ± 1.5	11.5 ± 6.6	--
Pholistoma racemosum	16.8 ± 8.8	18.6 ± 9.2	-1.61	--	--	--
Stelleria media	6.7 ± 3.3	13.5 ± 3.6	-3.57[1]	--	--	--
Riparian habitat plots						
Agrostis viridis	--	--	--	14.1 ± 7.3	25.7 ± 9.2	0.92
Brachypodium distachyon	--	--	--	10.4 ± 7.2	11.6 ± 7.0	0.94
Hainardia cylindrica	--	--	--	2.4 ± 1.0	1.2 ± 0.9	1.80
Juncus bufonius	20.6 ± 19.6	30.8 ± 12.4	--	--	--	--
Polypogon interruptus	40.4 ± 10.3	36.4 ± 1.2	--	13.2 ± 10.0	3.5 ± 2.4	--

[1] Significant at $p < 0.10$. Dashes indicate that a statistical test was not possible due to insufficient sample size.

b) Structure of scrub oak-dominated island chaparral

The mid- to upper-level layers of SOIC stands were significantly altered by the presence of bison ($M = 0.99$, $P = 0.01$) but the isolation between classes was not strong (Figure 12a; Stress = 0.16). Although univariate analyses are not entirely appropriate for description of overall habitat structure, they can provide insight into factors contributing to significant differences among SOIC habitats detected by ANOSIM. Univariate analyses suggest that differences in SOIC plot characteristics may be related to tree diversity and the number and size of snags (Table 18).

Table 18. Ground-level structural components (mean ± SD) of SOIC plots in Zone 1 (bison absent/pigs absent; N = 10), Zone 2 (bison present/pigs absent; N = 10), and Zone 3 (bison present/pigs present; N = 10) of Santa Catalina Island, California.

Parameter	Zone 1	Zone 2	Zone 3
Soil disturbance (all sources) (cm)	46.5 ± 132.5	97.4 ± 202.6	916.4 ± 1000.3
Litter depth (cm)	2.7 ± 0.9	2.2 ± 0.9	1.8 ± 0.74
Number of downed branches	58.2 + 24.8	54.6 ± 22.2	63.6 ± 26.4
Herb height (cm)	18.3 + 7.0	18.1 ± 7.5	16.1 ± 9.7

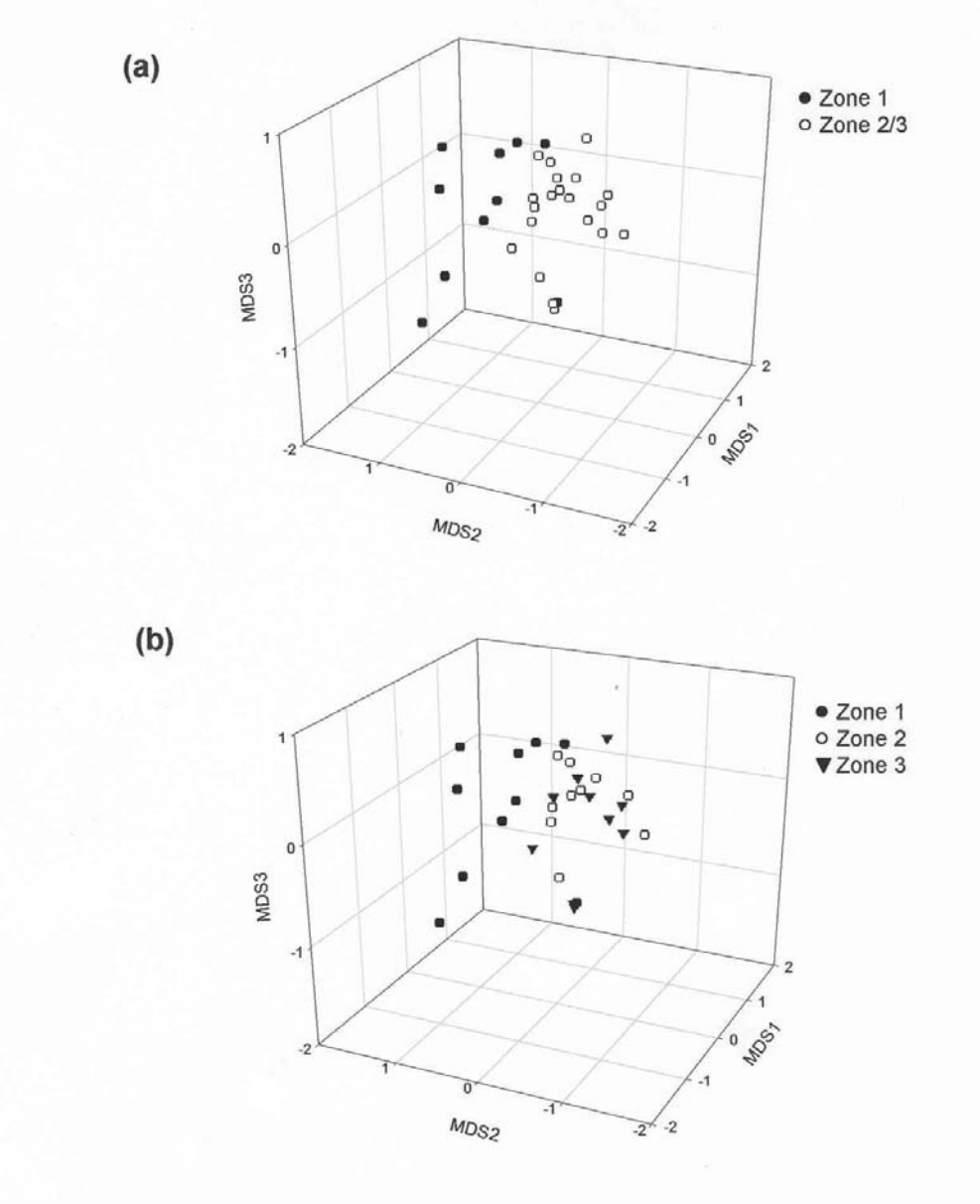

Figure 12. Habitat ordination using nMDS for (a) mid- to upper-layers of scrub oak-dominated island chaparral plots in Zone 1 (bison absent) and Zone 2/3 (bison present), and (b) lower layer of scrub oak-dominated island chaparral plots in Zone 1 (bison and feral pigs absent), Zone 2 (bison present, feral pigs absent), and Zone 3 (bison and feral pigs present) on Santa Catalina Island, California.

Ground cover was significantly affected by the presence of bison and feral pigs in SOIC habitats ($M = 0.78$, $P = 0.003$); however, when only sites from Zones 1 and 2 were compared, differences in ground structure were not evident ($M = 0.96$, $P = 0.14$). As with the mid- to upper-layers, compaction within classes was relatively good, but isolation of classes was not strong (Figure

12b, Stress = 0.16). Differences in SOIC structure at the ground level may be attributable to soil disturbance (rooting) by feral pigs (Table 19).

Table 19. Mid- and canopy-level structural components (mean ± SD) of SOIC plots in Zone 1 (bison absent; N = 10) and Zones 2/3 (bison present, N = 20) of Santa Catalina Island, California.

Parameter	Zone 1	Zones 2/3
Canopy height (m)	7.9 ± 4.8	6.6 ± 2.3
Canopy cover (%)	63.0 ± 9.4	69.8 ± 13.1
Number of shrubs	10.3 ± 6.1	10.2 ± 8.6
Tree dispersion (m)	5.7 ± 1.9	4.6 ± 1.5
Tree diversity (H')	0.7 ± 0.5	0.2 ± 0.1
Tree DBH (cm)	13.2 ± 3.5	13.0 ± 2.0
Broken branches per tree	1.0 ± 0.4	1.1 ± 0.3
Number of snags	12.4 ± 6.4	6.3 ± 3.8
Snag DBH (cm)	10.5 ± 2.9	8.7 ± 2.5
Broken branches per snag	1.2 ± 0.6	1.6 ± 1.0

c) Dispersal of non-native plant species

We extracted a total of 2,552 seeds from bison hair clumps collected at the 2002 roundup and 1,612 seeds in bison hair clumps collected at wallows. Analyses of seeds extracted from hair clumps collected during bison roundups revealed ≥ 5 species of non-native grasses and forbs but no seeds of plants native to the island (Table 20). Seeds extracted from hair clumps shed in wallows, however, revealed the presence of approximately similar numbers of non-native (≥ 6) and native (4) vascular plants (Table 20). Despite the similarity in the number of species, there were significantly more non-native species of seeds than native species of seeds (Table 20; t = 2.8, df = 36, P = 0.009). For both roundup and wallow hair samples, there were significantly more seeds of non-native forbs (roundup: 0 ± SE = 57.9 ± 13.0; wallows: 0 ± SE = 32.4 ± 10.6) than seeds of non-native grasses (roundup: 0 ± SE = 11.1 ± 3.0; wallows: 0 ± SE = 8.3 ± 4.8) (roundup: t = 3.6, df = 36, p = 0.001; wallows: t = -2.5, df = 36, P = 0.02). Although we failed to detect a significant relationship between the size of hair clumps and the number of seeds for roundup samples (Figure 13a), there was a significant relationship between mass of hair clump collected from wallows and seed number (Figure 13b). Thus, numbers of seeds lodged in wallow hair clumps are expected to increase with hair clump size as measured by hair clump mass (Figure 13b).

Table 20. Mean number of seeds (± 1 SE) collected during roundups in 2001 and from wallows in 2001 and 2002 on Santa Catalina Island, California.

Source/Taxon	Mean number
Roundup hair clumps (based on 332.5 g of hair examined)	
Native annual/perennial grasses	None detected
Non-native annual grasses[1]	11.11 ± 2.98
Non-native forbs	57.86 + 13.02
Marrubium vulgare	49.67 ± 13.15
Medicago polymorpha	0.51 ± 0.17
Medicago sativa	0.08 ± 0.06
Xanthium strumarium	7.60 ± 2.20
Total seeds/gram roundup hair examined[2]	29.67 ± 11.05
Wallow hair clumps (based on 167.3 g of hair examined)	
Native annual/perennial grasses (all *Nassella* spp.)	0.22 ± 0.19
Nonnative annual grasses[1]	8.30 ± 4.82
Native rushes	0.05 ± 0.05
Native forbs	2.62 + 1.70
Ambrosia chamissonis	0.03 ± 0.03
Microseries douglassii	2.60 ± 1.71
Nonnative forbs	32.35 + 10.66
Erodium spp.	9.97 ± 3.41
Marrubium vulgare	18.70 ± 9.23
Medicago polymorpha	1.05 ± 0.41
Xanthium spinosum	0.08 ± 0.04
Xanthium strumarium	2.54 ± 0.79
Total seeds/gram wallow hair examined[3]	10.39 ± 2.23

[1] Likely included more than one species of grass.
[2] Seed numbers represent totals removed from 37 clumps of hair shaved from the forelocks of bison during the October 2001 roundup. Although seed totals are expressed here as seeds/gram of hair to facilitate evaluating sampling effort, we detected no relationship between numbers of seeds and hair weight (see above).
[3] Seed numbers represent totals removed from 37 clumps of hair removed from wallows during spring/summer 2001 and 2002. Seed totals are expressed as seeds/gram of hair to facilitate evaluating sampling effort. Although seed totals are expressed here as seeds/gram of hair to facilitate evaluating sampling effort, we detected only a weak relationship between numbers of seeds and hair weight (see above).

There was a high rate of dormancy in seeds from hair clumps collected at roundups (0 ± SE = 47.8 + 14.4%) and wallows (0 ± SE = 68.6 + 11.4%) (Table 21). The majority of seeds of *Marrubium vulgare* (most abundant species in roundup and wallow hair; Table 20) were viable in hair clumps from roundups (85%) and wallows (100%) (Table 21). The viability of annual grasses was low in roundup hair samples (28.8%), but relatively high in wallow hair samples (61.1%). This was most likely due to differing amounts of time seeds were stored, as storage conditions can affect viability (Salisbury and Ross 1992). The majority (> 60%) of non-native legume seeds (*Medicago* spp.) were not viable (Table 21). Non-dormant seeds of *Xanthium strumarium* evidenced nearly 100% viability regardless of source (Table 21), and we commonly observed burs of *X. strumarium* on the faces, forelocks, and tails of adult and yearling bison.

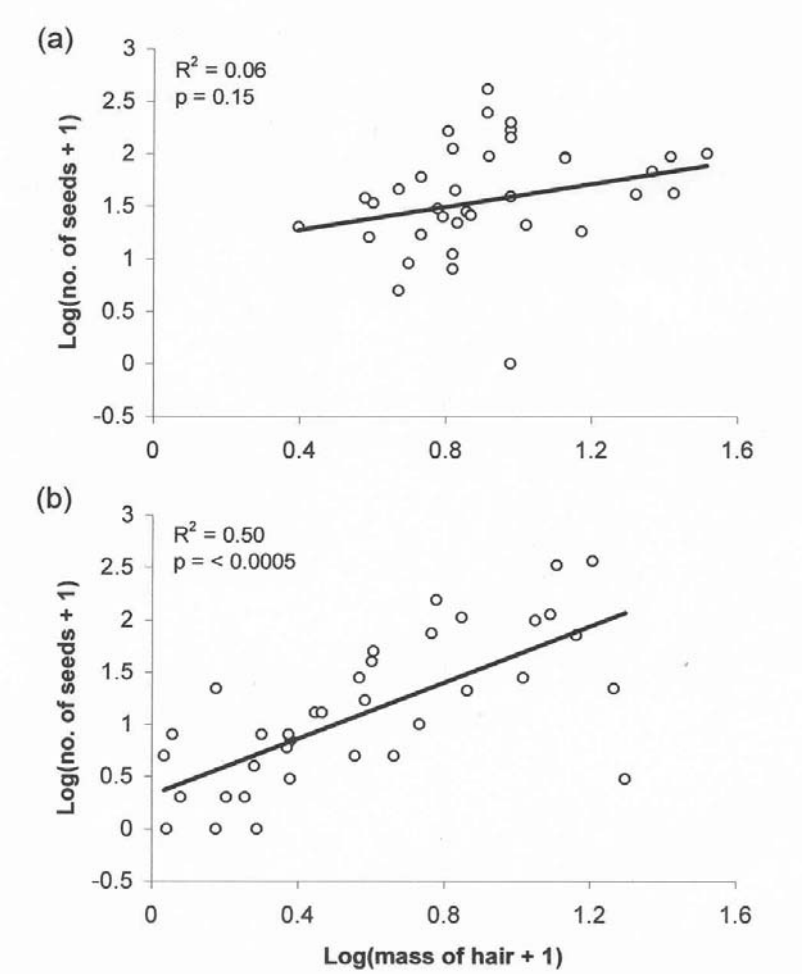

Figure 13. Linear regression relationships between numbers of seeds and mass of bison hair clumps (a) shaved from the forelocks of bison during the October 2000 roundup and (b) collected from active bison wallows in spring and summer 2001 and 2002 on Santa Catalina Island, California.

On average, seeds in hair clumps below a layer of soil were more likely to germinate (0 = 79.0% of pots had at least one seedling) than seeds in hair clumps left on the soil surface (0 = 24.8% of pots had at least one seedling). Although we last examined hair clump samples from 2002 after 48 days (rather than ending at 24 days as in 2001), doubling the length of the trial had no effect on the number of pots with seedlings. However, we were able to identify seeds to a lower taxonomic level in 2002 than in 2001. The majority of species growing from clumps of wallow hair were non-native (Table 22). The minimum mass of hair clump with seeds that germinated was 1.7 g and 0.2 g for the covered, and surface clumps, respectively.

Table 21. Viability of non-native and native seeds separated from bison hair clumps collected in roundups and at active wallows, Santa Catalina Island, California.

Species	Total tested	Dormant[3]	Not dormant[4]	
			Viable	Not viable
Roundup hair clumps[1]				
Non-native annual grasses[2]	69	10 (14.5)	17 (28.8)	42 (71.2)
Non-native forbs	350	185 (52.8)	140 (0.40)	25 (7.1)
Marrubium vulgare	200	140 (70.0)	51 (85.0)	9 (15.0)
Medicago polymorpha	40	25 (62.5)	2 (13.3)	13 (86.7)
Medicago sativa	10	8 (80.0)	0	2 (100)
Xanthium strumarium	100	12 (12.0)	87 (98.9)	1 (1.1)
Wallow hair clumps[1]				
Native grasses (*Nassella pulchra*)	7	0	5 (71.4)	2 (28.6)
Native rushes (*Juncus* sp.)	2	2 (100)	--	--
Native forbs				
Ambrosia chamissonis	1	1 (100)	--	--
Microseris douglasii	90	72 (80.0)	0	25 (100)
Non-native grasses[2]	24	6 (25.0)	11 (61.1)	7 (38.9)
Non-native forbs				
Erodium sp.	100	72 (72.0)	11 (39.3)	17 (60.7)
Marrubium vulgare	18	17 (94.4)	1 (100)	0
Medicago polymorpha	90	67 (74.4)	7 (30.4)	16 (69.6)
Xanthium strumarium	21	15 (71.4)	10 (100)	0

[1] Seeds from roundup samples were stored for approximately 13 months before testing, whereas seeds from wallow samples were stored for 7 to 9 months before testing.
[2] Likely includes more than one species of grass.
[3] Values in parentheses are percentages of total numbers of seeds tested.
[4] Values in parentheses are percentages of total number of seeds that were not dormant.

Table 22. Taxa sprouting from clumps of bison hair collected from wallows on Santa Catalina Island, California. Clumps grown in sterilized potting soil under greenhouse conditions in January 2001 (N = 34; 24 days) and October 2002 (N = 32; 48 days).

Plant taxon	Number of seedlings	
	2001	2002
Native grasses (*Nassella spp.*)	--	8
Non-native grasses	--	18
Brachypodium distachyon	--	2
Bromus spp.	--	16
Unknown annual grasses	61	11
Non-native forbs	13	34
Erodium botrys	2	--
Erodium cicutarium	3	3
Erodium spp.	--	1
Marrubium vulgare	--	5
Medicago spp.	--	3
Xanthium spinosum	--	2
Xanthium strumarium	8	20
Unknown annual forbs	4	1

Results from hair clump persistence trials during summer 2002 suggested that clumps of bison hair persisted in wallows for some time. After 60 days, 18 wallows retained marked clumps. Although hair clumps persisted, they did not remain intact with respect to size (indexed by mass). On average, hair clumps left in wallows lost nearly 40% of their original mass after 60 days (Table 23); small pieces of hair clumps were dispersed both above and below the surface of wallows. Fragmentation of hair clumps in wallows increased between 30 and 60 days, likely related to wallowing activity. For an individual bison hair clump shed during wallowing, there was an estimated 21.8% probability that at least one seedling would emerge from that clump (Appendix IX). Nevertheless, significant numbers of seedlings germinated from wallow soil independent of seedlings emerging from bison hair. Quantitatively, we detected no difference in the number of native seedlings between wallow soil samples with and without hair (all $P > 0.35$) (Figure 14a). We also failed to detect a difference in the number of non-native seedlings in pots with and without hair (all $P > 0.22$), although there was a trend for more non-native seedlings in soil samples with hair clumps (Figure 14b). As part of dung sampling/seedling germination experiments, seedlings germinated from 6 (33%) of 18 shredded and planted dung samples; these included 17 seedlings from annual grasses, one seedling of an unknown forb and no seedlings of native plants.

Table 23. Mean % original mass of marked hair clumps remaining in wallows after 30 days and 60 days (N = 20).

