

Climate alters response of an endemic island plant to removal of invasive herbivores

A. KATHRYN MCEACHERN,^{1,3} DIANE M. THOMSON,² AND KATHERINE A. CHESSE¹

¹U.S. Geological Survey, Western Ecological Research Center, Channel Islands Field Station,
1901 Spinnaker Drive, Ventura, California 93001 USA

²Joint Science Department, The Claremont Colleges, 925 N. Mills Avenue, Claremont, California 91711 USA

Abstract. Islands experience higher rates of species extinction than mainland ecosystems, with biological invasions among the leading causes; they also serve as important model systems for testing ideas in basic and applied ecology. Invasive removal programs on islands are conservation efforts that can also be viewed as powerful manipulative experiments, but few data are available to evaluate their effects. We collected demographic and herbivore damage data for *Castilleja mollis* Pennell, an endangered plant endemic to Santa Rosa Island, California, over a 12-year period before, during, and after the implementation of control for introduced cattle, deer, and elk. We used these long-term data to explore mechanisms underlying herbivore effects, assess the results of herbivore reduction at the scales of both individual plants and populations, and determine how temporal variability in herbivory and plant demography influenced responses to herbivore removals. For individual plants, herbivore effects mediated by disturbance were greater than those of grazing. Deer and elk scraping of the ground substantially increased plant mortality and dormancy and reduced flowering and growth. Stem damage from browsing did not affect survivorship but significantly reduced plant growth and flower production. Herbivore control successfully lowered damage rates, which declined steeply between 1997 and 2000 and have remained relatively low. *Castilleja mollis* abundances rose sharply after 1997, suggesting a positive effect of herbivore control, but then began to decline steadily again after 2003. The recent decline appears to be driven by higher mean growing season temperatures; interestingly, not only reductions in scraping damage but a period of cooler conditions were significant in explaining increases in *C. mollis* populations between 1997 and 2002. Our results demonstrate strong effects of introduced herbivores on both plant demography and population dynamics and show that climate-driven variation may counteract and mask positive responses to herbivore removal. Regional mean temperatures already have risen significantly over the last 50 years, suggesting that climate change could increasingly swamp the effects of management targeted at other environmental problems. Similar interactions between climate and invasive species will play an even greater role in future management, with long-term data sets like this critical to quantifying such effects.

Key words: biological invasions; *Castilleja mollis*; climate change; demography; endemic plant; environmental variation; eradication; herbivores; islands; population dynamics; Santa Rosa, Channel Islands, California, USA.

INTRODUCTION

Biological invasions have emerged as one of the most critical conservation issues of our time (Mack et al. 2000, Simberloff et al. 2005). Introduced species can change ecosystem structure and function, cause local extirpations and drive extinction of rare species (Ruesink et al. 1995, Mack and D'Antonio 1998, Wilcove et al. 1998). Island ecosystems are especially sensitive to introductions, given their high degree of endemism and a loss of defensive adaptations by native species due to the historical absence of large predators and herbivores

(Reaser et al. 2007). Almost all extinctions documented as caused by invasions have happened on islands; while the clearest cases involve predation, invasive plants and herbivores have been implicated in declines of natives as well (Clout 2002, Courchamp et al. 2003).

Invasions of island systems provide unique opportunities in both management and research. Islands have long served as important model systems in basic and applied ecology. Moreover, removal of invasive species is feasible for many islands, in contrast to most mainland invasions. Several major eradication programs for introduced vertebrates, including rats, goats, rabbits, and cattle, have been undertaken in recent years (Krajick 2005). These initiatives both represent critical conservation efforts and offer rare opportunities to study ecosystem responses to changes in community

Manuscript received 21 August 2008; revised 8 January 2009; accepted 13 January 2009. Corresponding Editor: R. A. Hufbauer.

³ E-mail: kathryn_mceachern@usgs.gov

composition and structure (Donlan et al. 2002, Sax et al. 2007). Detailed studies of island restoration projects can be used to gain insight into the underlying mechanisms of invasions and improve management strategies for both island and mainland systems.

Many effects of introduced vertebrates on island endemics are strong and obvious, and removal programs often have immediate benefits for native species (Donlan et al. 2002, Courchamp et al. 2003, Krajick 2005). However, the consequences of removals are not always clear, particularly in systems where multiple plant and animal invaders interact with each other as well as with native species, creating a strong potential for indirect effects. For example, eradication of an introduced grazer might benefit invasive plants at the expense of native species (Beatty and Licari 1992, Donlan and Martin 2004), and removal of large predators can lead to declines in native prey through mesopredator release of other invasive species (Rayner et al. 2007). Moreover, environmental changes due to species introductions, such as erosion, may not immediately reverse with their removal. Finally, island systems are experiencing a number of environmental impacts in addition to invasions, such as habitat loss and degradation and climate change. As a result, threatened species will not necessarily rebound even after eradication (North et al. 1994, Myers et al. 2000, Zavaleta et al. 2001).

Evaluating the effects of removal programs becomes even more complicated when logistical constraints prevent complete elimination of the introduced species. Challenges such as existing land-use agreements or logistical infeasibility may mean that a reduction in the density of introduced vertebrates is possible, but not total eradication (Campbell and Donlan 2005). It is difficult to weigh the costs and benefits of such partially successful removal programs without a clear understanding of their ecological effects. Given the recent increase in eradication efforts and the substantial time and money required for some of these programs, remarkably few studies documenting their effects have been published (Courchamp et al. 2003). In addition, previous research following introduced vertebrate removals has focused mostly on plant community responses, with an emphasis on more dominant and abundant species (Donlan et al. 2002, 2003).

The eight California Channel Islands (USA) are centers of high plant endemism, with 76 taxa occurring only on one or more of the islands (Raven 1967). The islands have no native ungulates, but over the past 150 years sheep, pigs, goats, cattle, deer, and elk were introduced through ranching and hunting operations. These introductions have been implicated in declines of rare endemic plants (Bowen and VanVuren 1997) and several vertebrates (Jones and Diamond 1976, McChesney and Tershy 1998, Roemer et al. 2002). The northern five islands have come under management of the National Park Service and The Nature Conservancy recently through land acquisition and agreements with

previous landowners, allowing for gradual implementation of introduced animal removal efforts. As a result, recent events in the Channel Islands encompass a range of island management opportunities and challenges, making them an excellent model system.

In this study, we collected and analyzed 12 years of demographic data, including records of damage to individual plants caused by vertebrate herbivores, for the endangered endemic *Castilleja mollis* Pennell (Scrophulariaceae, soft-leaved paintbrush) on Santa Rosa Island. The study spanned the period before, during and after cattle removal and the onset of major population reductions for deer and elk. Our goal was to explore the past and ongoing individual and population-level effects of vertebrate herbivory on *C. mollis*, as well as assess the effects of removal efforts on demographic rates and population trends.

