By 1990, the situation had changed dramatically. Since no other limiting factors changed between 1978 and 1990, the removal of feral sheep appears to have allowed for the survival of plant seedlings, with Bishop pine dominating new growth. Other species are also colonizing the area, but at much lower densities than Bishop pine as a result of fewer available seed sources. As these species grow old enough to disseminate their own seeds, their presence in the study area should increase markedly.

Summary/Conclusion

The TNC sheep removal program resulted in a remarkable recovery of the vegetation in the study area. The data collected in this study show that Bishop pine dominates the vegetation of the study area and will continue to do so in the near future. The reasons are as follows: (1) Bishop pine is longer lived than most other species in the study area, persisting even though no seedlings survived for close to 2 decades; and (2) It produces large numbers of seeds that are able to disperse over long distances. Additionally, other species not found when sheep were present are colonizing the area, and new species can be expected to occur in the future as seeds from less severely grazed areas are dispersed onto this site.

In a broader sense, this case study from Santa Cruz Island suggests that removing feral animals is a large step towards restoring island ecosystems that have been disturbed by human actions. Island biota are very vulnerable to nonnative herbivores, but in this case, Bishop pine showed remarkable recuperative abilities once the disturbance was removed.

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Vegetation Response to the Removal of Feral Sheep from Santa Cruz Island

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Abstract. From 1984 through 1993, we monitored the response of herbaceous vegetation in grasslands during and after the eradication of feral sheep (*Ovis aries*) from Santa Cruz Island. Although species diversity did not increase significantly between 1984 and 1993, herbaceous cover increased and bare ground decreased after sheep were eradicated from the island. The relative frequency of native herbaceous species was inversely related to increased frequency of nonnative species, while the number and relative frequency of nonnative species remained unchanged. There was no evidence that native species were being displaced by invading nonnative species, but rather the increase in cover was due to nonnative species that already occurred in an area. The composition of the herbaceous vegetation was independent of the number of species in each class but reflected the composition prior to the eradication and the ability of nonnative annuals to rapidly colonize disturbed areas. Measuring other parameters in addition to herbaceous vegetation would have given a more complete picture of the ecosystem's response to the eradication, and monitoring a variety of ecosystem parameters should be made a central part of any eradication program. Eradication programs should be designed to be only the first step in protecting and restoring biodiversity on the Channel Islands and not considered an end in themselves; other management programs will be necessary so that one type of nonnative impact is not replaced with another.

Keywords: Santa Cruz Island; eradication; feral animals; feral sheep; nonnative plants; monitoring; succession; restoration.

Introduction

For more than 150 years, the California Channel Islands have been impacted by feral animals, primarily sheep (*Ovis aries*), goats (*Capra hircus*), and pigs (*Sus scrofa*) (Coblentz 1977, 1978, 1980; Van Vuren 1981, 1984). These impacts were especially severe on Santa Cruz Island, where more than 50,000 sheep were estimated to be on the island in the 1890s. Attempts were made in the 1900s to control the sheep population by trapping and shooting, but the efforts were not successful (Van Vuren 1981). By the 1980s, there were an estimated 20,000 sheep on Santa Cruz. The density was more than double that of the maximum stocking rates of mainland sheep operations, and more than one-third of the island was classified as being heavily impacted (Van Vuren 1981). This resulted in an increase in bare ground and subsequently higher erosion rates, decreased herbaceous vegetation, reduction and modification of shrub communities, and a decrease in abundance and diversity of birds (Brumbaugh 1980; Hobbs 1980; Hochberg et al. 1980; Minnich 1980; Van Vuren 1981).

Beginning in late 1981, The Nature Conservancy (TNC) undertook a program to eradicate feral sheep from the 90% of Santa Cruz in which TNC had an interest. The goals of the program were to preserve, protect, and restore the natural systems, flora, and fauna of the island (Schuyler 1993). From 1981 through 1987, more than 36,000 sheep were shot on Santa Cruz.

In addition to the eradication efforts, a monitoring program was established to evaluate the response of herbaceous vegetation to the sheep eradication. In this paper, we present the general pattern of herbaceous species response to the eradication, test whether the frequency of occurrence and number of native species increased on Santa Cruz as a result of the eradication, and give recommendations for monitoring future feral-animal eradication programs.

Study Area

Santa Cruz Island is the largest of California's 8 Channel Islands. With a land area of more than 250 km^2, it is the most topographically and ecologically diverse of the islands. Santa Cruz is divided along its long axis by a central valley flanked by 2 east- to west-tending mountain ranges. Six major vegetation communities occur on Santa Cruz, including grasslands, chaparral, oak woodland, coastal scrub, pine forest, and riparian (Minnich 1980).

The Mediterranean climate is modified by the surrounding maritime conditions. Winters are cool and wet; late summer, spring, and fall are clear and warm; and early summer is foggy and cool. The 90-yr average rainfall is 30.7 cm (L. Laughrin, unpubl data), with about 90% of the precipitation occurring in November–April. Rainfall can vary in different parts of the island, but these patterns tend to be constant from year to year. A drought occurred from 1986 through 1990, when rainfall was only 45–70% of the average. The mean annual rainfall for the study period in the Central Valley of the island is presented in Table 1.

Table 1. Mean annual rainfall for Santa Cruz Island (Central Valley), 1984–1993.

