
Islands, Exotic Herbivores, and Invasive Plants: Their Roles in Coastal California Restoration

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Abstract

The Pacific islands off southern California, U.S.A. and Baja California, Mexico hold potential for the conservation and restoration of California Mediterranean coastal ecosystems. However, the presence of exotic herbivores and invasive plants pose threats to these systems. Here, we use introduced herbivore removal as a large-scale experimental manipulation to examine the importance of top-down and bottom-up processes to a large-scale restoration effort. Using a paired approach on the Todos Santos Islands, Mexico we removed herbivores from one island, while they temporarily remained on an adjacent and similar island. We augmented this experiment with smaller scale herbivore exclosures on the control island. At both scales we failed to detect an herbivore effect on the plant community; rather plant community dynamics appeared to be dominated by El Niño related precipitation and exotic annuals. A parallel experiment on the San Benito Islands, Mexico

revealed a different dynamic: Top-down effects on the plant community by exotic herbivores were evident. Differences in the response from the plant communities to both exotic herbivore presence and removal between these two island groups, along with Santa Barbara Island, U.S.A., where restoration has been on-going, raise important questions in ecosystem restoration. The history of anthropogenic disturbance, exotic plant abundance, and aridity play roles in postherbivore removal recovery. Although island conservation practitioners have honed the ability to remove exotic mammals from islands, development of invasive plant removal techniques is needed to fully capitalize on the conservation potential of California island ecosystems.

Key words: Baja California, Mexico, bottom-up, El Niño, eradication, introduced species, island conservation, large-scale experimental ecology, Mediterranean, rabbits, top-down.

Introduction

Mediterranean ecosystems are second only to lowland tropical rainforests in regional biodiversity (Cowling et al. 1996). Because of land conversion and incursion by exotic species they are also the most altered on earth (Rundel 1998). Southern California has suffered from significant landscape degradation, ecological perturbations, and biodiversity losses (Soulé et al. 1988; Walter 1998). Ecosystem protection in coastal southern California is scant, and areas available for protection often suffer from fragmentation and disturbance (Suarez et al. 1998; Crooks & Soulé 1999). Northwest Baja California, Mexico, where Mediterranean coastal vegetation continues southward from California, has also experienced recent accelerated development. As a result few undisturbed coastal lands exist on either side of the border (Reid & Murphy 1995; Esler et al. 1998).

Although little of this coastal bioregion is protected, all the Pacific islands on both sides of the border (hereafter California Islands) are either government owned or privately protected (Fig. 1) (SEDUE 1989; Halvorson 1994). Consequently, these islands hold potential for the conservation of California Mediterranean coastal ecosystems (Esler et al. 1998; Walter 1998). Restoration has been underway on U.S. California Islands for over 15 years (Davis et al. 1994; Halvorson 1998), and recent efforts have demonstrated the conservation value of islands in northwest Mexico (Donlan et al. 2000; Tershy et al. 2002; Donlan et al. in press). Despite these conservation gains, introduced species are still the greatest threat to these ecosystems.

Introduced species are present on all of the California Islands and are responsible for significant ecosystem degradation, including a number of extinctions (Mellink 1992; Halvorson 1998; Tershy et al. 2002). Introduced herbivores (e.g., goats and rabbits) have caused the greatest damage, including a number of plant extinctions on Guadalupe Island, Mexico (Coblentz 1978; Van Vuren & Coblentz 1987; Moran 1996). Consequently, restoration efforts have focused on removing exotic herbivores, with many successes (McChesney & Tershy 1998; Donlan et al. 2000). Exotic plants are also a threat and are becoming established at an increasing rate. For example, on Santa Cruz Island 36 exotic species were recorded at the turn of the century compared with the 170 now present (Junak et al. 1995). As we adopt food web and ecosystem approaches to

