HISTORY, HABITAT USE AND MANAGEMENT OF BISON ON CATALINA ISLAND, CALIFORNIA

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Abstract—Millions of American bison (*Bison bison*) once roamed prairies and other habitats of North America until widespread hunting in the 1800s decimated the species. Intensive conservation efforts in the early 1900s averted extinction by protective management and reintroductions to parks and natural areas. Related to their wide ecological tolerances, some bison populations now occur in areas not historically occupied by the species, including Catalina Island. In the period between 1924 and 1935, 24 bison were introduced to Catalina Island. By protective management and natural reproduction, the Catalina bison herd grew until nearly 400 animals roamed the island by 1969, when a program of regular culls was implemented to maintain a target population of 250–350 animals. The native fauna of Catalina Island did not include large ungulates, which has led to concern regarding the ecological effects of bison on native plants and animals. The Catalina Island Conservancy, a non-profit organization that owns and manages 88% of the island, has been actively working to protect and restore native flora and fauna including the removal of nonnative species. Notwithstanding the Conservancy's conservation mission, bison are culturally and economically significant to island residents, therefore making management of bison on Catalina Island controversial. Herein we review the history of bison on Catalina Island, provide detailed information on patterns of historic and current habitat use, qualitatively evaluate the importance of bison for tourism, and review multiple options for future management based on an island-wide model of carrying capacity and a conservation agenda of restoring the native flora and fauna of the island.

Keywords: bison, carrying capacity, conservation, restoration, tourism

INTRODUCTION

The history of the American bison (*Bison bison*) in mainland North America is well known. Prior to European settlement, the species was widely distributed in large numbers across prairie grasslands and other habitats. Following indiscriminate slaughter in the 1800s only a few hundred remained by 1900 (Shaw 1999). Protective management and intensive conservation efforts in the early 1900s averted extinction, however, when small populations of bison were reestablished in numerous national, state, and provincial parks in the United States and Canada, and on some private ranches (Berger and Cunningham 1994). Although bison are usually considered a prairie species, they occupied a diversity of habitats ranging from boreal forests to desert regions (Van Vuren 1987). Associated with their wide ecological tolerances, some bison populations now occur in areas not previously occupied by the species, including Catalina Island, California.

Bison are not native to coastal regions of California or the Channel Islands (Roe 1970). Additional historical detail will follow, but between 1924 and 1935, 23 bison were introduced to Catalina Island to film a movie (Gingrich 1974), and the small bison herd increased until around 400 bison roamed across the island by the 1960s (Lott and Minta 1983a). Due to concerns of overgrazing by livestock, bison, and other nonnative herbivores (feral pigs [*Sus scrofa]* and feral goats [*Capra hircus*]), a culling program was implemented in

1969. Bison are periodically captured in corrals and shipped off the island to buyers in different parts of the United States. Since 1970 the Catalina bison herd has been actively managed to maintain a smaller population and minimize their potential negative effects on native plants and animals.

The introduction of nonnative species to new areas is an important conservation problem in general but it is especially problematic on islands (Savidge 1987, Coblentz 1990, Cree et al. 1995), which typically have higher proportions of endemic species than mainlands and are more prone to invasion (Lodge 1993). Native organisms on islands are particularly vulnerable to pressures exerted by introduced species because they evolved in relative isolation under reduced interspecific competition, grazing, and predation (Bowen and Van Vuren 1997). Related to increased recognition of ecological problems caused by introduced species, the Santa Catalina Island Conservancy (hereafter Conservancy) implemented an active restoration program in the 1990s that included efforts to control weedy plants and eradicate feral goats and pigs (Schuyler et al. 2002). Bison are one of two remaining widespread free-ranging nonnative ungulates on the island; the other is mule deer (*Odocoileus hemionus*), which were introduced to the island in the 1930s and are currently abundant. Because of their size, nutritional needs, and gregarious nature, bison have the potential to substantially influence native plant and animal communities on Catalina Island (Damhoureyeh and Hartnett 1997, Fritz et al. 1999).

The small town of Avalon on Catalina Island was already a tourist destination in the early 1900s when bison were introduced, and as the bison herd grew it was rapidly embraced culturally and as another draw for tourism. Currently over one million visitors visit Catalina Island yearly, attracted by the diverse recreational opportunities, multiple hotels and resorts, and wildlife viewing. Many tourists and residents take advantage of Jeep® or bus tours, bicycling routes, hiking trails, and campgrounds to visit the island interior where it is advertised they will have the opportunity to observe American bison. Thus, and although bison are not native to Catalina Island, the combined cultural and economic significance of the species requires that the Conservancy consider herd management options that incorporate both ecological and socio-economic consequences of maintaining a free-ranging bison herd on the island.

To develop long-term and sustainable approaches to bison management, our objectives in this study were to (1) provide a detailed account of the history of bison on Catalina Island, (2) summarize and compare patterns of habitat use between the 1970s and present, and (3) review different management approaches for bison on Catalina Island that vary by emphases on economic and conservation considerations. We anticipate that a complete historical account of bison on Catalina Island will help clarify confusion regarding the population while providing important context for future studies. We also present a brief background on tourism as a form of recreation on Catalina Island, including a qualitative evaluation of the economic importance of bison for tourism. Finally, because detailed ecological research on the Catalina bison population was conducted in the 1970s prior to establishment of fences aiding feral pig and feral goat removal, a comparison of historic and recent patterns of habitat use may reveal whether the fences restrict or focus bison activities in some areas.

STUDY AREA

Description

Catalina Island is a 194-km^2 island located 40 km south of coastal Los Angeles, in Los Angeles County. Elevation on the island ranges from sea level to 640 m with a topography dominated by a northwest-southeast mountain range containing a series of lateral canyons (Schuyler et al. 2002). The climate is Mediterranean with relatively mild temperatures throughout the year and a long-term mean annual precipitation of 290 mm mostly occurring between November and April (Schoenherr et al. 1999, Santa Catalina Island Conservancy 2002). There are three major upland habitat types on the island: (1) coastal sage scrub, characterized by coastal sage (*Artemisia californica*) and prickly pear cactus (*Opuntia littoralis*); (2) grassland, dominated by exotic annual grasses and forbs, such as wild oats (*Avena fatua*) and storksbill (*Erodium* spp.), interspersed

with native bunch grasses (*Nasella* spp.); and (3) island chaparral, represented by evergreen and drought-resistant shrubs and low trees such as island scrub oak (*Quercus pacifica*) and lemonade berry (*Rhus integrifolia*). Riparian plant communities are limited to a few permanent or ephemeral streams in relatively deep lateral canyons and marshy wetland areas adjacent to artificial water impoundments (ponds) and one natural lake. Representative riparian plant species include cottonwood (*Populus trichocarpa*), willow (*Salix* spp.) various sedges and rushes, and mule fat (*Baccharis pilularis;* Knapp 2002).