Year	Rainfall (cm)
1984	25.4
1985	25.0
1986	49.5
1987	21.8
1988	24.3
1989	13.9
1990	10.0
1991	24.3
1992	32.9
1993	39.5

Methods

Because sheep primarily graze on herbaceous species, and about 50% of Santa Cruz Island is grassland (Minnich 1980), data were collected from 21 plots in grassland habitat sampled in 7 springs (March–May 1984–1993) (Table 2). Seven sites were selected along fencelines that divided areas with different initial sheep densities and impacts, with sampling done in plots on either side of the fence. Seven other plots were not divided by fences. Thirteen plots were in areas subjectively categorized as being heavily impacted by sheep, 3 in areas categorized as moderately impacted, and 5 in areas with light impacts. These proportions corresponded to islandwide estimates of sheep impacts, and were based on visual inspection of vegetation and soil conditions, as well as sheep density. The density was estimated from the total number of sheep killed in an area (Schuyler 1993), and is given in Appendix 1.

Table 2. Sampling effort for nested frequency plots monitoring the response of plant species to the removal of feral sheep on Santa Cruz Island, California. Sampling was not conducted in 1986, 1988, or 1990.

Year	No. plots	No. transects
1984	14	87
1985	14	87
1987	5	31
1989	7	42
1991	11	24
1992	14	54
1993	14	48

One to 8, 30-m transects were randomly selected perpendicular to a 30-m baseline within each plot. Twenty 2,500 cm^2 frames were spaced equidistantly along each transect, and the presence or absence of all herbaceous species was recorded in 1 of 4 square quadrats nested within each frame; nest sizes were 25 cm^2, 625 cm^2, 1,250 cm^2, and 2,500 cm^2 (U.S. Forest Service 1983). Estimates of the total percent cover of live vegetation, litter (dead or dry organic material), and bare ground were made for each frame. For the analyses in this study, cover estimates were converted to Daubenmire values (Bonham 1989) and frequency values were summed and standardized to the range 0–100% for each species (Smith et al. 1987).

We derived measures of species diversity (richness) (log series parameter *alpha*, Magurran 1988) and species similarity (simplified Morisita-Horn Index, Krebs 1989) from the total number of species in each year's sample. We analyzed changes between years in these parameters with a least-squares regression test.

We used discriminant function analysis to determine whether different years could be distinguished by differences in 6 predictor variables; the mean percent cover of herbaceous vegetation (Veg), litter (Litter), and bare ground (Bare) within each plot; the mean number of native and nonnative species/transect within each plot (Natvspec and Alnspec); and the mean percent relative frequency of native species within each plot (Natvfreq). We did not include the percent relative frequency of nonnative species in the model to avoid multicollinearity with the variable Natvfreq. Based on an analysis of the residuals, we arcsin transformed Veg, Litter, and Bare and log transformed Alnspec to improve the linearity, homoscedasticity, and normality of the data. The categorical variable Year had 7 levels corresponding to the years in which sampling was done at the different plots.

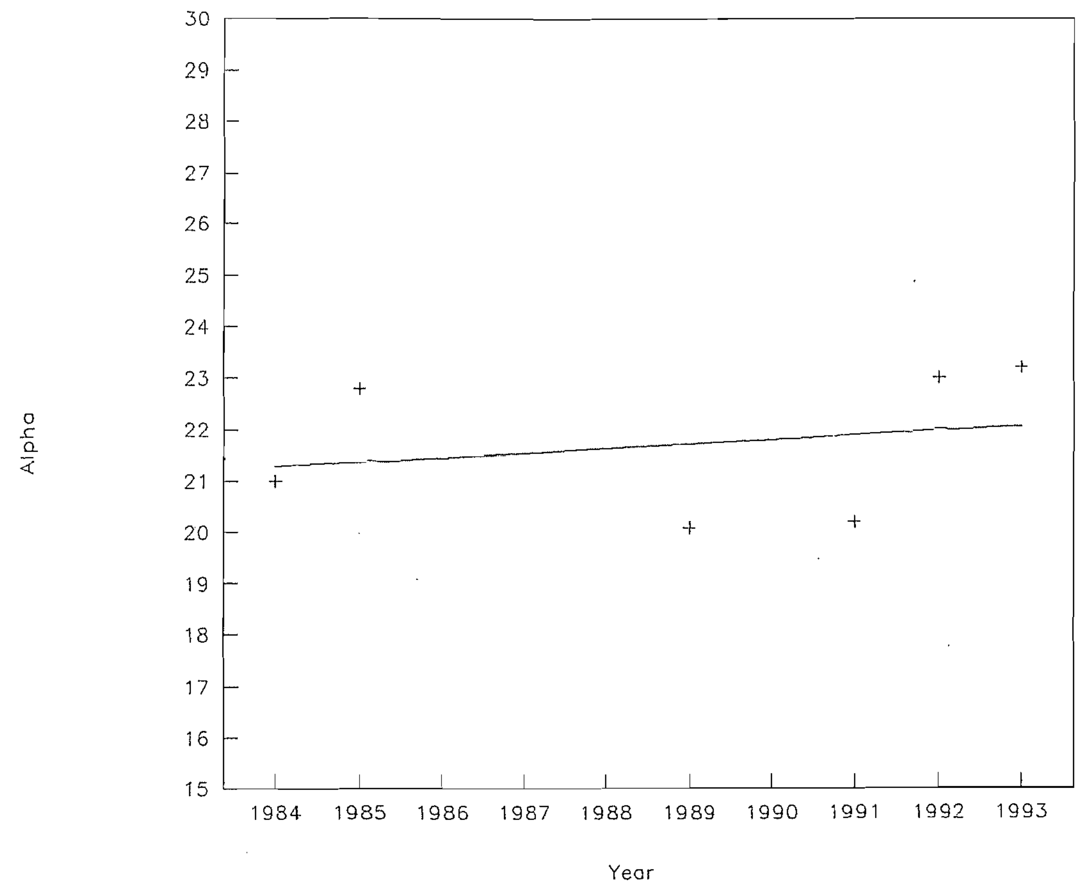

Figure 1. Species diversity (log series *alpha*) of herbaceous plants on Santa Cruz Island, California, 1984–1993.

