

# Rodent-limited establishment of bush lupine: field experiments on the cumulative effect of granivory

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## Summary

**1** Plants often suffer substantial loss of seeds to consumers. However, because the seed-to-seedling transition is frequently ignored, quantitative estimates of the effects of seed consumers on plant population dynamics are rare.

**2** We examined how post-dispersal seed predation by rodents affected seedling emergence and subsequent adult plant abundance of bush lupine (*Lupinus arboreus*), a large N-fixing shrub common to coastal dunes in California. We monitored patterns of seedling emergence and survival over 3 years for seeds sown into exclosed and control plots.

**3** We sowed additional cohorts of seeds in the second and third years and compared interannual variation in emergence patterns.

**4** Rodent exclusion substantially reduced seedling emergence, with an average of 109 seedlings emerging over 3 years from 476 seeds sown in rodent exclusion plots vs. 26 from control plots. The intensity of granivory, however, varied between years, with rodent exclusion increasing emergence from seeds sown in year one, but not in year two.

**5** Winter seedling mortality, due to cutworm herbivory, was similarly high in rodent-free and control plots, and its net impact was to reduce the difference in seedling abundance. Thus, by mid-summer in each of the three years, there were only marginally more seedlings in rodent-excluded vs. control plots.

**6** The cumulative effect of protecting seeds, was, however, large. After 3 years, an average of four adult lupines were established in rodent-free plots, whereas only 0.5 were found in control plots and lupine biomass was more than 5-fold higher in exclusion plots.

**7** Taken together, the results indicate that rodents play a critical role by limiting the abundance and biomass of a large N-fixing shrub in dunes.

*Key-words:* adult plant abundance, granivory, seed bank, seedling recruitment.

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## Introduction

Plants in almost all communities suffer loss of seeds to consumers (reviewed by Janzen 1971; Louda 1989; Crawley 1992; Hulme 1998). Seed predation can be substantial and sources of variability in loss can be manifold. Experiments have shown that flower and seed predators frequently consume 50–80% of either pre- (Waloff & Richards 1977; Louda & Potvin 1995; Maron 1998) or post-dispersed seeds (reviewed by Hulme 1993, 1998), with the magnitude of consumption varying greatly depending on seed size and density (Mittelbach & Gross 1984; Hulme 1994; Edwards

& Crawley 1999), habitat (Louda 1982; Willson & Whelan 1990; Maron & Simms 1997), season and year (Gashwiler 1970; Radvanyi 1970). Although our understanding of the magnitude and sources of variation in seed predation continues to expand, the consequences of this granivory for regeneration remain poorly understood. As such, the degree to which consumers control terrestrial plant abundance is often unclear (Crawley 1992; Hunter 1992; Louda & Potvin 1995).

Most research on post-dispersal seed predation has focused on birds, rodents or ants as dispersal agents, emphasizing behavioural patterns of these organisms (Vander Wall 1990), or the consequences of seed predation on community composition or structure (reviewed by Hulme 1998). These investigations either follow the fate or spatial arrangement of animal dispersed seed (Price & Jenkins 1986; Vander Wall 1994), or ask how seed size (Mittelbach & Gross 1984; Reader 1993;

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Hulme 1994), seed density (Casper 1988; Hulme 1994; Edwards & Crawley 1999) or habitat (Schupp 1988; Willson 1988; Maron & Simms 1997) correlates to predation risk. Experimental data relevant to the issue of how seed loss influences the magnitude of plant recruitment are, however, conspicuously lacking.

The effects of seed loss on plant abundance depend on the magnitude of the seed-to-seedling and seedling-to-adult transitions. Reductions in the abundance of dispersed seeds may have minimal impacts on adult plant abundance (Crawley 1989, 1992) if seeds saturate all safe-sites and recruitment is limited by safe-site availability or if compensatory density-dependent seedling mortality reduces any initial granivore-induced difference in seedling abundance. Alternatively, the seed-to-seedling and seedling-to-adult links can be strong, in which case seedling recruitment and adult plant establishment can directly correlate with previous or past year's seed production (Louda & Potvin 1995). Both seed predation and environmental cues that trigger germination can vary significantly from year to year, and determining how seed predators affect plant populations therefore also necessarily involves understanding how this variation modifies the cumulative effects of seed loss. While seed loss has been shown to reduce plant abundance (Louda 1982; Louda & Potvin 1995) and change community composition (Borchert & Jain 1978; Brown & Heske 1990; Ostfeld *et al.* 1997), multi-year experimental studies evaluating how seed predation influences recruitment are relatively rare. This is particularly true for plants that produce dormant seeds (but see Cabin *et al.* 2000). Dormancy may introduce considerable time lags in the population response to seed loss and the population-level impacts of seed predation for plants with seed banks is particularly uncertain (Crawley 1992; Maron & Gardner 2000).

In this paper we examine the degree to which rodent granivores influence the establishment of bush lupine (*Lupinus arboreus*), one of only a few large shrubs (others include *Baccharis pilularis* and *Lupinus chamissonis*) that provide structure in coastal dunes in California. Bush lupines are also prodigious nitrogen-fixers (Gadgil 1971; Palaniappan *et al.* 1979; Bentley & Johnson 1991, 1994) that create patches high in nitrogen within nutrient impoverished dunes (Alpert & Mooney 1996; Pickart *et al.* 1998) and grasslands (Maron & Connors 1996; Maron & Jefferies 1999). These patches are used by other plants, both while the lupines are alive and after they die (Alpert & Mooney 1996; Maron & Connors 1996).