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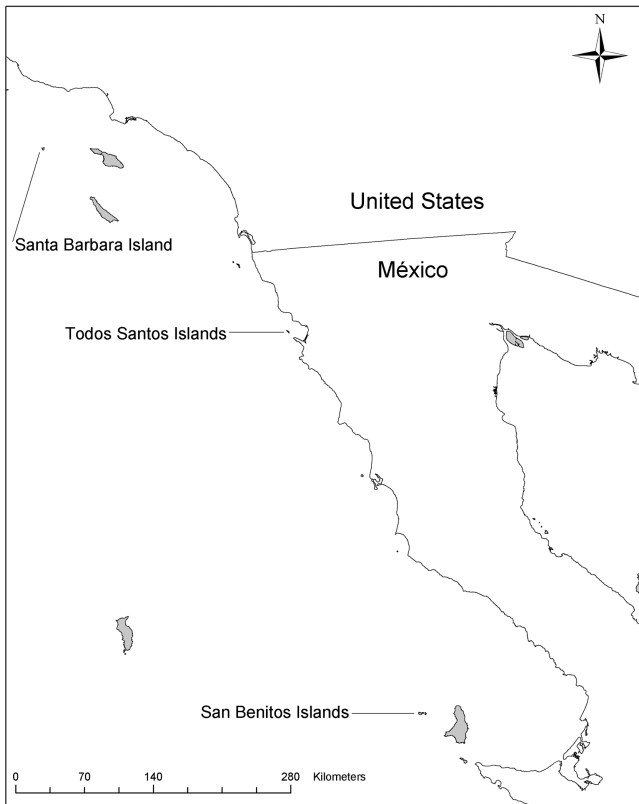


Figure 1. The California Islands. Introduced herbivores have been removed from many of the islands off California and Mexico, including Santa Barbara, Todos Santos, and the San Benitos Islands.

conservation and management (Power 2001), a large-scale holistic view, which includes the roles of exotic herbivores, invasive plants, and their interactions, will be needed for conservation success.

Here, we report on a large-scale experiment that integrates conservation action and experimental ecology. We use the removal of exotic herbivores from the Todos Santos Islands, Mexico to investigate the impact and recovery of an island plant community from herbivory (Fig. 1). We did this by contrasting one island where exotic herbivores were removed to an adjacent similar island where they remained. In addition, we gain insight and inference by combining this large-scale unreplicated manipulation with smaller scale replicated experiments in the form of herbivore exclosures (Frost et al. 1988; Donlan et al. 2002). We began this program with the intent of evaluating the following hypothesis: With herbivore removal plant community structure changes because of the release of top-down regulation.

We compare the results from the Todos Santos Islands with a parallel experiment on the San Benito Islands, Mexico (Donlan et al. 2002) and Santa Barbara Island, California where the U.S. National Park Service has conducted research and restoration for over 15 years (Fig. 1). The San Benitos are relatively intact with little influence by exotic plants; in contrast, Santa Barbara, like the Todos San-

tos Islands, is heavily influenced by exotic plants (Philbrick 1972; Junak & Philbrick 1994, 2000). We draw on these California Islands to discuss the roles of introduced herbivores and invasive plants in island conservation.

Methods

Background and Study Location

The Todos Santos Islands are two islands approximately 90 km south of the U.S.–Mexico border (Fig. 1). Most precipitation (approximately 90%) on the islands falls between November and April, with a mean annual rainfall of 255 mm (Junak & Philbrick 1994). The study system consisted of an experimental island (Todos Santos South, TSS) and a control island (Todos Santos North, TSN). TSS (1 km²) and TSN (0.3 km²) are separated by approximately 200 m and are similar both in vegetation and fauna. The islands are floristically diverse with 142 vascular plant taxa (Junak & Philbrick 1994). Five endemic vertebrates recently existed on the islands, but two species were driven to extinction by feral cats (Mellink 1992).