We used least-squares multiple regression to analyze the relationship between Natvspec, Alnspec, and Natvfreq (arcsin transformed) to 6 variables: Veg, Bare, rainfall (Rain), the year of the study (Year), sheep impacts (measured as the density of sheep prior to the eradication program) (Prednsty-log transformed), and the density of sheep within an area during a given year (Density-log transformed).

We identified 7 different classes of vegetation: native annual grasses, native annual herbs, native perennial grasses, native perennial herbs, nonnative annual grasses, nonnative annual herbs, and nonnative perennial herbs. The percent relative frequency of each vegetation class relative to the number of species in each class was analyzed with a Bonferroni simultaneous interval Chi-square procedure (Neu et al. 1974).

All statistical tests were considered significant if $p<0.05$. If $0.10>p>0.05$, the test was considered to be marginally significant.

Results

Species diversity did not increase significantly over the course of the study (1984–1993) (Fig. 1). Between-year similarity in species composition decreased significantly from 1984 through 1993, ($r=0.92$, 5 df, $p<0.01$). Using 1984 as the baseline year, the species similarity coefficients ranged between 0.83 and 0.89 from 1985 through 1989, then dropped to 0.17–0.20 from 1991 through 1993. There was no linear change in percent herbaceous cover or bare ground between 1984 and 1993 (Fig. 2), but cover increased directly with increased amounts of rainfall ($r = 0.53$, 109 df, $p = 0.000$).

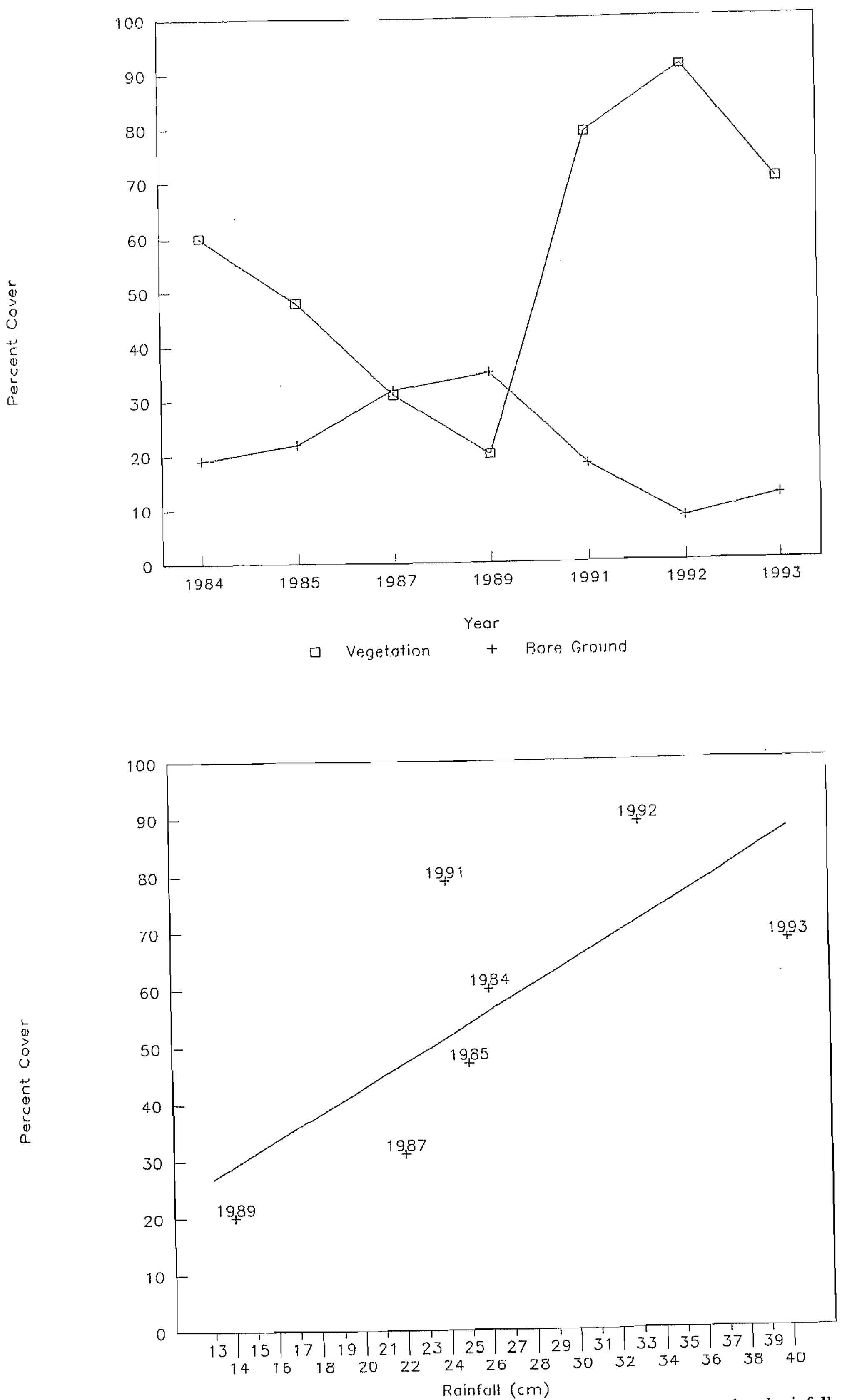

Figure 2. Percent cover of herbaceous species in relation to the year of feral sheep removal and rainfall on Santa Cruz Island, California.