At our coastal dune study site, rodents consume an average of 75% of newly dispersed bush lupine (hereafter 'lupine') seeds (Maron & Simms 1997). Although this predation can reduce seedling emergence in small (0.3 m × 0.3 m) plots in the year after seeds are sown, it is unclear how granivory affects seedling establishment or the abundance of adult lupines in dunes (Maron & Simms 1997). To understand fully how seed loss might

influence plants at the population level, one must ascertain how seed predation influences recruitment over the lifetime of seeds in the soil and whether processes that affect seedling survival compensate for seed loss. As lupine seeds are capable of dormancy (Maron & Simms 1997), short-term patterns of recruitment may not accurately reflect the population consequences of granivory.

Here we ask three questions:

1. Does granivory on a single cohort of seeds influence cumulative seedling recruitment into large plots across 3 years?
2. What is the magnitude of annual variation in the intensity of granivory and how does this, combined with carryover of dormant seeds, influence the overall population response to seed loss?
3. How do patterns of seedling mortality alter how granivore-driven reductions in recruitment ultimately affect adult lupine abundance?

## Methods

### STUDY SITE

This study took place at the University of California's Bodega Marine Reserve (BMR) located in central coastal California (see Barbour *et al.* 1973 for a complete description of the site). The site experiences a typical Mediterranean climate with a cool winter rainy season and extended summer drought. Bush lupines are community dominants in grasslands (Barbour *et al.* 1973; Heady *et al.* 1995) but occur at lower densities in adjacent (< 0.5 km away) dunes (Wagstaff 1938; Barbour & Johnson 1995) and are native at BMR and in similar habitats to the south. Dunes at BMR lie within the San Andreas Fault zone and consist of both open and stabilized sand. After overgrazing in the 1940s–1950s much of this dune system was planted with the European dune grass, *Ammophila arenaria*, which presently dominates large expanses of the dunes. Spring ephemeral forbs and grasses are common, but other woody plants in dunes at BMR include coyote bush (*Baccharus pilularis*), dune heather (*Ericameria ericoides*), and isolated populations of silver lupine (*Lupinus chamissonis*) on a few dune ridges and valleys.

Bush lupines produce mature seeds in late July and early August. Seeds are dispersed via explosive dehiscence, landing close to their parent bush, and many are consumed by rodents, especially in late summer (Maron & Simms 1997, unpublished data). Two granivorous rodents, deer mice, *Peromyscus maniculatus*, and western harvest mice, *Reithrodontomys megalotis*, are found at BMR and *Microtus californicus*, a primarily herbivorous vole, is also abundant but there are no seed-harvesting ants. Seeds escaping predation may germinate primarily between November–March (the period of heaviest rainfall) while ungerminated seeds can remain viable but dormant due to their hard seed coat (Quinlivan 1961, 1966). In grasslands, seeds are capable of extended

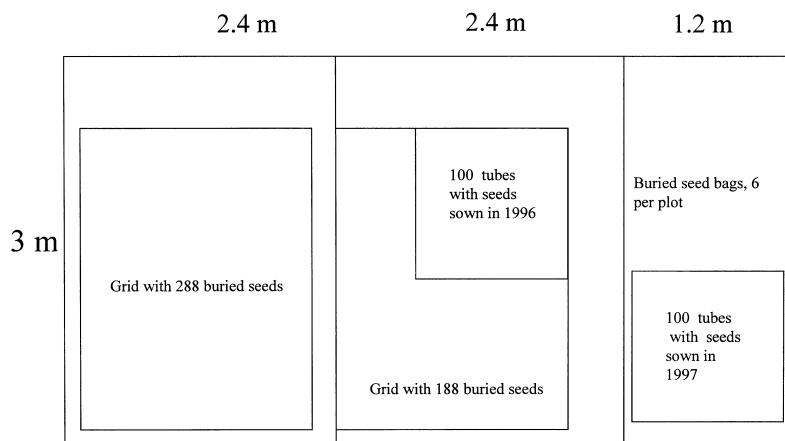


Fig. 1 Layout of seeds in each experimental plot.

dormancy and there is a large seed bank, whereas in dunes both seed dormancy (see results) and seed bank are reduced (Maron & Simms 1997).

#### INFLUENCE OF RODENT GRANIVORY ON LUPINE SEED BANK DYNAMICS AND RECRUITMENT

Rodent-exclusion and control plots were established at two dune sites, approximately 1 km apart. In July 1996, three pairs of 3 m × 6 m plots were randomly located in a 100 m × 100 m area within each site, in areas that were free from dense *Ammophila arenaria* dune grass. Plots were situated such that they were not near any existing bush lupines to prevent unwanted seeds from dispersing into plots. Plots belonging to the same pair were separated from each other by at least 5 m and pairs of plots were separated by at least 20 m. We randomly assigned one of each pair of plots to a rodent exclusion treatment consisting of fences which were 60 cm tall, buried to 25 cm, and made of galvanized hardware cloth (0.625 cm mesh size). Fences were supported every 3 m with metal rods which were 1.2 m tall and sunk into the sand. Each fence was topped by aluminium flashing (22.5 cm wide) riveted to the fencing. Control plots had metal rods (1.2 m high) placed at each corner but no fence. After constructing enclosures, Petri plates filled with lupine seeds were placed inside and outside of enclosures. After several days, mice had removed all seeds outside but none inside enclosures, showing that the fences were effective at keeping rodents from plots.