The Todos Santos Islands have a long history of anthropogenic disturbance. At the beginning of this study cats and European rabbits (*Oryctolagus cuniculus*) were present on TSS and cats, rabbits, and donkeys on TSN. Nonnative plants have recently become abundant: 34 species were recorded in 1994 compared with just 9 in 1950 (Moran 1950; Junak & Philbrick 1994).

Monthly precipitation data were obtained from the closest weather station located in Ensenada (Comision Nacional del Agua), 8 km east of the islands. Limited historical precipitation records (for Ensenada) were also obtained from the literature (Hastings & Humphrey 1969).

Introduced Herbivore Removal

The exotic herbivore eradication from Todos Santos was a part of a regional island conservation program (Donlan et al. 2000; Tershy et al. 2002). Rabbits and cats were removed from both islands; however, the removal on TSN was postponed to facilitate this large-scale experiment. Removal efforts began November 1997; approximately 30 cats and 40 rabbits were removed from TSS by hunting and trapping, yielding a pre-removal rabbit density estimate of 40 rabbits/km². Most animals (>95%, based on total rabbits removed) were removed between November 1997 and January 1998; complete removal was accomplished in spring 1998. Cats, rabbits, and four donkeys were present on TSN throughout the study. Three cats and approximately 30 rabbits were removed from TSN at the completion of this study, yielding a pre-removal density estimate of 100 rabbits/km². The comparison of rabbit density estimates are not ideal because they are from different time periods; however, when combined with comparative natural history observations TSN appeared to be a valid control in this study. Further, given the small num-

bers of donkeys (one to four) present on TSN both historically and just before the study, rabbits were considered the primary vertebrate herbivore on both islands.

Herbivores, Plant Cover, and Diversity

We measured changes in the plant communities by using (1) vegetation transects on both islands over a 17-month period and (2) herbivore exclosures and control plots established on TSN (where herbivores remained). Vegetation transects on TSS ($n = 30$) were permanent and sampled repeatedly. Because of access restrictions on TSN, new transects ($n = 20$) were sampled during each period. However, within island variances proved similar (Fig. 2). The start location of each 100-m transect was marked with a random GPS coordinate, and direction was determined from a random compass bearing. On TSS transects were sampled once before (November 1997) and three times after (April 1998, December 1998, and April 1999) the herbivore removal. On TSN transects were sampled consecutively with TSS (within 2 weeks). We were unable to sample TSN during the first sampling period.

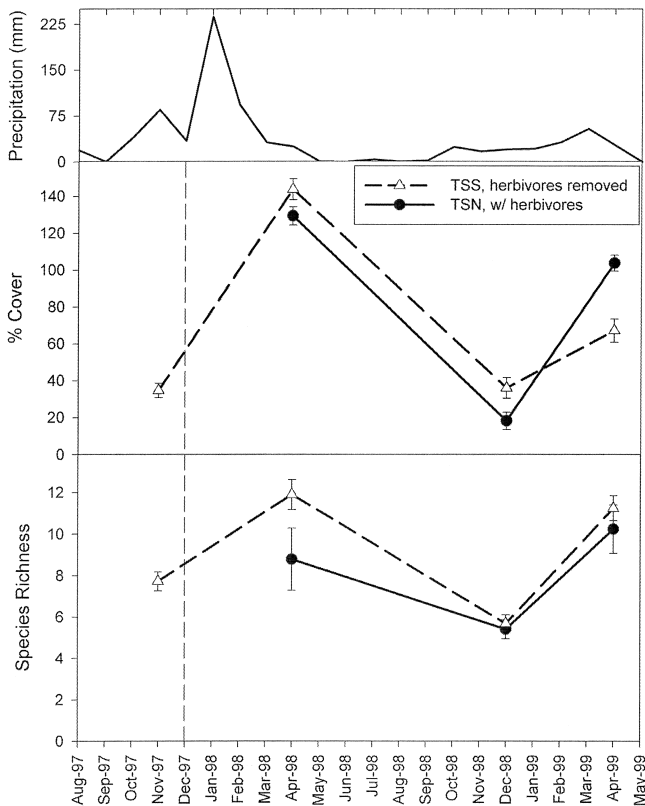


Figure 2. Changes in alpha diversity and vegetative cover on Todos Santos North (TSN) and South (TSS) over 18 months. Introduced herbivores were removed from TSS between November and December 1997 (indicated by the dashed line), whereas they remained on TSN for the entire study. Mean (SE): TSN = 20 transects, TSS = 30 transects.