Number of days	% On surface	% Under surface
30	64.3 $\pm$ 6.7	11.3 $\pm$ 5.8
60	49.8 $\pm$ 8.2	10.9 $\pm$ 5.6

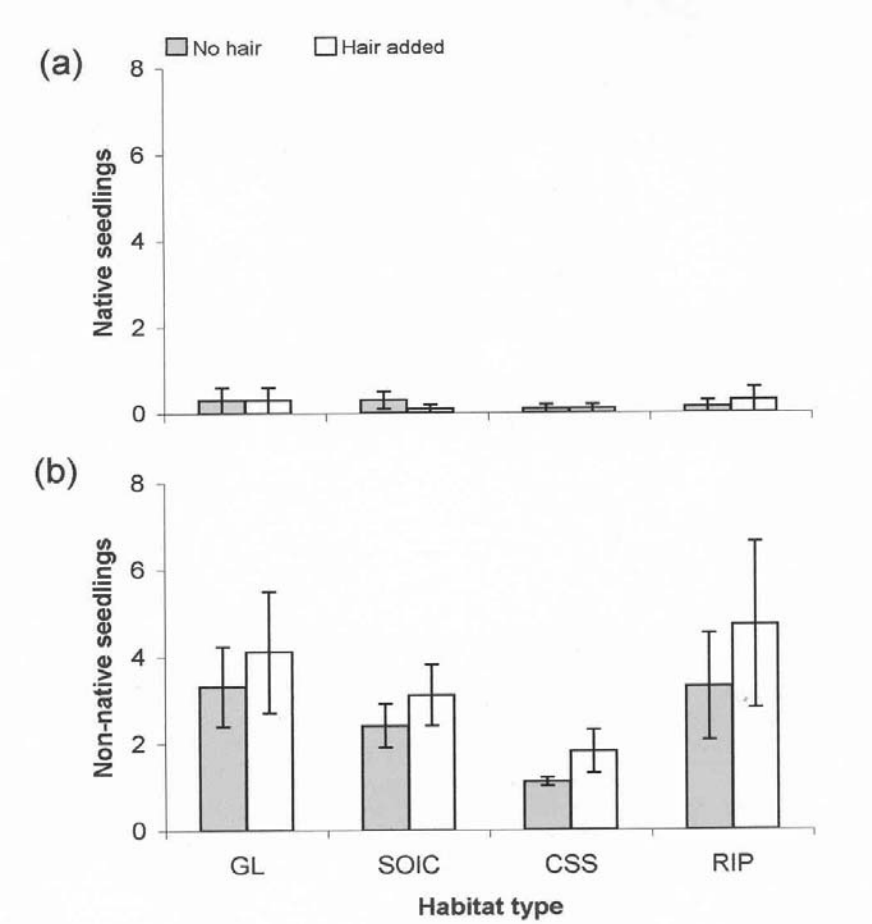

Figure 14. Mean (± SE) number of (a) native and (b) non-native seedlings observed germinating/sprouting from bison wallow soil with and without the addition of 0.6-23.6 g clumps of bison hair. Wallow soil was collected from seven different wallows each in grassland (GL), scrub oak-dominated island chaparral (SOIC), coastal sage scrub (CSS), and riparian habitats (RIP) on Santa Catalina Island, California, and watered/grown on the island in pots during summer 2002.

Effects on Terrestrial Vertebrates

a) Diversity and relative abundance of reptiles and amphibians

A total of four species of herptiles were captured during a total of 9 hours of time-constrained searches in Zone 1 and Zone 2 combined (Table 24). Notably, however, only a very few individuals were captured; eight total animals in Zone 2 and two in Zone 1 (Table 24). Small samples sizes precluded meaningful statistical analyses of potential differences in herptile communities between the bison-present area (Zone 2) and the bison-absent area of the island

(Zone 1), but three herptile species were observed in the bison-present area whereas only 2 species of herptiles (both reptiles) were detected in Zone 1 (Table 24). Temperature and wind speed did not differ between searches in Zone 1 and Zone 2 ($t = 0.5$, df = 16, $P = 0.65$ and $t = 0.1$, df = 16, $P = 0.91$, respectively), but there was significant variation in relative humidity ($t = 3.3$, df = 16, $P = 0.004$) between Zones. The structure of SOIC plots differed with respect to the presence of bison ($M = 0.74$, $P = 0.007$). However, isolation between classes and compaction within classes were not strong (Figure 15; Stress = 0.15). Tree richness, canopy cover, soil disturbance, and herb height may be related to the observed differences between Zones (Table 25).

Table 24. Number of reptiles and amphibians detected during visual encounter surveys in SOIC plots of Zone 1 (bison absent; N = 9) and Zones 2 (bison present, N = 9), Santa Catalina Island, California.

Class/Species	Zone 1	Zone 2
Amphibians		
Hyla regilla (Baird & Girard)	0	3
Batrachoseps pacificus (Cope)	0	1
Reptiles		
Elgaria multicarinata (Blainville)	1	0
Uta stansburiana Baird and Girard	1	4

Table 25. Structural components (mean ± SD) of herptile search plots in SOIC stands of Zone 1 (bison absent; N = 9) and Zones 2 (bison present, N = 9) of Santa Catalina Island, California.

Parameter	Zone 1	Zone 2
Canopy height (m)	5.9 ± 1.6	6.0 ± 2.2
Canopy cover (%)	56.4 ± 14.5	70.3 ± 8.4
Tree dispersion (m)	4.1 ± 1.4	3.8 ± 1.5
Tree richness	2.4 ± 2.1	1.4 ± 0.5
Number of shrubs	11.0 ± 4.7	9.8 ± 6.0
Soil disturbance (all sources) (cm)	54.1 ± 137.4	194.9 ± 138.0
Litter depth (cm)	2.7 ± 1.2	1.9 ± 0.5
Herb height (cm)	16.8 ± 7.9	10.0 ± 4.5
Number of downed logs	25.3 ± 15.5	24.7 ± 17.0
Number of rocks	35.1 ± 31.8	43.8 ± 46.8

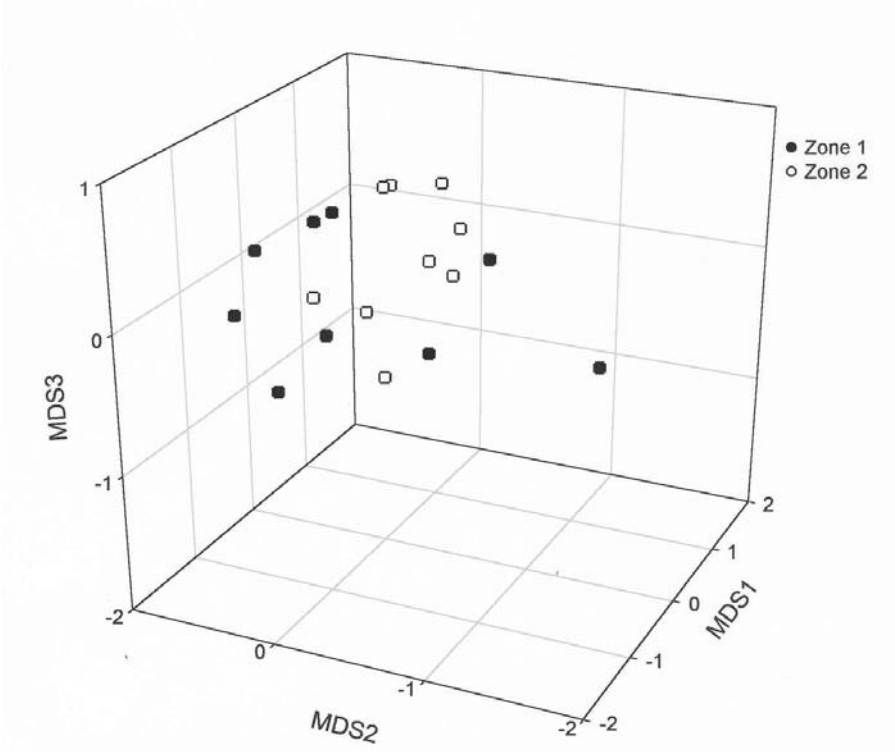

Figure 15. Habitat ordination using nMDS for reptile and amphibian visual encounter plots in Zone 1 (bison absent) and Zone 2 (bison present) on Santa Catalina Island, California.

b) Diversity and relative abundance of small mammals

During two periods of small mammal trapping (late summer/fall 2001 and 2002) we captured 3 total species including 2 of the 3 native small mammals considered present on the island (western harvest mouse, *Reithrodontomys megalotis*; deer mouse, *Peromyscus maniculatus*) and 1 of the 3 species of non-native small mammals known present (black rat, *Rattus rattus*). Overall, relative abundances of small mammals did not differ for plots in Zone 1 compared to plots in Zone 2 in either year of sampling (Figure 16; 2001: $t = -1.2$, df = 10, P = 0.25; 2002: Welch's adjusted $t = 1.7$, df = 8.7, $P = 0.12$). There was a trend for a difference in overall relative abundance between years. Sampling in 2001 suggested higher relative abundances of small mammals in Zone 2 compared to Zone 1, but this pattern was reversed in 2002 when somewhat higher relative abundances were detected in Zone 1 compared to Zone 2. The structure of mammal trapping plots in Zone 2 differed from the structure of mammal trapping plots in Zone 1 ($M = 0.70$, $P = 0.01$). As with the herptile habitat plots, however, isolation between classes and compaction within classes were not strong (Figure 17; Stress = 0.14). The

main factor contributing to observed differences between bison-present and bison-free plots was most likely increased soil disturbance in Zone 2 related to wallows (Table 26).

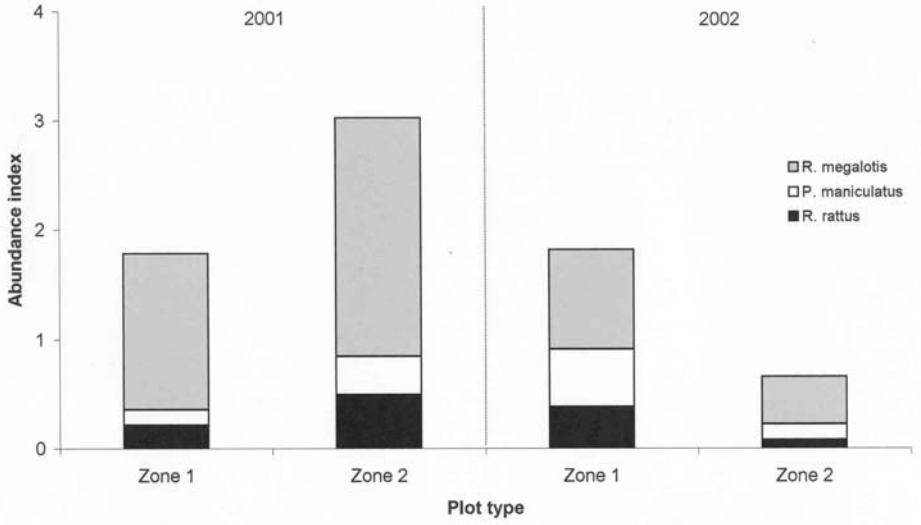

Figure 16. Estimated relative abundances based on captures/trap night for field mice and rats in Zone 1 (bison absent) and Zone 2 (bison present) on Santa Catalina Island, California.

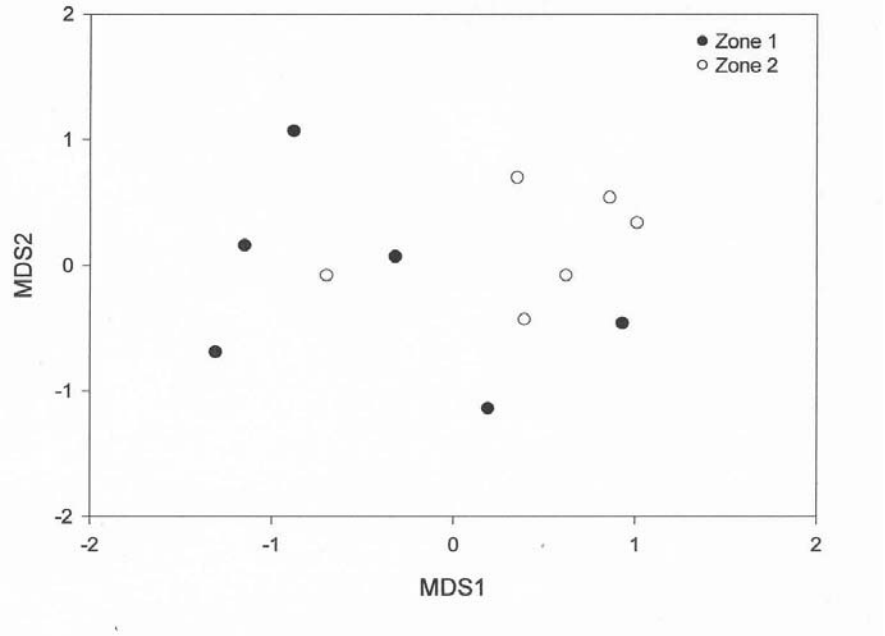

Figure 17. Habitat ordination using nMDS for small mammal trapping grids in Zone 1 (bison absent) and Zone 2 (bison present) on Santa Catalina Island, California.

Table 26. Structural components (mean ± SD) of small mammal trap grids in all habitats (Grassland, Coastal Sage Scrub, SOIC) of Zone 1 (bison absent; N = 6) and Zones 2 (bison present, N = 6) of Santa Catalina Island, California.

Parameter	Zone 1	Zone 2
Canopy cover (%)	21.1 ± 37.6	23.0 ± 35.8
Number of trees	5.2 ± 9.3	12.8 ± 19.8
Number of snags	0.8 ± 1.3	0.8 ± 1.6
Number of shrubs	9.7 ± 10.1	25.1 ± 27.3
Shrub richness	1.2 ± 1.0	1.4 ± 0.7
Number of cactus clumps	2.0 ± 3.1	4.0 ± 4.6
Soil disturbance (all sources) (cm)	45.9 ± 85.6	306.1 ± 218.0
Litter depth (cm)	2.2 ± 1.2	1.6 ± 1.4
Herb height (cm)	21.8 ± 4.3	21.3 ± 7.5
Number of downed logs	10.9 ± 17.8	3.4 ± 5.7

c) Associations with cowbirds and starlings

During bison group observations between January 2001 and August 2002, we recorded associations of starlings and/or cowbirds with 97 of 1,419 groups of bison (6.8 %). Among the bison groups associated with cowbirds or starlings, cowbirds were present in 21 groups, starlings were present in 52 groups, mixed flocks of cowbirds and starlings were present in 5 groups, and cowbirds or starlings that could not be identified to species were present with 19 groups. A logistic regression model revealed that cowbirds and starlings were more likely to occur in relatively large groups of bison that were near water sources associated with areas of human use/activities (Figure 18; Table 27)

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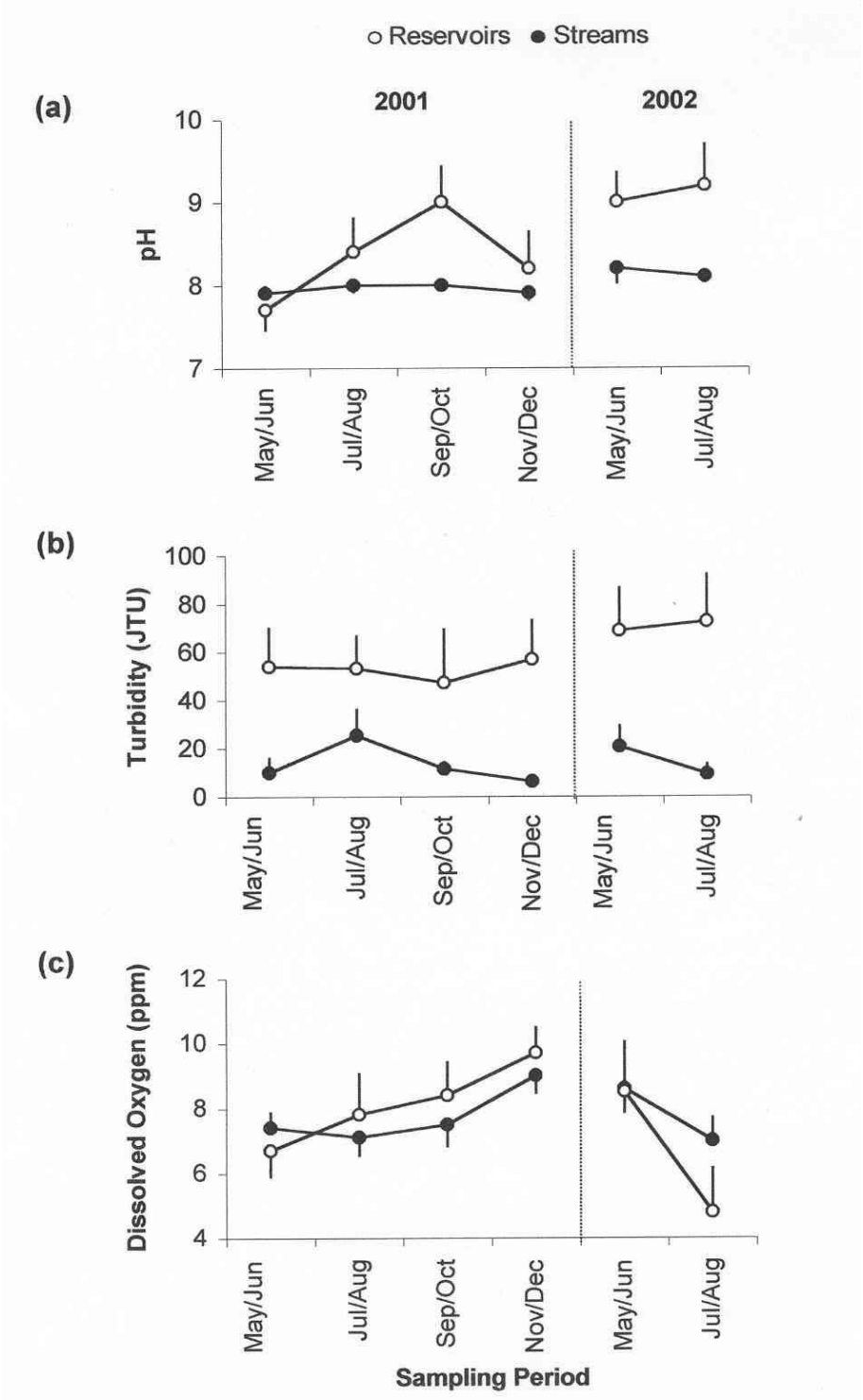


Figure 20. Mean (± SE) estimates of (a) pH, (b) turbidity, and (c) concentration of dissolved oxygen for six different two month sampling periods on Santa Catalina Island, California beginning in May/June 2001 and continuing through July/August 2002.

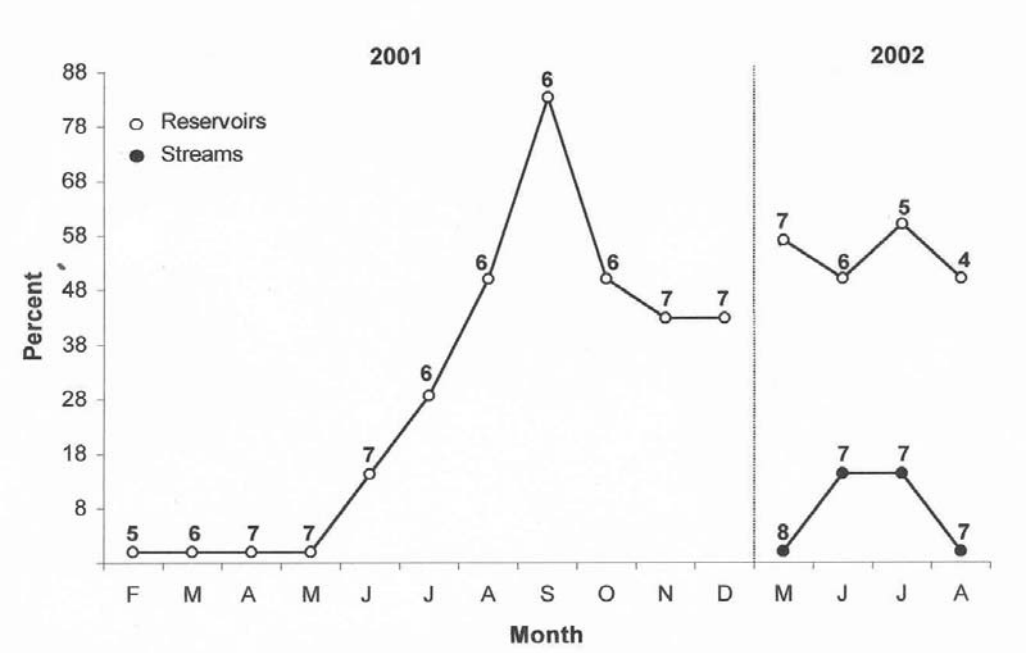


Figure 21. Proportions of reservoirs and streams on Santa Catalina Island, California with measured pH values > 8.5 from February to December 2001 and May to August 2002. Numbers above plot points represent sample sizes. No water samples collected from streams exceeded a pH of 8.5 during the two sampling periods.

Optimum Stocking Rate

Modeling estimates of the carrying capacity for bison on Santa Catalina Island indicated that as of August 2002, the bison population was at or near the ***maximum*** standard livestock carrying capacity estimate for a free-ranging herd over Zones 2, 3, and 4 (Tables 5, 28). However, the standard livestock carrying capacity estimate assumes that all annual grass biomass production except that required to prevent damage to plants is directed towards bison use. Thus, we estimated that only 189 bison could be supported under Management Option A when the same amount of biomass consumed by bison is reserved for use by native vertebrates and invertebrates of the island (moderate carrying capacity; Table 28), whereas only 95 animals could be supported when more plant material is reserved for native organisms than bison (light carrying capacity; Table 28). For Management Option B, the estimates for standard, moderate, and light carrying capacities were 241, 121, and 60 bison, respectively (Table 28). For Management Option C, the estimates for standard, moderate, and light carrying capacities were 33, 17, and 9 bison, respectively (Table 28). Because there are no detailed and quantitative data on forage and habitat needs for the multiple native organisms that directly compete with or otherwise rely on habitat provided by plant materials otherwise consumed by bison, we recommend that the maximum

stocking rates under each management option should be intermediate between the moderate and light carrying capacity estimates (Table 28).