To determine whether plots contained any dormant lupine seeds, we took four 30 cm × 30 cm × 20 cm deep soil samples per plot, before planting experimental seeds. We put soil samples through a 2-mm mesh sieve and material left in the sieve was carefully inspected for the large, easily identified lupine seeds (but none were found in any of the 48 samples across all plots). We have previously found that there is a small and likely transient lupine seed bank in these dunes, averaging 7–42 seeds m<sup>-2</sup> at several sites (Maron & Simms 1997, unpublished data).

In August 1996 we collected ripe lupine seeds from 20 mature bushes at each of the two sites at which we had established experimental plots, and combined most of these seeds into two bulk pools, one from each site. The remaining seeds from each shrub were used to represent maternal half-sib families in a separate study to determine the maternal and genetic components of dormancy.

We planted seeds drawn at random from the bulk pool and from the 20 half-sib families from that site into separate sections of each plot. We divided each plot into three sections (Fig. 1). Within the first (3 m × 2.4 m) section, 288 seeds were planted in a 18 × 16 grid pattern, with each grid point separated by 12.5 cm and a 15-cm buffer between grid and fence on two sides of the grid. This grid occupied a 2.12 m × 1.87 m area within the 3 m × 2.4 m section of the plot. In half of a second 3 m × 2.4 m section, a further 188 seeds were sown in a grid (shaped as an inverted 'L'), with equal spacing as above. The central portion of the remaining area within the second section was divided into a 10 × 10 grid (spacing 12.5 cm) and five progeny from each of 20 half-sib families were planted into each grid point.

To keep track of seed families, we surrounded each seed with a 3.5 cm by 5 cm deep plastic tube, open at both ends, that was pushed into the sand so that its lip protruded 1 cm from the sand. Seeds sown in tubes were placed on the soil surface, while seeds sown outside tubes were planted at a depth of approximately 3 cm to ensure that they would not blow away in the spring, when there are strong north-west winds at our site. In the final (1.2 m × 3 m) section of each plot, we buried six 13 cm × 10 cm bags, made of fibreglass window screen, containing one from each of 20 bushes and sealed with a soldering iron. Bags were covered on both sides with woven wire (mesh size = 0.635 cm) and buried 5 cm beneath the soil surface. They were excavated each summer and reburied after taking a census of the seeds. At the end of the experiment the bags were removed from the plots and all remaining seeds were counted. Previous work has shown that intact seeds within buried bags retain nearly 100% viability, and we

therefore assumed that all intact seeds were viable (Simms & Maron, unpublished data).

A total of 476 seeds were buried in each plot in 1996 (mean density of 44 seeds  $m^{-2}$ ) and a further 100 seeds (80  $m^{-2}$ ) were sown in tubes. A large lupine bush can produce 2000–3000 seeds (Maron 1998), the majority of which disperse within 5–10 m of the parent, giving a conservative estimate of the density of newly dispersed seeds around any one plant of 80 per  $m^2$ ; this is similar to or slightly above that in our experimental plots.

The following year (23–24 August 1997), we added a second grid of 100 tubes to each plot, identical to the one described above. This planting enabled us to: (i) estimate across years how granivory on newly dispersed seeds affects seedling recruitment; (ii) compare the magnitude of recruitment from newly dispersed seeds vs. seeds that had been dormant for one year; and (iii) compare how granivory differs between newly dispersed and dormant seeds and how this might influence patterns of seedling recruitment. The seeds used were collected in August 1997, primarily from the same 20 bushes per site, with five progeny planted for each half-sib family.

In each of 3 years, we carried out a census of plots (and tubes within plots) for newly emerged lupine seedlings. Plots were initially studied every 1–4 weeks, from November 25 1996 through March 1997, and sporadically thereafter; in the second and third years censuses started on December 5 1998 and January 3 1999, respectively. At each census, we recorded the number of seedlings that had emerged and marked them with dated plastic tags and noted if any previously marked seedlings had died.

One-year-old plants that had recruited into plots in 1997 started to produce fruit in summer 1998. Such fruit were removed while they were still green to prevent further seed input into plots confounding our study of how protecting seeds from granivores influenced the abundance of adult plants that ultimately established in plots. Understanding how granivores affect long-term lupine population dynamics depends on following the demographic fate of seeds produced by the adults that established as a result of our initial manipulation.

At the end of the experiment, in July 1999, we destructively harvested all adult lupines in each plot to quantify how 3 years of rodent exclusion affected total above-ground lupine biomass. Harvested plants were cut into small pieces, separated into leaves and branches and woody trunks and bagged. Plant material was brought back to the laboratory, dried at 75 °C for 30–60 hours and weighed. To estimate the percentage of experimentally sown seeds that remained buried and viable within plots, we removed tubes from rodent-free plots in July 1999 and carefully sieved out lupine seeds from the sand.