Ecological Resources

Los Angeles County has recognized 22 Sensitive Ecological Areas on Catalina Island (Ecological Restoration Department Map of Catalina Island). Sensitive Ecological Areas (SEAs) are diverse but may include habitat for rare or endangered species, represent regionally restricted biotic communities/assemblages, encompass areas of important habitat for species or groups of species for breeding, nesting, or migration, represent vestiges of undisturbed biotic communities, or are unique ecological areas of particular scientific interest (Anonymous 2002). Distributed across the island and within many of these 22 SEAs are six and 26 extant species of plants endemic to Catalina Island and the Channel Islands, respectively (Thorne 1976, Nixon and Muller 1994, Junak et al. 1995), and five endemic subspecies of terrestrial vertebrates (Collins and George 1990, Schoenherr et al. 1999).

Introduced Herbivores

Although no large native grazing animals historically occurred on Catalina Island, multiple species of domestic and feral ungulates were established during the past two centuries. Horses (*Equus caballus*), domestic cattle (*Bos taurus*), and sheep (*Ovis aries*) were introduced to the island in the 1800s, and ranching operations involving these ungulates were active in the island interior by the 1860s. All sheep were removed in the early 1920s. Bison were first introduced in 1924 and mule deer and feral pigs were introduced in the early and mid 1930s, respectively. After domestic cattle operations in the island interior ceased around 1960 there was growing concern over grazing impacts and disturbances promulgated by bison, feral pigs and goats (Baber and Coblentz 1986). After 1970 culling was used to maintain lower bison herd levels and several early control efforts directed at feral pigs and feral goats were initiated in the 1980s and early 1990s (reviewed by Garcelon et al. 1993). In the mid-1950s, the California Department of Fish and Game implemented a hunting program designed to control the burgeoning mule deer population (Melody and Garcelon 1999). This program has produced sporadic results and mule deer are considered a potential threat to many natural resources on the island. In the mid 1970s the island was considered to be recovering from overgrazing by domestic livestock. More recently the island can be considered as recovering from the activities of feral goats and feral pigs, following an intensive feral animal removal program that was initiated in the late 1990s and has resulted in the island-wide eradication of feral goats by 2002 and nearly all feral pigs by late 2003 (Schuyler et al. 2002).

Tourism

The potential for Catalina Island as a destination for tourism was recognized in the late 1880s by George Shatto who purchased the island with the goal of developing it as a resort. Shortly thereafter the Banning Brothers purchased Catalina Island, formed the Santa Catalina Island Company, and established the island as a tourist destination by developing hotels and campgrounds and initiating a passenger steamer service to the island. William Wrigley Jr. subsequently purchased the island in 1919 with plans to further develop it as a resort. Wrigley also held a strong conservation ethic, and under his and subsequent family members' guidance the Island Company initiated various conservation practices from the 1920s to the 1970s. In 1972 the Wrigley and Offield families formed the non-profit Santa Catalina Island Conservancy, which now owns and oversees conservation and restoration-oriented management of 88% of Catalina Island. The mission of the Conservancy is to serve as responsible stewards of the island through a balance of conservation, education, and recreation. Recreation includes tourism, and in association with the Island Company and other businesses the Conservancy provides visitors the opportunity to tour the island

interior by bus, Jeep®, bicycle, or on foot. A small airport near the middle of the island (Airport-In-The-Sky) is used by many to visit the island by private airplane.

The Island Company and Adventure Tours offer several short bus tours around the Avalon area. In addition, the Inland Motor Tour takes many visitors into the interior of the island where advertisements highlight the opportunity to view bison. This 45 km tour leaves Avalon via the main road to the Isthmus and includes stops at the Airport-In-The-Sky and El Rancho Escondido, both located in zone 2 (see below and Fig. 1). Bison are often observed at several points along this main road but frequently congregate in and around a shallow basin-like area near the Airport-In-The-Sky. Bison are also regularly observed along the main road near El Rancho Escondido, where sage scrub habitat was cleared and converted into grasslands when livestock operations were active in the island interior.

METHODS

History of Bison on Santa Catalina Island

We used a variety of mostly unpublished information to evaluate changes in bison population numbers over time. Records from periodic roundups were reviewed to estimate the number of bison shipped off the island and to estimate body masses for animals of different age and sex. Whenever possible, records from sales receipts and shipping receipts were used to cross reference information from roundups and determine actual numbers of animals removed from the island. Data on known bison mortalities were compiled from Conservancy records, direct observation, and reports from Conservancy personnel and volunteers. Data from literature references, Conservancy records, and periodic censuses were used to qualitatively track the size of the bison population from the 1930s to present. In recent years, multiple censuses of the bison herd were often undertaken. Data on estimated populations for years with multiple counts were taken as the number of bison enumerated in the late summer-fall period after adult cows had produced offspring. No census or count data were available after August 2002 so we estimated the number of bison likely present in August 2003 by subtracting the numbers of animals shipped from the island in October 2002 and adding in an estimated number of newborn calves based on average pregnancy rates for adult female bison on Catalina from serum progesterone levels (Sweitzer et al. 2003). Similarly, we estimated the projected number of animals present in January 2004 by subtracting the number of animals shipped off in November 2003 from the estimated August 2003 number.

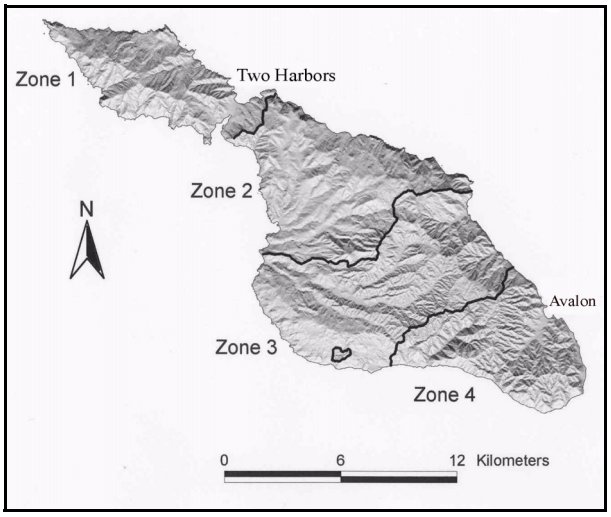

Figure 1. Feral animal removal zones on Catalina Island, CA as delineated by three cross-island fences. Zone 1 is bison free whereas zones 2, 3, and 4 are occupied by bison. Figure modified from Schuyler et al. (2002).