Table 28. Carrying capacity estimates (BY) for bison on Santa Catalina Island, California based on annual grass production within primary and secondary ranges and various inputs to a carrying capacity model (Table 4). For all model iterations the annual dry weight intake of forage was 1,719 kg/year/bison.

Management options[1]	Standard[2]	Moderate[3]	Light[4]	Recommended[5]
A. Herd allowed to free range	378	189	95	142
B. Herd confined to Zone 2	241	121	60	90
C. Herd confined to tour bus route	33	17	9	13

[1] See Figure 2 repeated below.
[2] Based on an allowable use factor (AUF; Table 4) of 0.5 or 50% for annual grasses in the model.
[3] Based on an AUF of 0.25 or 25% for annual grasses in the model
[4] Based on an AUF of 0.125 or 12.5% for annual grasses in the model.
[5] Based on a value intermediate between the moderate and light carrying capacity estimates for each area.

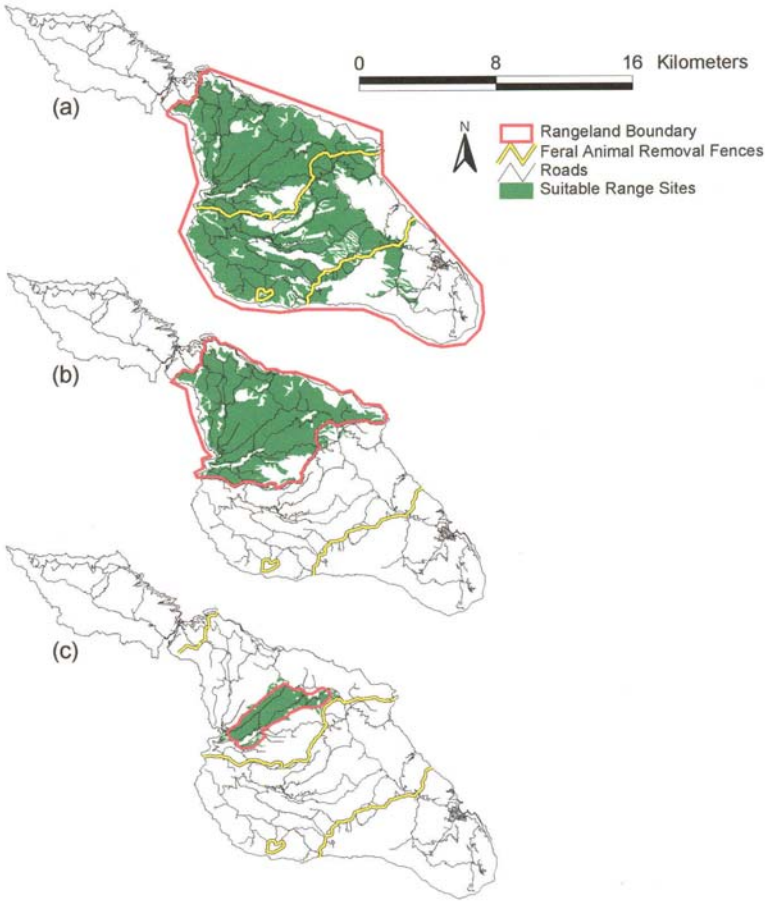


Figure 2. Maps of Santa Catalina Island identifying areas for three potential approaches to future management of bison, including (a) no change from current management (i.e. bison continue to range over Zones 2, 3, and 4); (b) restricting a small number of bison to the area defined as Zone 2; and (c) restricting a small number to a part of Zone 2. Suitable range sites were defined as areas with slope < 25 degrees and moderate to no erosion.

DISCUSSION

Introduced species are an important conservation concern, especially in island ecosystems that have a long history of reduced exposure to large-bodied animals (Coblentz 1990, Lodge 1993). Bison on Santa Catalina Island are especially problematic for resource management because although the island historically had a depauperate mammalian fauna entirely lacking large herbivores, bison have taken on important cultural and economic significance since being introduced in the 1920s. The challenge the Conservancy faces with potential changes in the future management of bison on Santa Catalina Island will be finding a reasonable balance between the short- and long-term ecological consequences of bison for the integrity of the island ecosystem and current economic and cultural considerations (see for example, the history of bison management in Colorado National Monument, Appendix III). This study focused entirely on the potential ecological effects of bison on the island, and we therefore will not delve into economic or cultural considerations or discuss in any great detail how those interests might be addressed by management decisions. In general, our results suggest a combination of negative, positive, and sometimes neutral implications for bison with respect to native and endemic plants and animals on the island. It is important to note, however, that from an ecological perspective, the research was conducted over a relatively short two-year time frame, thereby limiting our ability to extrapolate results to longer-term succession processes. Herein we discuss different aspects of our results on bison ecology, effects on terrestrial plants and vertebrates, effects on water quality, estimates of optimum carrying capacity/stocking density, and the management implications of the findings. Finally, because of the nature of terrestrial plant communities and the relatively slow pace of succession, we will return to the island in spring 2003 for a third season of vegetation sampling in bison exclosure and control habitat plots. An addendum to this report will be provided later in summer 2003 updating results, tables, and management implications as appropriate.

Bison Ecology

a) Population dynamics

Many aspects of the population ecology of bison on Santa Catalina Island are similar to mainland herds within the species' native range (McHugh 1958, Reynolds et al. 1982, Meagher 1986, Berger and Cunningham 1994). Potential differences compared to mainland populations include relatively low calving rates and a strongly skewed adult sex ratio. The skewed adult sex

ratio we noted is likely an artifact of periodic culling to reduce herd sizes; young males are disproportionately targeted for removal (Santa Catalina Island Conservancy unpubl. data; Appendix XI). Sport hunting or culling activities produced a similar skew in adult sex ratios in the Henry Mountains, Utah, and Konza Prairie, Kansas, where bulls and young males were disproportionately removed from populations (Van Vuren and Bray 1986, Towne 1999).
The relatively low calving rate observed among female bison may be due to the island's Mediterranean climate. The phenology of grasses and herbaceous plants on Santa Catalina Island is out of phase with the reproductive cycle of female bison (Mack and Thompson 1982, George et al. 2001). High quality, nutrient-rich forage is available only during late gestation, with grasses and herbaceous forage drying by late May and June during the energetically costly lactation period (George et al. 2001). Bison and other mammals typically experience a doubling or tripling of dietary energy needs during lactation compared to nonreproductive individuals of the same species (Vaughan et al. 2000). It is been hypothesized that nutritional stress results in asynchronous calving patterns (Berger and Cunningham 1994, Wolfe et al. 1999). Although we estimated that upwards of 90% of the calves on the island were born within 3 to 4 weeks from mid-April to early May, newborn calves were observed as late as September. In the last 10 years, newborn bison calves have occasionally been observed in December on the island (J. Eisenhut, pers. comm.).

Our analyses of data on body size, blood chemistry, and hematology support the hypothesis that bison on Santa Catalina Island are experiencing nutritional stress related to asynchrony in plant phenology and costs of reproduction. Bison on Santa Catalina Island are significantly smaller in body mass than mainland bison occupying prairie and mountainous rangelands (Figure 4). Adult male bison are especially small compared to mainland male bison (Figure 4). Among multiple blood chemistry and hematology parameters from October 2000 and 2002, cholesterol and blood urea nitrogen (BUN) values of the bison blood collected suggest that bison on Santa Catalina Island are dehydrated and malnourished compared to cattle (Table 7) and captive bison (Keith et al. 1978, Hawley and Peden 1982). Cholesterol levels were far lower than is typical for cattle in both years (Table 7), indicating insufficient energy intake (Keith et al. 1978, Hawley and Peden 1982). On the other hand, BUN values were higher than is typical for either cattle or captive bison (Table 7; Keith et al. 1978, Hawley and Peden 1982). Elevated levels of BUN are most likely a result of dehydration (i.e. waste nitrogen is not being excreted by the kidneys; C. Scott pers. comm.), but also may indicate insufficient energy intake and subsequent tissue catabolism (Hawley and Peden 1982, Hawley 1987). Also, glucose, red blood cell (RBC), and hematocrit values suggested that bison sampled in October 2002 were in poorer body condition

than bison sampled in October 2000, potentially due to significantly reduced forage availability in 2002 induced by drought (Figure 3). Bison sampled in October 2002 appeared to be either stressed or dehydrated compared to bison sampled in October 2000, as indicated by significant increases in RBC and hematocrit values in 2002 (Dunbar et al. 1999, Dunbar and Giordano 2002). Bison sampled in 2002 also appeared to be energetically stressed; blood-glucose concentration is positively related to energy intake (Keith et al. 1978, Hawley and Peden 1982), and bison sampled in October 2002 had lower blood-glucose values than bison sampled in October 2000. It should be noted that although the bison sampled in both years had higher blood-glucose values than those typical of cattle (Table 7), the values were comparable to those known for captive bison (Keith et al. 1978, Hawley and Peden 1982, Vestweber et al. 1991).

Although bison group size on Santa Catalina Island was smaller throughout the year than in mainland prairie populations (Table 9; Reynolds et al. 1982, Norland et al. 1985), our observed mean group size was consistent with sizes of bison groups occupying wooded or structurally heterogenous habitats in mainland situations (Reynolds et al. 1982, Berger and Cunningham 1994). However, it is possible that grouping behaviors of bison on the island were altered by establishment of feral animal removal fences. Throughout the 1970s, bison on Santa Catalina Island often formed two daily congregations of as many as 191 animals during rutting periods; large groups were often observed at the head of Cape Canyon and northwest of the western corrals (Galland 1989, D. Lott pers. comm.). Although we observed increasing size in mixed age/sex groups during the late spring/early summer, congregations of > 40 bison were very rare.

b) Habitat use

In portions of their native range, bison preferentially select open grassland over breaks, draws, or wooded areas (Norland et al. 1985, Berger and Cunningham 1994, Knapp et al. 1999). Data from group observations and dung transects during this study suggested that bison on Santa Catalina Island behave in a manner similar to their mainland counterparts. Our observations were also consistent with those of Galland (1989), who noted that bison on the island preferred grassland to scrubland, woodland, and barren or cultivated areas. However, the lack of seasonal variation in patterns of habitat use was somewhat surprising. In portions of their native range, bison exhibit seasonal differences in habitat use in response to a shifting mosaic of forage quality and quantity (Berger and Cunningham 1994, Knapp et al. 1999). We expected that bison on the island would preferentially graze on protected south-facing slopes in the spring (i.e., where soil temperatures are greater and grasses emerge earlier; Berger and Cunningham 1994), would shift to riparian areas with moist soil as uplands dried in the summer (Knapp et al. 1999), and might

also move to relatively steeper slopes later in the summer to graze as forage plants were depleted on milder slopes. Although we noted anecdotal differences in areas frequented by bison among seasons, these small-scale shifts in habitat use were not quantitatively significant (Figure 11).

Ultimately, the lack of strong seasonal shifts in patterns of habitat use by bison on the island results in relatively heavy and persistent use of a small number of areas. Specifically, open grassland areas with relatively mild slopes such as below El Rancho Escondido, Parishioner's Flats, lower Sheep Chute Road, the hayfields in Middle Canyon, open grasslands east of the Airport-in-the-Sky, the head of Cape Canyon, and the areas around Haypress and Patrick Reservoirs become focal points for bison activities. The activities of grazing ungulates in general have been shown to increase bare soil, reduce plant cover (Laughlin et al. 1994, Klinger et al. 1994), and reduce soil litter (Fleischner 1994). By the late dry season in any typical year on Santa Catalina Island, the grassland areas mentioned above appear heavily used by bison with high numbers of scattered dung piles, multiple wallow depressions, a relative lack of grasses and herbaceous forage, and denuded vegetation with expanses of nearly bare soil. Negative aesthetic impacts of bison are readily apparent when contrasting heavily used grassland areas in Zone 2 with similar grassland areas in Zone 1, where bison have never occurred in significant numbers.

c) Foraging behaviors and diets

Bison are a generalist herbivore with a well-developed multi-chambered stomach that allows them to consume and efficiently digest relatively coarse plant materials including cured grasses and parts of woody plants (Demarais and Krausman 2000). On Santa Catalina Island annual and perennial grasses and forbs are widespread and abundant and both bite count data and monthly diets estimated from microhistological analyses of feces indicated that they were the primary types of plants consumed by bison year round (Figure 10, Table 11). Except for in January 2002, 90% of the forage consumed by bison on Santa Catalina Island was grasses and forbs (Table 11). Forbs are typically very small components of bison diets regardless of location and even when they make up large proportion of available forage (Van Vuren 1984, Larter and Gates 1991, Shaw and Meagher 2000). Compared to some mainland herds of bison, bison on Santa Catalina Island consumed relatively high proportions of forbs (Table 11); averaged over all months forbs comprised 6.2% ± SE 0.9 of the diets of bison during the study. However, several other studies have reported proportions of forbs in the diets of bison similar to our values for Santa Catalina Island (Peden 1974, Wasser 1977, Norland 1985). Elsewhere in mainland North America bison were reported to consume primarily grasses and sedges (Van Vuren 1984, Waggoner and Hinkes 1989, Coppedge et al 1998, Demarais and Krausman 2000). Sedges/rushes are not widespread on

Santa Catalina Island, however, related to the limited distribution of riparian areas/habitats. At the outset of the study we had predicted that bison on Santa Catalina Island would alter their diets seasonally to consume relatively more woody shrubs and riparian vegetation (e.g., sedges/rushes) during the extended dry summer and fall period related to the Mediterranean climate of the region. Diet information supported this hypothesis for both sedges/rushes and woody shrubs. Bison in other mainland areas were reported to alter their diets to include more woody shrubs when other browse was unavailable (Waggoner and Hinkes 1989 for bison in Alaska) or of relatively poor quality (Peden 1974 for bison in Colorado). Similarly, in Oklahoma, bison in general but especially lactating adult females selected strongly for sedges in several seasons because of limited availability of high quality grasses (Coppedge et al. 1998). Another important component of the diets of bison on Santa Catalina Island during dry seasons was prickly pear cactus (*Opuntia littoralis*; Table 11), which may have been consumed for water. For example, Wasser (1977) noted that *Opuntia* was one of the ten most common diet components for bison at Colorado National Monument in Colorado, which he suggested they consumed for water.

We detected a trend for a relatively larger scale seasonal shift in the diets of bison on Santa Catalina Island when they diversified their diets to consume more shrubs/cactus and sedges/rushes during dry periods (Jun-Aug 2001 thru Dec–Feb 2002 and Jun-Aug 2002) as the nutritional quality of dried grasses deteriorated (Figure 11). Similar but more pronounced seasonal shifts in bison diets have been reported elsewhere where bison attempted to select for relatively low lignin and relatively high protein plants (Wasser 1977, Waggoner and Hinkes 1989, Larter and Gates 1991, Coppedge et al. 1998).

From a conservation perspective the most important issue related to foraging behavior and diets of bison is whether they are consuming significant proportions of Channel Island/Santa Catalina Island endemic plants. In three out of 16 months *Quercus pacifica* was detected in the diets of bison but in relatively small proportions (Table 11). Bison also consumed forbs in the genus *Lotus* and *Galium* during several months. These two genera are significant because they include several Channel Island/Santa Catalina Island endemics (Table 11). As part of microhistological analyses, however, the Washington State University lab we used was unable to discriminate to the species level for these genera and we were therefore unable to assess whether *Lotus argophyllus* var. *argenteus*, *Galium catalinense* ssp. *catalinense*, or *G. nutallie* ssp. *insulare* were consumed by bison on the island. We do know that native plants comprised 17.4 to 34.8% of the diets of bison over the months that diets were assessed. The corollary to this finding is that bison on Santa Catalina Island are consuming a relatively high proportion of non-native grasses, which may actually be beneficial in the short term. By consuming non-native grasses

bison are simultaneously removing some of the seeds produced by these plants before they are mature and removing significant non-native plant biomass, which may be important in limiting the spread and intensity of wildfire.

Effects on Native Plant Communities

a) Diversity and structure of herbaceous plant communities

Foraging, wallowing, and other activities of bison are known to strongly influence plant community composition and structure based on experimental studies in prairie ecosystems (Hartnett et al. 1996, Adler et al. 2001, Hart 2001). Our bison exclusion experiments in three different habitat types (grasslands, SOIC, riparian) on Santa Catalina Island were designed to assess the potential negative consequences of bison on plant communities that had previously experienced limited or no long-term exposure to intensive herbivory over evolutionary time scales. In general, plant community composition may show an immediate response to disturbances such as grazing, but may be very slow to indicate release from such pressure (Milchunas and Lauenroth 1993). We anticipated that this would be especially true for Santa Catalina Island because of the relatively recent history of high densities of non-native ungulates (feral goats, feral pigs, cattle, and bison). We also acknowledge that changes in plant community composition, while related to recent grazing history, may be importantly influenced by the combined and cumulative effects of past land use practices (Milchunas and Lauenroth 1993, Stromberg and Griffin 1996). For Santa Catalina Island, vestigial effects of feral ungulates including relatively intensive livestock grazing from the early 1900s to the 1950s may dampen the current ability of plant communities to respond quickly to reduced bison exposure. These considerations are important for interpreting results of our experimental assessment of the effects of bison on different plant communities on Santa Catalina Island.

Although there were relatively limited changes in plant community richness, diversity or heterogeneity for all habitats overall, we detected higher non-native cover (primarily from grasses) in bison-excluded plots than in plots grazed and trampled by bison. On mainland California and the Channel Islands, the removal of feral ungulates has been shown to result in the increased frequencies of a variety of non-native plant species (Talbot et al. 1939, Klinger et al. 1994, Laughrin et al. 1994). In Mediterranean-type systems, it appears that plants capable of the rapid formation of dense, tall stands (e.g., annual grasses) are likely to dominate areas protected by exclosures for several years (Noy-Meir et al. 1989). Dominance is perpetuated when a large amount of dead material is left as mulch in the dry season (Noy-Meir et al. 1989), which can have

important consequences for native plant communities. Non-native grasses compete for light, water, and nutrients, and can reduce recruitment and/or survival in native tree, shrub, and perennial grass seedlings (Gordon et al. 1989, D'Antonio and Vitousek 1992, Hamilton et al. 1999). In turn, grass invasions can alter abiotic disturbance regimes (e.g., fire) and the diversity and persistence of animal populations (D'Antonio and Vitousek 1992). In their native range, long-term grazing by bison results in the reduced cover and productivity of grasses and a concomitant increase in forbs (Knapp et al. 1999). Although it is possible that grazing by bison may currently play an important role in the control of annual grasses on Santa Catalina Island, their presence might result in sort of feedback loop. Evidence from California grasslands suggests that the input of nutrients (particularly in the form of nitrogen and phosphorus) significantly enhances the growth of non-native grasses to the detriment of native forbs (Hobbs and Huenneke 1992). The combined effect of a release from grazing and the slow leaching of nutrients from dung remaining on the plots could have contributed to the dominance of non-native grasses in our fenced plots.

Notably, our bison exclusion experiments suggest that grasslands have the potential to respond/recover more quickly after reduction or removal of foraging and wallowing by bison than SOIC plant communities (Tables 13, 14). Similarly, riparian habitat patches protected from bison for two years responded or changed in multiple mostly positive ways based on current knowledge of plant community structure and function (Tables 15, 16). Increases in species richness, species diversity and plant cover attributes in grassland habitats indicate that the current heavily used grassland areas with moderate to mild slopes may recover rather quickly if bison densities/activities are reduced, although this recovery may consist mostly of non-native annual grasses. For example, dramatic changes in vegetative cover and species diversity were noted within three years of a major reduction of the goat and feral pig populations (Laughrin et al. 1994), and in the San Joaquin valley shifts in plant species composition were apparent after two years in cattle-exclusion experiments (Talbot et al. 1939).