This unusually long-term data set also allowed us to explore several broad questions in ways not possible with most previous studies of plant-herbivore interactions. Hypotheses about herbivore impacts on plant populations play a central role in theory, for biological invasions specifically and community ecology in general. Yet most studies on herbivory are short-term and measure effects on individual plants, creating uncertainty about how these interactions influence population dynamics (Gomez 2005, Maron and Crone 2006). Our data allowed us to assess herbivore effects over a long time period, as well as test how impacts of herbivory on individual plant fitness interacted with other factors such as weather in changing population dynamics.

With this broader context in mind, in this paper we address the following specific questions: (1) How have levels of herbivore damage changed in response to cattle removal and reduction of deer and elk populations on Santa Rosa Island? (2) How do different kinds of herbivore damage affect survivorship, growth and reproduction of individual *C. mollis* plants? (3) How have *C. mollis* populations changed over time as herbivore management has changed? (4) How well do changes in the rates of herbivore damage explain the observed trends in *C. mollis* populations, and how does herbivory interact with other factors affecting persistence of this species?

METHODS

Study system

Santa Rosa is third largest of the U.S. California Channel Islands at 215 km². Ranching started in the 1840s, first with sheep and then cattle. In addition, pigs, elk (*Cervus elaphus*), and mule deer (*Odocoileus hemionus*) were introduced for sport hunting (Livingston 2006) after ranching began. The National Park Service purchased the island in 1987, and a special use permit allowed ranching and hunting to continue through 2011. However, a conservation lawsuit settlement resulted in the removal in 1998 of all cattle, whose numbers fluctuated between 3000 and 6000 annually. Deer

numbers were reduced by half and elk by about one-third between 1998 and 2000 in a planned stepped-down reduction to zero by 2011. Deer and elk are free-ranging on the island. Annual aerial game counts are made cooperatively by the National Park Service and the ranching operation, although counts are not available for some years. While the partners mutually verify the numbers, the associated detectability and error have not been quantified, and these counts are used only as broad estimates.

C. mollis is found only on Santa Rosa Island. It occurs as two disjunct populations within remnant coastal bluff scrub on the north shore of the island, on the bluffs of Carrington Point and nearly 13 km away on the near-shore marine terraces at Jaw Gulch. Scrub habitat is dominated by native coastal goldenbush (*Isocoma menziesii* var. *vernonoides*). *C. mollis* is hemi-parasitic, apparently using the goldenbush as its primary host, as plants are found mainly within 50 cm of a goldenbush individual.

C. mollis is a perennial subshrub with a growth form of sprawling, brittle stems that support leaves only during the growing season, typically January until about late June. Old stems are replaced by new ones each year. Plants sometimes die back and disappear completely at the end of the growing season, remaining dormant underground for one or more years before reappearing. Indeterminate inflorescences are produced at branch tips, with variable numbers of flowers enclosed in succulent lemon-yellow bracts. Plants can reproduce clonally via ramets as well as by seeds.

Demographic monitoring

In 1995, nine 5 × 5 m permanent study plots were established by stratified random methods, six at Carrington Point and three at Jaw Gulch. Demographic monitoring occurred annually from 1995 to 2006, except in 2002, at the end of the *C. mollis* growing season in late June to early July. Funding constraints required that we stop sampling half of two plots at Carrington Point in 2001.

At each annual census, plots were searched and new plants tagged. Each group of stems either arising from the same caudex or as a cluster from the soil was designated a separate ramet and recorded as an individual plant; no attempt was made to distinguish genets. Plants with cotyledons were labeled as seedlings of the year; otherwise new recruits were recorded as vegetative ramets. The number of stems, the length of the longest stem and the total number of inflorescences were recorded for each plant. Any plants present in previous years that could not be relocated were recorded as missing. Locations of plants missing in previous censuses were still checked in subsequent years, because individuals may remain dormant for several years before reappearing.

We recorded several distinct types of herbivore impacts in *C. mollis* populations. First, deer and elk

sometimes cause substantial soil disturbance and uprooting of *C. mollis* and their hosts, largely by scraping associated with rutting behavior concentrated in the fall and winter. We mapped scraping damage and noted the tag numbers of plants within the affected area. Since much of this damage occurs months before the demography census, we also documented scraping in plots several times between August and November in 1996 through 1998.

Second, ungulates damage stems directly, by browsing or trampling. For each plant, we recorded both the number of stems broken by trampling and the number browsed. From 1997 through 1999, we recorded additional information on damage and flower production at the scale of individual stems. We counted the number of inflorescences for all stems. We also randomly selected 10 plants per plot and for each counted the number of buds, partially open flowers, fully open flowers and fruits on every inflorescence, as well as classifying the inflorescence as either damaged or undamaged.

Data analysis

The ability of *C. mollis* to remain dormant underground for one or more years slightly complicated the assessment of mortality rates. We assumed that any plant growing in the exact location of a tagged individual missing in the previous year represented a return from dormancy. Eighty-six percent of individuals observed to go dormant and then reappear aboveground did so in the following year, and no plant stayed dormant longer than three years. We scored plants missing in 2006 as either dead or dormant based on preliminary results from the 2007 census; the 2007 data are not otherwise included in this analysis. We calculated between-year individual plant growth in size as the percent change in stem number, which generally explained more of the variation in plant performance than length of longest stem. All told, we analyzed 4461 records for individual plants in a given year, and 3352 observations of between-year transitions.

We used only data from the summer demographic census to track overall rates of scraping damage over time, so that sampling effort was comparable across years. To analyze the effects of ungulate scraping on individual plants we used all records; a plant was scored as “scraped” for a given year if its location in the plot was recorded as scraped at any point during that year, and otherwise as “not scraped.” We found no evidence that the consequences of stem breakage differed from those of browsing, so in our analysis individual stems and whole plants were categorized as “damaged” if they experienced either breakage or browsing, and “undamaged” if they did not.

Effects of herbivore damage on individual plants

Nearly 90% of the demographic records available for plants damaged by scraping were from years prior to

1999. We limited our comparison of not scraped to scraped individuals to the 1995–1998 data, to avoid confounding damage effects with other temporal changes. We used contingency table analyses to test whether damaged and undamaged plants differed in the frequencies with which they died, went dormant, or survived. We also used contingency tables to determine whether damage changed the probability of a plant flowering. This avoided problems with skew and numerous zero values in the data for numbers of flowers, and information on mean flower production did not add to the patterns we found in this categorical analysis. Likewise, we treated growth in individual plant size (stem number) as a categorical outcome (grew or remained stable/shrank) analyzed with contingency tables because this both dealt with severe non-normality in the percent growth data and captured the major patterns.