#### RODENT DENSITIES

We estimated rodent population densities in August 1996 and from August 1998 to August 1999. For the

1996 estimate, we established a grid of 36 Sherman live traps (each 6.25 cm  $\times$  12.5 cm) located 7-m apart in a square array covering 0.12 ha. This grid was immediately south of the northern-most experimental site. Traps were set and baited with peanut butter and rolled oats wrapped in waxed paper for four evenings following the new moon of 14 August 1996, and checked before sunrise. Animals were removed and identified although we did not differentiate between harvest mice (*Reithrodontomys megalotis*) and deer mice (*P. maniculatus*); the absence of marked dimorphism in body size among trapped mice (*R. megalotis* are generally smaller than *P. maniculatus*) suggests that harvest mice were not trapped during this census. Mice were marked by toe clipping and released at the site of capture. When voles (*M. californicus*) were trapped at a location, they were released unmarked and an additional trap was added to the grid point. No more than three traps were used at any grid location. Only once were two mice caught at the same grid location.

In 1998, we established two 7  $\times$  7 square trapping grids (7 m separation, total area 0.17 ha); a northern grid 50 m north of the northernmost experimental site, and a southern grid between the two sites. Each grid location was permanently marked with a polyvinylchloride plastic pipe (0.5–1.0 m tall). Because small mammals tend to be more active on dark nights, we endeavoured to confine each trapping session to within 4 days of the new moon. Most trapping sessions consisted of four consecutive nights of trapping (18–20 August 1998, 17–20 November 1998 and 10–13 May 1999), but two were divided into two bouts of two nights each (8–11 and 17–20 February 1999, and 2–5 and 9–12 August 1999).

Traps were baited and set as before but were also provisioned with spun polyester for warmth and placed under a 0.25 m  $\times$  0.25 m sheet metal shelter to protect any animals within from rain and heavy dew. Animals were removed from traps, weighed, identified to species, and marked with a numbered monel fingerling tag clipped to the right ear. Each animal was released where it had been caught. During the first two trapping sessions, we did not distinguish *P. maniculatus* and *R. megalotis* but subsequently we used a reliable dental characteristic of the top incisors to differentiate between the two species.

#### ANALYSES

##### *Main plots*

Preliminary analyses revealed that there were no significant differences in seedling emergence or survivorship between our two sites. Therefore, in all subsequent analyses we combined data from both sites. In each year, we tallied the total number of seedlings that emerged in each plot. For each plot, we also calculated the percentage of seedlings that died through the winter, between the census period when cumulative

seedling emergence peaked (15 February in 1997, 19 January in 1998, 26 January in 1999) and a late spring census (13 May in 1997, 14 June in 1998, 12 April in 1999). We compared seedling mortality (from time of emergence until mid-summer of the same year) in rodent-free and control plots in 1997 and 1998 using separate chi-squared tests. Seedling mortality in control plots in 1999 was not calculated since there was no emergence in three of the control plots, and since overall seedling numbers were extremely low in the remaining three control plots.

We used repeated measures ANOVA (rMANOVA) to compare the cumulative number of seedlings to emerge between rodent exclusion and control plots, with each of the 3 years of data as the repeated measure. We also used rMANOVA to determine whether there were differences between rodent-free and control plots in the number of seedlings that survived to the middle of summer for each of the 3 years of the experiment. We used a MANOVA to examine how rodent exclusion affected the correlated independent variables of final adult lupine abundance and biomass at the end of the experiment.

#### *Tubes*

We performed separate statistical analyses to compare the fate of seeds sown into tubes in 1996 and 1997 because these two groups of seeds were independent. To compare the effects of rodent exclusion and year on the total number of seedlings that emerged from tubes, we used a two-way ANOVA. The factor 'year' in this model is a comparison of the cumulative number of seedlings that emerged in 1997 from seeds sown in 1996 with the cumulative number of seedlings that emerged in 1998 from seeds sown in 1997. After finding a significant year by treatment interaction (see results), we used one-way ANOVAs to decompose the effects of rodent exclusion in each year. We used repeated measures ANOVA to compare the effects of rodent exclusion on the cumulative number of seedlings to emerge in 1997 and 1998 from tubes sowed with seeds in 1996. We used an identical analysis to compare the effects of rodent exclusion on the cumulative number of seedlings to emerge in 1998 and 1999 from tubes sowed in 1997. SYSTAT 8.0 (SYSTAT 1998) was used to analyse all data.

#### *Rodent densities*

We analysed mark-recapture data from 1996 in two ways. First, we used a Schnabel estimator, which is a modified Lincoln-Peterson estimator that accounts for multiple trapping occasions (Seber 1982). Secondly, we used the program CAPTURE for DOS (Rexstad & Burnham 1991), which estimated population density based on a model that assumed uniform trapping over time, uniform behaviour in the rodent population, and no heterogeneity in the population (White *et al.* 1982).

To analyse the 1998–1999 trapping data, we used Pollock's robust design modelling method (Pollock