Table 3. Canonical factor loadings and variance proportions of 6 predictor variables for 7 yr of sampling at 14 vegetation monitoring plots on Santa Cruz Island, California, 1984–1993.

Variable	CF1	CF2
Veg	-0.704	-0.075
Litter	0.825	-0.100
Bare	0.336	0.282
Natvspec	0.107	-0.675
Alnspec	0.113	-0.266
Natvfreq	0.084	-0.490
Variance (%)	38.7	25.1

The years 1984–1993 could be significantly distinguished by the linear combination of the predictor variables (Wilks' Lambda = 0.140, F = 9.34, df = 36 & 437, p=0.000). Two canonical factors accounted for 64% of the variation in the categorical variables. The first canonical factor was associated with the percent cover of vegetation and litter, while the second factor was associated with the number and frequency of native species (Table 3). Although the years 1991–1993 had greater vegetation cover and less litter than 1984–1989, the pattern did not move sequentially from one year to the next; 1984–1985 had more cover than did 1987–1989, while 1992 had more cover than 1991 and 1993 (Fig. 3). Likewise, there were years in which the number and frequency of native species were greater than others, but there was no sequential pattern of increase or decrease from year to year.

The regression of Natvspec on the 6 independent variables was significant (F = 3.09, df = 6 & 104, p = 0.008); however, the relationship was weak, with only 13% of the variability in the number of native species

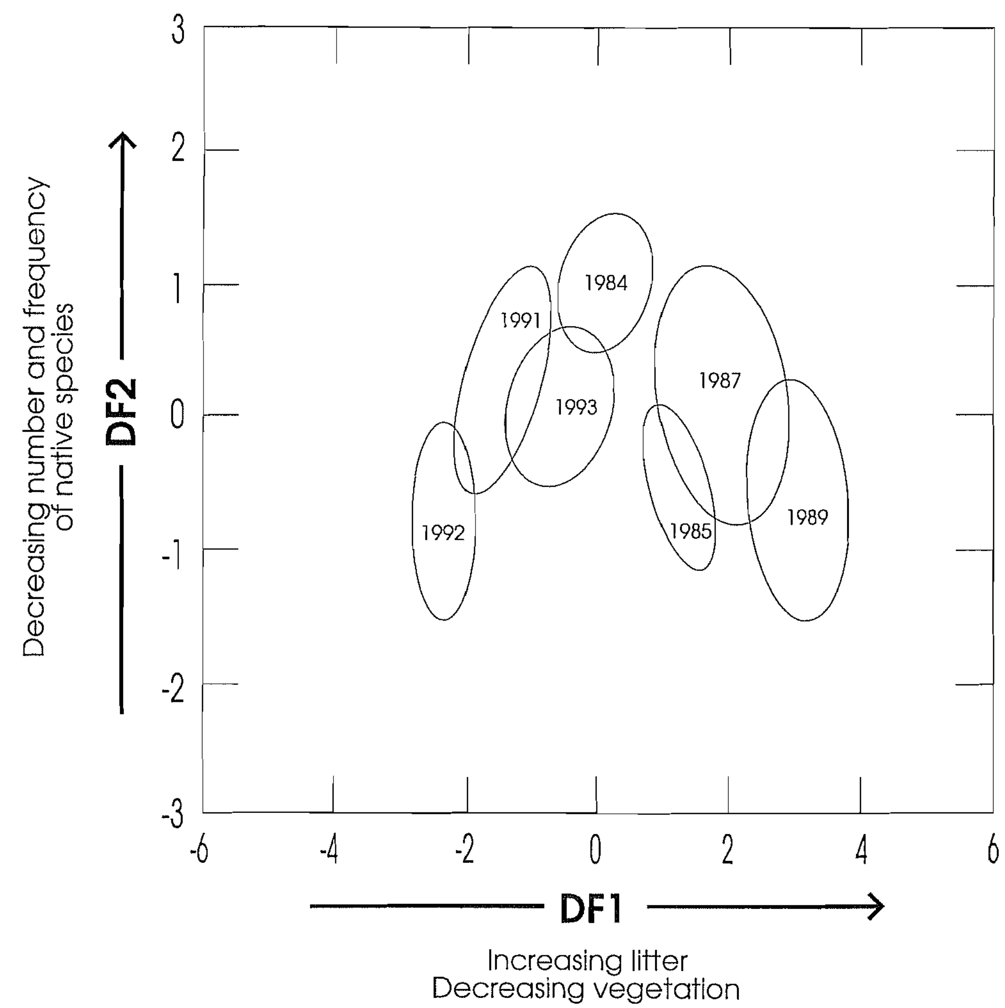

Figure 3. Ninety-five percent confidence ellipses for 2 canonical factors discriminating 7 yr in which herbaceous plants were sampled on Santa Cruz Island, California. (See text for details.)

accounted for. The variables Bare and Density had significant standardized regression coefficients, while the standardized beta weight for Prednsty was marginally significant (Table 4). The regression of Natvfreq on the 6 independent variables was significant and explained 31% of the variability in Natvfreq (F = 9.09, df = 6 & 104, p = 0.000). Three variables had significant standardized beta weights: Bare, Prednsty, and Veg. The standardized beta weight for Density was marginally significant (Table 4). There was no significant variation in Alnspec with the 6 independent variables.