For stem damage, untangling the effects on survivorship, growth and reproduction of individual plants proved challenging and required a more complicated set of analyses because herbivore damage was not random with respect to plant size. To quantify this problem, prior to the formal analysis we used binary logistic regression to explore the effects of plant stem number on the probabilities of plants experiencing damage, surviving and flowering. Accounting for differences between years, greater plant size significantly increased the probability of a plant experiencing stem damage in a given year (logistic regression, Wald statistic $\chi^2 = 262.7$, $n = 4461$ plants, $P < 0.001$). At the same time, larger plants were significantly more likely to survive into the following year ($\chi^2 = 125.9$, $n = 3124$, $P < 0.001$) and to flower ($\chi^2 = 522.6$, $n = 4461$, $P < 0.001$).

To clarify the relationship between plant size, damage, and plant performance, we divided the data set into five size categories: one-stem plants ($n = 643$ plants), two-stem plants ($n = 601$), three- to five-stem plants ($n = 1261$), plants with 6–10 stems ($n = 705$), and plants with more than 10 stems ($n = 198$). We then used contingency tables to check whether both damage and survivorship were independent of flowering within each size category before proceeding with further analysis. Plants that flowered were far more likely to be damaged (46–60%) than those that did not flower (15–30%; continuity corrected Pearson's $\chi^2 = 70.4$, 85.8, 160.7, 77.4, 8.5 for categories 1–5; $df = 1$; $P < 0.0001$ for categories 1–4 and $P = 0.004$ for category 5). Plants that flowered were also far more likely to survive for all size classes except the largest, with this difference particularly strong for one-stem plants ($\chi^2 = 38.06$, 19.15, 20.60, 18.92; $df = 1$, $P < 0.001$ for size categories 1–4).

In our final analysis, to better separate the effects of damage from those of plant size and flowering status we limited the comparison to flowering plants with at least two stems; this included 73% of the records for plants damaged by grazing. We then used forward stepwise logistic regression to test for the effects of damage on

survivorship, with the presence or absence of stem damage as a categorical independent factor and stem number and inflorescence number in the year of damage as continuous covariates. Due to evidence of a size by damage interaction for growth, we evaluated effects of damage on growth with separate 3×2 contingency tables for each size category, testing whether the frequency with which plants grew, remained stable or shrank in stem number varied between damaged and undamaged individuals. Finally, to estimate the effects of floral browsing on reproductive success we used a paired t test to compare mean flower numbers for browsed and unbrowsed inflorescences on the same stem from the 1997–1999 inflorescence censuses.

Herbivore damage and population growth

We used total stem numbers per plot to measure changes in *C. mollis* abundance; trends for stem and plant numbers were similar. We adjusted measures of abundance for two of the Carrington Point plots in 2003–2006 to reflect the fact that not all areas were recounted in those years, by using the fraction of plants present in the uncensused areas during 2001 to estimate the proportion of plants present but not counted.

To test for a link between levels of herbivore damage to individual plants and population trends, we looked at the relationship between both types of herbivore damage and observed population growth rates in individual plots. We calculated yearly population growth rates, or lambda (λ) values, by dividing stem numbers in year $t + 1$ by stem numbers in year t for each plot over the time period from 1996–2006. We then asked whether the variation in observed log lambda values was related to either (1) the amount of ungrate scraping as measured by the proportion of plants experiencing damage from scraping or (2) grazing damage, as measured by the fraction of stems in the plot either broken or browsed. In addition, we tested whether density dependence, site (Carrington Point or Jaw Gulch) or climate variation influenced *C. mollis* population growth. Initially, we explored a range of temperature and rainfall measures using data from the Santa Rosa Island weather station, including the amount of yearly rainfall, the amount of rainfall during the growing season (January to June), and both yearly and growing season temperatures. We screened these variables to avoid model over fitting; none of the independent variables used in the final model were tightly correlated with one another (observed $|r| \leq 0.37$).

Since measurements of lambda were taken in the same plots over multiple years, this analysis required a repeated measure model that would also accommodate covariates whose values fluctuated over time. We used a general linear mixed-model approach (GLMM) implemented in SPSS 16.0 (SPSS, Chicago, Illinois, USA) with the plots ($n = 9$) as subjects and the independent variables for effects of damage, climate and density in the previous year as continuous, fixed covariates. We fit

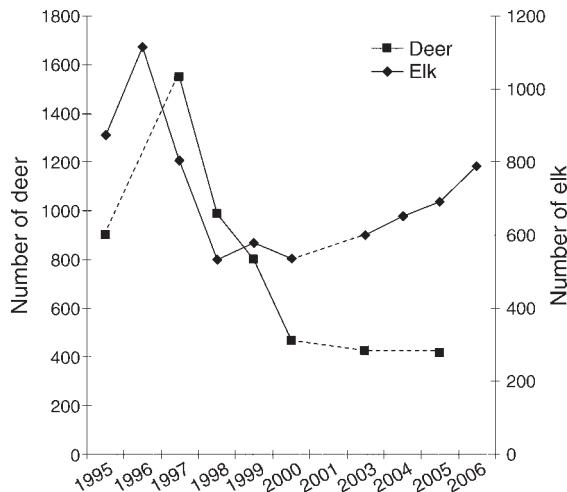


FIG. 1. Trends in estimated total numbers of deer and elk on Santa Rosa Island, California, USA, from 1995 to 2006. Dashed lines indicate years with no survey.

a range of models with different assumptions about variance-covariance structure to ensure that this choice did not influence the results, using AICs to compare fit. The strongest support was for the simplest variance-covariance structures tested, and the results of significance tests did not differ among a range of models with similar AICs. However, since there was some evidence in the data for differences in variances among years, although not for strong between-year correlations, we present results from the lowest-AIC model with heterogeneous variances.

RESULTS

Trends in herbivore abundance and damage

Recorded elk numbers peaked in 1996 at 1114 individuals, then declined to less than 600 by 1998 (Fig. 1); in spite of increasing slightly again between 2003 and 2006, they have remained at fewer than 800 individuals. Deer abundance peaked in 1997 at 1550 and then declined steeply in parallel to elk numbers until after 2000, when the population dropped and remained below 500 individuals (Fig. 1).

Damage due to ungulate scraping was highest at both Jaw Gulch (94% of plants) and Carrington Point (6% of plants) in 1996 and then dropped sharply until largely disappearing by 1999, soon after deer and elk reductions began. Scraping has never returned to the same levels, although at Jaw Gulch short-term increases occurred in 2003 and 2005 (Fig. 2A).

Similarly, grazing on stems was highest prior to 2000, with up to 60–70% of stems damaged per year, although this value fluctuated considerably (Fig. 2B). Grazing damage at Carrington Point in particular appeared to drop off after 1996 just as did ungulate scraping, but very high levels of stem breakage and browsing occurred in 1999, when *C. mollis* also flowered at much higher

rates than in previous years. Damage rates dropped off substantially after 1999 and with the exception of 2003 have remained under 10% in both sites since.