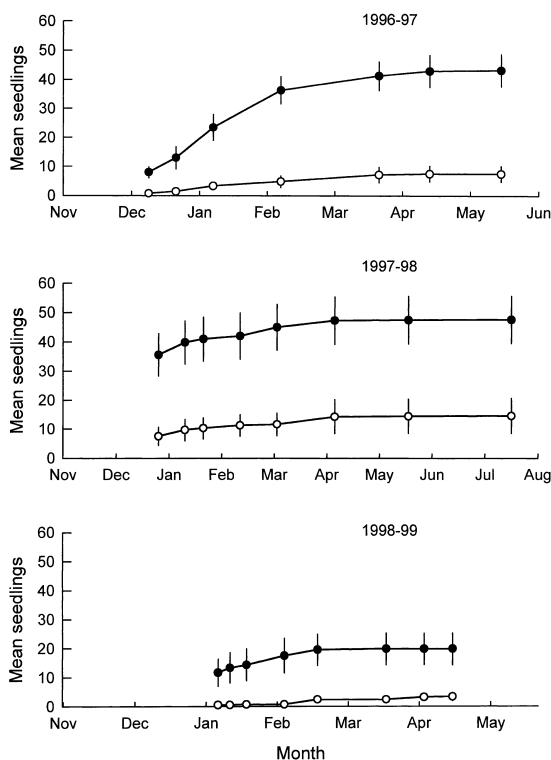
1982) in the program MARK (White 1999) to estimate the numbers of deer mice (*P. maniculatus*) and harvest mice (*R. megalotis*). We used the program to develop an unconstrained global model and models in which the likelihood of capture and recapture were constrained temporally and/or across species. Inference was through information theoretical means, and involved the ranking of corrected Akaike Information Criterion (AICc) values for each model (Burnham & Anderson 1998). Goodness-of-fit of the global model was tested with program MARK's integrated program CAPTURE goodness-of-fit routines.

Because the two species were not distinguished during the first two sessions, we first grouped data for both species and analysed it across all five sessions. We then analysed each species separately for the three sessions during which they were distinguished. We also used body masses to infer the numbers of each species during the first and second trapping sessions. Animals weighing 15 g or above were assumed to be *P. maniculatus* whereas animals below 15 g were assumed to be *R. megalotis*. We thus report the total number of animals trapped and our best estimates of the species to which they belong. However, none of these estimates were included in the data used in the models.

## Results

### SEEDLING EMERGENCE AND SURVIVAL, PLOTS

Exclusion of rodent granivores greatly increased the number of seedlings that emerged from plots (Fig. 2; rMANOVA across all 3 years,  $F_{1,10} = 53.5$ ,  $P < 0.0001$ ). In

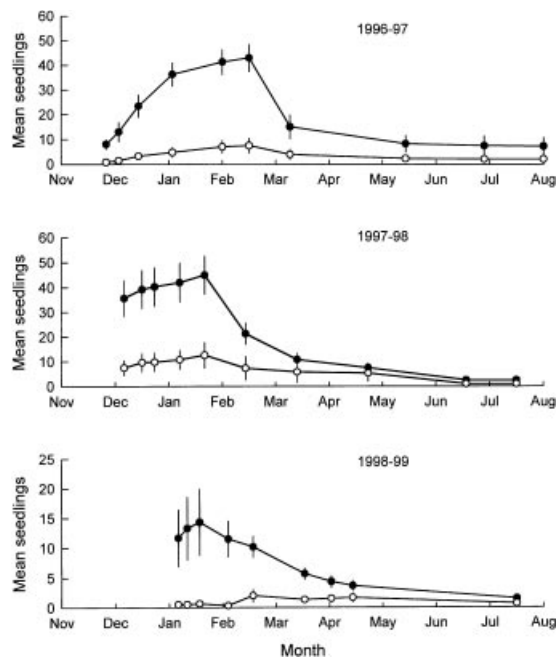


**Fig. 2** Mean ( $\pm 1$  SEM) cumulative (within a year) number of lupine seedlings to emerge in rodent exclusion (filled circles) and control (open circles) plots in each of the 3 years of the experiment. Seedling emergence in each year is from the cohort of 476 seeds we sowed in each plot in summer 1996.

not differ between treatments ( $\chi^2 = 2.82$  and  $1.87$  for 1997 and 1998, respectively,  $P > 0.05$ ). In rodent-free plots, mean seedling mortality through winter and spring was 85%, 95% and 54% in 1997, 1998 and 1999, respectively, whereas in control plots mean seedling mortality was 81% and 95% in 1997 and 1998, respectively. In mid-summer 1997, the number of seedlings that survived from those that germinated in the previous winter in control and rodent exclusion plots averaged 2.2 and 7.3, respectively, compared with 1.0 and 2.5 and 0.66 and 1.5 for 1997–1998 and 1998–1999 cohorts.

#### SEEDLING EMERGENCE AND SURVIVAL IN TUBES

Seedling emergence indicated significant among-year variability in the intensity of granivory (two-way ANOVA, treatment–year interaction,  $F = 19.2$ ,  $P < 0.0001$ ). Rodent exclusion had a large impact on seeds sown within tubes in 1996 (Fig. 4a), with an average of 20.3% of tubes producing seedlings in rodent exclusion plots, vs. 4.3% in control plots (two-way ANOVA, d.f.<sub>1,10</sub>,  $F = 31.6$ ,  $P < 0.0001$ ). Significantly higher emergence in tubes than that outside (9.1%;  $\chi^2$  with Yeat's correction = 4.0,  $P < 0.05$ ) was probably due to burial of seeds outside of tubes. Despite greater emergence from tubes in rodent exclusion vs. control plots, by mid-summer 1997, there was no significant difference between the mean



**Fig. 3** Mean ( $\pm 1$  SEM) number of lupine seedlings present in rodent exclusion (filled circles) and control (open circles) plots in each of the 3 years of the experiment.  $n = 6$ .