During our study, the second year of bison-exclusion experiments coincided with unusually dry weather conditions (Figure 2), which resulted in reduced plant productivity independent of bison activities and likely obscured potential bison-related changes observable in a more normal weather year. Because widely varying environmental conditions from 2001 to 2002 may result in differences in plant communities comparable to, or greater than, differences attributable to bison activities (see for example Noy-Meir et al. 1989, Milchunas and Lauenroth 1993), we will return to the island in 2003 for a third year of plant community sampling in bison exclosure and control plots. Evaluating community-level parameters in bison exclosure and control habitat plots after

three years of bison removal will allow us to refine our conclusions regarding the effects of bison on native plant communities.

b) Structure of scrub oak-dominated island chaparral

Within their native range bison can inflict a range of injuries to trees and woody shrubs by rubbing and horning behaviors (McHugh 1958, Campbell et al. 1994, Coppedge and Shaw 1997, Bowyer et al. 1998). Overall structural differences between patches of oak-dominated chaparral in areas with and without bison were primarily related to fewer snags and reduced diversity of trees. Rubbing behavior was likely responsible for our observation of fewer snags in SOIC stands with bison because small, dead trees can be easily pushed over by bison (Coppedge and Shaw 1997). Reduced tree diversity in areas with bison may be related to bison preferentially rubbing on/against smooth-barked trees (toyon, *Heteromeles arbutifolia*, lemonade berry, *Rhus integrifolia*) and reducing their survival (Coppedge and Shaw 1997). From an ecological perspective, high levels of biological and structural diversity in woodlands provides for increased habitat availability, thereby supporting higher a diversity of birds (e.g., snags provide nest sites for cavity nesters; Thomas 1979) and other vertebrates (e.g., bats use cavities in snags as roosts; Brigham et al. 1997, Betts 1998).

c) Dispersal of non-native plant species

It is widely hypothesized that many plant species native to the Mediterranean were inadvertently introduced to the Americas as fruits attached to the pelage of livestock (Sorenson 1986, D'Antonio and Vitousek 1992, Stromberg and Griffin 1996, Malo and Suárez 1997). Laboratory analyses, greenhouse germination trials, and field trials all indicated that seeds lodged in the hair of bison were viable under conditions typical on Santa Catalina Island, and would produce seedlings of primarily non-native plants (Tables 20, 21, 22, Figure 13). Our results in this area are significant in indicating that plant seeds that either become dislodged from bison hair or that are shed as part of a hair clump at a wallow can and will germinate on the island (Tables 21, 22. Thus, the presence of bison on Santa Catalina Island provides an additional mechanism for the dispersal and spread of non-native plants, which the Conservancy is actively attempting to control as part of island-wide restoration activities. Importantly, our detection of a significant positive relationship between the mass of wallow hair clumps and seed number (Figure 13b) indicates that the spread of non-native plants by bison is directly related to the number of bison on the island. Larger absolute numbers of bison will shed an absolute larger mass of hair

annually during the spring and early summer period, and therefore facilitate the spread of higher numbers of non-native plant seeds.

Notwithstanding the strong indication that bison can disperse seeds of non-native plants in their hair, it could be argued that bison hair does not add a significant number of seeds to the wallows when compared to the existing seed bank (i.e., a reserve of viable seeds present in the soil and on its surface; Russi et al. 1992). However, we cannot rule out the possibility that a large proportion of seeds in wallow soil are present because of the activities of bison. For example, the rough surfaces of wallows create sites where seedlings can become established (Hobbs and Huenneke 1992) and wallowing activity can bury seeds resting on the soil surface, ultimately resulting in higher overall germination rates (Stromberg and Griffin 1996). Importantly, seeds of non-native grasses in California are larger and produce longer radicles than those of native perennial grasses; thus, when they are buried they are more likely to germinate and then tolerate subsequent xeric conditions created by disturbance (Stromberg and Griffin 1996). Also, there is a strong tendency for established wallows to be visited/used by bison over multiple years (McHugh 1958, Polley and Wallace 1986), and active wallows tend to have higher proportions of weedy plants than inactive wallows or nearby undisturbed prairie (Polley and Collins 1984). Therefore, we conclude that the combined effects of physical disturbance and direct seed input via hair represents a significant mechanism for the maintenance and continuing spread of non-native plants on Santa Catalina Island.

Cattle dung has been implicated in the spread of exotic plants in tropical and temperate systems (Welch 1985, Malo and Suárez 1995, Radford et al. 2001). We detected limited evidence that seeds present in bison dung will germinate. Dried dung piles are highly hydrophobic until they begin to break down, however, and if mechanisms for dormancy are not in place, seeds in the interior of a dung pile are more likely to decay than germinate (Malo and Suárez 1995). Despite the fact that we collected fresh dung and broke up the samples to maximize seed exposure to moisture, we observed low rates of germination of primarily grasses (33%). Seed longevity of annual grasses is typically low (Russi et al. 1992, Bekker et al. 2000) and because bison dung piles on Santa Catalina Island may remain intact for more than two years it is unlikely that high numbers of non-native grass seeds in bison dung remain viable for extended periods.

Effects on Terrestrial Vertebrates

Large mammals can have profound and direct influences on vegetation and habitats used by smaller vertebrates by their foraging and other activities (Kuiters and Slim 2002, Johnson et al.

1999, Lusk et al. 1993, Singer et al. 1984). Changes in plant vegetative cover related to bison grazing, wallowing, and trampling (Knapp et al. 1999, Matlack et al. 2001, Meadows 2001), such as commonly observed around margins of lakes and streams or in heavily used grassland and SOIC habitats on Santa Catalina Island, may reduce forage availability and microhabitat characteristics important for small-bodied terrestrial vertebrates (small mammals, amphibians and reptiles). Despite some variation in structural components between habitats with or without bison, however, our results suggested limited effects of bison on small mammal populations (Figure 16). This finding was in contrast to other studies that found shifts in small mammal biomass/abundance and diversity linked to grazing by livestock (Reynolds and Trost 1980, Grant et al.1982, Hayward et al.1997). Research elsewhere has shown that the availability of cover has a very strong effect on small mammal abundances (Singer et al. 1984, Hayward et al. 1997), and that species characteristic of habitats with substantial ground cover are more abundant in ungrazed areas than grazed areas (Hayward et al. 1997, Woinarski and Ash 2002). Related to this point, our assessment of habitat attributes at small mammal trap grids suggested little variation in cover attributes (e.g. cactus clumps, shrubs, vegetation height, or logs) between grids in bison present areas (Zone 1) and grids in bison absent areas (Zone 2), potentially explaining the apparent lack of response by small mammal populations to the presence of bison. Among the relatively few species of small mammals present on Santa Catalina Island, Norway rats (*Rattus rattus)* are a non-native organism of significant conservation concern because of their known negative effects on a variety of vertebrates, invertebrates and plants (Palmer and Pons 1996, Hernandez et al. 1999, VanderWerf 2001, Campbell and Atkinson 2002). Importantly, our results suggested that any potential changes in habitat structure mediated by bison (i.e., amount of soil disturbance) were unlikely to positively affect *R. rattus* populations. Cyclic fluctuations in rodent populations are well known (e.g., Drost and Fellers 1991, Lambin et al. 2000), and although we detected potential interannual differences in abundance of small mammals, it was unlikely that any cyclic variation in rodent numbers was attributable to bison; interannual variation in rainfall, and food availability were several likely causative factors (Drost and Fellers 1991). Finally, responses of small mammals to grazing-induced changes in habitat structure vary by habitat (Fleischner 1994). Due to logistical constraints, however, we did not have sufficient replication within habitat types to examine each plant community separately. Notwithstanding this potential limitation of our study design, we detected no apparent bison-related differences in abundance of small mammals in any of the three habitats sampled on Santa Catalina Island.

We attempted to assess potential differences in abundances of amphibians and reptiles using data from time-constrained searches in SOIC habitats in Zone 1 (bison absent) and Zone 2 (bison

present). Capture success for herptiles was very low however, and only four species were detected in low numbers (Table 24). Our extremely low capture rates for herptiles precluded statistical comparisons and inferences regarding potential bison-related effects on these types of terrestrial vertebrates. However, a few predictions or suggestions for future research in this area can be made. First, although few data are available on the effects of activities of large mammals on amphibians, for aquatic-breeding amphibians proximity to water is more critical to diversity and abundance estimates than are the effects of grazing (Woinarski and Ash 2002). We would therefore expect that *Hyla regilla*, a pond- and stream-breeder (Stebbins and Cohen 1995), would be relatively unaffected by changes in habitat features in uplands. Second, the response of lizards to grazing is strongly related to their life history strategy and physiology. For example, widely ranging species that prefer open habitats, or highly heat-tolerant lizards, may prefer grazed sites over those that have not been grazed (Jones 1981, Read 2002). *Uta stansburiana* and *Elgaria multicarinata* are considered open-habitat species (Stebbins 1985) and it is possible that their numbers would tend to increase in areas occupied by bison.

Cowbirds and starlings, non-native bird species with important potential negative effects on native birds, may benefit by the presence of bison on Santa Catalina Island. Starlings and cowbirds are omnivores, with invertebrates and seeds of various grasses constituting the major components of their diets (Cabe 1993, Lowther 1993, Olsson et al. 2002). Large ungulates like bison may aid these species by exposing insects through trampling (Mayfield 1965). Our study design included recording the presence or absence of these two species *with* groups of bison being observed as part of other aspects of our research. Thus, we can comment on the distribution of cowbirds and starlings on the island only in relation to their association with bison groups; we are unable to provide information on the numbers of each species of bird on the island when they may occur independent of bison groups. Analyses of data on the distributions of cowbirds and starlings in relation to bison suggested that they were most positively associated with relatively large groups of bison, especially when those groups occupied areas near water and human-disturbed areas. Access to water in arid areas is known to be important to starlings for drinking and bathing (Cabe 1993), and cowbirds and starlings may associate with bison near areas with human activities because mowing (e.g., at Middle Ranch and El Rancho Escondido) and accumulating refuse in trash receptacles may provide important forage opportunities (Cabe 1993, Olsson et al. 2002). Large groups of bison may expose or disturb more invertebrates or provide more direct feeding opportunities than smaller groups. For example, it is possible that starlings are deriving nutrition directly from bison; we observed starlings feeding on blood and tissue from open sores on the backs and sides of two bison cows. Although blood or tissue

feeding is not reported for this species, oxpeckers (*Buphagus* spp.), a closely related bird in the same family as starlings, feed almost exclusively on blood from open sores or engorged ticks found on the backs and sides of large African mammals (Campbell and Lack 1985, Weeks 2000). In summary, cowbirds and starlings were sometimes associated with bison on Santa Catalina Island, but the relatively low percentage of bison groups associated with these birds, and the paucity of observations of cowbirds and starlings with smaller groups of bison more widely dispersed away from permanent water sources and high levels of human activities, suggests that the presence of bison may not be the primary factor influencing the distribution of these two bird species on Santa Catalina Island.

Effects on Water Quality

Urine and fecal deposition by bison directly into water or onto adjacent soils, and the foraging and trampling activities of bison around the relatively few sources of permanent water on Santa Catalina Island, may contribute to decreased water quality. Our relatively intensive water sampling regime directed at assessing this possibility suggested limited evidence that bison are having a quantifiable impact on the water quality of streams and reservoirs on Santa Catalina Island (Figure 20). The bulk of research assessing potential effects of ungulates on water quality in North America has involved domestic livestock, notably cattle (Kauffman and Krueger 1984, Belsky et al. 1999). Bison and cattle are often considered to be ecologically similar (Van Vuren 2001), suggesting that high densities of bison could have negative consequences for water quality. However, in the Henry Mountains, Utah, bison were less reliant on water sources than cattle (Van Vuren 2001), and on Santa Catalina Island, bison drink only 1 or 2 times per day, even during summer months (Lott 2002). Despite high levels of nitrogen-rich waste material (i.e., dung) on the landscape, ammonia and nitrate levels in most of the water bodies we sampled were not detectable. This result was in agreement with Dodds et al. (1996), who noted that ammonia and nitrate levels in water did not increase after the reintroduction of bison to watersheds in the Konza Prairie, Kansas. Nevertheless, our findings may be due to extended periods of low precipitation on the island (Caruso 2001, Scrimgeour and Kendall 2002). The mobile components of nitrogen (ammonia and nitrate) are carried by soil water, and downward or lateral nitrogen movement between rains is slow or nonexistent (Novotny and Olem 1994). Furthermore, ammonia and nitrate are readily taken up by microorganisms, soils, and vegetation when the environment is not already nitrogen-saturated (Tate 1990, Novotny and Olem 1994, Dodds et al. 1996, Kemp and Dodds 2002). Low yearly precipitation could have masked

differences in dissolved oxygen and turbidity that were actually related to bison. Decomposition of bison urine and dung in reservoirs and streams would result in reduced concentrations of dissolved oxygen, but during periods of low summer water levels, dissolved oxygen typically decreases because of increasing water temperatures (Cooke et al. 1996, Caruso 2001). Bison activity around the margins of streams and reservoirs may cause increased turbidity, but turbidity generally increases in streams during storm events and then decreases as flow declines throughout the dry months (Caruso 2001). Also, in small ponds with fine underlying sediments turbidity can fluctuate by evaporative water loss or via mixing of sediments in the water column induced by wind (Cooke et al. 1996). It is also possible that our failure to detect negative effects of bison on water quality was due to a combination of small sample sizes (Belsky et al. 1999, Scrimgeour and Kendall 2002) and relatively low variation in bison activity among watersheds. For example, we did not experimentally test for effects of bison on water quality by sampling at "control" sites with a history of a complete lack of bison activity.

Multiple small reservoirs on Santa Catalina Island provide important sources of water for island wildlife including bison. Measured pH values of water samples collected from reservoirs suggested pronounced increases in pH during the relatively dry summer and fall periods (Figure 21). This is important because relatively high pH levels (> 8.5) can cause reduced fertility and increased susceptibility to disease in cattle (Grant 1996). As previously noted, bison on Santa Catalina Island experience relatively low reproductive rates compared to mainland bison, and it is possible that the low pregnancy rates observed among adult female bison in fall 2002 was related to high reservoir pH values after July 2001 (Figure 21). Whether or not high reservoir pH values during dry periods directly influences bison reproduction on Santa Catalina Island, bison and other wildlife on the island are likely drinking water from reservoirs with high pH when streams dry and water volume in ponds decrease in drought years. The implications of this finding are unknown.

Optimum Stocking Density

After 1969 when a yearly cull was initiated in response to indications of overgrazing by livestock and non-native ungulates (O'Malley 1994), bison numbers on Santa Catalina Island have generally been maintained below 300 animals. Currently bison have relatively unrestricted access to most of Santa Catalina Island east of the isthmus at Two Harbors (Figure 2a), an area encompassing 19 different areas considered ecologically sensitive for Los Angeles County, California (F. Starkey, 2002 Ecological Restoration Department Map of Santa Catalina Island). If

bison are having significant negative effects on plants and animals on Santa Catalina Island or otherwise disrupting efforts at restoring the integrity of the island ecosystem, the Santa Catalina Island Conservancy will need to consider alternative approaches to future management. One of three future management options we evaluated as part of our carrying capacity or optimal stocking density model, was for no significant change from the present approach with bison having continued access to most of the island for foraging and all other activities (Management Option A Table 28, Figure 2a).

Our carrying capacity model suggested that the area of Santa Catalina Island excluding Zone 1 (Figure 2a) can maximally support around 378 animals, *but only when essentially all aboveground plant biomass within primary and secondary ranges for bison is reserved for use by bison*. The island harbors multiple native organisms that also rely on plant materials otherwise consumed by bison. We explicitly modeled for the forage needs of native organisms by altering our carrying capacity parameters to reserve some plant material for their use. Based on these model iterations, we estimated that under the status quo Management Option A, only 95 to 189 bison should reside on the island (Table 28).

Our estimate of carrying capacity for Management Option B (bison restricted to Zone 2, Figure 2b) was 241 animals when all aboveground plant biomass within primary and secondary ranges for bison is reserved for use by bison (Table 28). Importantly, however, we estimated that only 60 to 121 bison could be supported within Zone 2 when significant amounts of plant biomass production were reserved for use by native organisms in the area (Table 28). Important benefits of adopting this management option include protecting all but five of the island's 19 ecologically sensitive areas from bison activities and maintaining bison viewing opportunities in high human-use areas around the Airport-In-The-Sky, El Rancho Escondido, and part of the Inland Motor Tour route (Figure 2b). The major disadvantage of this management approach is that bison would continue to have unrestricted access to four ecologically sensitive riparian areas/corridors around Little and Shark Harbors, Lower Cottonwood Canyon, the drainage leading to Cottonwood Beach, and the small reservoirs immediately northwest of the Airport-In-The-Sky (2002 Ecological Restoration Department Map of Santa Catalina Island). Bison would also continue to have access to the ecologically sensitive high elevation habitats around Mt. Banning and Mt. Orizaba. Should the Conservancy consider adopting Management Option B for bison on the island, we recommend that approximately 90 bison be managed for in Zone 2 (Table 28). Maintaining an estimated 90 bison within this area would assure that sufficient forage would remain available for use as forage and habitat by island native vertebrates and invertebrates.

The final carrying capacity-based management option we considered (Option C) was restricting bison to a small 831 ha area within Zone 2 encompassing the Airport-In-The-Sky, El Rancho Escondido and part of the Inland Motor Tour route (Figure 2c). Our estimated maximum or standard carrying capacity for this area was 33 animals when essentially all aboveground plant biomass was reserved for use by bison, whereas the area would support between 9 and 17 bison when some plant biomass is reserved for use by native organisms (Table 28). Although a maximum of 33 bison in this area seems low compared to the current approximate 370 animals on the island (Table 5), bison would continue to be visible in and around high use areas for tourists. Further, restricting animals to this smaller island area would protect the five different ecologically sensitive areas encompassed by Zone 2 previously mentioned, as well as the other 14 ecologically sensitive areas outside of Zone 2. Importantly, however, Management Option C would require additional fencing, as well as the need to provide bison with one or several sources of water.

One final point related to our estimates of carrying capacity that is relevant to all three Management Options, biomass production values in the carrying capacity model are based on the current distribution and extent of grasslands within the primary and secondary ranges of bison on the island. Historically, however, relatively large areas of coastal sage scrub habitats were cleared and converted to grasslands when livestock were being produced on the island (Schuyler et al. 2002, P.Schuyler pers. comm.). As restoration of plant communities on Santa Catalina Island proceeds, it is likely that the areal extent of grassland habitat on the island will gradually diminish, especially if aided by active restoration-directed management. This is important because gradually reduced areas of grasslands will result in reduced grass and forb production, thereby reducing the carrying capacity for bison for different regions of the island (Table 28).

As part of the **MANAGEMENT IMPLICATIONS** we provide additional general recommendations related to the three carrying capacity-based management options for bison on Santa Catalina Island considered here. Also, one management option that we did not consider from a carrying capacity perspective was the complete removal of bison from Santa Catalina Island. A discussion of this management option is also presented as part of the **MANAGEMENT IMPLICATIONS** of this report.

MANAGEMENT IMPLICATIONS

In this study we assessed multiple potential ecological effects that bison may be having on Santa Catalina Island. Herein we summarize the major findings of this study as they relate to island-based ecological restoration activities and the major objective of this study to develop

recommendations and predicted outcomes of managing the bison on Santa Catalina Island at different levels. As a brief preamble to this section, it is important to note that failure to detect an important ecological effect after a relatively short time frame (2 for this study) does not mean an effect does not exist, especially for experimental research. Plant and animal communities are labile, and in ecological studies many years are often required to unequivocally identify important changes resulting from reduced exposure to a disturbance agent (bison in the case of this study) that might otherwise be masked by normal climatic or environmental variation. Also, this study was designed to address some of the ecological relationships that the Santa Catalina Island Conservancy will need to consider when managing bison on the island. We are aware that there are important social, cultural and economic considerations that will also need to be weighed as the Conservancy considers future management directions for bison on Santa Catalina Island, but these considerations were not part of our ecological research on the island bison.

Bison are non-native to Santa Catalina Island and Mediterranean climates in general, which is resulting in animals suffering relatively poor health and body condition (Figure 4, Table 7). Related to nutritional stresses induced by the dry summer to fall period, we determined that bison on Santa Catalina Island are smaller and their reproductive rates are relatively low (especially during drought periods; Tables 5, 6) compared to bison within their native range. Further, bison on Santa Catalina Island are frequently observed with open sores on their backs and sides, which are not nearly as common to the species within their mainland range (R. Sweitzer, D. Van Vuren, pers. obs.). Together these results/observations indicate that bison on the island are generally in poor health, especially during the relatively frequent drought cycles on the island (Figure 3). From a humanitarian perspective, the generally poor body condition of bison on Santa Catalina Island should be considered as the Conservancy discusses management options. For example, bison restricted to a small national monument in Colorado were determined to be in poor nutritional condition based on small body sizes and low reproductive rates relative to bison in other parts of North America (Wasser 1977, Bernard 1983). As reviewed in Appendix XI as a case history of recent controversy over bison management similar to controversies on Santa Catalina Island, part of the justification for the eventual management decision to remove the bison herd from Colorado National Monument was that the animals were suffering from overall poor health related to poor habitat conditions in the area (Wasser 1977, Bernard 1983).