Habitat Use

Information on habitat use by bison on Catalina Island was generated to understand how recently established cross-island fences may be altering bison movements and to identify areas where bison concentrate their activities. Bison currently have relatively unrestricted access to all areas of the island east of the Isthmus, where prior studies indicated they focus their foraging, wallowing and loafing activities in grassland, coastal sage scrub, island chaparral, and riparian habitats (Fig. 1; Lott and Minta 1983a, Galland 1989). Riparian habitats on the island include riparian corridors and marshy wetland areas associated with artificial water impoundments and Echo Lake (the only natural lake on the island). Bison were restricted from moving west of the Isthmus (zone 1) in the early 1990s by a new cross-island fence immediately east of the Isthmus (Fig. 1). Also, between December 1998 and July 1999 two more cross-island “feral

animal removal (FAR) fences" were established in support of a major eradication effort for feral pigs and feral goats (Schuyler et al. 2002). The FAR fences delimited four hunting zones from the northwestern area of the island west of the Isthmus to the southeastern area of the island including Avalon (Fig. 1). Although FAR fences include three modified cattle guards designed to permit bison to move among zones 2, 3, and 4, crossing points are limited and FAR fences may have restricted bison movements and habitat use after 1999.

Data on general aspects of habitat use by bison prior to 1999 were summarized from a review of the published literature, whereas data on current habitat use were collected as part of a larger study from January 2001 to May 2003 on the population ecology and ecological effects of bison on Catalina Island (Sweitzer et al. 2003). During the period from February 2001 to August 2002 we collected data on locations of bison groups noted during a variety of research activities, and performed transect-based surveys for dung to evaluate habitat use. For all bison groups observed over the course of five periodic ground-based censuses, regularly scheduled road surveys, and ad libitum observations, we recorded information on the location, group size, and age and sex composition of bison groups. We discriminated among four age and sex classes (calf, yearling, cow, bull) based on size, color, horn shapes, conformation and other traits (Berger and Cunningham 1994) and sex was assessed for yearlings whenever possible but not for calves. The five censuses occurred between April 2001 and August 2002 when we systematically searched island zones 2, 3, and 4 from the ground along a network of roads, including hiking into areas with poor visibility. During each census we marked the location of all bison groups on topographic maps and later used geographic information system (GIS) software (ArcView GIS 3.2; Environmental Systems Research Institute Inc. 1992–1999; hereafter ArcView) to assign approximate Universal Transverse Mercator (UTM) coordinates. Road surveys were conducted from February 2001 to July 2002 when we noted the primary habitat association for each group observed and estimated their geographic locations by applying Cartesian geometry to data on UTM coordinates for observer locations and estimated offset angles and distances to bison groups. Coordinates for observer locations were obtained using a Garmin GPS III Plus (Olathe, Kansas, USA), whereas a laser range finder, compass, and clinometer were used to measure offset distances and slopes to the approximate centers of bison groups. ArcView was used to (1) assign bison groups to one of 17 habitat classes (Appendix I), (2) measure the distance of groups to the nearest semi-permanent water (horse troughs, Echo Lake, 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.

Although bison group observations provided 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. To estimate habitat selection by bison on the island we conducted multiple bison dung belt transects (2 m × 100 m) across areas of the island with a recent history of use by bison (i.e., zone 1 was not included; Fig. 1) and within three focal habitats: grasslands, scrub oak-dominated island chaparral (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, so it was unlikely that fecal deposition rates differed between habitats by activity (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 most bison (95%) focused their activities in areas with <25° slope, and limited dung transects to such areas. ArcView was used to superimpose a 100-ha UTM grid (1000 x 1000 m) on the remaining sampling space and to randomly identify 20 possible dung transect start points within each cell. From the 20 potential dung transect start points within each cell, we selected two points that were within the two dominant focal 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. All bison dung piles along each dung transect 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 utilized (1) significantly more often than expected relative to availability (primary range), (2) in proportion to availability (secondary range), and (3) less than expected relative to availability (marginal range). Generalized Linear Models (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.

Bison Management

Notwithstanding their cultural and economic significance, future management of bison on Catalina Island should be compatible with the goal of maintaining viable native plant and animal populations and the different ecological processes that support those species over the long term. In association with research by Sweitzer et al. (2003) we developed a range of management options for consideration by the Conservancy that included: (1) continued maintenance of a free-ranging bison herd over most of the island excluding zone 1 and Avalon (2003 status quo option), (2) maintenance of a relatively small bison herd in zone 2 including the key portions of the Inland Motor Tour bus route encompassing the Airport-In-The-Sky and El Rancho Escondido, (3) restricting a small bison herd to a part of zone 2 encompassing the Airport-In-Sky and El Rancho Escondido, and (4) complete removal of the population. Fig. 2 provides maps of areas covered by the first three management scenarios.

To adequately consider these different management options a detailed model was used to estimate the optimum stocking density or carrying capacity of bison for Catalina Island (Sweitzer et al. 2003). Details on this carrying capacity model are available elsewhere (Sweitzer et al. 2003), but it integrated information on habitat use and diets of bison on Catalina to identify key forage classes and suitable range sites (areas with slopes <25° and moderate to no erosion), used data on body masses of bison on the island to estimate average annual forage intakes, and used estimated productivity values for island plant communities and key forage classes on different underlying soil types to estimate annual forage production (Cureton et al. 1955, Sweitzer et al. 2003). Also, and as further detailed by Sweitzer et al. (2003), the model was