Effects of ungulate scraping on individual plants

Scraping disturbance by deer and elk dramatically reduced *C. mollis* survivorship, growth and reproduction. Both mortality of damaged plants and the rate at which plants went dormant in the year scraping occurred were nearly triple that of undamaged plants (Fig. 3A, Pearson's $\chi^2 = 55.7$, $df = 2$, $P < 0.0001$). Effects of damage persisted into the year following the scraping as well (Fig. 3A). Only 65% of scraped individuals survived and appeared above ground in the following year, compared to 80% of unscraped plants ($\chi^2 = 4.23$, $df = 1$, $P = 0.025$). Scraped plants that did not die or go dormant were only about half as likely to grow in stem number (Fig. 3B, $\chi^2 = 6.1$, $df = 1$, $P = 0.047$) or

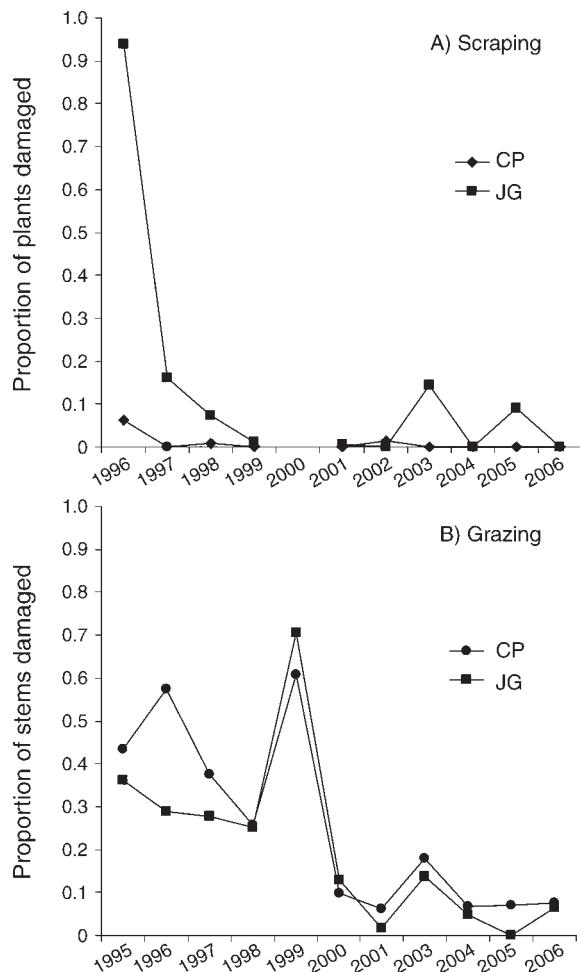


FIG. 2. Trends in herbivore damage on *Castilleja mollis*, an endangered perennial subshrub, from 1995 to 2006. (A) The proportion of plants damaged by ungulate scraping in the Carrington Point (CP) and Jaw Gulch (JG) populations. (B) The proportion of stems damaged by grazing at CP and JG.

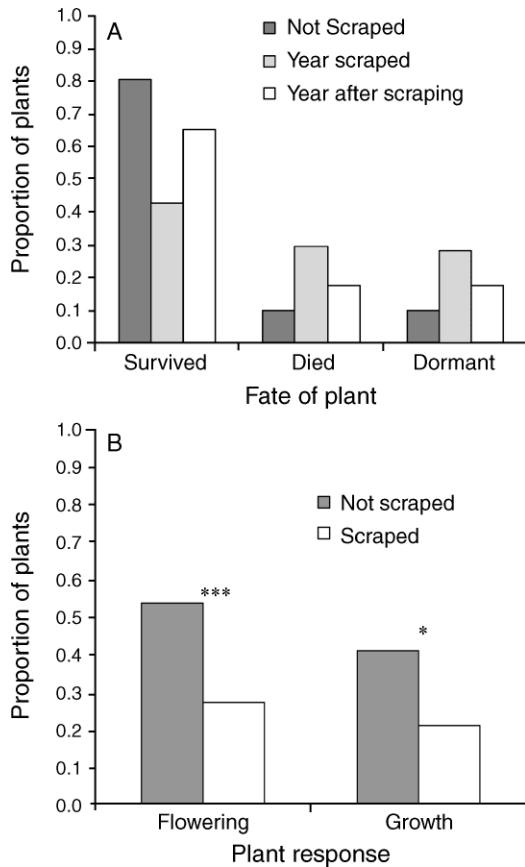


FIG. 3. (A) The effects of ungulate scraping on plant fates in both the year of damage and the year following damage. Plants survived, died, or entered or remained in a dormant state for the year. Data shown are for 1995–1998. (B) The effects of ungulate scraping on growth and flowering in the year of damage. Statistically significant differences are indicated by asterisks.

* $P < 0.05$; *** $P < 0.001$.

flower as undamaged individuals (Fig. 3B, $\chi^2 = 10.21$, $df = 1$, $P = 0.001$).

Effects of stem damage on individual plants

In contrast, stem grazing damage did not significantly affect survivorship (forward stepwise logistic regression, Wald statistic $\chi^2 = 0.87$, $n = 1373$ transitions, $P = 0.35$), although both larger plants and those that produced more inflorescences were more likely to survive ($\chi^2 = 7.6$ and 16.9 , respectively; $n = 1373$, $P = 0.006$ and $P < 0.001$). Stem damage to larger plants did not affect growth, but damage to smaller plants reduced growth. Damage did not affect whether plants grew, stayed the same size or shrank in the following year in size categories 3–5 (Fig. 4A; $\chi^2 = 1.31$, $df = 2$, $P = 0.52$ for category 3; $\chi^2 = 3.78$, $df = 2$, $P = 0.15$ for category 4; $\chi^2 = 1.15$, $df = 2$, $P = 0.56$ for category 5). However, category-2 plants were significantly less likely to grow if they experienced stem damage ($\chi^2 = 11.36$, $df = 2$, $P = 0.003$). Grazing damage reduced flower production; on