Bison on Santa Catalina Island are primarily consuming a mix of native and non-native annual and perennial grasses and forbs (Table 12a,b). As previously noted, reduction or removal of bison from the island would reduce grazing pressure on non-native annuals, but would also remove grazing pressure on several important native bunchgrasses (*Nassella pulchra*, *N. cernua*

and *N. lepida*). Within the native range of bison in mainland North America bunchgrasses are commonly a major part of their diets (Shaw and Meagher 2000). However, Mack and Thompson (1982) suggested that western bunchgrasses like those found in California (including *Nassella* spp.) are much more vulnerable to overgrazing than Great Plains bunchgrasses. Anecdotal observations suggest that grasses on Santa Catalina Island do not recover well from bison grazing, potentially because the dry summer climate limits plant regrowth. Although not yet demonstrated for native grasses on islands, Channel Island endemic woody shrubs were documented as lacking adequate chemical or mechanical defenses against large, grazing herbivores (Bowen and Van Vuren 1997), and it is possible that native species of grasses and forbs on Santa Catalina Island are unusually vulnerable to bison grazing.

Although bison exhibited a diet shift to include more woody plants/shrubs during the dry season on Santa Catalina Island, the only Channel Island endemic they consumed in detectable quantities was *Quercus pacifica*, the island scrub oak. Although bison consumed island scrub oak in relatively low quantities, this tree is the focus of conservation concern on the island because of a recent disease-related die-off on some parts of the island (Knapp 2002a). Further, natural regeneration of island scrub oak on Santa Catalina Island has been seriously reduced by recently high densities of feral pigs (rooting kills tree seedlings) and browsing by feral goats and mule deer (Knapp 2002a). Both feral goats and feral pigs have been nearly eradicated from the island, but mule deer and bison are still present in ecologically significant numbers. Although reduced densities of bison on Santa Catalina Island would reduce consumption of island scrub oak by the species, we have no indication that current levels of browsing on this endemic tree by bison is causing significant damage or mortality. Mule deer are likely the most important non-native ungulate on Santa Catalina Island threatening the long-term viability of SOIC woodlands.

Results from bison exclosure experiments indicate that bison are importantly altering multiple aspects of island plant communities in grasslands and riparian areas, but less so in SOIC habitats (Tables 13, 14, 16). Although we failed to detect a significant effect of bison on SOIC habitats as part of bison exclosure experiments, we did identify structural differences between SOIC habitats in Zone 2 (bison present-pigs absent) and Zone 1 (bison absent-pigs absent). Thus, for all three habitats that we focused on, bison were altering island plant communities. Maintenance of plant community structure and function is of obvious and profound importance to the ecological integrity of any ecosystem. The ecological integrity of plant communities on islands is especially important, however, because islands typically include proportionally more unique species than mainland areas (Reid and Miller 1989, Simberloff 1994). The Channel Islands of California are estimated to support 26 endemic species and 6 species have so far been

identified as occurring only on Santa Catalina Island (Minnich 1980, Davis et al. 1994). Thus, any change to plant communities on Santa Catalina Island identified as being caused by a non-native species like bison should be of important management concern (Van Vuren 1992). Nevertheless, and as was noted previously, Santa Catalina Island has a recent history of disturbance by many non-native ungulates (livestock, feral goats, feral pigs, bison) such that island plant communities were already significantly disturbed before the first arrival of bison in the 1920s. Related to this, one immediate response of plant communities to reduction or removal of bison on the island will be the proliferation of non-native annual grasses currently being grazed. To reiterate from above, the buildup of dry plant biomass over just a few years by reduced grazing pressure would require consideration of a fire management program, potentially including periodic controlled burning to reduce fuel loads in the event of wildfire. As a final note related to bison effects on island plant communities documented from exclosure experiments and from information on the diets of bison (Table 12a,b), previous research on grazing and herbivory indicates that ecosystems severely damaged by grazing (the highly eroded "Valley of the Moon" area on Santa Catalina Island is a good example) usually require a greater reduction in grazing pressure, or no grazing at all to allow for recovery compared to areas lacking a history of overuse (Van Vuren 1992). Importantly, once an ecosystem is seriously damaged by herbivores, even low densities of remaining herbivores may prevent recovery (Van Vuren 1992).

Results from our study indicate that bison are serving as important agents of dispersal of non-native grasses and forbs on the island. Weed removal and the control of non-native plants and shrubs has been an important component of resource management by the Conservancy's Department of Ecological Restoration over multiple years. Although we found no evidence that bison are facilitating the spread of non-native woody shrubs such as Mediterranean broom (*Genista linifolia*) and tree tobacco (*Nicotiana glauca*), bison are actively dispersing seeds of many non-native weedy grasses and forbs across large areas of the island via their wallowing activities. It was important that we detected a significant relationship between mass of wallow hair clumps and number of seeds (Figure 13). Ultimately, this result indicates that any future management option that reduces the number of bison below the current 185-250 management target will function to reduce dispersal of non-native weedy plants because fewer bison will shed a lower overall mass of hair in fewer wallows across the island.

We detected no indications that bison are negatively affecting herptile or small mammal communities by grazing or other activities in important habitats for these types of vertebrates (Figure 16, Table 24). Importantly, however, we note that our research in this area was entirely comparative in nature; parameters on terrestrial vertebrate community structure (relative

abundance, species richness, species diversity, etc.) were estimated and compared for several habitats sampled within Zone 1 (bison absent) and Zone 2 (bison present) and used to infer potential bison-related effects. Due to the relatively short duration of our research contract, we were unable to perform a true experimental study on the potential effects of bison on small terrestrial vertebrates, which is the best method of controlling for site-specific differences that can cause difficulties in drawing inferences from comparative studies.

Although brown-headed cowbirds and European starlings sometimes occurred among relatively large groups of bison on Santa Catalina Island, we cannot conclude from our research that the presence of these non-native birds on the island is being positively promoted by the presence of bison. As part of bison group and bison behavioral observations, the presence/absence of brown-headed cowbirds and European starlings was recorded. However, we did not conduct island-wide surveys for either of these species as the main focus of the study was bison. Our observations that cowbirds and starlings were disproportionately distributed among bison groups that were near permanent sources of water and/or close to areas of relatively high human use/disturbance suggests that other agents besides bison are facilitating these species on Santa Catalina Island. Nevertheless, both of these species are commonly associated with large, grazing herbivores, and potential reduced numbers of bison on Santa Catalina Island may therefore be expected to reduce the negative effects of native birds (Mayfield 1965, Ingold 1994, Hahn and Hatfield 1995).

Prior to this study, resource managers were concerned that bison were negatively affecting water quality on the island by trampling, and direct and indirect inputs of urine and feces into reservoirs and streams. Despite a fairly intensive sampling regime (Figure 19), we detected no significant negative effects of bison on any of the measures of water quality we monitored (Figure 20). But again, this part of our study did not include an experimental approach, and there were no areas in bison-absent Zone 1 to collect water samples from multiple streams and reservoirs for comparisons of data on water quality to areas of the island with bison. Any future change in management to reduce or remove bison from larger areas of the island will function to reduce aesthetically unpleasant trampling around reservoir and stream margins, but will likely not alter or improve measures of water quality.

Our estimates of carrying capacity suggest that if bison were the only species on Santa Catalina Island consuming or otherwise using the aboveground plant biomass produced in any given year, the area could support absolutely no more than 378 bison. Bison are a non-native species on the island, however, and there are multiple other native organisms that also require plant materials for foraging and cover that are otherwise being consumed by bison (). When at

least as much biomass as that consumed by bison was reserved for use by native organisms, we estimated that only 95 to 189 bison should be allowed to range over Zones 2, 3, and 4 of the island (Table 28). There is limited or no good information available on the total amount of plant biomass required for maintenance/persistence by the multiple other resident island species. Therefore, without first explicitly modeling carrying capacities for many of these other species as we did for bison, we recommend that the Conservancy adopt conservative approaches when reaching decisions on the numbers of bison supportable by different areas of the island. In Table 28 we provide recommended stocking rates for each of the three management options, which are intermediate between the moderate and light carrying capacity estimates produced by our model iterations (Table 28). Thus, we recommend a management target number of (1) 142 bison under Management Option A, (2) 90 bison under Management Option B, and (3) 13 bison under Management Option C (Table 28). These recommended management targets would be advantageous in allowing for flexibility in population control because immediate population management would not be required when the population is just below or just above a base stocking level (Norland et al. 1985). Secondly, this approach would reduce risk to all plant communities in all areas of the island (Norland et al. 1985). Finally, and of key ecological importance, this approach would provide an acceptable level of protection for the unique natural resources on the island, including sensitive riparian areas and Channel Island and/or Santa Catalina Island endemic plants and animals.

One management option that we did not consider from a carrying capacity perspective was the complete removal of bison from Santa Catalina Island. Our results suggest that the complete removal of all bison from the island would significantly improve habitat conditions in riparian areas and grasslands. Over the longer term bison removal would reduce pressure on SOIC habitats as well, potentially maintaining beneficial habitat conditions for cavity nesting vertebrates. This option would completely eliminate viewing opportunities for island residents and visitors, however, and over the short term would result in the proliferation of exotic grasses and forbs (Zavaleta et al. 2001). The buildup of dry plant biomass over several years by reduced grazing pressure would require consideration of a fire management program, potentially including periodic controlled burning to reduce fuel loads in the event of wildfire. A controlled burn schedule would be recommended because unusually hot fires carried by a heavy understory fuel load would significantly damage SOIC habitats including island endemic ironwood trees.

From a global conservation and restoration perspective, the ecological integrity of native plant and animal communities on islands is especially important because islands typically include proportionally more unique or endemic species than mainland areas. The Channel Islands of

California are estimated to support 26 endemic species and 6 species have so far been identified as occurring only on Santa Catalina Island. Thus, the changes to plant communities on Santa Catalina Island that were identified as being caused by bison in this study should be of important management concern. We therefore recommend that the Santa Catalina Island Conservancy consider a significant reduction in bison numbers on the island and restrict the herd to a smaller area of the island than is currently occupied by the species. One approach could be to initially restrict bison to Zone 2 for several years and then restrict them to the smaller area of Zone 2 in the future if significant ecological degradation persists or develops.

From an ecological perspective, even small numbers of a problematic non-native species occupying an insular ecosystem is cause for concern. Effective conservation often requires balancing multiple conflicting interests, however, and public acceptance of any change in bison management on Santa Catalina Island will be difficult. Nevertheless, the cost of maintaining the status quo on bison management will be significantly reduced ecological integrity of native plant communities on Santa Catalina Island.

LITERATURE CITED

Adler, P. B., D. A. Raff, and W. K. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465-479.

Altman, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227-265.

Barbour, M. G., J. H. Burk, W. D. Pitts, F. S. Gilliam, and M. W. Schwartz. 1999. Terrestrial plant ecology (Third edition). Benjamin/Cummings, Menlo Park, California.

Bekker, R. M., G. L. Verweij, J. P. Bakker, and L. F. M. Fresco. 2000. Soil seed bank dynamics in hayfield succession. Journal of Ecology 88:594-607.

Belsky, A. J., A. Matzke, and S. Uselman. 1999. Survey of livestock influences on stream and riparian ecosystems in the western United States. Journal of Soil and Water Conservation 54:419-431.

Berger, J. and C. Cunningham. 1994. Bison: mating and conservation in small populations. Columbia University Press, New York, New York.

Bernard, S. P. 1983. Too many bison at home on range. USA Today Journal, Grand Junction, CO, 21 March, 1983.

Betts, B. J. 1998. Roosts used by maternity colonies of silver-haired bats in northeastern Oregon. Journal of Mammalogy 79:643-650.

Blair, J. M., T. R. Seastedt, C. W. Rice, and R. A. Remundo. 1998. Terrestrial nutrient cycling in tallgrass prairie. Pp. 222-244 *in* Grassland dynamics (A. K. Knapp, J. M. Briggs, D. C.
Hartnett, and S. L. Collins, eds.). Oxford University Press, New York, NY.

Bock, C. E., H. M. Smith, and J. H. Bock. 1990. The effect of livestock grazing upon abundance of the lizard, *Sceloporus scalaris*, in southeastern Arizona. Journal of Herpetology 24:445-446.

Bowen, L. and D. Van Vuren. 1997. Insular endemic plants lack defenses against herbivores. Conservation Biology 11:1249-1254.

Bowman, R. H., R. E. Bishop, R. W. Griffin, and M. L. Jones. 1973. Soil survey: San Diego Area, California. Part II. Soil Conservation Service and Forest Service, United States Department of Agriculture.

Bowyer, R. T., X. Manteca, and A. Hoymork. 1998. Scent marking in American bison: morphological and spatial characteristics of wallows and rubbed trees. Pp. 81-91 *in* International symposium on bison ecology and management in North America (L. R. Irby and J. E. Knight, eds.). Montana State University, Bozeman, Montana.

Boydston, B. 1998. Catalina Island: where the buffalo roam. The Wall Street Journal, New York, New York, 20 February 1998.

Brigham, R. M., M. J. Vonhof, R. M. R. Barclay, and J. C. Gwilliam. 1997. Roosting behavior and roost-site preferences of forest-dwelling California bats (*Myotis californicus*). Journal of Mammalogy 78:1231-1239.

Cabe, P. R. 1993. European Starling (*Sturnus vulgaris*). *In* The Birds of North America, Number 48 (A. Poole and F. Gill, eds.). Philadelphia: The Academy of Natural Sciences, Washington, D. C.: The American Ornithologists' Union.

Campbell, B. and E. Lack, eds. 1985. A dictionary of birds. British Ornithologist's Union. Buteo Books, Vermillion, South Dakota.

Campbell, C., I. D. Campbell, C. B. Blyth, and J. H. McAndrews. 1994. Bison extirpation may have caused aspen expansion in western Canada. Ecography 17:360-362.

Campbell, D. J. and I. A. E. Atkinson. 2002. Depression of tree recruitment by the Pacific rat (*Rattus exulans* Peale) on New Zealand's northern offshore islands. Biological Conservation 107:19-35.

Campbell, J. E. and D. J. Gibson. 2001. The effect of seeds of exotic species transported via horse dung on vegetation along trail corridors. Plant Ecology 157: 23-35.

Carbyn, L. N., N. J. Lunn, and K. Timoney. 1998. Trends in the distribution and abundance of bison in Wood Buffalo National Park. Wildlife Society Bulletin 26:463-470.

Caruso, B. S. 2001. Temporal and spatial patterns of extreme low flows and effects on stream ecosystems in Otago, New Zealand. Journal of Hydrology 257:115-133.

Clothier, T. 2001. Annual/biennial seed germination database (online). Available Pp. 32.htm-34.htm *in* http://users.anet.com/~manytimes/ [Accessed 17 December 2002].

Coblentz, B. E. 1978. Effects of feral goats *Capra hircus* on island ecosystems. Biological Conservation 13:279-286.

Coblentz, B. E. 1990. Exotic organisms – a dilemma for conservation biology. Conservation Biology 4:261-265.

Coblentz, B. E. 1993. Invasive ecological dominants: environments boar-ed to tears and living on burroe-ed time. Pp. 223-224 *in* Biological Pollution (B. N. McKnight, ed.). Indiana Academy of Sciences.

Collins, P. W. and S. B. George. 1990. Systematics and taxonomy of island and mainland populations of western harvest mice (*Reithrodontomys megalotis*) in Southern California. Contributions in Science 420:1-26. Natural History Museum of Los Angeles County, Los Angeles, California.

Collins, S. L. 1992. Fire frequency and community heterogeneity in tallgrass prairie vegetation. Ecology 73:2001-2006.

Collins, S. L. and E. M. Steinauer. 1998. Disturbance, diversity, and species interactions in tallgrass prairie. Pp. 140-156 *in* Grassland dynamics (A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. L. Collins, eds.). Oxford University Press, New York, New York.

Colorado National Monument. 1984. Restore habitat damaged by introduced bison herd. Development/Study Package Proposal 501. National Park Service, U.S. Department of the Interior, Washington, D.C.

Cooke, G. D., E. B. Welch, S. A. Peterson, and P. R. Newroth. 1986. Lake and reservoir restoration. Butterworth Publishers, Stoneham, MA.

Coppedge, B. R. and J. H. Shaw. 1997. Effects of horning and rubbing behavior by bison (*Bison bison*) on woody vegetation in a tallgrass prairie landscape. American Midland Naturalist 138:189-196.

Coppedge, B. R., D. M. Leslie, and J. H. Shaw. 1998. Botanical composition of bison diets on tallgrass prairie in Oklahoma. Journal of Range Management 51:379-382.

Cree, A., C. H. Daugherty, and J. M. Hay. 1995. Reproduction of a rare New Zealand reptile, the tuatara, *Sphenodon punctatus*, on rat-free and rat-inhabited islands. Conservation Biology 9:373-383.

Crowell, T. M. 1983. Monument buffalo herd thinned to protect range. The Daily Sentinel, Grand Junction, Colorado, 31 August 1983.

Crum, S. 1983. Buffalo problems. *In* Speaking the public mind, The Daily Sentinel, Grand Junction, CO, 7 April 1983.

Cureton, H. H., J. W. Garlinghouse, L. Leifer, and C. Jensen. 1955. Conservation planning Santa Catalina Island April 25-27. Unpublished report to D. Propst, Santa Catalina Island Company, Avalon, California.

Daily Sentinel. 1983a. Buffalos may roam elsewhere. The Daily Sentinel, Grand Junction, CO, 25 March 1983.

Daily Sentinel. 1983b. Where buffalo roam. The Daily Sentinel, Grand Junction, CO, 22 May 1983.

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

Damhoureyeh, S. A. and D. C. Hartnett. 1997. Effects of bison and cattle on growth, reproduction, and abundances of five tallgrass prairie forbs. American Journal of Botany 84:1719-1728.

Davis, G. E., K. R. Faulkner, W. L. Halvorson. 1994. Ecological monitoring in Channel Islands National Park. Pages 465-482 *in* W. L. Halvorson and G. J. Maender, editors. Fourth California islands symposium: update on the status of resources. Santa Barbara Museum of Natural History, Santa Barbara, California.

Davitt, B. 2002. The Wildlife Habitat Nutrition Laboratory services and prices (online). Department of Natural Resource Sciences, Washington State University, Pullman, Washington. Available http://www.natural-resources.wsu.edu/Research/i-research.html [Accessed 12 January 2003].

Dodds, W. K., J. M. Blair, G. M. Henebry, J. K. Koelliker, R. Ramundo, and C. M. Tate. 1996. Nitrogen transport from tallgrass prairie watersheds. Journal of Environmental Quality 25:973-981.

Drost, C. A. and G. M. Fellers. 1991. Density cycles in an island population of deer mice, *Peromyscus maniculatus*. Oikos 60:351-364.

Dunbar, M. R. and M. R. Giordano. 2002. Abundance and condition indices of coyotes on Hart Mountain National Antelope Refuge, Oregon. Western North American Naturalist 62:341-347.

Dunbar, M. R., R. Velarde, M. A. Gregg, and M. Bray. 1999. Health evaluation of a pronghorn antelope population in Oregon. Journal of Wildlife Diseases 35:496-510.

Duncan, D. A. and R. G. Woodmansee. 1975. Forecasting forage yield from precipitation in California's annual rangeland. Journal of Range Management 28:327-329.

Duval, L. 2001. Catalina: island of calm with 1920s charm. The Seattle Times, Seattle, Washington, 29 July 2001.

Dyer, A. R. and K. J. Rice. 1999. Effects of competition on resource availability and growth of California bunchgrass. Ecology 80:2696-2710.

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

Fritz, K. M., W. K. Dodds, and J. Pontius. 1999. The effects of bison crossings on the macroinvertebrate community in a tallgrass prairie stream. American Midland Naturalist 141:253-265.

Fruita Times. 1983. Monument bison moved away. The Fruita Times, Fruita, CO, 16 November 1983.

Galland, J. C. 1989. Group size dynamics of herding animals. Unpublished Ph.D. Dissertation. University of California, Davis, California.

Garcelon, D. K., S. J. Escover, and S. F. Timm. 1993. Feral pig control methods on Santa Catalina Island, California. Pp. 44-45 *in* The wild pig in California oak woodland: ecology and economics (W. Tietje and R. H. Barrett, eds.). Integrated Hardwood Range Management Program, Department of Forestry and Resource Management, University of California, Berkeley, California.

Garcelon, D.K., B. Haveri, K. Ryan, and T. Manuwal. 2001. Feral goat and pig removal on Santa Catalina Island, California: 01 July 2000 – 30 June 2001. Unpublished report prepared for the Santa Catalina Island Conservancy, Avalon, California.