Table 4. Semipartial correlation coefficients (*sr*), standardized regression coefficients (B), test statistics (T), and probability values (P) for multiple regression analyses of variables significantly related to percent herbaceous vegetation cover and bare ground on Santa Cruz Island, 1984–1993.

Variable	*sr*	B	T	P
Number of native species (NATVSPEC)-R^2=0.125				
Bare	0.052	0.377	2.49	0.014
Density	0.035	-0.258	2.04	0.044
Prednsty	0.026	0.182	1.75	0.084
Relative frequency of native species (%) (NATVFREQ) - R^2 = 0.306				
Bare	0.118	0.568	4.21	0.000
Prednsty	0.093	0.346	3.73	0.000
Veg	0.036	0.312	2.33	0.022
Density	0.024	-0.212	1.88	0.062

The number of native species increased significantly as the number of nonnative species increased (r = 0.445, 109 df, p = 0.000), but decreased as the relative frequency of nonnatives increased (r = 0.685, 109 df, p = 0.000) (Fig. 4).

The relative frequency of occurrence of 3 of the 4 classes of natives was significantly less than expected relative to the number of species in each class, while 2 of the 3 classes of nonnative species were greater than expected (Table 5). Nonnative species comprised between 63 and 77% of the relative frequency across all years. Overall, the 49 nonnative species recorded during our study comprised 70% of the relative frequency (Appendix 2).

Discussion And Implications For the Channel Islands

An increase in herbaceous cover and decrease in bare ground was correlated with the eradication of feral sheep from Santa Cruz Island, but there was no appreciable change in species diversity. Although the species composition changed between 1984 and 1993, it was dominated by nonnative species in all years.

Rainfall was an important factor affecting the increase of vegetation cover, but the increase in cover was not associated with an increase in the number or relative frequency of native species. The number and relative frequency of native species appeared to be affected by factors related to sheep numbers. When the numbers of sheep on Santa Cruz were high, the number and relative frequency of native species were low; but after sheep were eradicated, natives were able to become established in open areas where sheep impacts had been relatively severe.

The signs of the standardized beta weights in the regression equations were indicative of the relationship between the independent variables and the number and relative frequency of native species. Although it appears counterintuitive that the percent cover of bare ground and vegetation would have the same sign in the relationship with the number of native species, this reflects 2 things: (1) the intercorrelation between variables in a regression equation can change the sign between 2 of those variables in a simple bivariate correlation (Sokal and Rohlf 1981), and (2) the abundance of native species is relatively greater in more open areas, but if the ground is totally devoid of vegetation one obviously would not find any species.

It has been assumed that removing nonnative grazers will lead to recovery of native species (Halvorson 1992); however, this did not appear to be the case on Santa Cruz between 1984 and 1993. The number of native species was not suppressed by nonnative species invading an area, but by an increase in cover from nonnative species already present in an area. Areas that had relatively high numbers of nonnative species also had relatively high numbers of native species, but the ratio of native:nonnative species tended to be lower where the relative frequency of nonnatives was high. This pattern probably reflects the historical effect of sheep grazing; the levels of species diversity, composition, and cover we observed in the initial parts of this study were established decades earlier, and ongoing grazing did not change them in any significant manner. Only after sheep were removed and environmental conditions were favorable (adequate rainfall) did vegetation cover have a chance to increase.

There are indications that the distributions and abundances of some species of rare plants across Santa Cruz Island have increased; however, the number of nonnative species has increased as well. Of 22 species of vascular plants found on Santa Cruz Island since 1987 that were never previously recorded from the island or were considered extirpated, 14 are nonnatives (S. Junak 1993, pers. comm.). Although their impact may be less obvious, nonnative plants can have many of the same detrimental effects to natural communities as feral animals (D'Antonio and Vitousek 1992; Halvorson 1992).

Schuyler (1993) noted that 4 processes needed to be monitored to document how the Santa Cruz Island ecosystem responded to the removal of feral sheep: (1) changes in vertebrate populations, (2) changes in nonnative plants, (3) changes in hydrologic regimes, and (4) changes in erosional processes and soil formation. Of these, only changes in nonnative herbaceous plants were monitored adequately during the Santa Cruz Island sheep

