

Islands and introduced herbivores: conservation action as ecosystem experimentation

C. JOSH DONLAN,*† BERNIE R. TERSHY*‡ and DONALD A. CROLL*†

*Island Conservation & Ecology Group, †Department of Biology and ‡Institute of Marine Science, University of California, Long Marine Lab, 100 Shaffer Road, Santa Cruz, CA 95060, USA

Summary

1. Overgrazing by exotic herbivores has a widespread impact on plant communities. We used the removal of exotic European rabbits, goats and donkeys from the San Benito Islands, Mexico, as an experimental manipulation to examine the importance of top-down and bottom-up processes in the impact and recovery of an island plant community.
2. Using a paired approach, we removed herbivores from one island, while they remained temporarily on an adjacent, similar island. We combined this large-scale manipulation with smaller-scale mechanistic experiments: herbivore food-preference trials and herbivore exclosures on the control island.
3. El Niño-related precipitation dominated vegetation dynamics early in the study. Differences in plant community structure due to selective herbivory between the experimental and control islands were detectable in the second year. Results from food-preference trials accurately predicted changes in the perennial plant community. When herbivores were removed from the experimental island, the abundance of their preferred plants increased while unpalatable species decreased. On the control island (herbivores present), we observed the opposite trend. However, we saw no recovery of vegetation inside the exclosures on the control island, constructed after the El Niño rains, probably due to the absence of rainfall.
4. While the relationship between herbivore food preference and changes in plant cover is strong evidence of a top-down effect by exotic species, the influence of El Niño precipitation highlights the importance of bottom-up factors, such as water availability, in the recovery of arid plant communities from long-term disturbance.

Key-words: Baja California, bottom-up, El Niño, exotic herbivory, large-scale experiments, Mexico, rabbits, top-down.

Journal of Applied Ecology (2002) **39**, 235–246

Introduction

A central question in ecology and conservation is the degree to which populations are limited by bottom-up vs. top-down forces (Pace *et al.* 1999; Polis 1999; Terborgh *et al.* 1999; Hunter 2001). Recent studies have shown that top-down processes in terrestrial systems can have fundamental effects on population demography and community composition (Pace *et al.* 1999; Terborgh *et al.* 1999; Maron & Simms 2001; Ripple *et al.* 2001; Roemer, Donlan & Courchamp 2002). However, abiotic forces, such as El Niño Southern Oscillation (ENSO) events, are important community

drivers (Meserve *et al.* 1999; Stapp, Polis & Sanchez Pinero 1999; Wright *et al.* 1999; Jaksic 2001). There is still only limited understanding of the degree to which interactions among species and the environment affect community processes (Oksanen & Oksanen 2000; Hunter 2001). A factor that has contributed to this limited understanding is the paucity of trophic studies that are both large in spatial scale and experimental in nature (Estes, Crooks & Holt 2001). Despite the challenges of large-scale experiments, they are both invaluable and irreplaceable in ecology (Likens 1985; Carpenter 1996).

Ecosystems are ‘the basic units of nature’ (Tansley 1935), and consequently the units of many applied ecological problems (Ormerod & Watkinson 2000). The importance of knowledge gained by large-scale and whole ecosystem experiments will increase as we adopt food web and ecosystem approaches to management and conservation (*sensu* Power 2001; Zavaleta, Hobbs

Correspondence: C. Josh Donlan, Island Conservation & Ecology Group, University of California, Long Marine Lab, 100 Shaffer Road, Santa Cruz, CA 95060, USA (fax 831 459 3383; e-mail jdonlan@islandconservation.org).

& Mooney 2001). A collaboration between ecological research and management offers a particularly promising opportunity to test experimentally ecological hypotheses at relevant spatial and temporal scales (Schmitz & Sinclair 1997). However, the integration of large-scale experiments with conservation application, in the spirit of adaptive management, has been limited largely to aquatic ecosystems (Walters 1986; Carpenter & Kitchell 1993). This lack of large-scale terrestrial experiments is partly due to intrinsic logistical and moral challenges coupled with the recent dominating influence by experimentalists on the methodological philosophy of ecology (Estes 1995; Oksanen 2001). Oksanen (2001) provides a philosophical framework that attempts to resolve some issues put forth by experimentalists (Hurlbert 1984). To overcome logistical and moral challenges, creative approaches are needed (Estes 1995). Examples include exploring (i) habitat fragments with and without predators; (ii) the recovery and/or decline of an over-exploited species; and (iii) reintroductions (Breitenmoser & Haller 1993; Estes & Duggins 1995; Crooks & Soulé 1999; Stahl *et al.* 2001). Here, using islands as a model system, we report on a novel approach to large-scale experiments with direct application to conservation and management.

Many island biotas now include exotic mammals. Due to the lack of both top predators and a history of vertebrate herbivory in the evolutionary background of island plants (Carlquist 1974; Bowen & Van Vuren 1997), exotic herbivores are known to play key roles in island ecosystems (Hunter 1992). The study of these herbivores offers an opportunity to explore potential top-down effects of species additions, and their removal provides a powerful approach to understanding these effects. While the eradication of non-native mammals from islands is important in conservation (Towns, Atkinson & Daugherty 1990; Donlan *et al.* 2000; Simberloff 2001), it also provides opportunities for large-scale applied experiments on ecosystems. These opportunities, which are morally justified due to conservation gains (Soule 1990), have been largely under-utilized by researchers (notable exceptions include Dilks & Wilson 1979; North, Bullock & Dulloo 1994).

In this study, we used the removal of exotic herbivores from the San Benito Islands, Mexico, to investigate the impact and recovery of an island plant community from herbivory. We did this by contrasting one island, from where exotic herbivores were removed, with another adjacent and similar island, where they remained. We began this programme with the intent of evaluating the following hypotheses: (i) with herbivore removal, plant community structure changes due to the release of top-down regulation; and (ii) the response by the plant community is predictable from the hierarchy of herbivore food preference. Specifically, we expected the largest relative increases by the most preferred plants.

An understanding of the community-level responses to exotic herbivory has important applied implications,

aiding in the management and restoration of grazing systems and degraded habitats (Bullock *et al.* 2001; Nugent, Fraser & Sweetapple 2001). However, the majority of evidence on community-wide impacts of exotic species remains anecdotal (Blossey 1999; Parker *et al.* 1999; although see Norbury 2001; Roemer, Donlan & Courchamp 2002). We therefore augmented our large-scale manipulation with smaller-scale replicated experiments. This approach allowed insight on both exotic herbivore and abiotic (i.e. precipitation) effects on an island plant community at the ecosystem scale.

BACKGROUND AND STUDY LOCATION

The San Benito Islands (Fig. 1; 28°18'30" N and 115°34'00" W) are located *c.* 65 km west of Point Eugenia, Baja California, Mexico, one of the driest areas in North America (mean annual rainfall < 100 mm; Crosswhite & Crosswhite 1982). These Sonoran desert islands are low in diversity but high in endemism, including at least eight endemic plants (Junak & Philbrick 2000). They have no native terrestrial mammals. The San Benito Islands are an important seabird nesting site, with 12 species nesting in large numbers (Boswell 1978). Seabirds probably play an important role in terms of nutrient input to the islands (C.J. Donlan, unpublished data; Anderson & Polis 1999). The study system consisted of an experimental island (San Benito West, SBW) and a control island (San Benito East, SBE). SBW (3.5 km²) and SBE (1.1 km²) are separated by *c.* 2 km and are similar both in vegetation and fauna (Junak & Philbrick 2000). The dominant plant community on both islands is maritime desert scrub, consisting of shrubs and suffrutescent perennials [*Agave sebastiana* (Greene), *Atriplex barclayana* (Benth.), *Euphorbia misera* (Benth.), *Frankenia palmeri* (I.M. Johnst.), *Lycium brevipes* (Benth.), *Lycium californicum* (Nutt.), *Malva pacifica* (M.F. Ray), *Suaeda moquimii* (Greene) and two species of cacti, as well as winter annuals, *Cryptantha* spp., *Eschscholzia ramosa* (Greene), *Hemizonia streetsii* (A. Gray) and *Perityle emoryi* (Torr.)] (Junak & Philbrick 2000).