Using the line-intercept method we estimated percent cover and species richness (i.e., alpha diversity) for each transect during each sampling period (for details see Mueller-Dombois & Ellenberg 1974). For percent cover the horizontal linear length to the nearest 1 cm was measured of each plant that intercepted the transect (intercepts were taken at any height above the ground; cover can exceed 100% due to overlapping species). Only plant species found on both islands were included for between-island species richness comparisons. Distributions of native and nonnative plant cover were tested for changes over time on each island using Kolmogorov-Smirnov tests. We also used linear correlations to test relationships between native and exotic vegetative cover each island for each sampling period. Cover data were arcsine transformed for statistical inference. Analyses were conducted using SYSTAT with an α level of 0.05 (Wilkinson 1998).

Herbivore Exclosures

We constructed three 27×27 -m exclosures on TSN (with herbivores) during May 1998. Locations of the exclosures were determined using random GPS coordinates. Exclosures were made of metal fence posts, chicken wire, and barbed wire, trenched approximately 0.5 m deep and extended 1.25 m high. Using random compass bearings, control plots (also 27×27 m) were located 25 m away from the exclosures. During all visits to the island (>150 days) we saw no evidence of rabbits or donkeys breaching the exclosures. We sampled the exclosures and control plots using five 25-m transects in each plot. All transects were at least 2 m away from the edge of the exclosure, thereby minimizing edge effects. Using the line-intercept method we estimated percent cover for each transect for three sampling periods: July 1998, December 1998, and July 1999. A one-way nested analysis of variance (transects nested in plots) was used to investigate a treatment effect (i.e., the exclusion of herbivores) during each of the three sampling periods.

Results

Herbivores, Plant Diversity, and Cover

During winter 1998 heavy rains, over twice the historical average, fell on the Todos Santos Islands between September 1997 and March 1998, coinciding with the start of an El Niño Southern Oscillation Event (ENSO; Fig. 2) (McPhaden 1999). After March 1998 rainfall declined to normal levels: 232 mm of rain fell between April 1998 and April 1999 (Hastings & Humphrey 1969).

Patterns of species richness and vegetative cover were similar on the experimental (TSS) and control island (TSN). Patterns paralleled changes in rainfall with richness and cover peaks in the spring (Fig. 2). Species richness was comparable on TSS and TSN throughout the study, with the exception of April 1998 where TSS diversity was slightly higher (Fig. 2). Vegetative cover was highest on both islands during April 1998, corresponding with ENSO-related pre-

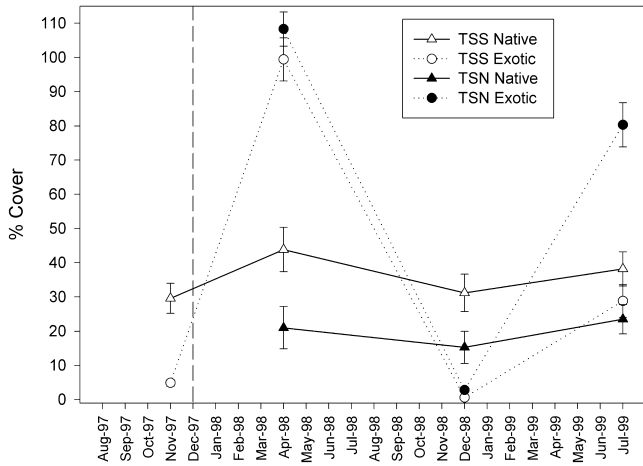


Figure 3. Native and nonnative vegetative cover on Todos Santos South (TSS) and North (TSN) over 18 months. Introduced herbivores were removed from TSS between November and December 1997 (indicated by the dashed line), whereas they remained on TSN for the entire study. Mean (SE): TSN = 20 transects, TSS = 30 transects.

precipitation, and cover on the islands was comparable during April 1998 and December 1998 (Fig. 2). Surprisingly, during April 1999 cover on TSS (herbivores removed) was less than TSN (with herbivores; Fig. 2).