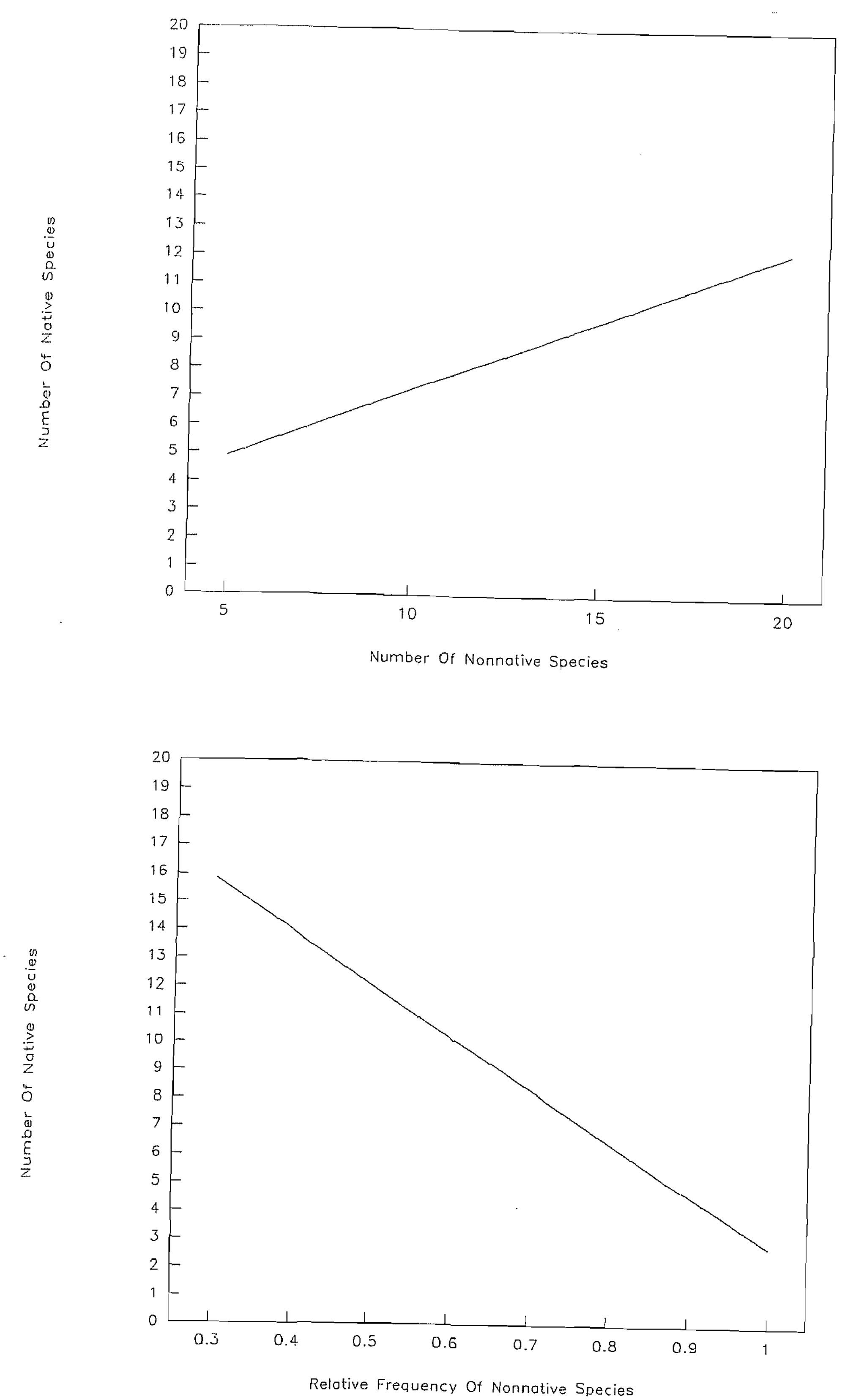

Figure 4. The relationship of the number of native herbaceous species to the number and relative frequency of nonnative herbaceous species on Santa Cruz Island, California, 1984–1993.

Table 5. Relative occurrence (with 95% Bonferroni confidence intervals) of 7 different herbaceous plant categories in relation to the number of species within each category on Santa Cruz Island, California, 1984–1993.

Category	Species (%)	Frequency of occurrence (%)		
Native annual grass	2.6	0.0<	0.8<	2.5
Native annual herb	42.6	32.6<	31.1<	29.6
Native perennial grass	4.5	6.5<	4.8<	3.0
Native perennial herb	16.1	6.7<	4.9<	3.2
Nonnative annual grass	11.6	30.6<	29.1<	27.6
Nonnative annual herb	18.1	28.6<	27.1<	25.6
Nonnative perennial herb	4.5	4.1<	2.3<	0.5

eradication. If the other processes had been monitored as Schuyler (1993) suggested, a more comprehensive evaluation of the ecosystem's response to the eradication could have been made.

It is important to note that, although this was a 10-yr study, it has only been 6 yr since sheep were eradicated on the western 90% of Santa Cruz Island. Whether it was dominated by nonnative species or not, the increase in cover was undoubtedly beneficial in reducing erosion and restoring natural hydrologic regimes. The recovery of Santa Cruz Island from the effects of sheep grazing will be ongoing for decades, and successional patterns may indeed begin to shift in favor of native species.

Eradication programs are controversial, high profile events, and private groups opposed to such programs can delay or inhibit the programs' implementation (Clifton 1991, PETA 1993). It is critical that conservation scientists and land managers explain the need for eradication programs and the likely outcomes, and demonstrate how the programs benefit ecosystems. At the present time, feral animal-eradication programs are underway or planned for at least 2 other Channel Islands (Santa Catalina and Santa Cruz) and have been completed recently on others (San Clemente, Santa Rosa). By designing extensive monitoring protocols as an integral part of any eradication program, conservation scientists will be able to better understand and communicate the need for the outcome of the program. A number of different ecosystem parameters should be monitored, monitoring should be initiated before eradication begins, and sampling should continue consistently throughout the eradication phase and at least several years beyond.