European rabbits *Oryctolagus cuniculus* (L.) were introduced to the San Benito Islands during the early 1990s and have since caused significant damage to the vegetation (Donlan *et al.* 2000). On SBW, rabbits were introduced in 1991; goats *Capra hircus* (L.) and donkeys *Equus asinus* (L.) have had a discontinuous presence since 1948 (Junak & Philbrick 2000). At the beginning of the study, rabbits were abundant and a few goats and donkeys (11 in total) were present on SBW. On SBE, rabbits were introduced between 1995 and 1996; rabbits were abundant by March 1996 (Donlan *et al.* 2000). There is no history of goats or donkeys on SBE. Given the small numbers of donkeys (one to four) and goats present on SBW, both historically (Moran & Lindsay 1951) and just prior to the study, rabbits were considered the primary vertebrate herbivore on both islands.

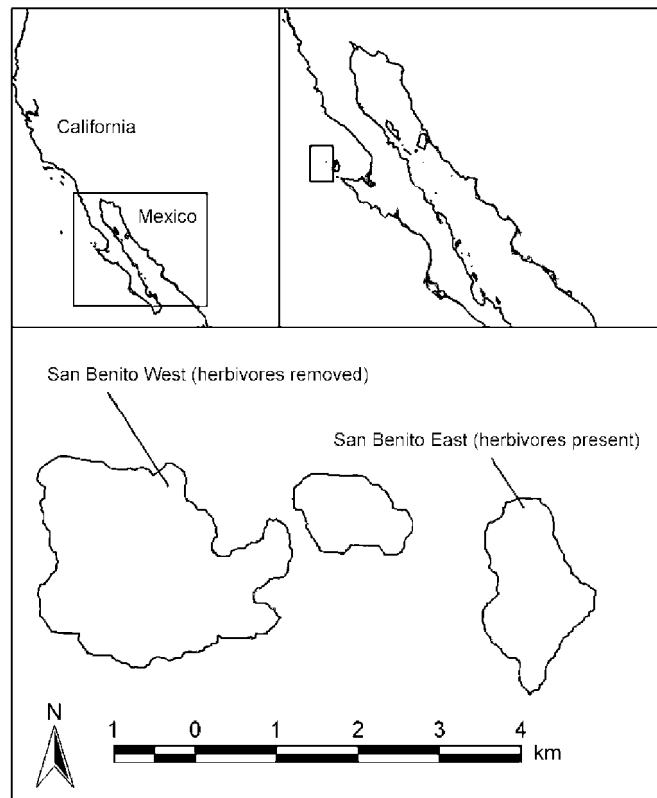


Fig. 1. The San Benito Islands, Baja California, Mexico.

Materials and methods

The eradication of exotic herbivores from the San Benito Islands was part of a regional island conservation programme (Donlan *et al.* 2000; Tershy *et al.* 2002). Herbivores were removed from both SBW and SBE; however, the removal on SBE was postponed to facilitate this large-scale experiment. Exotic herbivores on SBW were either removed by hunting and trapping (rabbits and goats) or they were permanently corralled (donkeys). Removal efforts began during January 1998; most rabbits (> 95%, based on total rabbits removed) and all seven goats were removed during the first 2 months. Complete removal was accomplished in spring 1998. Approximately 400 rabbits were removed from SBW, yielding a pre-removal rabbit density of 114 rabbits km⁻². Four donkeys were permanently corralled and provided with processed feed. Throughout the study, the rabbit population remained high on SBE. At its completion, rabbits were removed from SBE. Approximately 200 rabbits were removed between August and September 1999, yielding a pre-removal density of 181 rabbits km⁻². While estimated rabbit density was lower on SBW, the presence of the few larger herbivores on SBW may have compensated in terms of herbivore effects. The comparison of density estimates was not ideal because they came from different time periods (SBW prior to March 1998 and SBE after August 1999); however, when combined with comparative natural history

observations, SBE appeared to be a valid control in this study.

The postponement of the eradication on SBE did not jeopardize any conservation objectives. On the contrary, this study was planned around the conservation programme; rabbits were first eradicated from SBW due to a threatened endemic succulent (*Dudleya linearis* (Greene)) that is restricted to SBW (Donlan *et al.* 2000). Despite advantages of keeping rabbits on SBE for a longer period (i.e. extending the length of the experiment), we chose to remove rabbits from SBE in August 1999, both for the restoration benefit of the island and to remove the threat of rabbit reintroduction to SBW from SBE.

We examined herbivore effects on plant community structure by using three approaches: (i) permanent vegetation transects on both islands; (ii) food-preference trials on rabbits; and (iii) herbivore exclosures and control plots on SBE (with herbivores). Fieldwork was conducted during December 1997, June–July 1998, December 1998 and June–July 1999. Statistical analyses were conducted using SYSTATTM with an α -level of 0.05 (Wilkinson 1998).

HERBIVORES, PLANT COVER AND DIVERSITY

We measured changes in the plant communities on both islands using repeated-sampling permanent transects (21 on SBW, 11 on SBE) over a 20-month period. The start location of each 100-m transect was

marked with a random Global Positioning System (GPS) coordinate and direction was determined from a random compass bearing. We sampled both islands consecutively (within a period of 3 weeks), once prior to (December 1997) and three times (June–July 1998, December 1998 and June–July 1999) after herbivore removal on SBW. Using the line-intercept method (Mueller-Dombois & Ellenberg 1974), we estimated percentage cover and alpha diversity for each transect during each sampling period. For percentage cover, the horizontal linear length of each plant that intercepted the 100-m transect was measured (to the nearest 1 cm). To allow for between-island comparisons, only plant species found on both islands were included in computations of alpha diversity. Of the 51 vascular taxa found on the San Benito Islands, 22 are restricted to SBW. Most of these restricted taxa are rare annuals, some known from a single specimen (Junak & Philbrick 2000). The suite of plant species that characterize the islands are similar on SBW and SBE (see Background above; Junak & Philbrick 2000).

HERBIVORE PREFERENCE AND PLANT SPECIES ABUNDANCE

We performed a series of food preference tests with eight feral rabbits on SBE. Rabbits were captured, placed in a 3 × 3-m enclosure with no standing vegetation, and habituated for at least 24 h (the rabbits, originally from domestic stock, were relatively tame and thus habituated quickly). Five native, perennial, plants were chosen for preference tests: *Atriplex barclayana* (Chenopodiaceae), *Euphorbia misera* (Euphorbiaceae), *Lycium californicum* (Solanaceae), *Malva pacifica* (Malvaceae) and *Suaeda moquinii* (Chenopodiaceae). *Malva pacifica* is an island endemic; the remaining plants are native throughout Baja California (Junak & Philbrick 2000). Plants were chosen based on a priori field observations of rabbit browsing, browse damage and general plant abundance. On both islands, *Malva pacifica* and *Euphorbia misera* were heavily browsed; *Atriplex barclayana* showed some signs of browsing; and *Lycium californicum* and *Suaeda moquinii* showed no signs of herbivory. Plant specimens for trials were freshly picked and haphazardly collected from various locations on SBE.