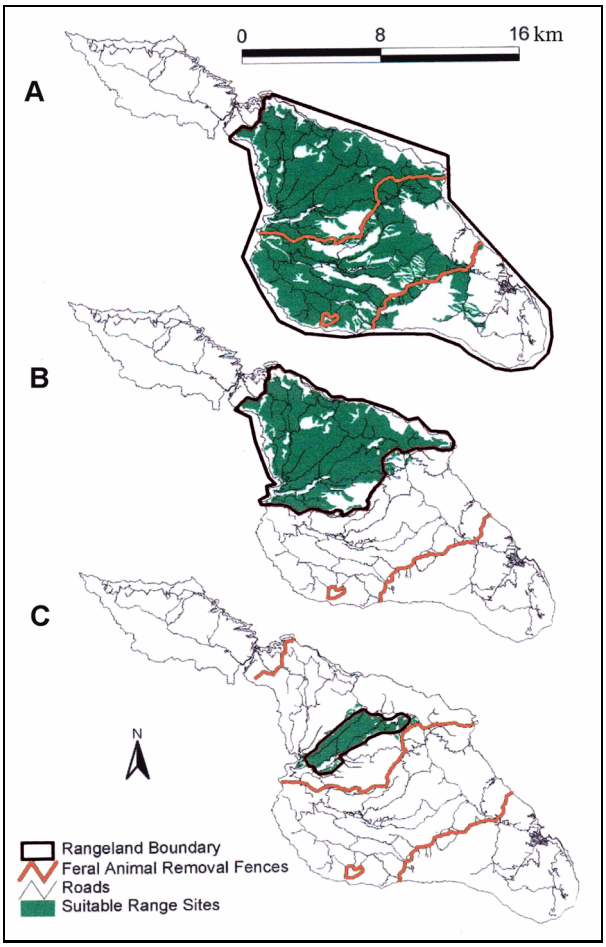

Figure 2. Maps of Catalina Island identifying three potential approaches to management of bison on carrying capacities. Option A is the "status quo" approach with bison continuing to range over zones 2, 3, and 4. Option B would restrict bison to the area defined as zone 2, including key portions of the Inland Motor Tour. Option C would restrict bison to a small portion of zone 2. Suitable range sites were areas with moderate to no erosion on slopes <25°.

designed to allow for altering the proportion of plant material that could be eaten and still preserve sufficient leaf area for plant recovery. By varying this "allowable use factor" we estimated the carrying capacity of bison in different areas of the island under a standard livestock grazing management regime (most or all consumable plant material considered available for bison use), moderate grazing regime (equal amounts of consumable plant material available to bison and native herbivores/consumers), and a light grazing regime (25% of consumable plant material available to bison and 75% reserved for native herbivores/consumers; Sweitzer et al. 2003).

Importance of Bison for Tourism

Although it is difficult to assign economic value to the cultural significance of bison, it is possible to appreciate their value for tourism using passenger and ticket sale data for bus and Jeep® tours. We used Conservancy records to summarize data on the annual numbers of passengers on Inland Motor Tours and Jeep® EcoTours for the period from 1999 to 2002. We calculated the estimated annual income from these tours based on current individual ticket prices (http://scico.com/html/discovery_land_tours_fr.html, accessed November 2003). Ticket prices for the Inland Motor Tour vary by age; tickets for adults and seniors are $47.25 and $42.50, respectively, whereas tickets for children are $23.75. To estimate monetary income from the annual numbers of passengers on the Inland Motor Tour we calculated a weighted average ticket price by assuming that 50% of annual passengers were adults, 25% were seniors and 25% were children. Notably, visitors take Inland Motor Tours and Jeep® EcoTours for other reasons besides seeing bison, and our purpose for summarizing these data was to provide a qualitative appreciation of bison-related tourism. For example, at least six other concessionaires offer tours into the interior of Catalina Island but we did not have ready access to passenger ticket sales/prices, nor did we attempt to compile data on sales of bison-related gifts, cards, etc., that are popular in the many shops in Avalon and at the Airport-In-The-Sky.

RESULTS

Management History

After the initial introduction of 14 bison to Catalina in 1924, a number of additional animals were transported to the island as replacements for illegally killed animals or to improve the genetics of the herd. In fall 1934, ten years after the original 14 animals were introduced, an additional nine bison were brought to the island to augment the herd (Table 1). Between 1934 and 1969 two bison were known to have been illegally shot, and the Island Company required the perpetrators to replace the animals with bison purchased and shipped from the mainland (Gingrich 1974). In 1969 and 1971 a combined total of 22 animals were introduced from different mainland areas to improve herd genetics, and then 12 more mainland bison were added to the herd in 1996 for similar purposes (Table 1).

Table 1. Summary of available data on numbers of bison added to the bison herd on Catalina Island (including animals from the original introduction) during the period from 1924 to the present. Data were compiled from Santa Catalina Island Company records, Conservancy records, and other documents or publications.

Year	Male calves	Yearling males	Yearling females	Adult males	Unknown sex/age	Totals	Source of bison
1924	-	-	-	-	14	14	Unknown
1934	-	-	-	-	9	9	Unknown
1934	-	-	-	-	1	1	Unknown
1968	-	-	-	-	1	1	Unknown
1969	15	-	-	-	-	15	Gillette, Wyoming
1971	-	7	-	-	-	7	Moiesa, Montana
1996	-	2	4	-	-	6	Palomar Mountain, California
1996	-	6	-	-	-	6	Loretta Leavitt
Totals	15	15	4	-	25	59	

Table 2. Summary of available data on minimum numbers of bison captured and shipped back to the California mainland from Catalina Island from 1969 to November 2003. Data were compiled from Santa Catalina Island Company records, Conservancy records, and various other documents.

	Males				Females				Unk. sex			
Year	Calves	Yearl	Adult	Unk	Calves	Yearl	Adult	Unk	Calves	Yearl	Adult/unk	Total
1969–73	–	–	–	97	–	–	–	10	–	–	–	107
1974	–	–	–	–	–	–	–	–	–	–	20	20
1976	–	–	27	–	–	–	5	–	–	–	–	32
1977	–	70	–	–	–	32	6	–	–	–	–	108
1978	–	–	"Minor shipment of young bulls"					–	–	–	–	Unk
1979	–	–	"Substantial heifer sale"				–	–	–	–	–	Unk
1980	–	–	"Buffalo sales lower than anticipated"						–	–	–	Unk
1984	–	–	–	–	–	–	–	65	–	55	–	120
1985	–	–	36	–	–	–	–	–	21	10	–	67
1986	–	–	8	–	–	–	23	–	5	28	–	64
1987	–	–	59	–	–	–	57	–	–	116	–	232
1988	–	–	49	–	–	–	44	–	–	–	–	93
1989	–	–	6	–	–	–	4	–	–	–	–	10
1990	–	–	15	–	–	–	68	–	26	132	–	241
1991	–	–	7	–	–	–	13	–	0	39	–	59
1992	–	–	20	–	–	–	5	–	0	19	–	44
1993	–	7	15	–	–	56	16	–	–	–	–	94
1994	–	29	17	–	–	30	9	–	–	–	–	85
1995	–	9	27	–	–	2	25	–	–	–	43	106
1996	–	14	7	–	–	18	26	–	–	–	–	65
1997	3	58	18	–	4	24	30	–	–	–	–	127
1998	–	14	4	–	–	20	8	–	–	–	2	48
2000	–	9	29	–	3	9	34	–	–	–	–	84
2002	13	1	25	–	–	4	59	–	–	–	–	102
2003	–	–	30	–	–	17	58	–	–	–	–	105
Column totals	16	211	399	97	7	212	490	75	52	399	65	2,013

We uncovered relatively limited information on the estimated size of the bison herd on Catalina Island from shortly after their introduction until the mid 1990s. Conservancy records and several references in the literature suggested that the bison population had increased to 400 animals by 1969 and then further grew to a probable all time high of around 524 animals in 1987 (Fig. 3; Gingrich 1974, Lott 1981, Lott and Minta 1983a). After the mid 1990s and including this study, censuses or counts of the bison herd were more regular (Table 3). From the mid 1990s to fall 2003 active management efforts maintained the herd around 275–300 animals (Fig. 3). The fall 2003 reduction to an estimated 206 animals marked the start of a program to manage the herd size at 150–200 animals.