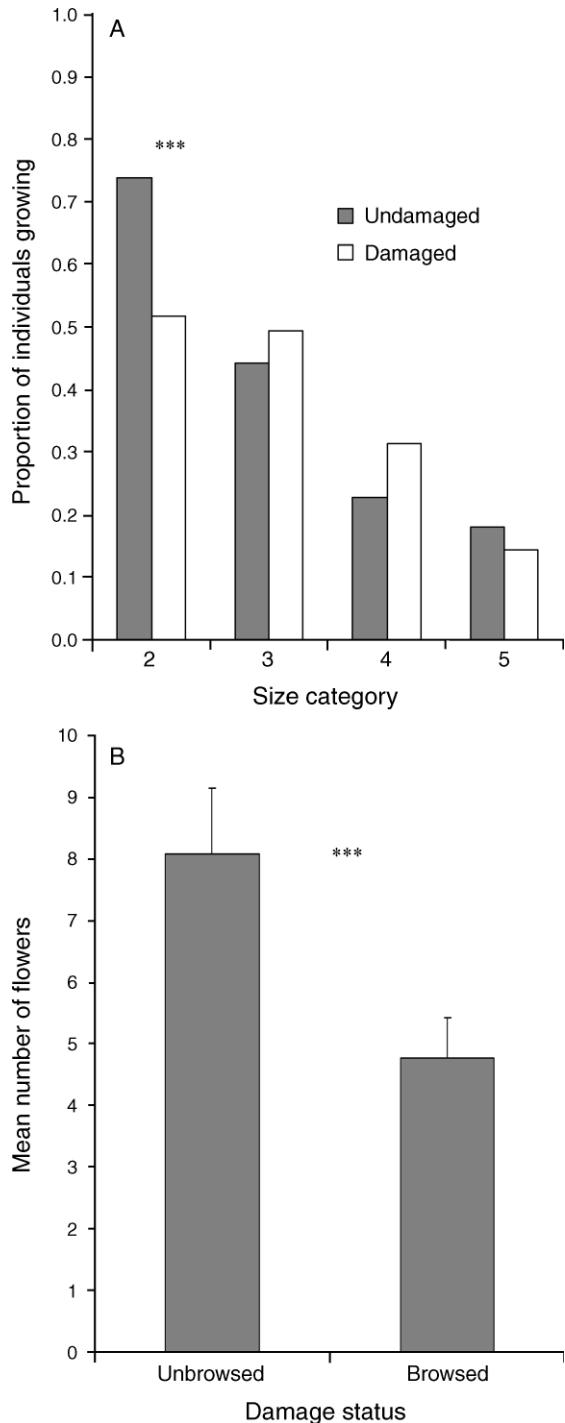


FIG. 4. Effects of herbivore grazing damage on (A) the probability of individual plants in the four largest size categories growing in stem number in the following year rather than remaining the same size or shrinking and (B) the mean number of flowers produced by a stem. Statistically significant differences between damaged and undamaged are indicated by asterisks.

* $P < 0.05$; *** $P < 0.001$.

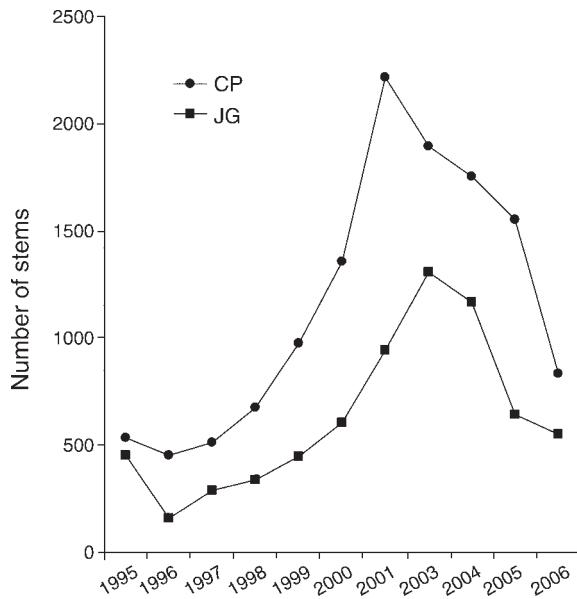


FIG. 5. Trends in population size of *Castilleja mollis* between 1995 and 2006 at Carrington Point (CP) and Jaw Gulch (JG), as measured by the total number of stems present in each population.

average, browsed inflorescences had 30% fewer flowers than unbrowsed ones on the same stem (Fig. 4B; paired *t* test, $t = 4.83$, $df = 33$, $P < 0.0001$).

Trends in plant abundance and demography

Abundances of *C. mollis* increased steadily after elk and deer abundances began to drop in 1996 and particularly after cattle removal in 1998, until peaking in 2001 (Carrington Point) or 2003 (Jaw Gulch; Fig. 5). However, *C. mollis* populations at both sites began to decline sharply again after 2003. By 2006, both total plant and total stem numbers were still greater than at the start of the study (a 42.4% increase in total plants

and a 40.4% increase for stems), but substantially lower than at the population peak in 2001.

Changes in multiple demographic rates may have contributed to this pattern of rise and decline in *C. mollis* abundances. In the period after herbivore reductions, the rate at which *C. mollis* individuals survived and appeared above ground in the following year rose from just under 70% in 1996–1997 to around 90% in 2000–2001 (Table 1). However, survivorship then steeply declined again and reached its lowest observed levels in 2006. Interestingly, the increase after herbivore control in year to year persistence above ground was driven mostly by reduced rates of dormancy; a total of 10.4% of all observed year-to-year transitions before 2000 involved plants going or remaining dormant, compared to 2.6% in 2000–2006. In contrast, the drop in above ground persistence after 2001 reflects increasing plant mortality rather than a return to greater dormancy levels (Fig. 3A, Table 1). Average plant growth in size was also low prior to 1998, increased dramatically during the period immediately following reductions in herbivore abundance (1999–2003), and then, like plant and stem numbers, dropped off sharply between 2004 and 2006 (Table 1).

Recruitment rates generally followed the same trends, although fluctuating considerably between years (Table 1). The majority of recruitment occurred through vegetative reproduction. Flowering appeared to be variable and episodic, with a greater proportion of plants flowering and much higher mean numbers of inflorescences per plant in a small number of years (e.g., 1999–2000; Table 1). Like flowering, sexual reproduction was very episodic; few seedlings were observed, almost all between 1999 and 2001 (Table 1).

Herbivore damage, climate, and population growth

In our initial screening of climate variables, none of the rainfall metrics, including total yearly rainfall and rainfall during the January to June growing season, showed any evidence of a relationship to population

TABLE 1. Yearly variation in demographic rates for *Castilleja mollis*, an endangered perennial subshrub endemic to Santa Rosa Island, California, USA.