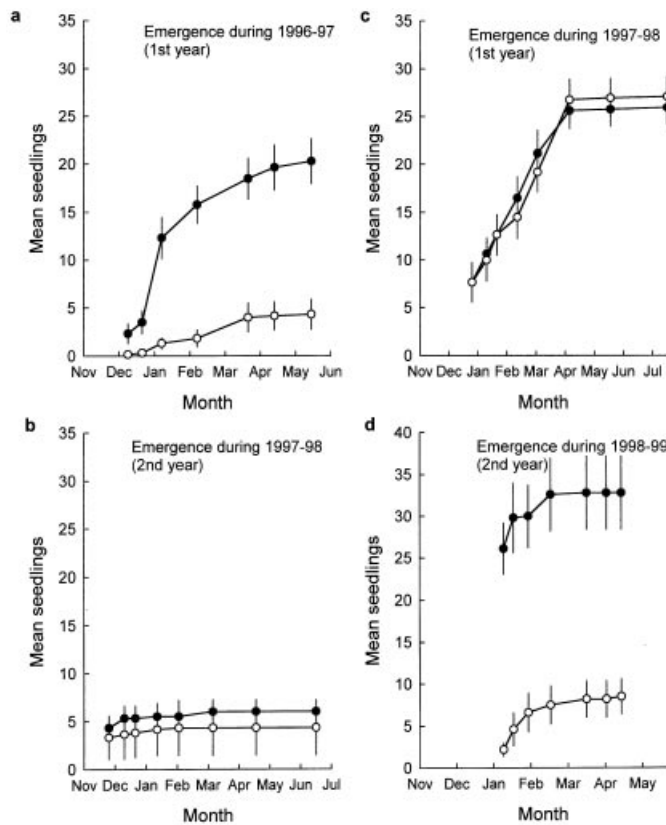
number of seedlings in these plots (Fig. 5; ANOVA,  $F_{1,10} = 3.7$ ,  $P = 0.08$ ).

For the cohort of seeds planted in 1997, there was no difference in seedling emergence between treatment and control plots in 1997–1998 (Fig. 4c; mean 26.0 and 27.1, respectively; ANOVA,  $F_{1,10} = 0.19$ ,  $F = 0.67$ ) nor in survival to summer 1998 (4.5 and 6.6 seedlings; Fig. 4c; rMANOVA,  $F_{1,10} = 1.18$ ,  $P = 0.30$ ). Seeds sown in 1996 also showed no difference in seedling emergence in the second year of the experiment (Fig. 4b; means 4.3 and 4.8, respectively; significant treatment by year interaction within rMANOVA;  $F_{1,10} = 21.6$ ,  $P < 0.001$ ). Thus, there was little evidence of intense granivory during 1997–1998 and the difference in emergence seen in seeds planted outside tubes may have been a carryover effect of granivory in the first year of the experiment. In 1999 only two seedlings (one in each treatment) emerged from tubes sown with seeds in 1996.

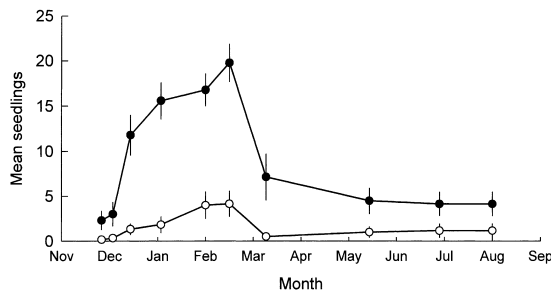
In 1999, rodent exclusion significantly increased the number of seedlings emerging from the dormant seeds remaining from the 1997 cohort (Fig. 4d; means 32.8 vs. 8.5, respectively; rMANOVA, significant treatment by year interaction,  $F_{1,10} = 36.2$ ,  $P < 0.0001$ ).

#### SEED DORMANCY

Only 4% of the original pool of 120 seeds we buried in bags were present 3 years later. All other seeds had either germinated or rotted. At the end of the experiment, only four seeds (0.069%) remained within tubes in rodent-free plots ( $n = 577$ , 23 tubes were not sampled because they had been disturbed, probably by deer).



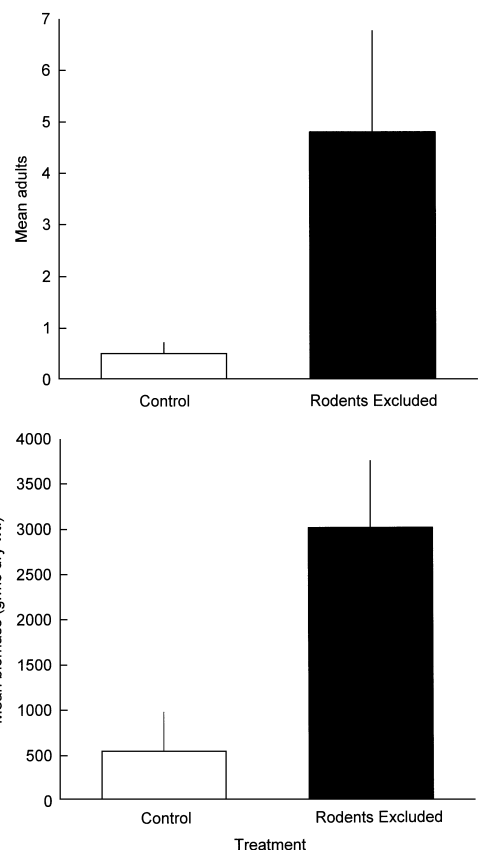
**Fig. 4** Mean ( $\pm 1$  SEM) cumulative (within a year) number of seedlings to emerge from 100 tubes sown with lupine seeds in 1996 (a, b) and 1997 (c, d) in rodent exclusion (filled circles) and control (open circles) plots. Top panels show seedling emergence in the first year seeds were sown; bottom panels show seedling emergence in the second year after seeds were sown.  $n = 6$ .