In 1969 a culling program was developed to reduce and stabilize the herd, which marked a shift from protective management to managing bison at lower herd levels to protect against overgrazing (O'Malley 1994). Between 1969 and 1977 approximately 267 bison were sold and shipped to the mainland (Table 2). Records on bison shipments were sparse between 1978 and 1983, but several notes we did find suggested that significant numbers of animals were removed. Records were more complete from 1984 to 2003 when a minimum total of 1,745 bison were sold and shipped off the island (Table 2). Early on in the culling program predominantly young bull bison were rounded up for removals, whereas in later years approximately equal numbers of male and female bison were

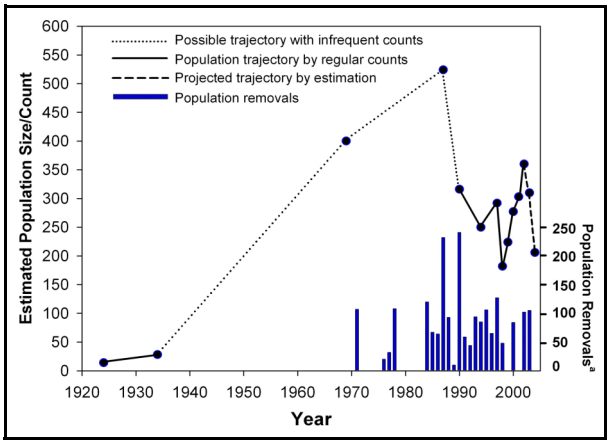

Figure 3. Estimated trend for the size of the bison population (line), and minimum population removals of bison (columns) on Catalina Island, CA. Records on the numbers of bison on the island from 1935 to the mid-1980s were limited. Methods used to estimate bison numbers after 1997 were primarily ground-based counts using the island road network. Minimum population removals were based on sales and shipping records (see Methods section).

removed (Table 2). Data on natural or management-related bison mortalities were very limited except for between 1994 and 2002 when managers reported 49 bison died or were euthanized due to poor health or injury.

Tourism

Between 1998 and 2002 an average of 102,824 tourists took the Inland Motor Tour to interior Catalina Island, which generated an estimated $4,133,541 annually over the period (Table 4). Similarly, as part of Jeep® EcoTours from 1999 to 2002 an average of 1,138 individuals visited the interior of Catalina Island each year for an estimated average of $89,882 in annual sales (Table 4). For the four years with data for both Inland Motor Tours and Jeep® EcoTours, there were an estimated 104,435 individual tourist excursions into the island interior, generating around $4,242,412 annually from these types of vehicle-based tours (Table 4).

Table 3. Summary of available census/count data for bison on Catalina Island from 1924 to August 2002. Data were compiled from Santa Catalina Island Company records, Conservancy records, and various other documents. See Methods for additional details.

Year	Period/ month	Yearl male	Adult male	Yearl female	Adult female	Unk sex calves/yearl	Unk sex adults	Unk sex/ age	Total
1924	December	-	-	-	-	-	-	14	14
1934	Summer	-	-	-	-	-	-	19	19
1934	Fall	-	-	-	-	-	-	28	28
1987	Summer	-	-	-	-	-	-	524	524
1990	February	-	-	-	-	-	-	316	316
1994	December	-	-	-	-	-	-	250	250
1997	August	-	-	-	-	89	203	0	292
1998	January	-	24	-	84	38	-	50	196
1998	September	-	-	-	-	-	-	182	182
1998	September	-	-	-	-	-	-	118	118
1999	April	-	-	-	-	-	-	166	166
1999	November	15	50	18	109	19	-	13	224
1999	December	27	41	13	120	-	-	-	201
2000	April	-	48	-	141	33	-	55	277
2001	April	3	50	13	128	38	3	44	279
2001	August	16	57	14	136	67	3	10	303
2001	November	7	57	3	123	64	10	36	300
2002	April	7	62	16	132	23	20	72	332
2002	August	14	95	14	157	62	12	6	360
2003[a]	August	-	-	-	-	-	-	-	310
2004[b]	January	-	-	-	-	-	-	-	206

[a] Estimated by subtracting the numbers of animals shipped off in October 2002 and adding in the estimated number of newborn calves in spring 2003 based on the estimated pregnancy rates of adult female bison from data on serum progesterone levels (Sweitzer et al. 2003).

[b] Projected by subtracting the numbers of bison that were shipped off the island in November 2003.

Table 4. Summary of recent data on tourist visits to the interior of Catalina Island on the Inland Motor Tour bus or by Jeep® EcoTour. At least six other companies provide tourist access to inland areas of Catalina Island as part of other recreational activities. Data are from Conservancy records.

	Inland Motor Tours		Jeep® EcoTours		Combined tours	
Year	Total people	Ticket sales ($)[a]	Total people	Ticket sales ($)	Total people	Ticket sales ($)
1998	100,935	4,057,587	-	-	-	-
1999	113,053	4,544,731	1,102	87,058	114,155	4,631,789
2000	111,337	4,475,747	1,118	88,322	112,455	4,564,069
2001	90,588	3,641,638	914	72,206	91,502	3,713,844
2002	98,209	3,948,002	1,417	111,943	99,626	4,059,945
Averages	102,824	4,133,541	1,138	89,882	104,435	4,242,412

[a] Estimated ticket sales were calculated based on advertised ticket prices in November 2003 (http://scico.com/html/discovery_land_tours_fr.html). Sales estimates for Inland Motor Tours were calculated as a weighted average of ticket prices for adults, seniors, and children (see Methods).