Year	Survived (%)	Dormant (%)	Died (%)	Flowered (%)	Growth (% change in stems)	Inflorescences/stem	Seedlings/plant	Vegetative recruits/plant
1995				70.00		1.43 ± 0.14		
1996	68.26	16.96	14.78	38.90	7.59 ± 9.23	0.52 ± 0.098	0.00	0.15 ± 0.009
1997	77.59	9.48	12.93	59.40	60.22 ± 11.84	0.98 ± 0.13	0.0045 ± 0.0006	0.34 ± 0.02
1998	82.46	11.57	5.97	52.90	63.25 ± 11.82	1.0 ± 0.11	0.00	0.36 ± 0.02
1999	85.34	5.57	9.09	79.00	114.69 ± 13.00	4.08 ± 0.61	0.042 ± 0.002	0.078 ± 0.003
2000	91.07	3.17	5.76	87.30	58.86 ± 9.52	4.74 ± 0.39	0.049 ± 0.004	0.42 ± 0.02
2001	86.47	2.92	10.61	70.20	81.62 ± 9.04	2.1 ± 0.15	0.14 ± 0.008	0.32 ± 0.009
2003				58.20		0.98 ± 0.07	0.00	0.36 ± 0.01
2004	82.40	1.32	16.28	31.90	17.52 ± 4.02	0.43 ± 0.06	0.00	0.070 ± 0.002
2005	67.88	2.18	29.95	33.40	19.45 ± 5.99	0.71 ± 0.14	0.00	0.015 ± 0.0006
2006	62.31	4.27	33.42	61.70	26.38 ± 9.57	3.28 ± 0.43	0.00	0.026 ± 0.0006

Notes: Data shown are for all individuals, irrespective of population. The columns represent the percentage of plants surviving and appearing aboveground, in dormancy or dead; percentage of plants flowering; mean percentage change in stem number (growth); mean number of inflorescences per stem in individuals that flowered; mean number of seedlings per plant; and mean number of vegetative recruits per plant. Means \pm SE are shown.

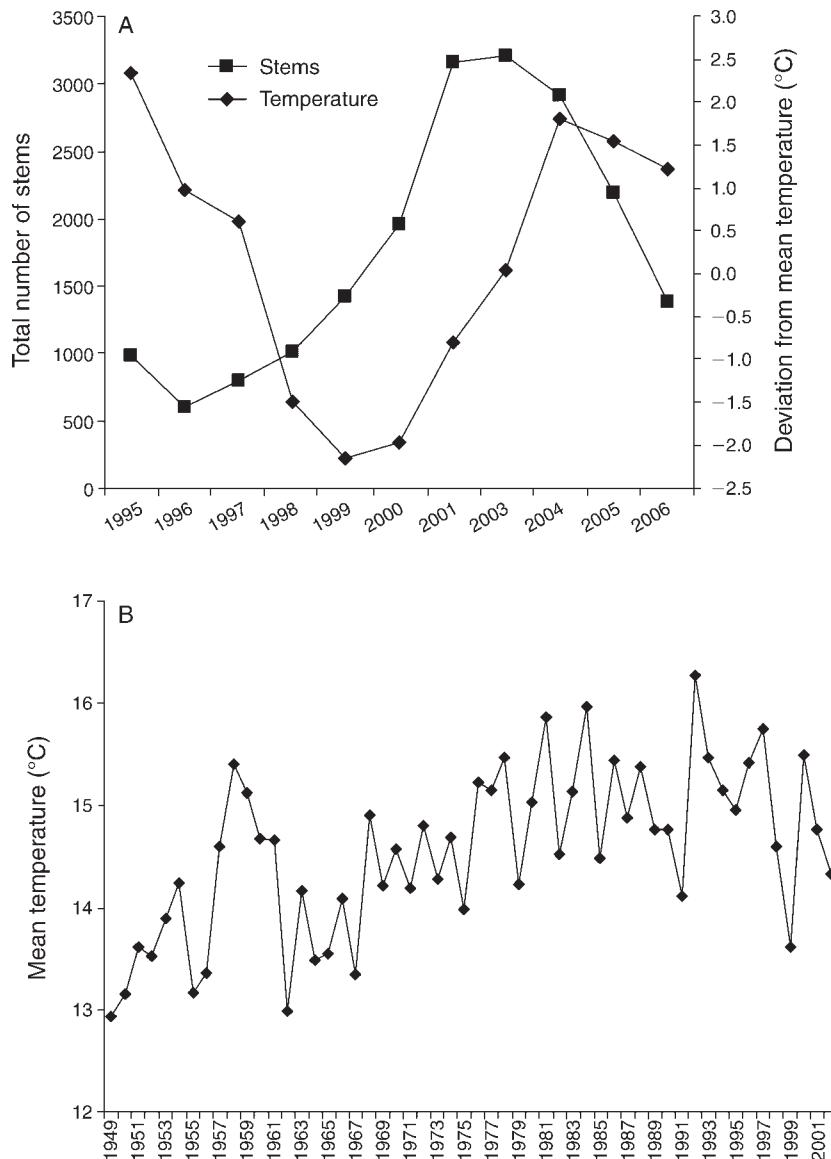


FIG. 6. The association between temperature trends and changes in *Castilleja mollis* population size. (A) Data from 1996–2005 for total numbers of *C. mollis* stems for both populations combined and for the deviation of the mean growing season temperature (January–June) in that year from the mean taken over all years between 1990 and 2006. (B) Trend in mean growing-season temperature for the Oxnard weather station from 1949 to 2002, which is increasing significantly over time ($P < 0.001$).

growth rates (Spearman's rank correlation $|r| \leq 0.18$). In contrast, we found that the years of highest *C. mollis* population growth tended to correspond with lower-than-average growing season (January to June) temperatures ($r = -0.533$; Fig. 6A). Therefore, we included annual variation in growing season temperatures, expressed as the deviation from the average at Santa Rosa Island between 1990 and 2006, in our final analysis.

Ungulate scraping damage had a strong, significant negative relationship with *C. mollis* population growth ($F_{1,59,29} = 10.53$, $P = 0.002$). *C. mollis* also showed significantly higher growth rates in years with below

average growing season temperatures ($F_{1,65,14} = 28.18$, $P < 0.0001$). The proportion of stems damaged by grazing did not significantly relate to population growth ($F_{1,65,04} = 1.47$, $P = 0.24$), and we found no evidence of significant density dependence ($F_{1,65,03} = 2.16$, $P = 0.15$) or of differences between the two sites ($F_{1,23,96} = 0.59$, $P = 0.49$).

Given that higher temperatures were associated with reduced *C. mollis* population growth, we also asked whether the range of growing season temperatures observed during our study was typical of what this species experiences over long time scales. Temperature records for Santa Rosa Island only date back to 1990, so

we used the closest weather station with longer-term data available (Oxnard, 1949–2002). At the Oxnard station, average growing season temperatures have risen significantly over the last 50 years, at an estimated rate of $0.03 \pm 0.006^\circ\text{C}$ per year (mean \pm SE; linear regression, $F_{1,52} = 26.41$, $P < 0.001$; Fig. 6B).