Each trial was performed on a single rabbit that was provided a choice of two plant species. Each rabbit was tested for all 10 pairwise combinations of the five plant species and the entire experiment was replicated five times for each rabbit. Equal proportions (by size) of plants were used and small samples were placed adjacent to each other inside the enclosure. The order of the dichotomous tests and the relative position of the two plants (left or right side) were random. Trials were conducted on three rabbits during July 1998 and five rabbits during July 1999. The first plant species consumed by the rabbit was scored as preferred for each trial conducted. A food preference index (P) was calculated for each plant species from the equation:

$$P(x) = \frac{\text{number of times plant species } x \text{ was chosen}}{\text{number of choice tests that included plant species } x}$$

Results from the food preference trials were used to predict a priori the direction and magnitude of perennial plant cover change on both islands. Ordered heterogeneity tests were performed for each island using percentage cover change (December 1997–July 1999) for the five plant species (Rice & Gaines 1994a,b). Using cover change from the plant transects for each of the five plant species, Friedman tests were used to test for heterogeneity through time (Neter *et al.* 1996). In addition, we used linear regression models to test relationships between rabbit plant preference and plant species cover on both islands. Models were developed for each of the four sampling periods to test for a time effect on each island.

HERBIVORE EXCLOSURES

We constructed three 27 × 27-m exclosures on SBE (with herbivores) during July 1998. The locations of the exclosures were determined using random GPS coordinates. The exclosures were made of metal fence posts and chicken 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 (> 100 days) we saw no evidence of rabbits 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 percentage cover for each transect for three sampling periods: July 1998, December 1998 and July 1999. A one-way nested ANOVA (transects nested in plots) was used to investigate a treatment effect (i.e. the exclusion of herbivores) during each of the three sampling periods.

PRECIPITATION

Monthly precipitation data were obtained from the closest weather station, Exportadora de Sal S.A. meteorological department located on Cedros Island (27 km east of the San Benito Islands). Limited historical precipitation records (for Cedros Island) were also obtained from the literature (Hastings & Humphrey 1969).

Results

HERBIVORES, PLANT DIVERSITY AND COVER

From August 1997 to March 1998, heavy rain (over twice the historical average) fell on the San Benito Islands coinciding with the onset of a strong ENSO

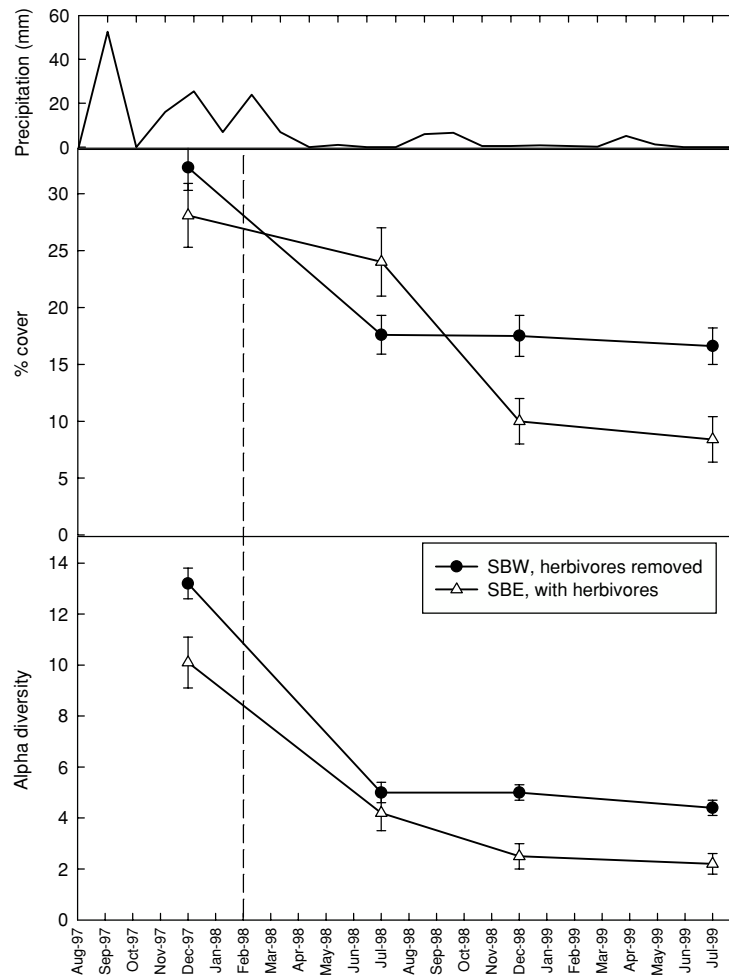


Fig. 2. Changes in alpha diversity and vegetative cover on San Benito West (SBW) and East (SBE) over 20 months. Introduced herbivores were removed from SBW between January and February 1998 (indicated by the dashed line), while they remained on SBE for the entire study. Mean (SE), SBW = 21 transects, SBE = 11 transects.

(Fig. 2; McPhaden 1999). Very little rain (22 mm; less than half the historical average) fell during the remainder of the study (Fig. 2).

Percentage cover and alpha diversity were influenced by rain and the subsequent effects of grazing (Fig. 2). During December 1997, in response to ENSO-related precipitation, cover and alpha diversity of the plant communities were elevated on both SBW and SBE. With the return to arid conditions, diversity and cover declined to similar levels on both islands by July 1998. During the final sampling periods, diversity continued to decline on SBE (with herbivores) but remained constant on SBW (herbivores removed). On SBW, vegetative cover levelled off (16.6–17.5%), after the initial decline due to annual senescence (Fig. 2). On SBE, cover declined throughout the study due to a combination of annual senescence and selective herbivory (28.1–8.4%; Fig. 2).

HERBIVORE PREFERENCE AND PLANT SPECIES ABUNDANCE

All eight rabbits preferred the five perennial species in an identical order (Kendall coefficient of concordance

= 1.0), with the endemic *Malva pacifica* (0.96 ± 0.02 , mean preference index \pm SE) being the most preferred, followed by *Euphorbia misera* (0.73 ± 0.02), *Atriplex barclayana* (0.50 ± 0.02), *Lycium californicum* (0.31 ± 0.02) and *Suaeda moquinii* (0.01 ± 0.01). The latter species was almost never eaten by rabbits. Differences between food preference indices were significant (Friedman test statistic = 32.0; $P < 0.001$). Results of the food-preference trials showed a strict hierarchical pattern. *Malva pacifica* was always preferred over the other four plants; *Euphorbia misera* was always chosen over the remaining three species, and so on.