Current 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 (Fig. 4). Because bison were restricted from ranging into zone 1 by the FAR fence and seldom moved past the cattle guard near Haypress reservoir into zone 4, the activities of bison were focused in the central portion of the island (zones 2 and 3; Fig. 4). The majority of the bison groups (98%) were observed in zones 2 and 3, with a heavy concentration of bison activity around the centers of these areas (Fig. 4). Approximately 87% of all bison groups were

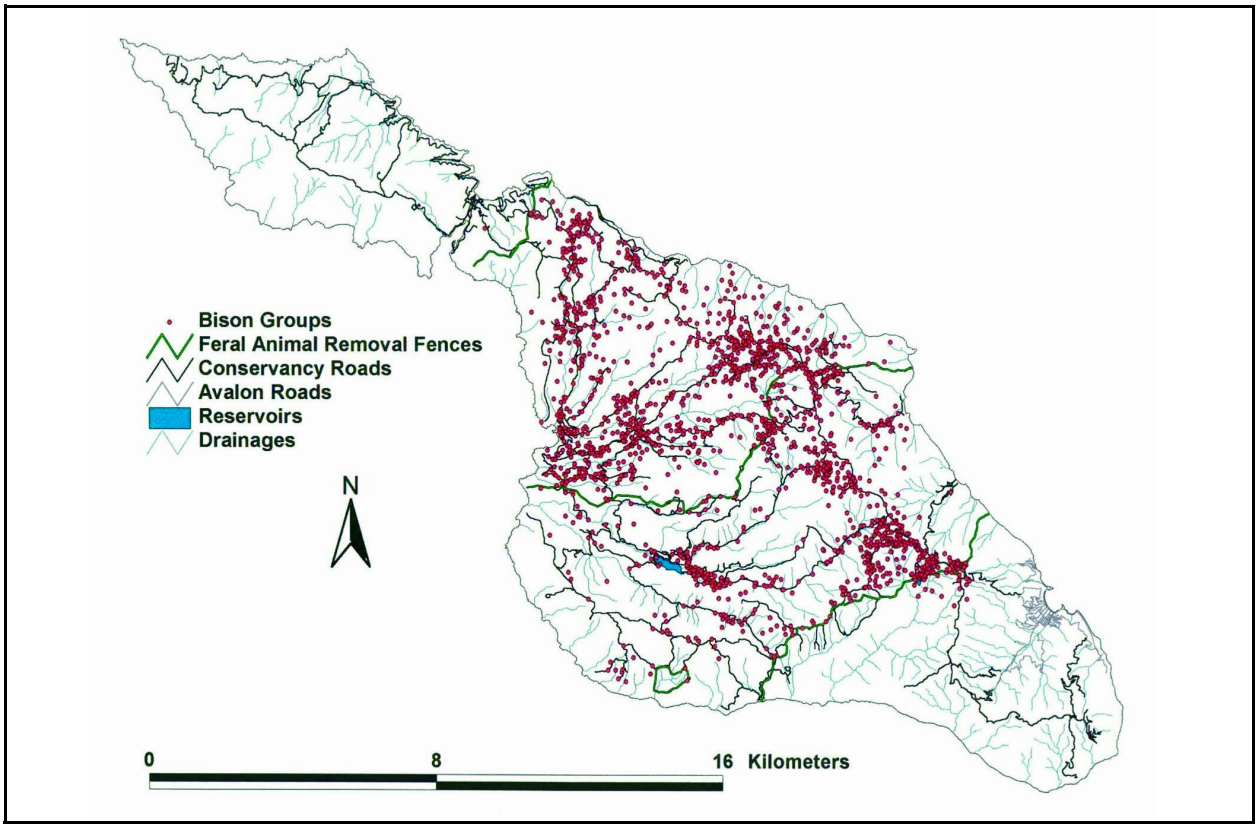

Figure 4. Estimated or measured locations of bison groups on Catalina Island, CA noted as part of bison group observations and five periodic bison censuses or counts from April 2001 to August 2002. See Methods section for details on census/counts.

Table 5. Distribution of bison groups (%) in 17 different physiographic/vegetation types on Catalina Island, California.

Habitat type	Area of Zones 2 and 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/ 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

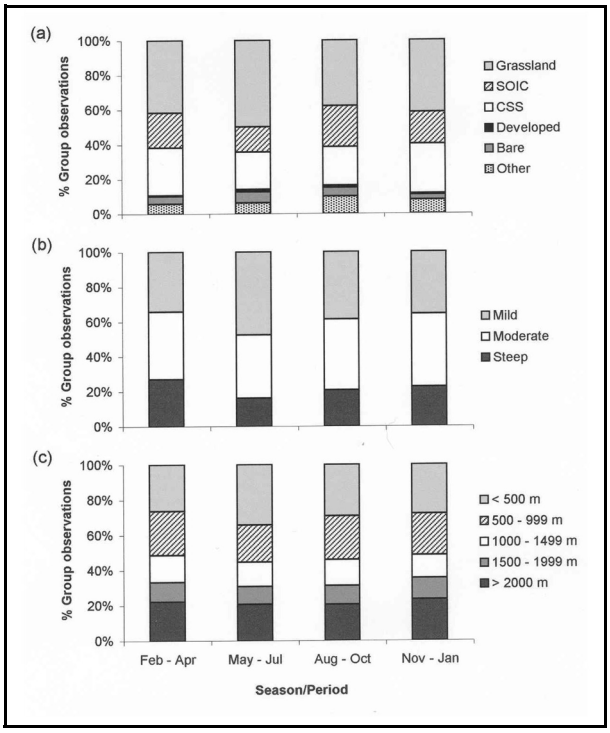

Figure 5. Seasonal variation in different aspects of habitat use by bison on Catalina Island, CA illustrated by: a) bison group observations in multiple different physiographic/vegetations classes, b) bison group observations on island terrains of different slopes, and c) bison group observations at different distances from water sources. Seasons were three month periods with Nov.– Jan. and Feb.– Apr. encompassing the wet season, and May – Jul. and Aug.– Oct. encompassing the dry period.

recorded in grassland, coastal sage scrub, or island chaparral habitat (Table 5). 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 (Fig. 5; Log-ratio Chi-square = 8.8, df = 15, P = 0.89) or differing slopes (Fig. 5; 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 (Fig. 5; 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 periods.

Analyses of data from 213 dung transects indicated that grassland habitats were strongly preferred by bison, whereas SOIC and coastal sage scrub were used less than expected relative to availability (Fig. 6). General Linear Model analysis suggested bison activity in any given area was related to the major and minor habitat types present, slope, and vegetation density (Table 6). 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.