Although native cover showed little change, exotic cover showed dramatic seasonal fluctuations on both islands (Fig. 3). Native cover on TSS was consistently higher than TSN; perennials dominated percent cover of native vegetation. Except for the annual *Marah macrocarpus* (wild cucumber; cover, 5–8%), native annuals were rare on both islands (cover < 2%). With the exception of *M. macrocarpus* on both islands and two additional annuals on TSS, changes of native annual and perennial cover were not significant over time on both islands (six perennials and six annuals on each island, Kolmogorov-Smirnov test, $p > 0.05$, TSS = 30, TSN = 20). In contrast, cover changes of all exotic annuals with the exception of *Mesembryanthemum crystallinum* (iceplant) were significant over time on both islands (five species, Kolmogorov-Smirnov test, $p < 0.05$, TSS = 30, TSN = 20). During April 1998 exotic annual cover on both islands was more than 100%, and cover the following winter was less than 1%. During April 1999 exotic cover on TSS was low compared with TSN (28% and 80%, respectively; Fig. 3). The exotic annual *Malva parviflora* (cheeseweed) was the dominant species on both islands during spring 1998 and 1999.

Negative correlations between native and exotic cover were present on both islands during select sampling periods. During spring sampling periods with high exotic cover native and exotic cover was negatively correlated (TSN spring 1999 $r_p = -0.52$, TSN spring 2000 $r_p = -0.74$, TSS spring 1999 $r_p = -0.56$, $p < 0.05$ for all periods). On TSS during spring 2000 there was no correlation between native and exotic cover ($p = 0.65$). With the exception of TSS winter 1999

Table 1. Vegetative cover of herbivore exclusion and control plots on Todos Santos North during three sampling periods.

	May 1998	December 1999	April 1998
Exclusion			
1*	103.0 (6.1)	0	116.4 (8.4)
2	172.1 (28.2)	58.3 (42.7)	109.1 (36.2)
3	178.4 (43.3)	75.0 (14.8)	131.3 (13.5)
Control			
1*	122.4 (23.0)	6.2 (10.4)	122.7 (24.2)
2	181.1 (38.4)	37.3 (20.0)	136.3 (26.3)
3	184.5 (16.9)	91.2 (34.6)	116.5 (17.3)

Values are mean cover, with standard deviation in parentheses. No differences were detected between exclusion and control plots for any time period (one-way nested analysis of variance: $p > 0.17$, $n = 6$ [3 replicates within the two treatments, five transects per replicate]). Because of nonsignificant differences between the nested transects, estimates of variation were pooled to increase statistical power. However, no differences were detected between treatments ($p > 0.10$). * Plot consisted entirely of *Malva parviflora*.

($r_p = -0.63$, $p < 0.001$), there was no correlations on TSS or TSN between native and exotic cover during winter sampling periods, when exotic cover was low ($p > 0.26$).

Herbivore Exlosures

We found no differences in cover between the exclusions and control plots on TSN throughout the study. One exclusion and control plot were exclusively *M. parviflora*; in both plots cover was high during spring (>100%) and low during December 1999 (<6%). The additional plots consisted of both native and exotic species; vegetative cover changes were similar in the exclusion and control plots (Table 1). No differences existed between transects nested within plots at a $\alpha = 0.25$; therefore, the pooling of estimates of variation is warranted while controlling for type II error (Underwood 1997). Despite increased statistical power from post-hoc pooling of estimates of variation, we found no differences between the treatment (Table 1; power analysis: $1 - \beta > 0.86$ for all three sampling periods, effect size = 0.25) (Cohen 1977).