It is also important to recognize that eradication programs should only be considered a first step for protecting and restoring native species' diversity. It is likely that environmental factors influencing the response of plant and animal species to eradication programs will vary unpredictably, as rainfall patterns did on Santa Cruz Island during our study. This may produce successional patterns that are relatively undesirable; management activities will probably be needed to prevent unwanted outcomes from eradicating feral animals, such as the displacement of native herbaceous species by nonnative grasses and forbs that occurred on Santa Cruz.

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Appendix 1. Estimated sheep density (#km^2) on Santa Cruz Island, California. After 1987, no sheep occurred on the western 90% of the island.

Pasture	1982	1983	1984	1985	1986	1987
Light impact						
La Punta	26.0	0.0	0.0	0.0	0.0	0.0
Cabrillo	43.5	43.5	43.5	0.0	0.0	0.0
Portezuela	12.0	12.0	12.0	12.0	0.9	0.9
Moderate impact						
Alberts	64.2	5.7	14.2	0.0	2.2	4.7
Pozo/Sauces	131.8	131.8	131.8	131.8	76.5	0.4
Heavy impact						
Dos Cuevas	200.9	74.7	3.2	1.2	0.0	0.0
North Shore	287.6	198.3	198.3	5.5	0.9	1.7
Laguna	291.2	291.2	291.2	291.2	225.8	1.7
Willows	265.6	265.6	265.6	265.6	199.5	1.1

Appendix 2. Herbaceous vascular plant species recorded from plots monitoring the recovery of vegetation from feral sheep grazing. Santa Cruz Island, California, 1984–1993.

Species	Relative frequency	Species	Relative frequency
Native annual grasses		**Native perennial herbs (continued)**	
Bromus carinatus	0.003	*Allium praecox*	0.025
Bromus maritimus	0.030	*Asclepias fascicularis*	0.008
Hordeum californicum	0.050	*Atriplex californica*	0.134
Hordeum depressum	0.402	*Bloomeria crocea*	0.214
		Brodiaea jolonensis	0.018
Native annual herbs		*Calochortus albus*	0.003
Achyrachaena mollis	0.027	*Calystegia macrostegia*	0.077
Agoseris heterophylla	0.055	*Cardionema ramosissimum*	0.546
Amsinckia intermedia	0.096	*Chenopodium californicum*	0.045
Amsinckia menziesii	0.045	*Cirsium occidentale*	0.003
Antirrhinum nuttalianum	0.002	*Dichelostemma pulchellum*	0.662
Astragalus didymocarpus	0.151	*Epilobium ciliatum*	0.005
Bowlesia incana	0.040	*Frankenia salina*	0.042
Calandrinia ciliata	0.264	*Galium angustifolium*	0.003
Camissonia robusta	0.007	*Galium nuttallii*	0.007
Chorizanthe staticoides	0.040	*Lomatium utriculatum*	0.002
Claytonia perfoliata	0.101	*Lupinus concinnus*	0.077
Crassula erecta	2.004	*Marah macrocarpus*	0.010
Cryptantha clevelandii	0.030	*Sanicula arguta*	0.099
Daucus pusillus	0.148	*Scutellaria tuberosa*	0.017
Dodecatheon clevlandi	0.007	*Sidalcea malviflora*	0.044
Eremocarpus setigerus	4.423	*Sisyrinchium bellum*	0.082
Erodium macrophyllum	0.089	*Stachys bullata*	0.008
Eschscholzia californica	0.002	*Zauschneria californica*	0.024
Filago arizonica	0.805		
Filago californica	1.125	**Nonnative perennial grasses**	
Gilia angelensis	0.289	*Avena barbata*	10.652
Gilia clivorum	0.034	*Avena fatua*	0.229
Gnaphalium bicolor	0.119	*Bromus diandrus*	4.724
Gnaphalium californicum	0.015	*Bromus mollis*	8.954
Gnaphalium chilense	0.055	*Bromus rubens*	6.131
Gnaphalium microcephalum	0.709	*Gastridium ventricosum*	0.109
Hemizonia fasciculata	0.099	*Hordeum geniculatum*	0.338
Heterotheca grandiflora	1.592	*Hordeum leporinum*	1.128
Lasthenia californica	0.941	*Hordeum murinum*	0.091
Layia platyglossa	0.214	*Lamarkia aurea*	1.503
Lepidium nitidum	1.069	*Lolium multiflorum*	0.079
Linanthus androsaceus	0.002	*Lolium perenne*	0.054
Linaria texana	0.002	*Parapholis incurva*	0.018
Lotus micranthus	0.078	*Phalaris minor*	0.392
Lotus strigosus	0.081	*Vulpia bromoides*	0.953
Lotus subpinnatus	0.414	*Vulpia myuros*	4.788
Lupinus bicolor	0.989		
Micropus californicus	2.345	**Nonnative annual herbs**	
Montia fontana	0.005	*Anagallis arvensis*	0.212
Navarretia atractyloides	0.124	*Brassica geniculata*	0.008
Orthocarpus attenuatus	0.163	*Brassica nigra*	0.639
Orthocarpus purpurascens	0.010	*Capsella bursa-pastoris*	0.008
Pectocarya linearis	0.114	*Centaurea melitensis*	1.261
Plagiobothrys canescens	0.003	*Centaurea solstitialis*	0.136
Plagiobothrys collinus	0.124	*Cerastium glomeratum*	0.435
Psilocarphus tenellus	0.177	*Erodium botrys*	3.401
Pterostygia drymarioides	0.020	*Erodium cicutarium*	6.219
Ranunculus californicus	0.044	*Erodium moschatum*	0.274
Spergularia marina	0.131	*Galium aparine*	0.136
Stylocline gnaphalioides	0.479	*Gnaphalium luteo-album*	0.059
Thysanocarpus curvipes	0.008	*Hypochoeris glabra*	5.314
Trifolium albopurpureum	0.479	*Madia sativa*	0.008
Trifolium amplectens	1.835	*Malva parviflora*	0.092
Trifolium ciliolatum	0.002	*Matricaria matricarioides*	0.002
Trifolium depauperatum	0.002	*Medicago polymorpha*	3.300
Trifolium fucatum	0.044	*Rigiopappus leptocladus*	0.062
Trifolium gracilentum	0.045	*Senecio vulgaris*	0.131
Trifolium microcephalum	1.056	*Silene gallica*	4.494
Trifolium microdon	0.437	*Silybum marianum*	0.039
Trifolium tridentatum	0.010	*Sisymbrium officinale*	0.030
Trifolium variegatum	0.012	*Sonchus asper*	0.249
Viola pedunculata	0.795	*Sonchus oleraceous*	0.313
		Spergula arvensis	0.003
Native perennial grasses		*Stellaria media*	0.301
Aristida adscensionis	0.108	*Torilis nodosa*	0.205
Aristida divericata	0.434		
Stipa cernua	0.015	**Nonnative perennial herbs**	
Stipa diegoensis	0.143	*Aster chilensis*	0.002
Stipa lepida	0.126	*Atriplex semibaccata*	0.893
Stipa pulchra	2.668	*Convolvulus arvensis*	0.397
		Cotula australis	0.050
Native perennial herbs		*Foeniculum vulgare*	0.343
Achillea millefolium	0.010	*Rumex crispus*	0.061