**Fig. 5** Mean ( $\pm 1$  SEM) number of lupine seedlings within tubes during 1997 in rodent exclusion (filled circles) and control (open circles) plots.  $n = 6$ .

**ADULT PLANT ABUNDANCE AND BIOMASS, PLOTS AND TUBES**

After 3 years, almost an order of magnitude (4.8 vs. 0.5 lupines per plot) more adult lupines established in rodent exclusion vs. control plots (Fig. 6, Table 1), if plants produced from seeds sown both inside and outside tubes were included. Considering only the original cohort of 476 seeds sown outside tubes in each plot, an average of 0.6% produced an adult plant in rodent exclusion plots whereas an average of 0.1% produced an adult plant in control plots. The strong effects of rodent exclusion on adult plant abundance translated into substantial impacts on overall lupine biomass. There was a highly significant 5.5-fold increase in lupine biomass in rodent-free plots



**Fig. 6** (a) Number and (b) above-ground biomass of adult lupines (mean + 1 SEM) in control and rodent exclusion plots.

**Table 1** MANOVA testing the effects of rodent exclusion on abundance and biomass of adult lupines in plots. Wilks' lambda = 0.48,  $F_{2,9} = 4.9$ ,  $P = 0.036$ 

	d.f.	Mean squares	<i>F</i>	<i>P</i>
Lupine abundance	1	52.08	5.6	0.039
Error	10	9.2		
Biomass	1	18305900	8.4	0.016
Error	10	2173015		

**Table 2** Numbers of animals trapped during each trapping session. *Peromyscus maniculatus*, deer mice, and *Reithrodontomys megalotis*, harvest mice, were not distinguished during the first two sessions. For those sessions, we report the summed numbers and our best estimate of numbers by species (in parentheses) as deduced from body masses

Date	Both species	<i>P. maniculatus</i>	<i>R. megalotis</i>
<i>(a) Northern grid</i>			
August 1998	19	(7)	(12)
November 1998	46	(28)	(18)
February 1999	11	10	1
May 1999	5	3	2
August 1999	9	9	0
<i>(b) Southern grid</i>			
August 1998	8	(6)	(2)
November 1998	41	(21)	(20)
February 1999	14	5	9
May 1999	3	3	0
August 1999	8	8	0

compared to control plots (Table 1; 3012 g dry wt. vs. 432 g dry wt.).

#### DENSITIES OF GRANIVOROUS RODENTS

Mark-recapture estimates of the 1996 mouse population within the 0.12 ha trapping grid varied from  $12 \pm 1.1$  SE (CAPTURE estimate) to 17.7 (Schnabel estimate; no standard error available) individuals.

**Table 3** Population estimates from each trapping session. Because the two species were not distinguished during the first two sessions, we first analysed the summed data across all five sessions. We then analysed the data from each species for those sessions in which they were distinguished

Date	Both species	<i>P. maniculatus</i>	<i>R. megalotis</i>
<i>(a) Northern grid</i>			
August 1998	$22.0 \pm 1.7 \times 10^{-5}$	—	—
November 1998	$45.0 \pm 0$	—	—
February 1999	$11.0 \pm 7.4 \times 10^{-15}$	$10.0 \pm 5.7 \times 10^{-17}$	$1.0 \pm 3.2 \times 10^{-24}$
May 1999	$5.0 \pm 1.6 \times 10^{-5}$	$3.0 \pm 0$	$2.0 \pm 0$
August 1999	$9.0 \pm 2.0 \times 10^{-17}$	$9.0 \pm 0.002$	$0.0 \pm 0$
<i>(b) Southern grid</i>			
August 1998	$9.4 \pm 2.2$	—	—
November 1998	$49.4 \pm 4.2$	—	—
February 1999	$17.0 \pm 2.2$	$5 \pm 1.4 \times 10^{-4}$	$9 \pm 2.3 \times 10^{-4}$
May 1999	$3.2 \pm 1.0$	$3 \pm 1.6 \times 10^{-5}$	$2480 \pm 1128737^*$
August 1999	$9.5 \pm 1.7$	$8 \pm 1.7 \times 10^{-6}$	$318 \pm 0^*$

\*Unreliable estimates, which probably result from too few captures.

The numbers of granivorous rodents trapped during 1998–1999 are presented in Table 2. Table 3 presents model estimates of numbers. Estimates with particularly small standard errors arise from too few captures and are probably suspect. With the exception of *R. megalotis*, which was not trapped in the southern grid during the last two trapping sessions, model estimates agreed well with actual numbers of animals trapped. Because of the distance between traps in the grids, all values may underestimate actual densities.

Although our trapping methods preclude estimating absolute density, they do provide relative comparisons across time of granivorous rodent numbers near our exclosures. It is clear that these values fluctuate through time. In the grids trapped during 1998 and 1999, both species peaked in number in November 1998 and subsequently declined. The number estimated in 1996, obtained from a slightly different trapping protocol, was near the high end of the later range.