Discussion

Vegetative dynamics were similar on both the experimental (TSS, herbivores removed) and control (TSN, with herbivores) islands during the first 16 months after the removal of herbivores (Figs. 2–3). As seen elsewhere (Polis et al. 1997; Donlan et al. 2002), ENSO-related precipitation contributed to high levels of vegetative cover during April 1998. Cover patterns paralleled rainfall during the remainder of the study. Similar results were observed in the exclusions and control plots on TSN: Cover changes paralleled rainfall and an herbivore effect was not detected, despite sufficient statistical power (see Results). Although changes in species richness on TSS and TSN were also influenced by rainfall, ENSO-related precipitation appeared to have little effect: Richness during April 1998 and April 1999 were similar on both islands.

Exotic annuals dominated the plant community on both islands. Homogenous stands (2 m tall) of *Malva parviflora* (hereafter *Malva*) covered much of the islands during the spring sampling periods (40–70%). In addition, exotic annual grasses were abundant, and *Mesembryanthemum crystallinum* (hereafter *Mesembryanthemum*) was locally common. Although ENSO-related precipitation likely played a role in the widespread germination of exotic annuals during spring 1998, exotic cover was also high the following spring with normal precipitation.

In contrast to exotics, native vegetation showed little change in response to either rainfall or herbivore removal. This response differs from exotic herbivore removal studies elsewhere (Coblentz 1978; Ebenhard 1988). Overall, patterns of vegetative cover and species richness on the experimental (TSS) and control (TSN) islands, coupled with the results of the enclosure experiments, suggest that the effects of exotic herbivores on the Todos Santos plant communities were negligible at the resolution of our 18-month study. These results, along with the negative relationships between exotic and native cover, suggest that exotic annuals may be the major community driver in this insular system.

A concurrent study, on the San Benito Islands, Mexico, revealed a different dynamic: Top-down effects on the plant community by introduced rabbits were evident. On the experimental island (herbivores removed) preferred plants increased in abundance, whereas unpalatable species decreased with herbivore removal. In contrast, on the control island (with herbivores) preferred plants declined approaching extinction, whereas unpalatable plants increased in abundance (Donlan et al. 2002). Despite not knowing herbivore preferences on Todos Santos, we observed no between-island differences in the vegetation dynamics.

The differences in the short-term response of plant communities to herbivore removal between Todos Santos and San Benito Islands raise important questions in island restoration. Differences in native versus exotic plant dominance may play a key role in these observed differences. The arid San Benito Islands are dominated by native vegetation, with few nonnative plants (Junak & Philbrick 2000). In contrast, the Todos Santos Islands have a long history of disturbance and subsequently have been dominated by exotic annuals (Junak & Philbrick 1994). The native-dominated San Benito plant community showed rapid signs of recovery toward pre-disturbance conditions; in contrast, Todos Santos showed no such signs after herbivore removal and remain an altered ecosystem dominated by exotic plants.

Two nonexclusive explanations exist for the failure of the herbivore removal to have a short-term impact on the Todos Santos plant communities. First, through bottom-up factors (i.e., precipitation), exotic annuals (*Malva* and others) swamped any top-down effect by rabbits. Second, rabbit densities on TSS were too low to exhibit an herbivore effect on the plant community. The latter explanation

is unlikely. The presence of feral cats may have suppressed rabbit densities; however, enclosures showed no signs of a herbivore effect on TSN, where density estimates were comparable with densities on the San Benito Islands (115–193 rabbits/km²), where herbivore effects were widespread (Donlan et al. 2002).