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Flowers Visited by Honey Bees and Native Bees on Santa Cruz Island

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Abstract. European honey bees (*Apis mellifera* L.) were introduced to Santa Cruz Island more than 110 yr ago. Feral honey bee populations occupy most of the island and share floral resources with many native bees. Studies are being conducted to determine the impact of honey bees on native bees and pollination of flowering plants on Santa Cruz Island, as well as the effects of removal of honey bees from a closed system. Foraging honey bees tend to concentrate on introduced weedy plant species. Honey bees overlap primarily with generalist native bees in exploitation of pollen and nectar resources. Removal of honey bees from Santa Cruz Island is predicted to (1) increase food availability for native bees, (2) reduce seed set of some introduced weedy flowering plants, and (3) have little or no negative impact on seed production of most native plants.

Keywords: Feral honey bees; *Apis mellifera*; Africanized honey bees; native bees; nonnative bees; nonnative weeds; endemic plants; biodiversity; biogeography; food resource use; food resource overlap; pollen; nectar; pollination; keystone species; Santa Cruz Island.

Introduction

Considerable controversy exists regarding the impact of honey bees, (*Apis mellifera* L.), on the flora and fauna of various areas of the world where it has been introduced by humans (Roubik 1989; Pyke 1990; Wills et al. 1990; Sugden and Pyke 1991; and Paton 1993). Most were races of European honey bees (EHB) introduced to provide honey and beeswax. More recently a genotype from Africa introduced to Brazil to improve honey production has spread rapidly through the Americas displacing European strains in tropical and subtropical areas. This is the African or Africanized honey bee (AHB) that has received so much attention in the popular press (often known as "killer bees") due to their vigorous colony defense behavior that has resulted in numerous domestic animal and human deaths in the areas they have invaded. This genetic type has become established in Texas (since 1990), Arizona (since 1992) and most recently in New Mexico (1993), and is expected to arrive in California any time.

In most areas of introduction, honey bees have successfully established feral populations by swarming from commercial colonies and have become naturalized. Feral colonies differ from commercial colonies in many characteristics: smaller colony populations, smaller nest cavity size, continued presence if environment permits, and frequent swarming (Seeley 1985; Thorp 1987). These features affect the potential impact on local flora and competition with native bees. Densities of commercial honey bee colonies can be controlled and their effects may be intense, but temporary and sporadic. Densities of feral EHB colonies and their population sizes are greatly affected by fluctuations in floral and water resources. Densities of feral AHB are reported to be greater than those of EHB in tropical areas due to smaller colony sizes, nest cavities occupied, and more frequent swarming (Roubik 1989).

Honey bees were introduced to Santa Cruz Island before 1880 (Wenner and Thorp 1993, 1994). Wenner (1989) proposed a phased removal of them from Santa Cruz Island along with studies on concomitant changes in the flora and fauna. Because honey bees have not become established on any of the other northern Channel Islands, this appears to be a unique opportunity to evaluate the impact of removal of honey bees from a closed system, an opportunity not feasible in mainland habitats due to the widespread naturalization of feral populations. Thus, we set out to determine the diversity of plants used as pollen and/or nectar resources by honey bees in comparison to those used by native bees on Santa Cruz Island. This was deemed basic to questions as to the extent of resource sharing and where to look for the most intensive overlap and, thus, potential competition for food. In order to compare interactions for floral resources between honey bees and other bees on Santa Cruz Island with those of mainland communities, we also investigated the biodiversity, floral specializations, and biogeographic origins of the native bee fauna on Santa Cruz Island.