## Discussion

### EFFECTS OF GRANIVORY ON SEEDLING RECRUITMENT

Intense granivory on an experimentally sowed cohort of lupine seeds substantially reduced lupine seedling recruitment. Cumulatively over 3 years, an average of 109 seedlings emerged (from an initial pool of 476 seeds) in rodent exclusion plots whereas only an average of 26 seedlings emerged in control plots. Thus, mice severely limit lupine recruitment within coastal dunes at our site. While the overall cumulative impact of granivory was large, separate cohorts of seeds sown in tubes showed sizeable interannual differences in granivore impacts on plant recruitment. Although year-to-year variation in the magnitude of seed predation is common, such variation is not often explicitly linked to annual variability in plant recruitment (Louda 1989) as can be seen here. Heavy predation of seeds in the first year of the experiment



resulted in fewer seedlings emerging in control vs. rodent-free plots. This treatment effect disappeared in year two but reappeared in year three.

The relative densities of granivorous rodent populations at our sites do fluctuate through time but with no data from 1997 we cannot determine whether the differences in seed predation between 1996 and 1997 were due to changes in rodent density. Deer mice are omnivorous and other factors, such as changes in alternate food sources, could have driven the observed changes in seed predation.

#### EFFECTS OF SEEDLING SURVIVAL ON PATTERNS OF ESTABLISHMENT

A key question in studies such as ours is how consumer-driven reductions in plant recruitment translate to overall adult plant abundance. That is, do seed consumers that substantially reduce seedling abundance actually affect overall adult plant abundance? Quantifying this link is a key, but often overlooked, step in establishing the overall impact of seed consumers on plant population abundance. A variety of compensatory processes, such as density-dependent seedling survival, can potentially greatly reduce the magnitude of the population impact of seed consumers.

We found that high winter mortality of seedlings in all plots effectively shrank the difference in emergence between treatments, so that by mid-summer there were only modest differences in seedling density between rodent-free and control plots (Fig. 3). Seedlings were widely spaced throughout plots and did not compete for light, and mortality was greatest during the wet winter months of February–March (Fig. 3), when competition for water is implausible. Mortality was not therefore due to interactions between densely growing seedlings but to insect herbivory by cutworm larvae (family Noctuidae). Excavated dead lupine seedlings exhibited telltale signs of feeding by cutworms and we frequently found cutworm larvae feeding directly below the soil surface on seedling roots. Moreover, in separate experiments in which we applied a below-ground insecticide, there was significantly higher seedling survival in insecticide-treated vs. control plots (Maron *et al.*, unpublished data). Interestingly, herbivory by another root feeder, the ghost moth (*Hepialus californicus*), kills lupine seedlings in grasslands (Strong *et al.* 1999; Maron *et al.*, unpublished data). Seedling density did not affect mortality but if below-ground herbivory is density-dependent these herbivores could have compensatory impacts on lupine populations. Insect herbivores and rodent granivores may have interesting additive or even interactive effects on lupine establishment (Maron & Simms 1997; Maron 1998).

#### SEED DORMANCY

By the third year of the experiment, the number of seedlings that emerged in rodent-free plots was much

reduced (approximately half) compared with seedling emergence in years one and two (Fig. 2), probably due to a greatly reduced pool of dormant seeds. Few buried seeds (4%) survived for 3 years or remained in tubes at the end of the experiment (1.6%). Thus, the majority of seeds in the cohort we originally sowed into plots probably either germinated but failed to emerge or rotted.

#### EFFECTS OF GRANIVORY ON ADULT PLANT ABUNDANCE

Despite the compensatory effects of seedling mortality, heavy granivory had the cumulative effect of lowering the number of adult lupines that established in exclosed plots. Thus, mouse predation on seeds reduced both seedling regeneration and, within a relatively short time interval, adult bush lupine abundance. Protecting seeds from rodents for only 2 years resulted in a large increase in the number of adult shrubs that established by the end of the third year. Over longer time spans, we predict that protection from rodents may have an even greater impact on lupine abundance, although ultimately other density-dependent processes should set some upper limit to lupine density.

Granivores can play a keystone role in systems if their impacts on population, community or ecosystem processes are disproportionate to their biomass. Granivores at our site play such a role because their feeding activities limit the establishment of one of the few large woody shrubs that grow in coastal dunes, and thus influence its structure and function. White-crowned sparrows (*Zonotrychia leucophrys*) and song sparrows (*Melospiza melodia*) use these bushes for nesting, and *Peromyscus maniculatus* often builds nests around the base of bushes (Maron & Simms, personal observation). Functionally the plants fix a tremendous amount of nitrogen (Gadgil 1971; Palaniappan *et al.* 1979; Baker *et al.* 1986; Bentley & Johnson 1991, 1994); from N-rich leaf litter alone a large lupine growing in grasslands can conservatively add 18 g N to soil each year (Maron & Jefferies, unpublished data). Assuming similar N addition rates in dunes, rodent exclusion, at a minimum, may increase N inputs by 5.4 g N/m<sup>2</sup> year<sup>-1</sup>.

Seed predation, whether at the pre- or post-dispersal stage, is a common feature of most communities. Despite this fact, our understanding of how ubiquitous seed consumers influence the fundamental structure of plant communities and the dynamics of particular plant populations is still in its infancy. In systems such as ours, where seed-limited recruitment is probably the norm, heavy predation on seeds can greatly alter the dynamics of even a transient seed bank, and over time serve as a major source of mortality to a structurally and functionally important nitrogen fixing plant. As plant-consumer studies begin to examine the seed to seedling transition in more detail, we may gain an increased appreciation for the fundamental role consumers play in altering vegetation abundance, and even long-term dynamics, in complex ecosystems.

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