As predicted, the changes in relative abundance of the five plant species were positively correlated with the preference hierarchy on SBW (herbivores removed), whereas on SBE (herbivores present) the correlation was negative (Fig. 3). The trends on both islands were statistically significant (Fig. 3). Changes in regression models over time were consistent with the hypothesis that introduced herbivores exhibit top-down control of the plant community (Fig. 4). On SBE (with herbivores), we found no relationship between rabbit food preference and plant cover during the first sampling

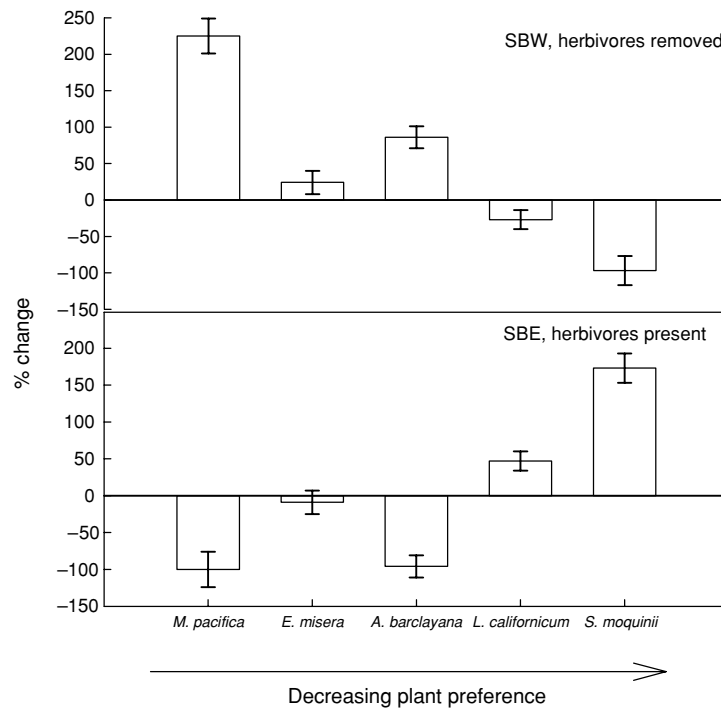


Fig. 3. Mean percentage cover change (SE) for five perennial species on San Benito West (SBW, $n = 21$) and East (SBE, $n = 11$) between December 1997 and July 1999. Introduced herbivores were removed from SBW, while they remained on SBE for the entire study. Plant species are arranged in order of rabbit preference (see the Methods), the most preferred plant being *Malva pacifica*. Trends on both islands are significant (ordered heterogeneity test; SBW: OH = 0.89, $P < 0.001$; SBE: OH = 0.72, $P = 0.01$).

period (Fig. 4a), but strong negative relationships for the subsequent three periods (Fig. 4b–d). We found the opposite trend on SBW (herbivores removed): strong negative relationships during the first two sampling periods, followed by non-significant relationships during the last two periods (Fig. 4e–h). The slopes of the SBE models showed an initial negative increase (December 1997–July 1998), while the slopes of the SBW models changed from negative to positive through time. While the absolute cover of the perennial plant species was low (0–5%), this was partly a reflection of the sparse vegetation in this desert ecosystem. These five perennial species are dominant, in terms of abundance, on both islands.

HERBIVORE ENCLOSURES

We found no differences in cover between enclosure and control plots on SBE (Table 1). The plots were constructed and first sampled in July 1998, after the ENSO-related precipitation. Cacti [*Opuntia* sp. nova and *Mammillaria neopalmeri* (Craig)] dominated one enclosure and control plot; cover in both of these plots remained relatively constant throughout the study (16–20%; Table 1). Due to heavy herbivory by rabbits prior to enclosure construction, the additional two enclosure and control plots were low in cover (< 2.0%) during the initial sampling period and remained low. By the last sampling period, the two control plots were completely denuded of vegetation (Table 1). No germination was

Table 1. Vegetative cover of herbivore enclosure and control plots on San Benito East during three sampling periods, mean cover (SD). No differences were detected between enclosure and control plots for any time period [one-way nested ANOVA: $P > 0.90$, $n = 6$ (three replicates within the two treatments, five transects per replicate)]. Due to non-significant differences between the nested transects, estimates of variation were pooled to increase statistical power. However, no differences were detected between treatments ($P > 0.11$)

	July 1998	December 1998	July 1999
Enclosure			
1	1.58 (0.58)	1.97 (0.40)	1.24 (0.28)
2*	18.64 (1.60)	22.19 (1.68)	16.41 (0.83)
3	0.22 (0.010)	1.51 (0.96)	1.55 (0.29)
Control			
1	0.05 (0.05)	0.28 (0.28)	0.0
2†	20.06 (0.91)	20.62 (0.92)	20.15 (0.32)
3	0.06 (0.06)	0.0	0.0

*Cover by cacti = 12.5, 16.2, 13.2 for respective periods.

†Cover by cacti = 14.8, 16.1, 16.7 for respective periods.

observed. No differences existed between transects nested within plots at an α -level = 0.25; therefore, the pooling of estimates of variation was warranted while controlling for type II error (Underwood 1997). In spite of 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).

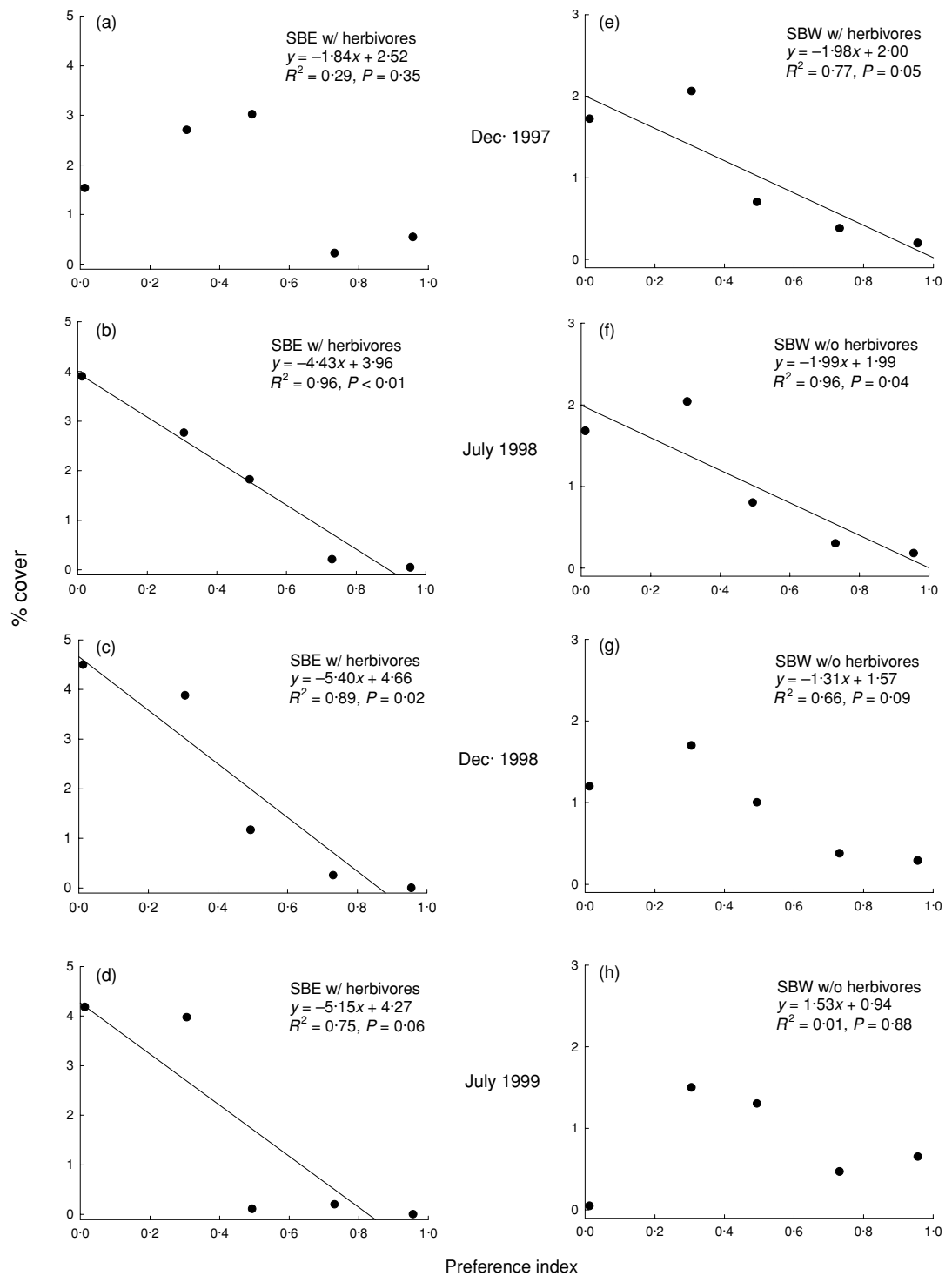


Fig. 4. Linear regression models with mean rabbit food preference index as the independent variable and corresponding mean plant species cover as the dependent variable. (a–d) From San Benito East (SBE) for each sampling period; negative relationships are present with the exception of the first sampling period. (e–h) From San Benito West (SBW), where introduced herbivores were removed after the first sampling period; negative relationships exist during the first two sampling periods and are lacking thereafter.