Management Options

Assuming a 2003 status quo management approach, we estimated that Catalina Island could support 378 bison under a standard grazing regime, 189 animals under a moderate bison grazing pressure approach, and 95 animals with light bison grazing pressure (Table 7). If bison were confined to zone 2, we estimated carrying capacities of 241 bison under a standard grazing regime, 121 bison with the moderate grazing regime, and 60 bison under a light-grazing regime (Table 7). If bison were restricted to a part of zone 2, we estimated a standard carrying capacity of 33, a moderate

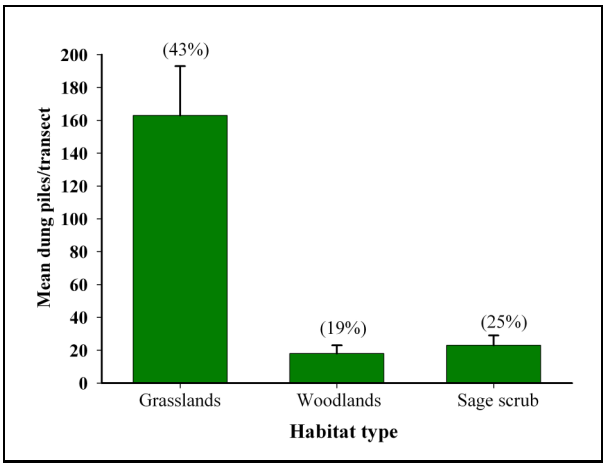

Figure 6. mean (±SE) numbers of dung/piles/transect along multiple belt transects in three habitat types on Catalina Island during May and June 2002. Numbers in parentheses above bars represent the proportion of all group observations observed in each habitat type. Habitats were designated as primary or marginal based on results of Chi-squared tests comparing use to availability.

carrying capacity of 17, and a light carrying capacity of nine bison (Table 7).

DISCUSSION

Management History

In general, very little detailed information was available on the early history of bison on Catalina Island other than that they were to be used while filming a movie. However, there has been some uncertainty regarding which movie bison were shipped to Catalina Island to be included in because there was no actual footage of bison in the movie "The Vanishing American" that they were purportedly used for. Nevertheless, the consensus is that bison were to be filmed for "The Vanishing American" (Gingrich 1974). At the time that the bison herd was becoming established on Catalina Island in the 1930s bison numbers were very low throughout their native range (Berger and Cunningham 1994). Considering that William Wrigley Jr. held a strong conservation ethic and was likely aware of problems with diminished populations of bison in their native range, it is conceivable that ranch managers working for the Island Company considered the bison on Catalina Island very valuable for conserving the species. This idea helps explain the rationale for importing 22 new animals from the mainland in 1969 and 1971 to genetically mix with the island herd and maintain population health (Lott and Minta 1983a). Twelve additional bison were brought to Catalina Island from the mainland in 1996 for the same reason. Notably, 30 of the 34 bison introduced from mainland sources after 1934 were males, reflecting the idea that new male bison might be more effective for rapidly integrating new genes into a polygynous breeding population than females. It is not known how effective these efforts at population management were for maintaining genetic diversity in the Catalina bison herd because no genetic research has been conducted.

Habitat Use

There was little evidence for altered patterns of habitat use by bison on Catalina Island related to the establishment of FAR fences. Our recent data were generally consistent with those of Galland (1989) and Lott and Minta (1983a, b) from work in the 1970s when bison on the island preferred grasslands over scrublands, occasionally foraged and loafed in scrub oak woodland habitats, and avoided barren or cultivated areas. More specifically, Galland (1989) noted: (1) a strong positive relationship between group size and vegetative community type [large groups of bison (44 animals) were most often observed in grassland and coastal sage scrub habitats], (2) a positive relationship between group size and ponds/water sources (most large groups of bison were observed

Table 6. Results of general linear model analyses assessing factors influencing bison activity based on the distribution of dung piles on Catalina Island. The overall model explained 59% of the variation in bison activity ($R^2 = 0.59$)

Parameter	SS	Df	MS	F-ratio
Major habitat[a]	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	

[a] Major habitats were defined as the habitat that comprised >60% of belt transect area whereas minor habitats comprised 20–40% of the belt transect area (see Methods).
*$P < 0.05$, **$P < 0.001$

Table 7. Estimates of carrying capacity for bison on Catalina Island under three different management scenarios (see Sweitzer et al. 2003 for additional details).

Management option	Standard[a]	Moderate[b]	Light[c]
A. Bison in most of Zone 2, 3, and 4 excluding Avalon (Status Quo)	378	189	95
B. Bison restricted to Zone 2	241	121	60
C. Bison restricted to a portion of Zone 2 along major tour bus route	33	17	9

[a] Assumes that 100% of consumable aboveground annual grass biomass is used by bison.
[b] Assumes that 50% of consumable aboveground annual grass biomass is used by bison and 50% is used by native herbivores/consumers.
[c] Assumes that 25% of consumable aboveground annual grass biomass is used by bison and 75% is used by native herbivores/consumers.

near ponds/water sources), and (3) a significant negative relationships between group size and slope and elevation (most large groups were observed on shallow slopes at relatively low elevations such as upland benches or valley bottoms). Galland (1989) further reported that bison most often occurred on northwest facing slopes, congregated around a few artificial water impoundments during rut periods, and that bison cows used thick scrub oak woodland habitats during the spring calving period (Galland 1989). Also of interest was Lott and Minta's (1983a, b) indirect suggestion that bison seldom ranged into the southeastern area of the island (zone 4), which closely matched our recent observations that very few bison used this part of the island (Fig. 4). Also, although bison had ready access to the west end of the island in the 1970s, Lott (2002) and Lott and Minta (1983a, b) reported that they seldom ventured there because of steep topography, limited forage and severe habitat degradation caused by feral goats.

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 from this study suggested that bison on Catalina Island behave in a manner similar to their mainland counterparts. 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 Catalina Island would preferentially graze on protected south-facing slopes in the spring where new grasses would emerge earliest due to warm soil temperatures (Berger and Cunningham 1994), but then shift to riparian areas in the summer as forage in upland habitats became depleted and dry and senescent (Knapp et al. 1999). Although we noted anecdotal differences in areas frequented by bison among seasons, these small-scale shifts in habitat use were not quantitatively significant. Ultimately, the apparent lack of strong seasonal shifts in patterns of habitat use by bison on Catalina Island resulted in relatively heavy and persistent use of a small number of open grassland areas with relatively mild slopes including the broad bench near El Rancho Escondido, the open grasslands east of the Airport-in-the-Sky, and near where the main road enters zone 2 heading into the island interior.

Tourism

Bison have long been culturally important in the United States, but notably so once their imminent extinction was narrowly averted at the end of the 19th century (Lott 2002). Bison numbers in North America were very low but increasing in 1924 when they were first introduced to Catalina Island. It is therefore not surprising that the growing bison population after 1934 was rapidly embraced by island residents as a symbol of the island's rugged interior, and that the bison herd soon became a draw for tourism (Boydston 1998, Mecoy 2002). Our summary of recent data on bus and Jeep® tours indicate that these two types of tourism generate significant sales annually (Table 4). Tourists clearly visit the interior of Catalina Island for reasons other than viewing bison, but it

is likely that fewer would be interested in doing so if bison were not present or if they were present in sufficiently low numbers that they would seldom be observed along tour routes. It is fortunate that several preferred foraging and loafing areas for bison are near the Airport-In-The-Sky and El Rancho Escondido because tourists viewing the island by bus, Jeep®, and airplane frequently have the opportunity to observe them (Fig. 4).