DISCUSSION

Short-term research focusing on the effects of single factors in isolation usually fails to capture the full complexity of ecological systems (Agrawal et al. 2007, Didham et al. 2007), but remarkably few studies have explored how several stressors work together to threaten species persistence across a range of environmental conditions (Davidson and Knapp 2007). In this study, we observed a seemingly straightforward pattern emerge in the first few years after herbivore control, with *C. mollis* showing strong increases in both individual plant performance and population size. Short-term monitoring might easily have led to the conclusion that changes in herbivore pressure alone caused this response. Likewise, when growth in *C. mollis* populations reversed into steady declines, this pattern on the surface called into question the benefits of herbivore removal. Only a long-term data set integrating information on individual plant demography with population trends allowed the more nuanced story to emerge: both climate and herbivore removal were important drivers of observed population changes. As our results illustrate, risk assessments that fail to integrate multiple threats can lead to poor predictions, especially when based on short-term data sets.

We found compelling evidence that herbivores had strong negative effects on *C. mollis*, but the strengths of effects varied among types of damage. Measurement of individual plant demographic rates demonstrated that scraping behavior had devastating impacts on *C. mollis* survivorship, dormancy, growth, and flowering persisting for several years. Stem browsing damage was also frequent in *C. mollis* populations prior to 2000 and still occurs, but the effects were more subtle. Direct grazing lowered mean flower production by nearly a third, but stem damage did not affect survivorship and reduced plant growth only for small individuals.

In contrast to most studies of herbivory (Halpern and Underwood 2006), we were also able to ask directly how these demographic changes linked to population trends. Data on individual plant fitness did provide good estimates of how the population as a whole would respond. Scraping damage clearly translated into major effects on population growth. However, adding the weaker effects of stem grazing on plant fates did not significantly improve model predictions of population growth.

The lack of a clear signal for stem grazing effects in the population trends does not necessarily indicate their unimportance for population dynamics. First, herbivores appeared to increase grazing on *C. mollis* in

response to greater abundance of inflorescences, for reasons that are not entirely clear but may relate to the succulent floral bracts. Thus, it is possible that grazing pressure has not risen in recent years even with moderate increases in total herbivore densities (e.g., the estimated total number of deer and elk broke 1100 individuals again in 2005) in part because *C. mollis* has flowered much less under the warmer conditions prevalent in these years (mean \pm SE annual probability of flowering from 2003 to 2006 = $46\% \pm 7.9\%$, compared to $65\% \pm 6.2\%$ from 1995 to 2001). To predict the long-term effects of continued elk and deer grazing, such responses of herbivores to changes in native plant populations must be taken into account.

Second, because the life history of *C. mollis* includes a long-lived adult stage and strong dormancy, short-term population dynamics are likely to be dominated by the fates of established individuals that are relatively unaffected by stem grazing. Stem damage primarily influenced seed production and growth of smaller individuals, processes linked to recruitment, and recruitment was very episodic. We observed little reproduction, either via seeds (0.024 ± 0.015 seedlings \cdot plant $^{-1}\cdot$ yr $^{-1}$ [mean \pm SE]) or vegetative propagation (0.21 ± 0.05 recruits \cdot plant $^{-1}\cdot$ yr $^{-1}$). About 99% of the seedlings appeared between 1999 and 2001 and 64% of all vegetative recruits in 2000–2001 or 2003. Nevertheless, maintenance of some recruitment is critical to long-term persistence, and grazing effects unimportant in most years may still reduce recruitment in unusual but key years. In general, herbivore effects on individual fitness may give a misleading picture of their population-scale consequences, so a careful, formal modeling approach is necessary to fully elucidate how herbivores influence population growth and extinction risk (Halpern and Underwood 2006, Maron and Crone 2006).

Previous studies of introduced herbivore effects in mainland systems have found population-level effects on native plants ranging from strongly negative to positive. Disturbance may benefit some native herbaceous plants by removing competing vegetation, while consumption of plant tissue generates more negative impacts (Bastrenta et al. 1995, Lennartsson and Oostermeijer 2001, Maron and Crone 2006). In contrast, we found a strong detrimental effect of scraping disturbance on *C. mollis*. There are several possible explanations. First, as an island endemic with brittle stems, succulent inflorescences and no previous exposure to vertebrate herbivores, *C. mollis* does not appear tolerant of herbivores. Second, most previous studies have focused on short-lived species with substantial reproduction from seed, which may be more strongly influenced by interspecific competition and better able to exploit grazer-generated gaps than the longer-lived, primarily clonal *C. mollis*. Our results reinforce that responses to herbivores are likely to vary substantially among plants with different life histories, so that attempting to predict the effects of changes in herbivore density based on the limited

number of population studies currently available is potentially very problematic (Maron and Crone 2006).

Our analysis confirms the importance of herbivore impacts for *C. mollis*, but we found that a shift from warmer to cooler growing season temperatures also played a very strong role in the observed increase in *C. mollis* populations between 1997 and 2003. Conversely, increased temperatures appear to be largely responsible for declines from 2003–2006. The mechanism for this effect is not completely clear, as growing season temperatures are likely to be correlated with a number of other environmental factors affecting *C. mollis*. One possibility is that temperatures are related to summertime cloud shading and coastal fog, shown to be important factors regulating the growth of a tree endemic to Santa Rosa Island (Williams et al 2008). While more difficult to capture in a single metric, such effects may ultimately matter more to population growth than total rainfall, given that much of the precipitation in this system is concentrated in a small number of storms between January and March.

We also explored the potential contributions of intraspecific density dependence or plant community changes to *C. mollis* declines after 2003. Since *C. mollis* is hemiparasitic, herbivore removal might have caused indirect effects mediated through host plants. However, data on community composition from nearby sites over the same time span showed no major shifts in the abundance of important hosts such as goldenbush (Channel Islands National Park, *unpublished data*). Likewise, we found no evidence that intraspecific density-dependence strongly limited population growth.

The strong effects of climatic variation raise important questions for conservation of *C. mollis* and other island species. Under favorable conditions, control of scraping damage to low levels appeared adequate to promote *C. mollis* population growth; the reduced numbers of vertebrate herbivores now present on Santa Rosa Island might not threaten the short-term persistence of this species if demographic rates were always as high as during 1999–2003. Fully assessing how climatic variation interacts with herbivore effects is difficult, because we observed the highest levels of herbivory under cooler, more favorable conditions. However, the dramatically reduced survival and reproduction observed from 2003–2006 suggest that the ability of these populations to tolerate even low levels of herbivore damage could be markedly lower than the early years of this study indicated.

More broadly, our results reinforce that to adequately predict and evaluate responses to large-scale herbivore removals we must understand them within the context of important year-to-year environmental variation that drives population dynamics. More troubling, our data suggest that *C. mollis* may be currently experiencing warmer average growing season temperatures than in the past and is likely to continue doing so. Although weather records specific to Santa Rosa Island date back

only to 1990, data from the closest mainland weather station showed a clear increasing trend in growing season temperature over the last 50 years.