Discussion

LARGE-SCALE EXPERIMENTS IN APPLIED ECOLOGY

Two main obstacles in conducting large-scale experiments are valid controls and replication (Diamond 1986).

Due to ethical or logistical circumstances, these obstacles are often insuperable. Many studies of plant–herbivore dynamics have been plagued by shortcomings in experimental design, particularly spatial scale (Crawley 1990) and statistical inferences resulting in pseudoreplication (Hurlbert 1984; Brown & McDonald 1995). While in this study an adjacent island served as

a large-scale control, the treatment effects at the level of islands were not replicated. Rather, we gain insight and inference by combining the large-scale manipulation with smaller-scale replicated mechanistic experiments (Frost *et al.* 1988). This integrative approach avoids problematic issues with statistical inference (Hurlbert 1984) and extrapolations from small-scale studies to larger scales (Crawley 1990; Carpenter 1996). The value of this approach is especially apparent in this study. The inevitable lack of replication at the island scale, the conservation objectives outweighing the possibility for additional temporal data collection pre-eradication, and the environmental variance imposed by ENSO-related precipitation make inferences challenging. The combination of large- and small-scale approaches allows for such inferences.

Large-scale experiments are scaled properly for important management issues and thus will play a critical role in resource management in the face of environmental change (Carpenter 1990). An ecosystem approach to conservation and restoration will also play a decisive role (Power 2001; Zavaleta, Hobbs & Mooney 2001). A blend between ecosystem restoration and large-scale experimentalism has much to offer conservation and ecology. The restorationist provides the large-scale manipulation, while the ecologist provides a quantitative assessment of the restoration action. Ecologists exploiting such opportunities to overcome the obstacles of large-scale experiments will greatly benefit pure ecology and environmental problem-solving (Walters & Holling 1990; Ormerod & Watkinson 2000).

EL NIÑO, HERBIVORE RELEASE AND TOP-DOWN EFFECTS

Deserts are stressed environments with low primary productivity and scarce, variable rainfall, and consequently are viewed as pulse-reserve ecosystems regulated by abiotic factors, particularly water availability (Noy-Meir 1973; Evenari, Noy-Meir & Goodall 1985; although see Polis 1991). As a result, ENSO-related precipitation events have large impacts on arid ecosystems (Brown & Heske 1990; Meserve *et al.* 1999; Jaksic 2001). For example, during the 1992–93 ENSO, Polis *et al.* (1997) documented dramatic changes on small island communities in the Gulf of California, Mexico (i.e. an increase in mean plant cover from 1% to 40%).

Heavy rain on the San Benito Islands during the 1997–98 ENSO resulted in elevated vegetative cover and diversity (Fig. 2). The germination of annuals resulting from the precipitation dominated plant community structure on both islands early in the study, whereas post-ENSO vegetative changes showed island differences attributable to selective herbivory. On SBE (with herbivores), vegetative cover and diversity declined due to a combination of a return to arid conditions and selective herbivory, while cover and diversity on SBW (herbivores removed) levelled off after an initial decline (Fig. 2). The ENSO rains and the release

of herbivory facilitated the germination and growth of select perennials on SBW. For example, following herbivore removal localized flowering patches of the previously rare *Malva pacifica* were common on SBW. In contrast, rabbits on SBE had almost extirpated this once abundant endemic perennial in less than 3 years (Junak & Philbrick 2000; Fig. 3). The plant community differences at the island scale attributed to selective herbivory are corroborated by the results of the food-preference trials.

Food-preference trials show that the endemic *Malva pacifica* is overwhelmingly preferred by rabbits. Historically, anecdotal data also suggest a strong herbivore preference for the endemic *Dudleya linearis* (Moran & Lindsay 1951). Shortly after the introduction of rabbits, *Dudleya linearis* became increasingly rare, approaching extinction (Donlan *et al.* 2000). The precipitous decline of *Dudleya linearis* and *Malva pacifica* on the San Benito Islands is probably due to the polyphagous but hierarchical diet of rabbits (Crawley 1983; Thompson & King 1994). Rabbits with their catholic diet can switch forage species, permitting an abundant rabbit population despite a decrease in preferred plant species. Despite diet switching, the presence of rabbits prevents new recruitment of preferred species. Suppression of recruitment and subsequent depletion of the seed bank leads towards extinction (Hunt 2001). The results of the food-preference trials, coupled with anecdotal data, lend support to the generalization that herbivores prefer insular endemic plants to non-endemic native species (Carlquist 1974; Bowen & Van Vuren 1997).

The strong relationship between rabbit food preference and changes in plant species cover is evidence of a strong top-down effect on the perennial plant community (Figs 3 and 4). On SBE (with herbivores), the perennial plant community appears to have come under top-down regulation, whereas on SBW (herbivores removed) the community appears to have been released from top-down control. The time series of regression models illuminate this pattern (Fig. 4). By December 1997, rabbits had been present on SBE for 2–3 years. Although their impact on preferred plant species was observable, their herbivory failed to explain the abundance of perennials (Fig. 4). Perennial plant abundances may have been influenced by ENSO precipitation and the short duration of herbivore presence. By July 1998, herbivory shifted perennial plant community structure: preferred plants declined and non-preferred species increased in abundance. The strong inverse relationship between preference and cover was present on SBE for the remainder of the study. On SBW, rabbits had been present for approximately 6 years (by December 1997) and rabbit preference correlated strongly with the abundance of perennial plant species. Following rabbit removal, preferred plants increased and non-preferred species declined in abundance. By July 1999, there was no relationship between preference and plant cover, suggesting a release from top-down control (Fig. 4).

This overall pattern of a decrease in abundance of preferred plants and the increase of unpalatable species due to exotic herbivory has been observed in other insular communities (Coblentz 1978; Leader-Williams, Scott & Pratt 1981; Loope & Scowcroft 1985; Chapuis, Bousses & Barnaud 1994; Abbott, Marchant & Cranfield 2000; Bullock *et al.* 2002). The dynamics of the perennial plant community on San Benito Islands are consistent with a positive correlation between palatability and competitive ability (Harper 1969; Crawley 1983). Altered species composition is a general feature of mammalian herbivore–plant interactions in many ecosystems (reviews by Bryant *et al.* 1991; Augustine & McNaughton 1998). Some of these plant community changes are a result of introduced herbivores, livestock and native predator-free herbivores (e.g. white-tail deer *Odocoileus virginianus* (Zimmerman) in eastern North America; McShea, Underwood & Rappole 1997; Hunt 2001; Bullock *et al.* 2002). In some cases these changes can lead to alternate ecosystem states (Augustine, Frelich & Jordan 1998; Mack & D'Antonio 1998) and can also affect ecosystem processes, such as nutrient cycling (Bryant *et al.* 1991; Pastor & Cohen 1997; Maron & Jefferies 1999). These changes in species composition and ecosystem processes are of fundamental concern (Chapin *et al.* 1997; Hooper & Vitousek 1997). Of primary importance is under what circumstances these changes are reversible (D'Antonio, Meyerson & Denslow 2001).