Gary, H. L., S. R. Johnson, and S. L. Ponce. 1983. Cattle grazing impact on surface water quality in a Colorado Front Range stream. Journal of Soil and Water Conservation 1983:124-128.

George, M., G. Nader, N. McDougald, M. Connor, and B. Frost. 2001. Annual rangeland forage quality. Rangeland Management Series Publication 8022. University of California, Agriculture and Natural Resources, Oakland, California.

Goguen, C. B. and N. E. Mathews. 2002. Songbird community composition and nesting success in grazed and ungrazed pinyon-juniper woodlands. Journal of Wildlife Management 62:474-484.

Gordon, D. R., J. M. Welker, J. W. Menke, and K. J. Rice. 1989. Competition for soil water between annual plants and blue oak (Quercus douglasii) seedlings. Oecologia 79:533-541.

Grant, W. E., E. C. Birney, N. R. French, and D. M. Swift. 1982. Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. Journal of Mammalogy 63:248-260.

Grant, R. 1996. Water quality and requirements for dairy cattle. NebGuide Publication G93-1138-A (online). Institute of Agriculture and Natural Resources, University of Nebraska-Lincoln, NB. Available http://www.ianr.unl.edu/pubs/Dairy/g1138.htm#check [Accessed 12 November 2002].

Grazing Lands Technology Institute. 1997. National range and pasture handbook. National Resources Conservation Service, U. S. Department of Agriculture, Washington, D. C.

Gringrich, R. 1974. The Buffalo of Catalina. Unpublished document, Santa Catalina Conservancy, Avalon, California.

Hahn, D. C. and J. S. Hatfield. 1995. Parasitism at the landscape scale: cowbirds prefer forests. Conservation Biology 9:1415-1424.

Halloran, A. F. 1960. American bison weights and measurements from the Wichita Mountains Wildlife Refuge. Proceedings of the Oklahoma Academy of Science 41:212-219.

Halloran, A. F. 1968. Bison (Bovidae) productivity on the Wichita Mountains Wildlife Refuge, Oklahoma. Southwestern Naturalist 13:23-26.

Hamilton, J. G., C. Holzpfel, and B. E. Mahall. 1999. Coexistence and interference between a native perennial grass and non-native annual grasses in California. Oecologia 121:518-526.

Hart, R. H. 2001. Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. Plant Ecology 155:111-118.

Hartnett, D. C., K. R. Hickman, and L. E. Fischer. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. Journal of Range Management 49:413-420.

Hartnett, D. C., A. A. Steuter, and K. R. Hickman. 1997. Comparative ecology of native and introduced ungulates. Pp. 72-101 in Ecology and conservation of Great Plains vertebrates (F. L. Knopf and F. B. Samson, eds.). Springer-Verlag, New York, New York.

Hawley, A. W. 1987. Identifying bison ration groups by multivariate analysis of blood composition. Journal of Wildlife Management 51:893-900.

Hawley, A. W. and D. W. Peden. 1982. Effects of ration, season, and animal handling on composition of bison and cattle blood. Journal of Wildlife Diseases 18:321-338.

Hayes, M. J. 2002. What is drought?: Drought indices (online). National Drought Mitigation Center, University of Nebraska, Lincoln, Nebraska. Available http://www.drought.unl.edu/whatis/indices.htm. [Accessed 28 December 2002].

Hayward, B., E. J. Heske, and C. W. Painter. 1997. Effects of livestock grazing on small mammals at a desert ceinaga. Journal of Wildlife Management 61:123-129.

Hernandez, M. A., M. Aurelio, and M. Nogales. 1999. Breeding success and predation on artificial nests of the endemic pigeons Bolle's Laurel pigeon (*Columbia bollii*) and white-tailed Laurel Pigeon (*Columbia junoniae*) in the laurel forest of Tenerife (Canary Islands). Ibis 141:52-59.

Heske, E. J. and M. Campbell. 1991. Effects of an 11-year livestock exclosure on rodent and ant numbers in the Chihuahuan Desert, Southeastern Arizona. Southwestern Naturalist 36:89-93.

Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster, eds. 1994. Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington and London.

Hickman, J. C., ed. 1993. The Jepson manual: higher plants of California. University of California Press, Berkeley, California.

Higgins, K. F., J. L. Oldemeyer, K. J. Jenkins, G. K. Clambey, and R. F. Harlow. 1994. Vegetation sampling and measurement. Pp. 567-591 *in* Research and management techniques for wildlife and habitats, Fifth Edition (T. A. Bookhout, ed.). The Wildlife Society, Bethseda, Maryland.

Hobbs, R. J. and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324-337.

Holochek, J. L., M. Vavra, and R. D. Pieper. 1982. Botanical composition determination of range herbivore diets: A review. Journal of Range Management 35:309-315.

Hosmer, D. W. and S. Lemeshow. 1989. Applied logistic regression. John Wiley & Sons, Inc., New York, NY.

Hudson, R. J. and S. Frank. 1987. Foraging ecology of bison in aspen boreal habitats. Journal of Range Management 40:71-75.

Hufstader, R. W. 1976. Precipitation, temperature, and the standing crop of some southern California grassland species. Journal of Range Management 29:433-435.

Ingold, D. J. 1994. Influence of nest-site competition between European starlings and woodpeckers. Wilson Bulletin 106:227-231.

Johnson, C. F., R. M. Cowling, and P. B. Phillipson. 1999. The flora of the Addo Elephant National Park, South Africa: are threatened species vulnerable to elephant damage? Biodiversity and Conservation 8:1447-1456.

Jones, K. B. 1981. Effects of grazing on lizard abundance and diversity in western Arizona. Southwestern Naturalist 26:107-115.

Jones, H. L. 1990. Annotated checklist of the birds of Santa Catalina Island and adjacent waters. Santa Catalina Island Conservancy, Avalon, California.

Junak, S., T. Ayers, R. Scott, D. Wilken, and D. Young. 1995. A flora of Santa Cruz Island. Santa Barbara Botanic Garden, Santa Barbara, California. 397 pp.

Junak, S., S. Chaney, R. Philibrick, and R. Clark. 1997. A checklist of vascular plants of Channel Islands National Park. Southwest Parks and Monuments Association, Tucson, Arizona.

Kauffman, J. B. and W. C. Krueger. 1984. Livestock impacts on riparian ecosystems and streamside management implications…a review. Journal of Range Management 37:430-439.

Keith, E. O., J. E. Ellis, R. W. Phillips, and M. M. Benjamin. 1978. Serologic and hematologic values of bison in Colorado. Journal of Wildlife Diseases 14:493-500.

Keith, L.D. 2002. California island assesses impact of bison boom. The Sunday Oregonian, Portland, Oregon, 17 February 2002.

Kemp, M. J. and W. K. Dodds. 2002. The influence of ammonium, nitrate, and dissolved oxygen concentrations on uptake, nitrification, and denitrification rates associated with prairie stream substrata. Limnology and Oceanography 47:1380-1393.

Kimzey, J. B. 1983. Buffalo memories. *In* Speaking the public mind, The Daily Sentinel, Grand Junction, Colorado, 12 May 1983.

Kirkpatrick, J. F., J. C. McCarthy, D. F. Gudermuth, S. E. Shideler, and B. L. Lasley. 1996. An assessment of the reproductive biology of Yellowstone bison (*Bison bison*) subpopulations using noncapture methods. Canadian Journal of Zoology 74:8-14.

Klinger, R. C., P. T. Schuyler, and J. D. Sterner. 1994. Vegetation response to the removal of feral sheep from Santa Cruz Island. Pp. 341-350 *in* Fourth California Islands symposium: Update on the status of resources (W. L. Halvorson and G. J. Maender, eds.). Santa Barbara Museum of Natural History, Santa Barbara, California.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. Bioscience 49:39-50.

Knapp, D. A. 2002a. The status of island scrub oak (*Quercus pacifica*) on Catalina Island, California. *In* Proceedings of the fifth symposium on oak woodlands: Oaks in California's changing landscape. October 22-25, 2001, San Diego, California. USDA Forest Service Gen. Tech. Rep. PSW-GTR-184.

Knapp, D. 2002b. Santa Catalina Island vegetation mapping project report. Unpublished report prepared for Santa Catalina Island Conservancy, Avalon, California.

Komers, P.E., F. Messier, and C. G. Gates. 1993. Group structure in wood bison: nutritional and reproductive determinants. Canadian Journal of Zoology 71:1367-1371.

Krebs, C. J. 1999. Ecological methodology, Second Edition. Addison-Wesley Educational Publishers, Inc., Menlo Park, California.

Kruskal, J. B. and M. Wish. 1978. Multidimensional scaling. Sage University Paper Series on Quantitative Applications, 07-011 (E. M. Uslander, ed.) Sage Publications, Beverly Hills, California.

Kuiters, A. T. and P. A. Slim. 2002. Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. Biological Conservation 105:65-74.

Lambin, X., S. J. Petty, and J. L. Mackinnon. 2000. Cyclic dynamics in field vole populations and generalist predation. Journal of Animal Ecology 69:106-118.

Larter, N. C. and C. C. Gates. 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. Canadian Journal of Zoology 69:2677-2685.

Laughrin, L., M. Carroll, A. Bromfield, and J. Carroll. 1994. Trends in vegetation changes with removal of feral animal grazing pressures on Santa Catalina Islands. Pp. 523-529 *in* Fourth California Islands symposium: Update on the status of resources (W. L. Halvorson and G. J. Maender, eds.). Santa Barbara Museum of Natural History, Santa Barbara, California.

Lee, P. F. 1990. Bison nutrition. Pp. 79-97 *in* Buffalo producer's guide to management and marketing (K. Dowling, ed.). R. R. Donnelley and Sons Co., Chicago, IL.

Lewis, R. 1983. Save the buffalo. *In* Speaking the public mind, The Daily Sentinel, Grand Junction, CO, 20 March 1983.

Litvaitis, J. A., K. Titus, and E. M. Anderson. 1994. Measuring vertebrate use of terrestrial habitats and food. Pp. 254-274 *in* Research and management techniques for wildlife and habitats, Fifth Edition (T. A. Bookhout, ed.). The Wildlife Society, Bethseda, MD.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution 8:133-137.

Lombardo, C. A. and K. R. Faulkner. 2000. Eradication of feral pigs (*Sus scrofa*) from Santa Rosa Island, Channel Islands National Park. Pp. 300-306 *in* Proceedings of the fifth California Islands Symposium, 29 March – 1 April. Santa Barbara Museum of Natural History, Santa Barbara, California. CD-ROM.

Lott, D. F. 1979. Dominance relations and breeding rate in mature male American bison. Z. Tierpsychol. 49:418-432.

Lott, D. F. 2002. American bison: a natural history. University of California Press, Berkeley and Los Angeles, California.

Lott, D. F. and J. C. Galland. 1985. Parturition in American Bison: precocity and systematic variation in cow isolation. Z. Tierpsychol. 69:66-71.

Lott, D. F. and J. C. Galland. 1987. Body mass as a factor influencing dominance status in American bison cows. Journal of Mammalogy 68:683-685.

Lott, D. F. and S. C. Minta. 1983. Random individual association and social group instability in American Bison (*Bison bison*). Z. Tierpsychol. 61:153-172.

Lowther, P. E. 1993. Brown-headed cowbird (*Molothrus ater*) *In* The Birds of North America, Number 47 (A. Poole and F. Gill, eds.). Philadelphia: The Academy of Natural Sciences, Washington, D. C.: The American Ornithologists' Union.

Lusk, M. R., M. J. Lacki, and R. A. Lancia. 1993. Responses of deer mice (*Peromyscus maniculatus*) to wild hog rooting in Great Smoky Mountains National Park. Brimleyana 19:169-184.

Mack, R. N. and J. N. Thompson. 1982. Evolution in steppe with few large, hooved mammals. American Naturalist 119:757-773.

Mac Nally, R., A. Parkinson, G. Horrocks, L. Conole, and C. Tzaros. 2001. Relationships between terrestrial vertebrate diversity, abundance, and availability of coarse woody debris on south-eastern Australian floodplains. Biological Conservation 191-205.

Malo, J. E. and F. Suárez. 1995. Cattle dung and the fate of *Biserrula pelecinus* L. (Leguminosae) in a Mediterranean pasture: seed dispersal, germination, and recruitment. Botanical Journal of the Linnean Society 118:139-148.

Malo, J. E. and F. Suárez. 1997. Dispersal mechanism and transcontinental naturalization proneness among Mediterranean herbaceous species. Journal of Biogeography 24:391-394.

Martin, A. C., H. S. Zwim, and A. L. Nelson. 1951. American wildlife and plants. Dover Publications, New York, New York.

Matlack, R. S., D. W. Kaufman, and G. A. Kaufman. 2001. Influence of grazing by bison and cattle on deer mice in burned tallgrass prairie. American Midland Naturalist 146:361-368.

Mayfield, H. 1965. The brown-headed cowbird, with old and new hosts. Living Bird 4:13-29.

McHugh, T. 1958. Social behavior of the American Buffalo (*Bison bison bison*). Zoologica 43:1-41.

McInnis, M. L., M. Vavra, and W. C. Krueger. 1983. A comparison of four methods used to determine the diets of large herbivores. Journal of Range Management 36:302-306.

McKee, T. B., N. J. Doesken, and J. Kleist. 1993. The relationship of drought frequency and duration to time scales. Pp. 179-184 *in* Preprints, 8th Conference on Applied Climatology, 17-22 January 1993, Anaheim, California.

Meadows, D. W. 2001. Effects of bison trampling on stream macroinvertebrate community structure on Antelope Island, Utah. Journal of Freshwater Ecology 16:83-92.

Meagher, M. 1986. *Bison bison*. Mammalian Species 266:1-8.

Mecoy, L. 2002. Island of the brown bison. The Sacramento Bee, Sacramento, CA, 3 November 2002.

Melody, K., and D. K. Garcelon. 1999. Potential impacts of introduced mule deer on the ecology of Santa Catalina Island, California. Unpublished research report, Institute for Wildlife Studies, Arcata, California.

Mesa Conservation District. 1982. Soil and water conservation plan, Colorado National Monument (bison range). Soil Conservation Service, U. S. Department of Agriculture, Washington, D. C.

Mian, M. A. R., R. M. Skirvin, M. A. Norton, and A. G. Otterbacher. 1995. Drying interferes with germination of blackberry (*Rubus* sp.) seeds in vitro. HortScience 30:124-126.

Milchunas, D. G. and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63:327-366.

Miller, P. H. 1964. The ecological distribution of mammals in Colorado National Monument, Mesa County, Colorado. Unpublished MS thesis. Oklahoma State University, Stillwater, Oklahoma.

Minnich, R. A. 1980. Vegetation of Santa Cruz and Santa Catalina Islands. Pp. 123-137 *in* The California Islands: Proceedings of a multidisciplinary symposium (D. M. Power, ed.). Santa Barbara Museum of Natural History, Santa Barbara, California.

Munro, C. and G. Stabenfeldt. 1984. Development of a microtitre plate enzyme immunoassay for the determination of progesterone. Journal of Endocrinology 101:41-49.

Murphy, A. H. 1970. Predicted forage yield based on fall precipitation in California annual grasslands. Journal of Range Management 23:363-365.

National Audubon Society. 2002. The Christmas bird count historical results (online). Available http://www.audubon.org/bird/cbc [Accessed 18 December 2002].
Nixon, K. C. and C. H. Muller. 1994. New names in California oaks. Novon 4:391-393.
Norland, J. E., L. R. Irby, and C. B. Marlow. 1985. Determination of optimum bison stocking rate in Theodore Roosevelt National Park, North Dakota. Journal of Environmental Management 21:225-239.
Novotny, V. and H. Olem. 1994. Prevention, identification, and management of diffuse pollution. Von Nostrand Reinhold, New York, New York.
Noyes, J. H., G. Sasser, B. K. Johnson, L. D. Bryant, and B. Alexander. 1997. Accuracy of pregnancy detection by serum protein (PSPB) in elk. Wildlife Society Bulletin 25:695-698.
Noy-Meir, I., M. Gutman, and Y. Kaplan. 1989. Responses of Mediterranean grassland plants to grazing and protection. Journal of Ecology 77:290-310.
O'Malley, P. G. 1994. The Catalina Conservancy's First 20 Years: Private conservation comes of age. Pp. 149-155 *in* Fourth California Islands symposium: Update on the status of resources (W. L. Halvorson and G. J. Maender, eds.). Santa Barbara Museum of Natural History, Santa Barbara, California.
Olsson, O., M. Bruun, and H. G. Smith. 2002. Starling foraging success in relation to agricultural land-use. Ecography 25:363-371.
Ortega, I. M., F. C. Bryant, and D. L. Drawe. 1995. Contrasts of esophageal-fistula versus bite-count techniques to determine cattle diets. Journal of Range Management 48:498-502.
Palmer, M. and G. X. Pons. 1996. Diversity in western Mediterranean islets: effects of rat presence on a beetle guild. Acta Oecologica 17:297-305.
Peart, D., D. T. Patten, and S. L. Lohr. 1994. Feral pig disturbance and woody species seedling regeneration and abundance beneath coast live oaks (*Quercus agrifolia*) on Santa Cruz Island, California. Pp. 313-322 *in* Fourth California Islands symposium: Update on the status of resources (W. L. Halvorson and G. J. Maender, eds.). Santa Barbara Museum of Natural History, Santa Barbara, California.
Peden, D. G., G. M. Van Dyne, R. W. Rice, and R. M. Hansen. 1974. The trophic ecology of Bison bison L. on shortgrass plains. Journal of Applied Ecology 11:489-497.
Polley, H. W. and S. L. Collins. 1984. Relationships of vegetation and environment in buffalo wallows. American Midland Naturalist 112:178-186.
Polley, H. W. and L. L. Wallace. 1986. The relationship of plant species heterogeneity to soil variation in buffalo wallows. Southwestern Naturalist 31:493-501.
Radford, I. J., D. M. Nicholas, J. R. Brown, and D. J. Kriticos. 2001. Paddock-scale patterns of seed production and dispersal in the invasive shrub *Acacia niltotica* (Mimosaceae) in northern Australian rangelands. Austral Ecology 26:338-348.
Read, J. L. 2002. Experimental trial of Australian arid zone reptiles as early warning indicators of overgrazing by cattle. Austral Ecology 27:55-66.
Reid, W. and K. Miller. 1989. Keeping options alive: The scientific basis for conserving biodiversity. World Resources Institute, Washington, D.C.
Reynolds, H. W., R. D. Glaholt, and A. W. L. Hawley. 1982. Bison: *Bison bison*. Pp. 972-1006 *in* Wild mammals of North America: Biology, management, economics (J. A. Chapman and G. A. Feldhamer, eds.). John Hopkins University Press, Baltimore, MD.
Reynolds, H. W., R. M. Hansen, and D. G. Peden. 1978. Diets of Slave River lowland bison herd, Northwest Territories, Canada. Journal of Wildlife Management 42:581-590.
Reynolds, T. D. and C. H. Trost. 1980. The response of native vertebrate populations to crested wheatgrass planting and grazing by sheep. Journal of Range Management 33:122-125.
Rich, T. D. 1978. Cowbird parasitism of Sage and Brewer's Sparrows. Condor 80:348.
Roe, F.G. 1970. The North American buffalo: a critical study of the species in its wild state. University of Toronto Press, Toronto, Ontario, Canada.

Rosing, M. N., M. Ben-David, and R. P. Barry. 1998. Analysis of stable isotope data: a K nearest-neighbors randomization test. Journal of Wildlife Management 62:380-388.

Rutberg, A. T. 1986. Lactation and fetal sex rations in American bison. American Naturalist 127:89-94.

Russi, L., P. S. Cocks, and E. H. Roberts. 1992. Seed bank dynamics in a Mediterranean grassland. Journal of Applied Ecology 29:763-771.

Rutley, B. D. and R. J. Hudson. 2001. Activity budgets and foraging behavior of bison on seeded pastures. Journal of Range Management 54:218-225.

Salisbury, F. B. and C. W. Ross. 1992. Plant physiology. Wadsworth Publishing Company, Belmont, California.

Sampson, A. W., A. Chase, and D. W. Hedrick. 1951. California grasslands and range forage grasses. Bulletin 724. California Agricultural Experiment Station, College of Agriculture, University of California, California.

Sanders, K. D., B. E. Dahl, and G. Scott. 1980. Bite-count vs fecal analysis for range animal diets. Journal of Range Management 33:146-149.

Santa Catalina Island Conservancy. 2002. Rainfall data (online). Available http://www.catalinaconservancy.org/ecology/weather/index.asp [Accessed 28 December 2002].

Sasser, R. G., C. A. Ruder, K. A. Ivani, J. E. Butler, and W. C. Hamilton. 1986. Detection of pregnancy by radioimmunoassay of a novel pregnancy-specific protein in serum of cows and a profile of serum concentrations during pregnancy. Biological Reproduction 35:936-942.

Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. Ecology 68: 660-668.

Schoenherr, A. A., C. R. Feldmeth, and M. J. Emerson. 1999. Natural history of the islands of California. University of California Press, Berkeley, California.

Schuyler, P.T., D. K. Garcelon, and S. Escover. 2002. Eradication of feral pigs (*Sus scrofa*) on Santa Catalina Island, California, USA. Pp. 274-286 *in* Turning the Tide: the eradication of invasive species (C. R. Veitch and M. N.Clout, eds.). IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, United Kingdom.

Scrimgeour, G. J. and S. Kendall. 2002. Consequences of livestock grazing on water quality and benthic algal biomass in a Canadian natural grassland plateau. Environmental Management 29:824-844.

Shaw, J. H. and T. S. Carter. 1989. Calving patterns among American bison. Journal of Wildlife Management 53:896-898.

Shaw, J. H. 1999. American bison. Pp 342-343 *in* The Smithsonian book of North American mammals (D. E. Wilson and S. Ruff, eds.). Smithsonian Institution Press, Washington, D.C.

Shaw, J. H. and M. M. Meagher. 2000. Bison. Pp. 447-466 *in* Ecology and management of large mammals in North America (S. Demarais and P. R. Krausman, eds.). Prentice-Hall, Inc., Upper Saddle River, NJ.

Shipman G. 1969. Soil survey Santa Catalina Island, California. USDA Natural Resources Conservation Service**.** Lancaster, California

Simberloff, D. 1994. Conservation biology and the unique fragility of island ecosystems. Pp. 1-10 *in* Fourth California islands symposium: Update on the status of resources (W. L. Halvorson and G. J. Maender, eds.). Santa Barbara Museum of Natural History, Santa Barbara, California.

Singer, F. J., W. T. Swank., and E. E. C. Clebsch. 1984. Effects of wild pig rooting in a deciduous forest. Journal of Wildlife Management 48:464-473.

Sneva, F. A. and D. N. Hyder. 1962. Estimating herbage production on semiarid ranges in the Intermountain Region. Journal of Range Management 15:88-93.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research, Second Edition. W. H. Freeman and Company, New York, NY.

Sorenson, A. E. 1986. Seed dispersal by adhesion. Annual Review of Ecology and Systematics 17:443-463.

Sparks, D. R. and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscopic technique. Journal of Range Management 21:264-265.

Stebbins, R. C. 1985. Peterson field guide to western reptiles and amphibians. Houghton Mifflin, Boston, Massachusetts.

Stebbins, R. C., and N. W. Cohen. 1995. A natural history of amphibians. Princeton University Press, Princeton, New Jersey.

Stratton, L. 2002. Oak restoration trials: Santa Catalina Island. *In* Proceedings of the fifth symposium on oak woodlands: Oaks in California's changing landscape. October 22-25, 2001, San Diego, California. USDA Forest Service Gen. Tech. Rep. PSW-GTR-184.

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.

Sweitzer, R. A. and D. H. Van Vuren. 2002. Rooting and foraging effects of wild pigs on tree regeneration and acorn survival in California's oak woodland ecosystems. *In* Proceedings of the fifth symposium on oak woodlands: Oaks in California's changing landscape. October 22-25, 2001, San Diego, California. USDA Forest Service Gen. Tech. Rep. PSW-GTR-184.

Talbot, M. W., H. H. Biswell, and A. L. Hormay. 1939. Fluctuations in the annual vegetation of California. Ecology 20:394-402.

Tate, C. M. 1990. Patterns and controls of nitrogen in tallgrass prairie streams. Ecology 71:2007-2018.

Thomas, J. W. 1979 Wildlife habitats in managed forests: the blue mountains of Oregon and Washington. USDA Forest Service Agriculture Handbook No. 553. Wildlife Management Institute, Washington D.C.

Thorne, R. F. 1967. A flora of Santa Catalina Island, California. Aliso 6:1-77.

Thorne, R. F. 1969. A supplement to the floras of Santa Catalina and San Clemente Islands, Los Angeles County, California. Aliso 7:73-83.

Thorne, R. F. 1976. Conservation and management of the natural flora of Santa Catalina Island. Unpublished report prepared for the Center for Natural Areas, Washington, D.C.

Towne, E. G. 1999. Bison performance and productivity on tallgrass prairie. Southwestern Naturalist 44:361-366.

Uchytil, R. J. 1992. *Xanthium strumarium*. *In* Fire Effects Information System (online). U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire
Sciences Laboratory (2002, September). Available http://www.fs.fed.us/database/feis/ [Accessed 17 December 2002].

Van Dyne, G. M., N. R. Brockington, Z. Szocs, J. Duek, and C. A. Ribic. 1981. Large herbivore subsystem. Pp. 269-537 *in* Grasslands, systems analysis, and man (A. I. Breymeyer and G. M. Van Dyne, eds.). Cambridge University Press, Cambridge, United Kingdom.

Van Sickle, J. 1997. Using mean similarity dendrograms to evaluate classifications. Journal of Agricultural, Biological, and Environmental Statistics. 2:370-388.

Van Sickle, J. 1998. Documentation for MEANSIM, Version 6.0 (online). U. S. Environmental Protection Agency, Western Ecology Division, Corvallis, OR. Available http://www.epa.gov/naaujydh/pages/models/dendro/meansim6.htm [Accessed 12 January 2003].

Van Vuren, D. 1984. Summer diets of bison and cattle in southern Utah. Journal of Range Management 37:260-261.

Van Vuren, D. 2001. Spatial relations of American bison (*Bison bison*) and domestic cattle in a montane environment. Animal Biodiversity and Conservation 24:117-124.

Van Vuren, D. 1987. Bison west of the Rocky Mountains: An alternative explanation. Northwest Science 61:65-69.

Van Vuren, D. 1992. Eradication of feral goats and sheep from island ecosystems. Proceedings of the Vertebrate Pest Conference 15:377-381.

Van Vuren, D. and M. P. Bray. 1986. Population dynamics of bison in the Henry Mountains, Utah. Journal of Mammalogy 67:503-511.

Van Vuren, D., and B. E. Coblentz. 1987. Some ecological effects of feral sheep on Santa Cruz Island, California, USA. Biological Conservation 41:253-268.

VanderWerf, E. A. 2001. Rodent control decreases predation on artificial nests in O'ahu 'Elapaio habitat. Journal of Field Ornithology 72:448-457.

Vaughan, T. A., J. M. Ryan, and N. J. Czaplewski. 2000. Mammalogy (fourth edition). Brooks/Cole. United States.

Vavra, M., R. W. Rice, and R. M. Hansen. 1978. A comparison of esophageal fistula and fecal material to determine steer diets. Journal of Range Management 31:11-13.

Vestweber, J. G., D. E. Johnson, G. L. Merrill, and J. J. Staats. 1991. Hematological and blood chemistry profiles of American bison grazing on Konza Prairie of Kansas. Journal of Wildlife Diseases 27: 417-420.

Waggoner, V. and M. Hinkes. 1986. Summer and fall browse utilization by an Alaskan bison herd. Journal of Wildlife Management 50:322-324.

Wasser, C. H. 1977. Bison-induced stresses on canyon-bottom ecosystems in Colorado National Monument. Unpublished report prepared for Resource Management, Colorado National Monument, National Park Service, U.S. Department of the Interior.

Weeks, P. 2000. Red-billed oxpeckers: vampires or tickbirds? Behavioral Ecology 11:154-160.

Wehtje, W. 1994. Response of a Bishop pine (*Pinus muricata*) population to removal of feral sheep on Santa Cruz Island, California. Pp. 331-340 *in* Fourth California Islands symposium: Update on the status of resources (W. L. Halvorson and G. J. Maender, eds.). Santa Barbara Museum of Natural History, Santa Barbara, California.

Welch, D. 1985. Studies in the grazing of heather moorland in north-east Scotland. Journal of Applied Ecology 22:461-472.

Woinarski, J. C. Z. and A. J. Ash. 2002. Responses of vertebrates to pastoralism, military land use, and landscape position in an Australian tropical savanna.

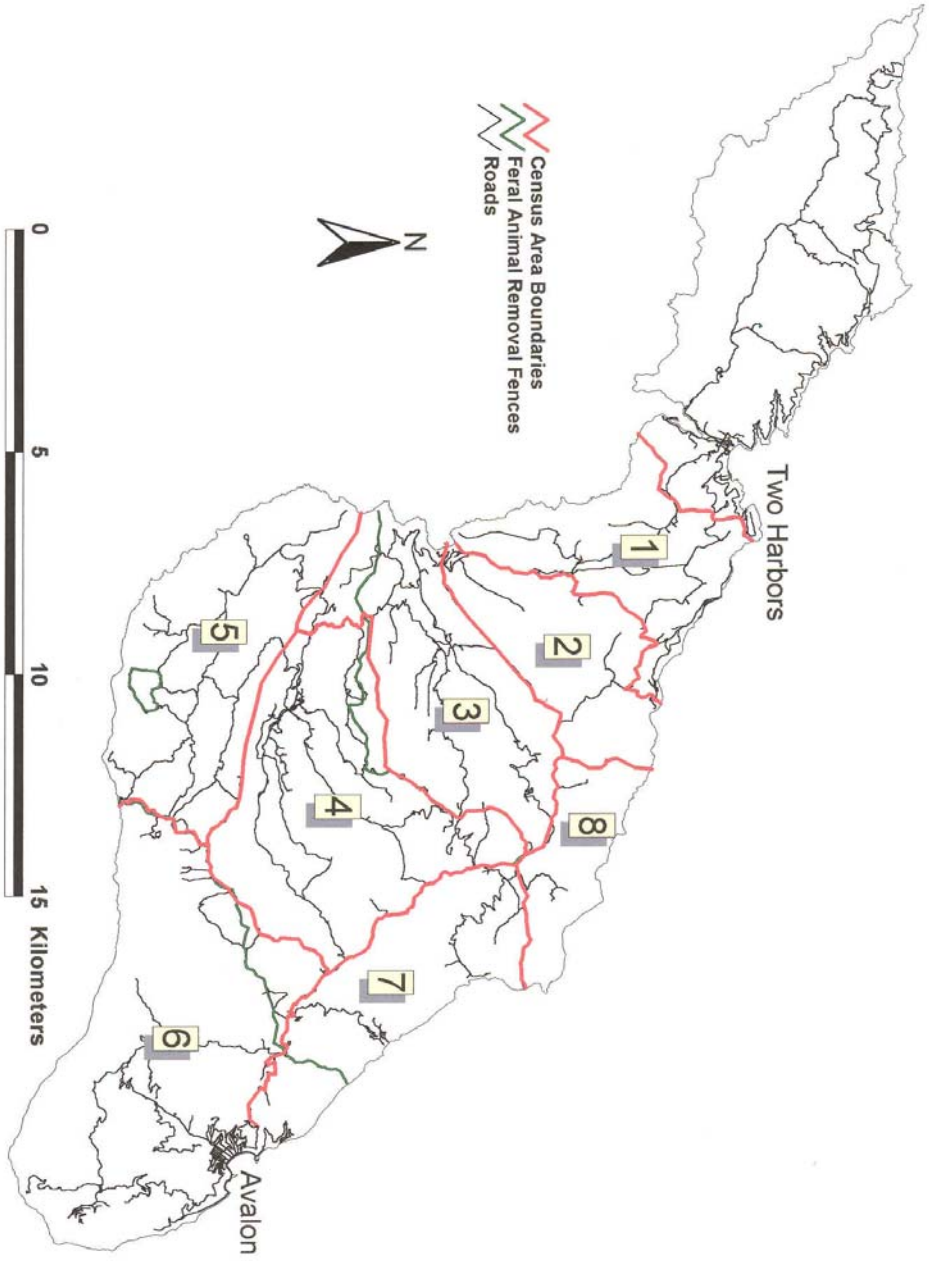
Wolfe, M. L., M. P. Shipka, and J. F. Kimball. 1999. Reproductive ecology of bison on Antelope Island, Utah. Great Basin Naturalist 59:105-111.

Zar, J. H. 1999. Biostatistical analysis, Fourth Edition. Prentice-Hall, Inc., Upper Saddle River, NJ.

Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution 16: 454-459.

APPENDICES

APPENDIX I. Map illustrating eight different areas used for ground-based counts/censuses of bison on Santa Catalina Island, California during the study period (January 2001 to August 2002).



APPENDIX II. Microsoft® Excel 2000 routine used to correct geographic locations recorded during bison group observations on Santa Catalina Island, California.

Let:

UTM_E = UTM easting at observer's location.
UTM_N = UTM northing at observer's location.
OS = offset slope (%) to center of bison group, from observer's location
OD = offset distance (m) to center of bison group, from observer's location
OA = offset angle (^{o}) to center of bison group, from observer's location

Then, adjusted offset slope is:

AOS = ((100-ABS(OFFSET SLOPE))/100)*OD

And the corrected UTM coordinates are:

UTM_E_Corrected = UTM_E+(IF(AND(OA>90, OA<270),-1,1))*(SIN(RADIANS
(IF(OA<90,OA,(IF(OA<180,OA-90,(IF(OA<270, OA-180,
(IF(OA<360,OA-270,"X")))))))))*AOS)

UTM_N_Corrected = UTM_N+(IF(AND(OA>180, OA<360),-1,1))*(COS(RADIANS
(IF(OA<90,OA,(IF(OA<180,OA-90,(IF(OA<270,OA-180,
(IF(OA<360,OA-270,"X")))))))))*AOS)

APPENDIX III. Relative percent observations of bison engaged in major behavior categories by habitat type on Santa Catalina Island, California. Data summarized from group observations (number of bison contributing to each category in parentheses) during the period between January 2001 and August 2002.

Habitat	Feed	Stand	Rest	Other
Coastal sage scrub	33.1 (1277)	20.4 (784)	33.3 (1283)	13.1 (504)
Grassland	33.3 (2607)	19.8 (1548)	33.3 (2609)	13.6 (1065)
SOIC	31.7 (780)	20.2 (499)	34.5 (850)	13.5 (333)

APPENDIX IV. Sampling methods for characterizing habitat structure of SOIC plots with and without bison and pigs on Santa Catalina Island, California. Habitat plots consisted of perpendicular 2-m x 20-m belt transects and a 30-m diameter circular plot (divided into quarters), centered on randomly selected midpoint.

Structural component	Method
Topography	
Slope	Angle of slope, measured with clinometer from midpoint.
Aspect	Direction of slope, measured with compass from midpoint.
Tree Cover	
Percent canopy cover	Mean densiometer reading at midpoint and at each end of perpendicular belt transects.
Canopy height	Overstory tree height, measured with clinometer.
Size of trees	Mean diameter at breast height (cm) of trees (DBH > 3.5 cm) in circular plot.
Diversity of trees	Richness and evenness of tree species in circular plot.
Frequency of broken branches	Mean number of broken branches (diameter > 2.5 cm) per tree in circular plot
Number of snags	Total number of snags (stem height > 2 m, DBH > 3.5 cm) in circular plot.
Size of snags	Mean diameter at breast height (cm) of snags (DBH > 3.5 cm) in circular plot.
Overstory tree dispersion	Mean distance (m) from midpoint to nearest overstory tree, in quarters of circular plot.
Ground Cover	
Number of shrubs	Mean number of shrubs (stem height 0.5 – 2 m, DBH < 3.5 cm) along perpendicular belt transects.
Vegetation height	Mean height (cm) of vegetation at midpoint and at each end of perpendicular belt transects.
Number of downed branches	Total number of downed branches (length > 0.5 m, diameter > 2.5 cm) in circular plot.
Litter depth	Mean depth of penetration (cm) by ruler into litter material at midpoint and at each end of perpendicular belt transects.
Litter type	Most common litter type at midpoint and at each end of perpendicular belt transects.
Ground Disturbance	
Disturbance by bison	Mean distance (cm) disturbed by bison along centerline of perpendicular belt transects.
Disturbance by wild pigs	Mean distance (cm) rooted by wild pigs along centerline of perpendicular belt transects.
Disturbance by rodents	Mean distance (cm) disturbed by rodents along centerline of perpendicular belt transects.
Game trails	Mean distance (cm) disturbed by game trails (deer, pigs, bison) along centerline of perpendicular belt transects.
Other disturbance	Mean distance (cm) disturbed by road construction, foot traffic, and unidentifiable causes along centerline of perpendicular belt transects.
Frequency of use by bison	
Dung piles	Total number of bison dung pats in circular plot.
Wallowing activity	Total number of circle quarters with wallowing activity.
Rubbing activity	Total number of trees and snags with clumps of bison hair on branches and/or stems.

APPENDIX V. Sampling methods for characterizing visual encounter survey plots for reptiles and amphibians in SOIC plots with and without bison on Santa Catalina Island, California. Habitat plots consisted of perpendicular 2-m x 20-m belt transects and a 30-m diameter circular plot (divided into quarters) centered on selected midpoint.

Structural component	Methods
Topography	
Slope	Angle of slope, measured with clinometer from midpoint.
Aspect	Direction of slope, measured with compass from midpoint.
Tree Cover	
Percent canopy cover	Mean densiometer reading at midpoint and at each end of perpendicular belt transects.
Canopy height	Overstory tree height, measured with clinometer.
Richness of trees	Total number of tree species in circular plot.
Number of snags	Total number of snags (stem height > 2 m, DBH > 3.5 cm) in circular plot.
Overstory tree dispersion	Mean distance (m) from midpoint to nearest overstory tree, in quarters of circular plot.
Ground Cover	
Density of shrubs	Mean number of shrubs (stem height 0.5 – 2 m, DBH < 3.5 cm) along perpendicular belt transects.
Vegetation height	Mean height (cm) of vegetation at midpoint and at each end of perpendicular belt transects.
Density of cover objects	Total number of rocks and logs in circular plot.
Litter depth	Mean depth of penetration (cm) by ruler into litter material at midpoint and at each end of perpendicular belt transects.
Litter type	Most common litter type at midpoint and at each end of perpendicular belt transects.
Ground Disturbance	
Disturbance by bison	Mean distance (cm) disturbed by bison along centerline of perpendicular belt transects.
Disturbance by wild pigs	Mean distance (cm) rooted by wild pigs along centerline of perpendicular belt transects.
Disturbance by rodents	Mean distance (cm) disturbed by rodents along centerline of perpendicular belt transects.
Game trails	Mean distance (cm) disturbed by game trails (deer, pigs, bison) along centerline of perpendicular belt transects.
Other disturbance	Mean distance (cm) disturbed by road construction, foot traffic, and unidentifiable causes along centerline of perpendicular belt transects.

APPENDIX VI. Sampling methods for characterizing habitat structure of mammal trapping grids in grassland, SOIC, and coastal sage scrub plots with and without bison on Santa Catalina Island, California. Habitat plots consisted of perpendicular 2-m x 20-m belt transects and a 20-m diameter circular plot (divided into quarters) centered on randomly selected trap.

Structural component	Methods
Topography	
Slope	Angle of slope, measured with clinometer from trap.
Aspect	Direction of slope, measured with compass from trap.
Tree Cover	
Percent canopy cover	Mean densiometer reading at trap and at each end of perpendicular belt transects.
Canopy height	Overstory tree height, measured with clinometer.
Size of trees	Mean diameter at breast height (cm) of trees (DBH > 3.5 cm) in circular plot.
Richness of trees	Total number of tree species in circular plot.
Number of snags	Total number of snags (stem height > 2 m, DBH > 3.5 cm) in circular plot.
Size of snags	Mean diameter at breast height (cm) of snags (DBH > 3.5 cm) in circular plot.
Overstory tree dispersion	Mean distance (m) from trap to nearest overstory tree, in quarters of circular plot.
Ground Cover	
Density of shrubs	Total number of shrubs (stem height 0.5 – 2 m, DBH < 3.5 cm) along perpendicular belt transects.
Richness of shrubs	Total number of shrub species in circular plot.
Density of cactus	Total number of cactus clumps ($\geq$ 3 cactus plants) in circular plot.
Vegetation height	Mean height (cm) of vegetation at trap and at each end of perpendicular belt transects.
Density of downed logs	Total number of downed logs (length > 1m, DBH > 3.5 cm) in circular plot.
Litter depth	Mean depth of penetration (cm) by ruler into litter material at trap and at each end of perpendicular belt transects.
Litter type	Most common litter type at trap and at each end of perpendicular belt transects.
Ground Disturbance	
Disturbance by bison	Mean distance (cm) disturbed by bison along centerline of perpendicular belt transects.
Disturbance by wild pigs	Mean distance (cm) rooted by wild pigs along centerline of perpendicular belt transects.
Disturbance by rodents	Mean distance (cm) disturbed by rodents along centerline of perpendicular belt transects.
Game trails	Mean distance (cm) disturbed by game trails (deer, pigs, bison) along centerline of perpendicular belt transects.
Other disturbance	Mean distance (cm) disturbed by road construction, foot traffic, and unidentifiable causes along centerline of perpendicular belt transects.
Frequency of use by bison	
Dung piles	Total number of bison dung pats in circular plot.
Wallowing activity	Total number of wallows in circular plot.