Although many authors have suggested that interactions between climate change and other environmental impacts such as invasions are likely to be of increasing importance in the future (Weltzin et al. 2003), we are aware of little empirical work that has measured such effects already occurring. Our results illustrate the many challenges such interactions will pose, in both untangling the most important causes of species declines and in predicting the outcomes of management changes. Given that managers cannot directly control effects of changing climate on threatened species, it is all the more important not only to minimize other impacts, but to integrate the effects of current and future environmental variation in weighing the relative payoffs of management strategies.

ACKNOWLEDGMENTS

We thank D. Rodriguez and C. Cowan for substantial assistance with data collection, and J. Levine, N. Pavlovic, K. Faulkner, J. Howell, J. Hatfield, and J. Yee for many helpful comments on the manuscript. Funding for this work was provided by the National Park Service, by National Science Foundation grant 0353608, and the U.S. Geological Survey. Our work was conducted under U.S. Fish and Wildlife Service Recovery Research Permit #TE-044846.

LITERATURE CITED

- Agrawal, A. A., et al. 2007. Filling key gaps in population and community ecology. *Frontiers in Ecology and the Environment* 5:145–152.
- Bastrenta, B., J. D. Lebreton, and J. D. Thompson. 1995. Predicting demographic change in response to herbivory: a model of the effects of grazing and annual variation on the population dynamics of *Anthyllis vulneraria*. *Journal of Ecology* 83:603–611.
- Beatty, S. W., and D. L. Licari. 1992. Invasion of fennel into shrub communities on Santa Cruz Island, California. *Madrono* 39:54–66.
- Bowen, L., and D. VanVuren. 1997. Insular endemic plants lack defenses against herbivores. *Conservation Biology* 11:1249–1254.
- Campbell, K., and C. J. Donlan. 2005. Feral goat eradications on islands. *Conservation Biology* 19:1362–1374.
- Clout, M. N. 2002. Biodiversity loss caused by invasive alien vertebrates. *Zeitschrift Fur Jagdwissenschaft* 48:51–58.
- Courchamp, F., J. L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. *Biological Reviews* 78:347–383.
- Davidson, C., and R. A. Knapp. 2007. Multiple stressors and amphibian declines: dual impacts of pesticides and fish on yellow-legged frogs. *Ecological Applications* 17:587–597.
- Didham, R. K., J. M. Tylianakis, N. J. Gernmell, T. A. Rand, and R. M. Ewers. 2007. Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution* 22:489–496.
- Donlan, C. J., D. A. Croll, and B. R. Tershy. 2003. Islands, exotic herbivores, and invasive plants: their roles in coastal California restoration. *Restoration Ecology* 11:524–530.
- Donlan, C. J., and P. S. Martin. 2004. Role of ecological history in invasive species management and conservation. *Conservation Biology* 18:267–269.
- Donlan, C. J., B. R. Tershy, and D. A. Croll. 2002. Islands and introduced herbivores: conservation action as ecosystem experimentation. *Journal of Applied Ecology* 39:235–246.

- Gomez, J. M. 2005. Long-term effects of ungulates on performance, abundance, and spatial distribution of two montane herbs. *Ecological Monographs* 75:231–258.
- Halpern, S. L., and N. Underwood. 2006. Approaches for testing herbivore effects on plant population dynamics. *Journal of Applied Ecology* 43:922–929.
- Jones, H. L., and J. M. Diamond. 1976. Short-time-base studies of turnover in breeding bird populations on the California Channel Islands. *Condor* 78:526–549.
- Krajick, K. 2005. Ecology: winning the war against island invaders. *Science* 310:1410–1413.
- Lennartsson, T., and J. G. B. Oostermeijer. 2001. Demographic variation and population viability in *Gentianella campestris*: effects of grassland management and environmental stochasticity. *Journal of Ecology* 89:451–463.
- Livingston, D. S. 2006. Ranches in the sea: a history of the islands within Channel Islands National Park. Draft Technical Report. Department of the Interior, National Park Service, Channel Islands National Park, Ventura, California, USA.
- Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13:195–198.
- Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10:689–710.
- Maron, J. L., and E. Crone. 2006. Herbivory: effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B* 273:2575–2584.
- McChesney, G. J., and B. Tershy. 1998. History and status of introduced mammals and impacts to breeding seabirds on the California Channel and northwestern Baja California Islands. *Colonial Waterbirds* 21:335–347.
- Myers, J. H., D. Simberloff, A. M. Kuris, and J. R. Carey. 2000. Eradication revisited: dealing with exotic species. *Trends in Ecology and Evolution* 15:316–320.
- North, S. G., D. J. Bullock, and M. E. Dulloo. 1994. Changes in the vegetation and reptile populations on Round-Island, Mauritius, following eradication of rabbits. *Biological Conservation* 67:21–28.
- Raven, P. H. 1967. The floristics of the California Islands. Pages 57–67 in R. N. Philbrick, editor. *Proceedings of the Symposium on the Biology of the California Islands*. Santa Barbara Botanic Garden, Santa Barbara, California, USA.
- Rayner, M. J., M. E. Hauber, M. J. Imber, R. K. Stamp, and M. N. Clout. 2007. Spatial heterogeneity of mesopredator release within an oceanic island system. *Proceedings of the National Academy of Sciences (USA)* 104:20862–20865.
- Reaser, J. K., et al. 2007. Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environmental Conservation* 34:98–111.
- Roemer, G. W., C. J. Donlan, and F. Courchamp. 2002. Golden Eagles, feral pigs, and insular carnivores: how exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences (USA)* 99:791–796.
- Ruesink, J. L., I. M. Parker, M. J. Groom, and P. M. Kareiva. 1995. Reducing the risks of nonindigenous species introductions: guilty until proven innocent. *BioScience* 45:465–477.
- Sax, D. F., J. J. Stachowicz, J. H. Brown, J. F. Bruno, M. N. Dawson, S. D. Gaines, R. K. Grosberg, A. Hastings, R. D. Holt, M. M. Mayfield, M. I. O'Connor, and W. R. Rice. 2007. Ecological and evolutionary insights from species invasions. *Trends in Ecology and Evolution* 22:465–471.
- Simberloff, D., I. M. Parker, and P. N. Windle. 2005. Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment* 3:12–20.
- Weltzin, J. F., R. T. Belote, and N. J. Sanders. 2003. Biological invaders in a greenhouse world: will elevated CO₂ fuel plant invasions? *Frontiers in Ecology and the Environment* 1:146–153.
- Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *BioScience* 48:607–615.
- Williams, A. Park, C. J. Still, D. T. Fischer, and S. W. Leavitt. 2008. The influence of summertime fog and overcast clouds on the growth of a coastal Californian pine: a tree-ring study. *Oecologia* 156:601–611.
- Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* 16:454–459.