The island-wide vegetation response to herbivore removal (Fig. 2), coupled with the predictable perennial plant species responses (Figs 3 and 4), suggest that the herbivore-induced changes are reversible on the San Benito Islands. However, this evidence of a strong reversible herbivore effect is disparate with the outcome of the enclosure experiments on the control island (SBE). For example, we observed germination of the preferred *Malva pacifica* on SBW, but not inside the SBE enclosures. In fact, we observed no germination or increase in cover in any of the enclosures despite the release of herbivory. The timing of enclosure construction and the subsequent interaction between top-down and bottom-up processes could explain this difference. It is possible that on SBW, ENSO precipitation and the removal of herbivores synergistically facilitated the germination and survival of *Malva pacifica* between January and July 1998 (Fig. 3). In contrast, herbivore pressure was high on SBE throughout the ENSO rains and enclosures were not constructed until July 1998, 4 months after any precipitation on the island (Fig. 2). Despite the absence of herbivory inside the SBE enclosures after July 1998, germination did not occur due to lack of water availability (July 1998–July 1999 rainfall = 21 mm). Alternatively, *Malva pacifica* seed was not present inside the enclosures although this is unlikely, due to the presence of dead plants inside the enclosures, its widespread abundance historically on the island, and a persistent seed bank (B.R. Tershy, personal observation; Kivilaan & Bandurski 1981; Junak & Philbrick 2000). Thus, it appears that while exotic herbivores

exhibit a top-down effect on the perennial plant community, recovery after the removal of herbivores may be limited by a bottom-up mechanism (i.e. water availability).

The predictable herbivore impacts and signs of recovery after eradication are indeed short-term and may not forecast the island's long-term dynamics. The interaction between herbivore and abiotic effects, and subsequent management implications, could be better understood by extending the short-time period of this study. While eradications cannot often be postponed due to conservation priorities, islands with planned eradications can be identified early during planning stages, thus allowing for a longer time series of data collection pre-eradication. Long-term monitoring post-eradication with a sampling interval of a few years will also help to identify the relative importance of biotic and abiotic factors influencing the ecosystem (Brown *et al.* 2001). Bullock, North and colleagues have followed the ecology of Round Island (Mauritius) for 10 years following rabbit and goat eradication (North & Bullock 1986; North, Bullock & Dulloo 1994; Bullock *et al.* 2002). Vegetation responses were predictable in the short term, but some long-term changes were dramatic and unpredictable, particularly an increasing influence by exotic plants (Bullock *et al.* 2002). The undesirable increase in abundance and influence of exotic plants after exotic herbivore removal has also been observed on Carnac Island, Australia (Abbott, Marchant & Cranfield 2000) and the Channel Islands, USA (Halvorson, Fenn & Allardice 1988; Klinger, Schuyler & Sterner 1994). However, the interaction between exotic herbivores and invasive plants remains largely unstudied and examples are mostly anecdotal (Driesche & Driesche 2000). Exotic plants are not present in high abundance on the San Benito Islands, and low, variable, rainfall is likely to play a role [mean exotic cover was less than 3.1% (SBW) and 9.3% (SBE) during all sampling periods]. Arid ecosystems that lack large influences by exotic plants may require less management, from an ecosystem perspective, following exotic herbivore removal, compared with more mesic systems (Donlan 2000).

Exotic herbivores have affected islands for over a century, leading to numerous plant extinctions (Wallace 1892; Melville 1979). Our study demonstrates that introduced herbivores can change plant community structure through selective herbivory. This top-down effect led, in this case, to the increase of unpalatable plants species and the decline of preferred species toward extinction. While top-down effects of herbivores might damage communities rapidly, recovery can depend on the bottom-up effects of resources, such as water availability. In desert ecosystems with low and variable rainfall, island recovery may be delayed by prolonged drought. However, the reduced presence of exotic plants, as found on the arid San Benito Islands, may aid in the recovery towards original pre-disturbance conditions. This study is unique in that

we exploited the conservation action of exotic herbivore removal as a large-scale controlled experiment. Large-scale experimental approaches combined with smaller-scale mechanistic experiments, particularly the exploitation of conservation action as a perturbation, might offer useful models in applied ecology more widely.

Acknowledgements

We thank J. C. Hermsillo, M. A. Hermsillo, J. A. Sanchez, J. C. Salinas and especially B. Wood of the Island Conservation and Ecology Group. We thank S. Junak, J. L. Alguilar and the many field assistants that made this research possible. We thank our conservation partners SEMARNAP, INE and *Pescadores Nacionales de Abulón*. Funding for this conservation and research was provided by the American Museum of Natural History Theodore Roosevelt Memorial Fund, Grants-in-Aid of Research from the National Academy of Science through Sigma Xi, the Packard Foundation and the Switzer Foundation. C.J. Donlan also thanks J. Estes, L. Fox, I. Parker and G. Roemer, all of whom provided invaluable support and improved earlier copies of this manuscript. N. Biavaschi provided assistance with figures. This research was conducted under permit 750–10291 *Secretaría del Medio Ambiente, Recursos Naturales y Pesca*. This work is in partial fulfilment of the requirements of the degree of Masters of Arts at the University of California Santa Cruz (to C.J. Donlan). D. J. Bullock, S. North and two anonymous referees greatly improved this manuscript.

References

Abbott, I., Marchant, N. & Cranfield, R. (2000) Long-term change in the floristic composition and vegetation structure of Carnac Island, Western Australia. *Journal of Biogeography*, **27**, 333–346.

Anderson, W.B. & Polis, G.A. (1999) Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia (Berlin)*, **118**, 324–332.

Augustine, D.J. & McNaughton, S.J. (1998) Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management*, **62**, 1165–1183.

Augustine, D.J., Frelich, L.E. & Jordan, P.A. (1998) Evidence for two alternate stable states in an ungulate grazing system. *Ecological Applications*, **8**, 1260–1269.

Blossey, B. (1999) Before, during and after: the need for long-term monitoring in invasive plant species management. *Biological Invasions*, **1**, 301–311.

Boswell, J. (1978) The birds of the San Benito Islands, Lower California, Mexico. *Bristol Ornithology*, **11**, 23–32.

Bowen, L. & Van Vuren, D. (1997) Insular endemic plants lack defenses against herbivores. *Conservation Biology*, **11**, 1249–1254.

Breitenmoser, U. & Haller, H. (1993) Patterns of predation by reintroduced European lynx in the Swiss Alps. *Journal of Wildlife Management*, **57**, 135–144.

Brown, J.H. & Heske, E.J. (1990) Temporal changes in a Chihuahuan desert rodent community. *Oikos*, **59**, 290–302.

Brown, J.H. & McDonald, W. (1995) Livestock grazing and conservation on southwestern rangelands. *Conservation Biology*, **9**, 1644–1647.

Brown, J.H., Whitham, T.G., Ernest, S.K.M. & Gehring, C.A. (2001) Complex species interactions and the dynamics of ecological systems: long-term experiments. *Science*, **293**, 643–650.

Bryant, J.P., Provenza, F.D., Pastor, J., Reichardt, P.B., Clausen, T.P., Toit, J.T.D. (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics*, **22**, 431–446.

Bullock, J.M., Franklin, J., Stevenson, M.J., Silvertown, J., Coulson, S.J., Gregory, S.J. & Tofts, R. (2001) A plant trait analysis of responses to grazing in a long-term experiment. *Journal of Applied Ecology*, **38**, 253–267.