APPENDIX VIIa. Production potential of annual grass, perennial grass, and forbs during favorable and unfavorable years in vegetation classes used by bison on Santa Catalina Island, California for Management Option A (bison herd allowed to free-range over Zones 2, 3, and 4; Figure 2).

Vegetation class[1]	Production in favorable years (kg)[2]				Production in unfavorable years (kg)[2]			
	Annual grass	*Perennial grass*	*Forbs*	*Total*	*Annual grass*	*Perennial grass*	*Forbs*	*Total*
Primary range								
Valley and foothill grassland	1,785,843	172,751	284,927	2,243,522	729,676	70,584	116,418	916,678
Mule fat scrub	518	50	83	651	151	15	24	190
Non-native herbaceous	50,978	4,931	8,133	64,043	15,969	1,545	2,548	20,061
Riparian herbaceous	5,740	555	916	7,211	1,644	159	262	2,065
Secondary range								
Developed	23,540	2,277	3,756	29,573	8,996	870	1,435	11,301
Non-native chaparral/non-native woodland	11,857	1,147	1,892	14,896	4,792	464	765	6,020
Southern riparian woodland	48,767	4,717	7,781	61,265	18,731	1,812	2,989	23,532
Marginal range								
Coastal sage scrub	1,787,849	172,945	285,247	2,246,042	656,819	63,537	104,794	825,150
Island chaparral	2,808,036	271,632	448,016	3,527,683	1,167,666	112,953	186,299	1,466,918
Island woodland	19,187	1,856	3,061	24,104	8,590	831	1,370	10,791

[1] Primary (use greater than expected), secondary (used in proportion to availability) and marginal (lower than expected use) ranges are delineated on the basis of Chi-square tests ($P<0.05$) on vegetation class availability vs fecal counts or group observations.

[2] Based on 79.6% annual grass, 7.7% perennial grass, and 12.7%, as determined from biomass clip plots. We defined "favorable" years as average or above-average precipitation and "unfavorable" years as below-average precipitation.

APPENDIX VIIb. Production potential of annual grass, perennial grass, and forbs during favorable and unfavorable years in vegetation classes used by bison on Santa Catalina Island, California for Management Option B (small herd of bison confined to Zone 2; Figure 2).

Vegetation class[1]	Production in favorable years (kg)[2]				Production in unfavorable years (kg)[2]			
	Annual grass	*Perennial grass*	*Forbs*	*Total*	*Annual grass*	*Perennial grass*	*Forbs*	*Total*
Primary range								
Valley and foothill grassland	1,169,972	113,176	186,666	1,489,814	480,181	46,450	76,612	603,243
Non-native herbaceous	3,480	337	555	4,372	1,006	97	161	1,264
Riparian herbaceous	3,580	346	571	4,498	1,014	98	162	1,274
Secondary range								
Developed	12,047	1,165	1,922	15,135	5,399	522	861	6,783
Southern riparian woodland	23,305	2,254	3,718	29,277	10,065	974	1,606	12,644
Marginal range								
Coastal sage scrub	900,340	87,093	143,647	1,131,080	329,707	31,894	52,604	414,205
Island chaparral	1,598,655	154,644	255,062	2,008,361	680,901	65,866	108,636	855,403
Island woodland	12,968	1,254	2,069	16,292	5,836	565	931	7,331

[1] Primary (use greater than expected), secondary (used in proportion to availability) and marginal (lower than expected use) ranges are delineated on the basis of Chi-square tests ($P<0.05$) on vegetation class availability vs fecal counts or group observations.

[2] Based on 79.6% annual grass, 7.7% perennial grass, and 12.7%, as determined from biomass clip plots. We defined "favorable" years as average or above-average precipitation and "unfavorable" years as below-average precipitation.

APPENDIX VIIc. Production potential of annual grass, perennial grass, and forbs during favorable and unfavorable years in vegetation classes used by bison on Santa Catalina Island, California for Management Option C (small herd of bison confined to tour bus route within Zone 2; Figure 2).

Vegetation class[1]	Production in favorable years (kg)[2]				Production in unfavorable years (kg)[2]			
	Annual grass	*Perennial grass*	*Forbs*	*Total*	*Annual grass*	*Perennial grass*	*Forbs*	*Total*
Primary range								
Valley and foothill grassland	174,857	16,915	27,898	219,669	60,388	5,842	9,635	75,864
Non-native herbaceous	3,480	337	555	4,372	1,008	97	161	1,264
Secondary range								
Developed	8,160	789	1,302	10,251	3,650	353	582	4,585
Southern riparian woodland	9,271	897	1,479	11,648	4,072	394	650	5,116
Marginal range								
Coastal sage scrub	185,128	17,908	29,537	232,573	68,582	6,634	10,942	86,158
Island chaparral	267,282	25,855	42,644	335,781	110,227	10,663	17,586	138,476

[1] Primary (use greater than expected), secondary (used in proportion to availability) and marginal (lower than expected use) ranges are delineated on the basis of Chi-square tests ($P<0.05$) on vegetation class availability vs fecal counts or group observations.

[2] Based on 79.6% annual grass, 7.7% perennial grass, and 12.7%, as determined from biomass clip plots. We defined "favorable" years as average or above-average precipitation and "unfavorable" years as below-average precipitation.

APPENDIX VIII. Vascular plant species present in 24 plots (12 control and 12 experimental) in grassland (GL), scrub-oak dominated island chaparral (SOIC), and riparian (RIP) habitats during April and May 2001 and 2002 on Santa Catalina Island, California.

Species	GL	SOIC	RIP
DICOTYLEDONS			
Apiaceae			
***Bowlesia incana* R. Lopez & Pavón**		X	
Bowlesia. Native annual.			
***Sanicula arguta* J. Coulter & Rose**	X		
Sanicle. Native perennial.			
***Torilis* spp.**		X	
Hedge parsley. Non-native annual.			
Asteraceae			
***Baccharis pilularis* DC.**			X
Coyote brush. Native shrub.			
***Centaurea melitensis* L.**			X
Tocalote. Non-native annual.			
***Cirsium occidentale* (Nutt.) Jepson**			X
California thistle. Native biennual.			
Cotula coronopifolia L.			X
Brass buttons. Non-native annual/perennial			
Filago gallica L.	X		X
Narrow-leaved filago. Non-native annual.			
***Gnaphalium bicolor* Bioletti**			X
Two-tone everlasting, bicolored everlasting. Native biennial/perennial.			
Gnaphalium luteo-album L.			X
Weedy cudweed. Non-native annual.			
Hemizonia fasciculata (DC.) Torrey & A. Gray	X		
Common tarweed. Native annual.			
Hypochaeris glabra L.	X		X
Smooth cats ear. Non-native annual.			
Isocoma menziesii (Hook. & Arn.) G. Nelson			X
Coast goldenbush. Native shrub.			
Madia gracilis (Smith) Keck		X	X
Slender madia/tarweed. Native annual.			
Rafinesquia californica Nutt.		X	X
California chicory. Native annual.			
Sonchus asper (L.) Hill			X
Prickly sow thistle. Non-native annual.			
Sonchus oleraceus L.	X		
Common sow thistle. Non-native annual.			
***Stebbinsoseris heterocarpa* Nutt**	X		
Brown microseris. Native annual.			
Xanthium strumarium L.			X
Cocklebur. Native annual to California, introduced to Santa Catalina Island.			
Boraginaceae			
***Amsinckia menziesii* Lehm.**		X	X
Common fiddleneck. Native annual.			
Brassicaceae			
***Brassica nigra* (L.) Koch**			X
Black mustard. Non-native annual.			
Capsella bursa-pastoris (L.) Medikus	X		
Shepherd's purse. Non-native annual.			
***Hirschfeldia incana* (L.) Lagr.-Fossat**	X	X	X
Mediterranean mustard, short-podded mustard. Non-native perennial.			

Lepidium latipes (Hook)			X
Dwarf peppergrass. Native annual.			
***Lepidium nitidum* Torry & A. Gray**			X
Shining peppergrass. Native annual.			
***Lepidium strictum* (S. Watson) Rattan**			X
Peppergrass, prostrate peppergrass. Native annual.			
***Rorippa nasturtium-aquaticum* (L.) Hayek**			X
Water cress. Non-native perennial.			
Sisymbrium orientale L.			X
Oriental mustard. Non-native annual.			
Caryophyllaceae			
Silene gallica L.	X	X	X
Catchfly, windmill pink. Non-native annual.			
Stellaria media (L.) Villars		X	
Common chickweed. Non-native annual.			
Chenopodicaceae			
Atriplex semibaccata R. Br.	X		
Australian saltbush. Non-native subshrub/perennial.			
Beta macrocarpa Junak & Hoefs	X		
Wild beet. Non-native biennial.			
Chenopodium californicum (S. Watson) S. Watson		X	
California goosefoot, soaproot. Native perennial.			
Fabaceae			
Lotus purshianus (Benth.) Clements & E.G. Clements			X
Spanish clover. Native annual.			
Lotus strigosus (Nutt.) E. Greene			X
Bishop's lotus. Native annual.			
Medicago polymorpha L.	X		X
Bur-clover. Non-native annual.			
Medicago sativa L.	X	X	X
Alfalfa. Non-native perennial.			
Melilotus albus Medikus	X		X
White sweet clover. Non-native annual/biennial.			
Fagaceae			
***Quercus pacifica* Nixon & Mueller**		X	X
Island scrub oak. Native tree/shrub.			
Gentianaceae			
***Centaurium venustum* (A. Gray) Robinson**	X		
Canchalagua. Native annual.			
Geraniaceae			
Erodium brachycarpum (Godron) Thell.	X		X
Storkbill. Non-native annual.			
Erodium cicutarium (L.) L'Hér.	X	X	X
Redstem filaree. Non-native annual.			
Erodium moschatum (L.) L'Hér.	X	X	X
Whitestem filaree. Non-native annual.			
Hydrophyllaceae			
Eucrypta chrysanthemifolia (Benth.) E. Greene		X	
Eucrypta. Native annual.			
Pholistoma racemosum (Nutt.) Constance		X	
White fiesta flower. Native annual.			
Lamiaceae			
***Marrubium vulgare* L.**	X	X	X
Horehound. Non-native perennial.			
Malvaceae			
***Malva parviflora* L.**	X	X	X

Cheeseweed. Non-native annual.			
Plantaginaceae			
Plantago erecta			X
California plantain. Native annual.			
Polygonaceae			
***Polygonum arenastrum* Boreau**			X
Common knotweed. Non-native annual.			
Rumex crispus L.			X
Curly dock. Non-native perennial.			
Portulaceae			
***Calandrinia ciliata* (Ruíz Lopez & Pavón) DC.**			X
Red maids. Native annual.			
***Claytonia perfoliata* Willd.**		X	
Miner's lettuce. Native annual.			
Primulaceae			
***Anagallis arvensis* L.**	X		X
Scarlet pimpernel. Non-native annual.			
Ranunculaceae			
***Clematis ligusticifolia* (Nutt.)**			X
Virgin's bower, creek clematis. Native vine.			
Rubiaceae			
***Galium aparine* L.**		X	
Cleavers, goose grass. Native annual.			
Saururaceae			
Anemopsis californica (Nutt.) Hook & Arn.			X
Yerba mansa. Native perennial.			
Urticaceae			
Parietaria hespera B.D. Hinton		X	
Pellitory. Native annual.			
Urtica urens L.		X	
Dwarf nettle. Non-native annual.			
MONOCOTYLEDONS			
Juncaceae			
Juncus acutus L. ssp. *leopoldii* (Parl.) Snog.			X
Spiny rush. Native perennial.			
Juncus bufonius L.			X
Toad rush. Native annual.			
Liliaceae			
***Bloomeria crocea* (Torrey) Cov.**	X		
Common golden star. Native perennial.			
***Calochortus catalinae* S. Watson**	X		
Catalina mariposa. Native perennial.			
***Dichelostemma capitatum* (Benth.) A. W. Wood**	X	X	
Blue dicks. Native perennial.			
Poaceae			
Agrostis viridis Gouan			X
Water bentgrass. Non-native perennial.			
Avena barbata Link	X		X
Slender wild oats. Non-native annual.			
Avena fatua L.	X		
Wild oats. Non-native annual.			
Brachypodium distachyon (L.) Beauv.	X	X	X
False brome. Non-native annual.			
***Bromus carinatus* Hook & Arn.**	X		
California brome. Native perennial.			

Bromus diandrus Roth Ripgut brome. Non-native annual.	X	X	X
Bromus hordeaceus L. Soft chess. Non-native annual.	X	X	X
Bromus madritensis (L.) Red brome. Non-native annual.		X	X
Cynodon dactylon (L.) Pers. Bermuda grass. Non-native perennial.	X		X
Desmazeria rigida (L.) Tutlin Desmazeria. Non-native annual.			X
***Distichlis spicata* (L.) E. Greene** Saltgrass. Native perennial.			X
Gastridium ventricosum (Gouan) Schinz & Thell. Nit grass. Non-native annual.	X		
Hainardia cylindrica (Willd.) Greuter Thin tail. Non-native annual.	X	X	X
Hordeum intercedens Nevski Foxtail barley, vernal barley. Non-native annual.	X		
Hordeum marinum Hudson Mediterranean barley. Non-native annual.			X
Hordeum murinum L. Glaucous foxtail, foxtail. Non-native annual.	X	X	X
Lamarckia aurea (L.) Moench Goldentop. Non-native annual.			X
Lolium multiflorum Lam. Italian ryegrass. Non-native annual/biennial.	X		X
Lolium perenne (L.) English ryegrass, perennial ryegrass. Non-native perennial.	X		X
Nassella pulchra (A. Hithchc.) Barkworth Purple needlegrass. Native perennial.	X		
Phalaris minor Retz. Mediterranean canary grass. Non-native annual.	X		X
Poa annua L. Annual bluegrass. Non-native annual.			X
Polypogon interruptus Kunth Ditch beard grass. Non-native perennial.			X
Polypogon monspeliensis (L.) Desf. Rabbitsfoot grass. Non-native perennial.			X
Vulpia bromoides (L.) S.F. Gray Brome fescue. Non-native annual.	X		X
Vulpia myuros (L.) C. Gmelin Foxtail fescue. Non-native annual.	X		
Typhaceae			
***Typha domingensis* Pers.** Southern cattail, Narrow-leaved cattail. Native perennial.			X

APPENDIX IX: Description of methods used to estimate the probability of seed germination from individual bison hair clumps in wallows.

First, we assume that on average, 50% of the original mass of hair clumps will persist on the surface of wallows, and 11% of the original mass will persist below the soil surface based on results from wallow experiments described in text. Therefore, if the minimum final weight of a hypothetical clump of bison hair found resting on the surface of a wallow was 1.7 g, its original weight must have been $\geq$ 3.4 g. Similarly, if the minimum final weight of a hypothetical clump of bison hair found just below the soil surface in a wallow was 0.2 g, the original weight would have been approximately 1.8 g. Second, based on results from seed germination experiments in the University of North Dakota greenhouse, the following equation was derived to estimate sprouting/germination probability:

If:

P(A) = P(piece of clump on surface after 60 days)*
P(piece on surface will sprout)*P(original clump size $\geq$ 3.4 g)

P(B) = P(piece of clump below surface after 60 days)*
P(piece below surface will sprout)*P(original clump size $\geq$ 1.8)

Let:

P(A or B) = P(A) + P(B) + P(A and B)
= (0.800)(0.248)(0.341) + (0.350)(0.790)(0.603) –
(0.250)(0.248)(0.790)(0.341)
= (0.06765 + 0.16673) – 0.01670
= 0.218

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APPENDIX X. Number of bison removed in yearly roundups from Santa Catalina Island, California from 1996-2002, inclusive (Santa Catalina Island Conservancy, unpubl. data).

Year	Number of animals culled	% Γ	% E
1996	25	72	28
1997	80	66	34
1998	48	42	58
1999	0	--	--
2000	56	68	32
2001	0	--	--
2002	102	38	62

APPENDIX XI. Timeline-based description of a controversy over the ecological effects of a small herd of bison introduced to Colorado National Monument, Colorado between 1925 and 1928. Related to the observed and perceived negative effects and eventual ecological research to document those effects, the bison herd was eventually removed from the national monument after a series of public hearings over the economic and cultural significance of the bison herd to local communities/citizens.

Case History: Colorado National Monument

Colorado National Monument (COLM) encompasses approximately 7126 ha in west central Colorado. The vegetation is typical of xeric Great Basin forms, with a dominant shrub cover (*Sarcobatus vermiculatis* and *Artemisia tridentata*) and lesser cover by annual and perennial grasses and *Atriplex canescens* (Miller 1964). Although there is some evidence that bison were native to north central Colorado, there are no data to suggest that bison ever inhabited the area now encompassed by COLM (Miller 1964; Wasser 1977). Beginning in 1925, bison were introduced to an 1165 ha fenced section of the monument (approximately 0.06 times the size of Santa Catalina Island) as a tourist attraction (Wasser 1977). Significant damage to the park was noted as early as 1943, and a control program was instituted in 1945. Eventually, however, the National Park Service (NPS) opted to remove the entire bison population, both for the integrity of the COLM ecosystem and the health of the bison. Below we provide a detailed timeline of bison management in COLM.

1923: Funds are obtained to fence an 1165 ha of COLM (Wasser 1977).

1925-1928: Eight bison are introduced to COLM as a tourist attraction (Wasser 1977).

1938: A regional biologist with NPS recommends that the bison herd be maintained at $\leq$ 20 animals due to the limited amount of suitable range (Wasser 1977).

1942: The herd reaches its maximum known size (approximately 46 bison) (Wasser 1977).

1943: The range is considered to be in very poor condition. Plans are made to reduce the bison population to approximately 20 animals, but no significant action is taken until 1945 (Wasser 1977).

1945-1969: Periodic culls of the herd are made, with the goal of maintaining 10 to 20 bison. There are no known culls after 1969 (Wasser 1977).

1975-1977: A study is commissioned by NPS to examine the potential ecological effects of bison in COLM. Park personnel are concerned that bison are causing damage to the COLM ecosystem and that bison are malnourished, diseased, and/or inbred. Results of the study suggest that bison grazing has significant impacts on the soils of the monument and that plant species favored by bison as forage are being overutilized (Wasser 1977). In addition, the bison appear to be smaller than plains bison (see also Berger and Cunningham 1994) and during drought years many animals have prominent ribs and a "languid disposition". Wasser (1977) recommends that the NPS should (1) reduce the herd from 31 animals to 10 animals, (2) regularly supply phosphorus and protein supplementation, (3) improve existing water supplies, (4) use fire as a management tool to increase the growth of grasses and forbs and to inhibit the growth of shrubs potentially toxic

to bison (e.g., *A. tridentata*), and (5) hire a resource manager to supervise the bison herd and other wildlife in COLM.

1982: The Soil Conservation Service of the USDA compiles a soil and water conservation plan for COLM. The agency estimates that only 60% of the fenced area is available for use by bison due to steep slopes. The range is considered to be in a declining trend and from clip plot data and range surveys, the current carrying capacity of the COLM bison range is estimated at 3 animals (10% of the 1982 population) (Mesa Conservation District 1982). Even at that population level, the agency suggests that the grazing regime will have to be closely managed (e.g., by rotational grazing, seeding, etc.) to prevent a further decline in the quality of the range.

1983: Park Service personnel hold a month of public hearings to discuss the future of bison in COLM (Daily Sentinel 1983a). The NPS feels that a bison herd is not appropriate for COLM due to: (1) the severely stressed condition of the COLM ecosystem (Bernard 1983), (2) the potential for competition between bison and native wildlife (Daily Sentinel 1983b), and (3) the general poor health of the bison, as indicated by low reproductive rate and small body size (Bernard 1983, Crowell 1983, Daily Sentinel 1983c). Public opinion is varied. At one end of the spectrum, there is support for the decision because of the condition of the bison and the park (Bernard 1983, Crum 1983), but on the other end, the decision is considered inappropriate, in part because of the historical significance of the bison (Bernard 1983, Kimzey 1983, Lewis 1983). Ultimately, NPS decides to remove the remaining 35 to 38 animals; most are shipped to Badlands National Park, South Dakota (Daily Sentinel 1983b, Fruita Times 1983).

1984: Funds are requested to begin an intensive restoration program for the area of COLM grazed by bison, including removal of exotic plants, and restoration of soils and native vegetation (Colorado National Monument 1984).