Dominant exotics annuals on Todos Santos include *Malva*, *Mesembryanthemum*, and European annual grasses (*Bromus* spp. [brome], *Avena* spp. [oat], *Hordeum murinum* [barley]). A recent history of human-caused fires on the islands likely facilitated the spread of exotic annuals, particularly hard-seeded exotic annuals like *Malva* that are encouraged by fire (Makowski & Morrison 1989; Junak & Philbrick 1994; Milberg & Lamont 1995). With its competitive ability, persistent seed bank (>100 years), and ability to inbreed (Kivilaan & Bandurski 1981; Milberg & Lamont 1995), *Malva*'s presence may be permanent once established. Control of this species elsewhere has been minimally effective (Milberg & Lamont 1995). Also facilitated by fire, *Mesembryanthemum* causes ecosystem-level changes by altering soil characteristics (Vivrette & Muller 1977). By accumulating high levels of salt in its tissues and subsequently leaching them into the soil at death, *Mesembryanthemum* prevents the growth of nontolerant plants by changing the osmotic environment and facilitates the spread of itself and other salt-tolerant exotics such as *Malva* spp. and *Hordeum* spp. (N. Vivrette, Ransom Seed Laboratory, personal communication, 2000; Vivrette & Muller 1977; Makowski & Morrison 1989). Exotic grasses have also been shown to have ecosystem-level impacts through resource competition, geomorphological changes, and alteration of fire regimes (Mack 1981; D'Antonio & Vitousek 1992). In coastal scrub ecosystems exotic grasses persist even after the removal of disturbances such as grazing and fire (Eliason & Allen 1997). Even if the potential for fire and other disturbances were removed from the Todos Santos Islands, removing these ecosystem-level impacts from these exotics will prove difficult.

Three hundred kilometers to the north, a similar dynamic is occurring on Santa Barbara Island (Fig. 1). With similar climate and subsequent plant community Santa Barbara, like Todos Santos, has a long history of anthropogenic disturbance, including exotic herbivores, invasive plants, and fire (Philbrick 1972). Fire, goats, European rabbits, and exotic annuals (including *Malva*, *Mesembryanthemum*, and exotic grasses) were introduced to the island before the 1900s. Rabbits and *Mesembryanthemum* populations rapidly expanded in the 1950s; these exotics along with fire caused widespread destruction of native vegetation (Philbrick 1972). In 1981 the U.S. National Park Service removed rabbits. Although a succulent (*Dudleya traskiae*; Santa Barbara Island live-forever) once on the verge of extinction is recovering (Clark & Halvorson 1987), the native plant community is not. Exotic grasses, *Mesembryanthemum*, and bare soil still dominate the island after 19 years of minimal anthropogenic disturbance (Halvorson et al. 1988; D'Antonio et al. 1992). Recent res-

toration efforts by the Park Service, including revegetation and erosion control, show some progress but are labor intensive (D'Antonio et al. 1992; Halvorson 1994). Reversing the impacts of invasive plants will undoubtedly prove more challenging than exotic herbivore removal. But without success in such efforts the full conservation potential of the California Islands will not be realized.

The California islands, on both sides of the border, are likely the remaining candidates for the permanent restoration of coastal California habitat due to the ability to remove anthropogenic disturbances (e.g., exotic species removals), protect against future disturbances (e.g., plant invasions and fire), and minimize pressure of human development. In arid ecosystems or where anthropogenic disturbance has been minimal, the removal of exotic herbivores may be sufficient to allow for natural recovery of native plant communities without need of active management. However, evidence from this study and Santa Barbara Island suggests that for disturbed ecosystems herbivore removal alone is not enough. As we adopt ecosystem approaches to management, an understanding of the interactions of exotic herbivores and invasive plants is needed. Recently developed techniques have facilitated introduced mammal removals on larger and biologically complex islands (Donlan et al. in press). Similar techniques are needed for plant eradication, a daunting challenge for ecologists, managers, and conservationists. On most of the California islands a long-term commitment that includes intensive on-the-ground restoration, applied research, and adaptive management will be a prerequisite for restoration success.

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