Bullock, D.J., North, S.G., Dulloo, M.E. & Thorson, M. (2002) The impact of rabbit eradication on the ecology of Round Island, Mauritius. *Turning the Tide: The Eradication of Invasive Species* (eds C.R. Veitch & M.N. Clout). Invasive Species Specialist Group of the World Conservation Union (IUCN), Auckland, New Zealand.

Carlquist, S. (1974) *Island Biology*. Columbia University Press, New York, NY.

Carpenter, S.R. (1990) Large-scale perturbations: opportunities for innovation. *Ecology*, **71**, 2038–2043.

Carpenter, S.R. (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology*, **77**, 677–680.

Carpenter, S.R. & Kitchell, J.F. (1993) *The Trophic Cascade in Lakes*. Cambridge University Press, Cambridge, UK.

Chapin, F.S. III, Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E. & Tilman, D. (1997) Biotic control over the functioning of ecosystems. *Science*, **277**, 500–504.

Chapuis, J.L., Bousses, P. & Barnaud, G. (1994) Alien mammals, impact and management in the French subantarctic islands. *Biological Conservation*, **67**, 97–104.

Coblentz, B.E. (1978) The effects of feral goats (*Capra hircus*) on island ecosystems. *Biological Conservation*, **13**, 279–285.

Cohen, J. (1977) *Statistical Power Analysis for the Behavioral Sciences*, rev. edn. Academic Press, New York, NY.

Crawley, M.J. (1983) *Herbivory, the Dynamics of Animal–Plant Interactions*. University of California Press, Berkeley, CA.

Crawley, M.J. (1990) Rabbit grazing, plant competition and seedling recruitment in acid grassland. *Journal of Applied Ecology*, **27**, 803–820.

Crooks, K.R. & Soulé, M.E. (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400**, 563–566.

Crosswhite, F.S. & Crosswhite, C.D. (1982) The Sonoran desert. *Reference Handbook on the Deserts of North America* (ed. G.L. Bender), pp. 163–295. Greenwood Press, Westport, CT.

D'Antonio, C., Meyerson, L.A. & Denslow, J.S. (2001) Exotic species and conservation: research needs. *Conservation Biology: Research Priorities for the Next Decade* (eds M.E. Soule & G.H. Orians), pp. 59–80. Island Press, Washington, DC.

Diamond, J. (1986) Overview: laboratory experiments, field experiments, and natural experiments. *Community Ecology* (eds J. Diamond & T.J. Case), pp. 3–22. Harper & Row, New York, NY.

Dilks, P.J. & Wilson, P.R. (1979) Feral sheep and cattle and royal albatrosses on Campbell Island; population trends and habitat changes. *New Zealand Journal of Zoology*, **6**, 127–139.

Donlan, C.J. (2000) *Islands and introduced herbivores: using conservation to investigate top-down and bottom-up processes*. MA Thesis. University of California, Santa Cruz, CA.

Donlan, C.J., Tershy, B.R., Keitt, B.S., Wood, B., Sanchez, J.A., Weinstein, A., Croll, D.A. & Alguilar, J.L. (2000) Island conservation action in northwest Mexico. *Proceedings of the Fifth California Islands Symposium* (eds D.H. Browne, H. Chaney & K. Mitchell), pp. 330–338. Santa Barbara Museum of Natural History, Santa Barbara, CA.

- Driesche, J.V. & Driesche, R.V. (2000) After the sheep are all gone, the recovery of Santa Cruz Island after 140 years of grazing. *Nature Out of Place, Biological Invasions in the Global Age* (eds J.V. Driesche & R.V. Driesche), pp. 153–176. Island Press, Washington, DC.
- Estes, J.A. (1995) Top-level carnivores and ecosystem effects: questions and approaches. *Linking Species and Ecosystems* (eds C.G. Jones & J.H. Lawton), pp. 151–158. Chapman & Hall, New York, NY.
- Estes, J.A. & Duggins, D.O. (1995) Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs*, **65**, 75–100.
- Estes, J., Crooks, K. & Holt, R. (2001) Ecological role of predators. *Encyclopedia of Biodiversity* (ed. S. Levin), pp. 857–878. Academic Press, San Diego, CA.
- Evenari, M., Noy-Meir, I. & Goodall, D.W. (1985) *Hot Deserts and Arid Shrublands*. Elsevier, New York, NY.
- Frost, T.M., DeAngelis, D.L., Bartell, S.M., Hall, D.J. & Hurlbert, S.H. (1988) Scale in design and interpretation of aquatic community research. *Complex Interactions in Lake Communities* (ed. S.R. Carpenter), pp. 229–258. Springer-Verlag, New York, NY.
- Halvorson, W.L., Fenn, D.B. & Allardice, W.R. (1988) Soils and vegetations of Santa Barbara Island Channel Islands National Park California USA. *Environmental Management*, **12**, 109–118.
- Harper, J.L. (1969) The role of predation in vegetational diversity. *Brookhaven Symposia in Biology*, **22**, 48–62.
- Hastings, J.R. & Humphrey, R.R. (1969) *Climatological data and statistics for Baja California*. Technical Reports on the Meteorology and Climatology of Arid Regions, No. 18. University of Arizona, Tucson, AZ.
- Hooper, D.U. & Vitousek, P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302–1305.
- Hunt, L.P. (2001) Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. *Journal of Applied Ecology*, **38**, 238–252.
- Hunter, M. (2001) Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: experiments, life tables, and time-series analysis. *Basic and Applied Ecology*, **2**, 294–311.
- Hunter, M.D. (1992) Interactions within herbivore communities mediated by the host plant: the keystone herbivore concept. *Effects of Resource Distribution on Animal–Plant Interactions* (eds M.D. Hunter, T. Ohgushi & P.W. Price), pp. 287–325. Academic Press, San Diego, CA.
- Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–212.
- Jaksic, F.M. (2001) Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography*, **24**, 241–250.
- Junak, S.A. & Philbrick, R. (2000) Flowering plants of the San Benitos Islands, Baja California, Mexico. *Proceedings of the Fifth California Islands Symposium* (eds D.H. Browne, H. Chaney & K. Mitchell), pp. 235–246. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Kivilaan, A. & Bandurski, R.S. (1981) The one hundred-year period for Dr Beal's seed viability experiment. *American Journal of Botany*, **68**, 1290–1292.
- Klinger, R.C., Schuyler, P.T. & Sterner, J.D. (1994) Vegetation response to the removal of feral sheep from Santa Cruz Island. *The Fourth California Islands Symposium, Update on the Status of Resources* (eds W.L. Halvorson & G.J. Mender), pp. 341–350. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Leader-Williams, N., Scott, T.A. & Pratt, R.M. (1981) Forage selection by introduced reindeer on South Georgia, and its consequence for the flora. *Journal of Applied Ecology*, **18**, 83–106.
- Likens, G.E. (1985) An experimental approach for the study of ecosystems. *Journal of Ecology*, **73**, 381–396.
- Loope, L.L. & Scowcroft, P.G. (1985) Vegetation response within exclosures in Hawaii: a review. *Hawaii's Terrestrial Ecosystems: Preservation and Management* (eds C.P. Stone & J.M. Scott), pp. 377–421. University of Hawaii Press for Cooperative National Park Resources Study Unit, Honolulu, HI.
- Mack, M.C. & D'Antonio, C.M. (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution*, **13**, 195–198.
- McPhaden, M.J. (1999) Genesis and evolution of the 1997–98 El Niño. *Science*, **283**, 950–954.
- McShea, W.J., Underwood, H.B. & Rappole, J.H. (1997) *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institution Press, Washington, DC.
- Maron, J.L. & Jefferies, R.L. (1999) Bush lupine mortality, altered resource availability, and alternative vegetation states. *Ecology*, **80**, 443–454.
- Maron, J.L. & Simms, E.L. (2001) Rodent-limited establishment of bush lupine: field experiments on the cumulative effect of granivory. *Journal of Ecology*, **89**, 578–588.
- Melville, R. (1979) Endangered island floras. *Plants and Islands* (ed. D. Bramwell), pp. 361–370. Academic Press, New York, NY.
- Meserve, P.L., Milstead, W.B., Gutierrez, J.R. & Jaksic, F.M. (1999) The interplay of biotic and abiotic factors in a semiarid Chilean mammal assemblage: results of a long-term experiment. *Oikos*, **85**, 364–372.
- Moran, R. & Lindsay, G. (1951) San Benito Islands. *Desert Plant Life*, **23**, 78–83.
- Mueller-Dombois, D. & Ellenberg, H. (1974) *Aims and Methods of Vegetation Ecology*. Wiley, New York, NY.
- Neter, J., Kutner, M.H., Nachtsheim, C.J. & Wasserman, W. (1996) *Applied Linear Statistical Models*, 4th edn. Irwin, Chicago, IL.
- Norbury, G. (2001) Conserving dryland lizards by reducing predator-mediated apparent competition and direct competition with introduced species. *Journal of Applied Ecology*, **38**, 1350–1361.
- North, S.G. & Bullock, D. (1986) Changes in the vegetation and populations of introduced mammals of Round Island and Gunner's Quoin, Mauritius. *Biological Conservation*, **37**, 99–117.
- North, S.G., Bullock, D.J. & Dulloo, M.E. (1994) Changes in the vegetation and reptile populations on Round Island, Mauritius, following eradication of rabbits. *Biological Conservation*, **67**, 21–28.
- Noy-Meir, I. (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 25–41.
- Nugent, G., Fraser, W. & Sweetapple, P. (2001) Top down or bottom up? Comparing the impacts of introduced arboreal possums and 'terrestrial' ruminants on native forests in New Zealand. *Biological Conservation*, **99**, 65–79.
- Oksanen, L. (2001) Logic of experiments in ecology: is pseudoreplication a pseudoissue? *Oikos*, **94**, 27–38.
- Oksanen, L. & Oksanen, T. (2000) The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist*, **155**, 703–723.
- Ormerod, S.J. & Watkinson, A.R. (2000) Large-scale ecology and hydrology: an introductory perspective from the editors of the *Journal of Applied Ecology*. *Journal of Applied Ecology*, **37** (Supplement 1), 1–5.
- Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution*, **14**, 483–488.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Holle, B.V., Moyle, P.B., Byers, J.E. & Goldwasser, L. (1999) Impact:

- toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3–19.
- Pastor, J. & Cohen, Y. (1997) Herbivores, the functional diversity of plants species, and the cycling of nutrients of ecosystems. *Theoretical Population Biology*, **51**, 165–179.
- Polis, G.A. (1991) Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist*, **138**, 123–155.
- Polis, G.A. (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos*, **86**, 3–15.
- Polis, G.A., Hurd, S.D., Jackson, C.T. & Pinero, F.S. (1997) El Nino effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology*, **78**, 1884–1897.
- Power, M.E. (2001) Field biology, food web models, and management: challenges of context and scale. *Oikos*, **94**, 118–129.
- Rice, W.R. & Gaines, S.D. (1994a) Extending nondirectional heterogeneity tests to evaluate simply ordered alternative hypothesis. *Proceedings of the National Academy of Sciences of the USA*, **91**, 225–226.
- Rice, W.R. & Gaines, S.D. (1994b) The ordered-heterogeneity family of tests. *Biometrics*, **50**, 746–752.
- Ripple, W.J., Larsen, E.J., Renkin, R.A. & Smith, D.W. (2001) Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation*, **102**, 227–234.
- Roemer, G.W., Donlan, C.J. & Courchamp, F. (2002) Golden eagles, feral pigs and insular carnivores: how exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences*, **99**, 791–796.
- Schmitz, O.J. & Sinclair, A.R.E. (1997) Rethinking the role of deer in forest ecosystem dynamics. *The Science of Overabundance: Deer Ecology and Population Management* (eds W.J. McShea, H.B. Underwood & J.H. Rappole), pp. 201–223. Smithsonian Institution Press, Washington, DC.
- Simberloff, D. (2001) Eradication of island invasives: practical actions and results achieved. *Trends in Ecology and Evolution*, **16**, 273–274.
- Soule, M.E. (1990) The onslaught of alien species and other challenges in the coming decades. *Conservation Biology*, **4**, 233–239.
- Stahl, P., Vandel, J.M., Herrenschmidt, V. & Migot, P. (2001) Predation on livestock by an expanding reintroduced lynx population: long-term trend and spatial variability. *Journal of Applied Ecology*, **38**, 674–687.
- Stapp, P., Polis, G.A. & Sanchez Pinero, F. (1999) Stable isotopes reveal strong marine and El Nino effects on island food webs. *Nature*, **401**, 467–469.
- Tansley, A.G. (1935) The use and abuse of vegetational concepts and terms. *Ecology*, **16**, 284–387.
- Terborgh, J., Estes, J.A., Paquet, P., Ralls, K., Boyd-Heger, D., Miller, B.J. & Noss, R.F. (1999) The role of top carnivores in regulating terrestrial ecosystems. *Continental Conservation: Scientific Foundations of Regional Reserve Networks* (eds M.E. Soulé & J. Terborgh), pp. 39–64. Island Press, Washington, DC.
- Tershy, B.R., Donlan, C.J., Keitt, B., Croll, D., Sanchez, J.A., Wood, B., Hermosillo, M.A. & Howald, G. (in press) Island conservation in northwest Mexico: a conservation model integrating research, education and exotic mammal eradication. *Turning the Tide: The Eradication of Invasive Species* (eds C.R. Veitch & M.N. Clout). Invasive Species Specialist Group of the World Conservation Union (IUCN), Auckland, New Zealand.
- Thompson, H.V. & King, C.M. (1994) *The European Rabbit: The History and Biology of a Successful Colonizer*. Oxford University Press, New York, NY.
- Towns, D.R., Atkinson, I.A.E. & Daugherty, C.H. (1990) *Ecological Restoration of New Zealand Islands: Papers Presented at Conference on Ecological Restoration of New Zealand Islands, University of Auckland. 20–24 November 1989, Auckland, New Zealand*. Department of Conservation, Wellington, New Zealand.
- Underwood, A.J. (1997) *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, New York, NY.
- Wallace, A.R. (1892) Island life, or, the phenomena and causes of insular faunas and floras. *Including a Revision and Attempted Solution of the Problem of Geological Climates*. Macmillan, London, UK.
- Walters, C.J. (1986) *Adaptive Management of Renewable Resources*. Macmillan, New York, NY.
- Walters, C.J. & Holling, C.S. (1990) Large-scale management experiments and learning by doing. *Ecology*, **71**, 2060–2068.
- Wilkinson, L. (1998) *Systat 8.0*. SPSS Inc., Chicago, IL.
- Wright, S.J., Carrasco, C., Calderon, O. & Paton, S. (1999) The El Nino Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology*, **80**, 1632–1647.
- Zavaleta, E.S., Hobbs, R.J. & Mooney, H.A. (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution*, **16**, 454–459.

Received 30 May 2001; final copy received 17 December 2001