Management Options

Currently bison have relatively unrestricted access to most of Catalina Island east of the Isthmus (Fig. 4), an area that encompasses 19 different areas considered ecologically sensitive for Los Angeles County. Our carrying capacity model suggests that the area of Catalina Island excluding zone 1 may maximally support around 378 animals, but only under a standard livestock grazing regime in which essentially all preferred aboveground plant biomass is reserved for use by bison. However because Catalina Island harbors multiple native organisms that also rely on plant materials for forage or habitat, we estimated carrying capacities under lower levels of bison use as 189 (moderate bison grazing) and 95 bison (light bison grazing). Relatively lower assumptions of forage availability and forage use by bison can be thought of as effectively reserving herbaceous forage for use by the suite of native species on the island. Further, lower grazing pressure by bison based on lower stocking rates would result in less impact to the 19 different SEAs in zones 2, 3 and 4. From the perspective of tourism, the 2003 status quo management approach with lower stocking rates based on the lighter grazing regime assumptions would continue to provide viewing opportunities.

A second management option is to use the existing FAR fences to restrict bison to zone 2. This would require modifications to two cattle guards to render them impassable to bison. The ecological advantage of restricting bison to zone 2 is that 67% of the island would be protected from grazing and other activities of bison (Coppedge and Shaw 1997), and only five of the island's SEAs would be exposed to bison. Restricting bison to zone 2 would continue to provide viewing opportunities around key areas for bus tours and private plane traffic.

A third management option is to restrict bison to a relatively small portion of zone 2 encompassing the Airport-In-The-Sky and El Rancho Escondido. Although this area would support between nine and 33 bison depending on the three grazing regime assumptions, some bison would continue to be visible in and around high use areas for tourists. A key advantage of restricting animals to this smaller area of the island is that it would protect all five of the SEAs in zone 2 as well as the other 14 SEAs in zones 3 and 4. Disadvantages include the potential for a rapid buildup of thatch from nonnative plants, additional fencing to contain the bison within part of zone 2, and the need to establish one or several artificial sources of water for the bison.

Although the fourth management option of completely removing bison from the island might be appealing from a strict conservation perspective, there are several reasons that this approach may not be feasible in the near term. Results of detailed research by Sweitzer et al. (2003) indicated that when small areas of habitat in grasslands and scrub oak woodlands were protected from bison, multiple species of nonnative grasses and forbs proliferated. This was not surprising because data on the diets of bison on the island indicated that they consumed the most readily available plants; abundant nonnative grasses and forbs (Sweitzer et al. 2003). It is very likely that the rapid or complete removal of bison would result in a buildup of dry plant biomass, which might increase the intensity of occasional wildfires and damage SOIC habitats and endemic island ironwood tree groves. To reduce this threat, a fire management program, including periodic controlled burning, would need to be considered. Complete removal of the bison would eliminate bison viewing opportunities and potentially reduce the numbers of tourists visiting the interior of the island via bus or Jeep® tours and airplanes. We did not attempt to estimate the potential loss in tourism-related income by complete removal of the bison.

From a global conservation and restoration perspective the ecological integrity of native and endemic plant and animal communities on islands is especially important. The Channel Islands of California are estimated to support 26 endemic plants, in addition to the six species of plants known to occur only on Catalina Island (Nixon and

Muller 1994, Junak et al. 1995). From an ecological perspective, even small numbers of a large-bodied non-native herbivore occupying an insular ecosystem is cause for concern, and recent research has linked changes in Catalina Island's plant communities to the activities of bison (Sweitzer et al. 2003). Effective conservation often requires balancing multiple conflicting interests, and public acceptance of any change in bison management on the island will be difficult without serious consideration of the cultural and economic importance of the species to the island residents. Three of the four possible management options we reviewed provide for continued bison viewing opportunities in the island interior.

Current Management

Based on research results provided by Sweitzer et al. (2003) on the ecological effects of bison on Catalina Island, the Conservancy held a series of meetings in winter and spring 2003 to discuss bison management and is now beginning to implement several management recommendations from the study. A goal of maintaining a bison herd size of 150–200 animals primarily in zones 2 and 3 was approved by the Conservancy's Board of Directors in April 2003. In November 2003, 105 bison were shipped of the island as the first step to reducing the herd size to 150. Additional animals will be shipped in 2004 to reach the target of 150 animals. Once the target has been reached, the herd will be allowed to reproduce until the upper goal of 200 is approached. In addition, the Conservancy is beginning to assess the feasibility of contraception to reduce herd growth, which would also reduce the costs of management. A bison herd size of 150–200 falls within the moderate grazing regime approach suggested by Sweitzer et al. (2003) and presented here under the status quo management option (Table 7).

To address some of the potential impacts mentioned by Sweitzer et al. (2003) the Conservancy is preparing a wildland fire management plan, will explore additional range management techniques to reduce negative grazing impacts, and will further explore the relationship between bison grazing and nonnative annual grasses and forbs. Regular censuses will be conducted, more accurate herd health and management data will be collected, and periodic reassessments of the impacts of bison will be conducted. Notably, the reduction in herd size will help protect the natural resources of Catalina Island while not eliminating the opportunity for island residents and tourists to view and enjoy this culturally significant large mammal that has been roaming the interior of Catalina Island since 1924.

ACKNOWLEDGMENTS

Funding and logistical support for this study were provided by the Santa Catalina Island Conservancy and the University of North Dakota. H. Saldaña, D. Propst, B. Guay and L. Alther helped with historical data. M. Kleinfelter and R. Loggins provided aid with ArcView procedures. We had assistance in the field from N. Kadrmas, P. Isakson, J. Costa and D. McDonald. D. McDonald was especially helpful during multiple aspects of the study and D. Knapp assisted with data on island vegetation. Multiple volunteers and volunteer groups aided the research at various times and are listed by name by Sweitzer et al. (2003). P. Novak-Echenique, V. Smothers, and S. Jewett of the USDA Natural Resources Conservation Service provided information on the soils of Santa Catalina Island and the San Diego area. C. Schwemm, B. Weckerly, and an anonymous reviewed provided constructive comments for improving the manuscript.

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Appendix 1. Physiographic/vegetation classes on Santa Catalina Island, California based on Knapp 2002.

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