

## Fire and dynamics of granivory on a California grassland forb

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**Abstract.** This study examines the effects of burning and granivory on the reproductive success of the rare plant *Amsinckia grandiflora* (Boraginaceae). Fire is often used in California grasslands as a means of exotic species control, but the indirect effects these controls have on the reproductive ecology of native plants are rarely assessed. The interaction of fire with granivory of *A. grandiflora* seeds was examined in California grasslands over five years (1998–2002). In 1998 and 1999, both burned and unburned plots had bird-exclusion (netted) and no-exclusion (open) treatments. Predation rates were high (51–99%) and final predation rates did not differ among treatments. In 2000, granivory rates in the unburned, open plots were lower than in previous years (14%), and rodent trapping yielded only a single animal. Low granivory rates were observed in 2001 for unburned, open plots (47%). In 2001, burned/open plots experienced significantly more granivory (87%) than either burned/netted plots (37%) or unburned/open plots (47%). In 2002, every seed was taken from burned, open plots. Granivory was highly variable, ranging from 4 to 100% per plot over a 3-week period. Nearly all plots were discovered (>10% predation) by granivores in all trials in all years. When data from all treatments were combined, significant differences in granivory rates occurred among years, indicating stronger inter-year effects than within-year effects due to burning or bird exclusion. Fire affects granivory when overall predation rates are low, but when predation levels are high (as they were in 1998 and 1999), fire may not affect granivory occurring within the same year. Models extending seed survivorship through the dry summer indicate that most seeds are eaten, even when granivory rates are low.

### Introduction

California native forbs are often sensitive to light availability, responding negatively to competition for light, particularly in the germination and early growth stages. There is evidence that competition by invasive exotic annual grasses reduces fecundity in *Amsinckia grandiflora* (Gray) Kleeb. ex Greene, a federally-listed endangered borage native to California grasslands (Carlsen et al. 2000). This reduction in fecundity has been found in other native species, both annual and perennial (Guerrant 1992; Gordon and Rice 1993; Pavlik et al. 1993). In California, fire has been used to control exotic annual grasses and remove thatch to stimulate native forb populations and to also re-establish native perennial bunch grasses (George et al. 1992; Menke 1992; Meyer and Schiffman 1999). While fire is a management tool to control invasive species in California, exotic annual grass

presence has also been associated with an increased frequency and intensity of wildfires in California (Brooks 1999). While fire may have a beneficial impact on California native forbs by reducing competition from exotic grasses, fire may also have other impacts on the life cycle of rare native plants. In this study, we begin to examine the effect of fire on granivory of *A. grandiflora* seeds.

Granivory has been shown to have an effect on species abundance in California grasslands (Batzli and Pitelka 1970; Bouchert and Jain 1978). The relatively large *A. grandiflora* seeds, or nutlets (approximately 4 mg) should be attractive to granivores (Hoffmann et al. 1995). Granivorous mammals such as deer mice (*Peromyscus maniculatus*), Heermann's kangaroo rats (*Dipodomys heermanni*) and valley pocket-gophers (*Thomomys bottae*) have been trapped at the experimental location. In addition, seed-eating birds such as savannah sparrows (*Passerculus sandwichensis*) and towhees (*Pipilo* sp.) have been observed foraging at the site (T. Carlsen, unpublished data). Other studies have shown that birds and rodents have distinct foraging strategies, with separate prey preferences, temporal dynamics, and feeding intensities (Pulliam and Brand 1975; Inouye et al. 1980; Howe and Brown 1999). *A. grandiflora* does not maintain a large seed bank (Pavlik 1995) and so is highly dependent on between-year seed survival for population sustainability.

We hypothesized that burned areas would suffer more granivory than unburned areas, because of greater visibility of the nutlets and fewer ambient seeds competing for granivore attention (Hassan and West 1986). We expected that rodents would be risk-averse and less likely to forage in open areas created by burning and that birds would be the dominant granivore of *A. grandiflora* nutlets in the burned plots.

## Methods

### *Experiment area*

Tests were performed within a reintroduced population of *A. grandiflora*. This population occurs less than 500 m from a native population. The reintroduced and native populations have similar slope, aspect, and community characteristics and occur at Site 300 in the Corral Hollow area of the Altamont Hills in California, USA (Figure 1). Site 300 is a Lawrence Livermore National Laboratory high-explosives facility operated by the University of California for the U.S. Department of Energy. Censuses of flowering plants over the years have shown similar interyear dynamics in demography at these neighboring populations (Carlsen et al. 2001).

Two areas within the reintroduced population were chosen for study. Area 1 was the 25 × 30 m portion of the population that had been sown in 1993 (Carlsen et al. 2002). This area had a 0.8 m tall metal flashing installed in 1993 to a depth of 0.4 m as part of a rodent prevention strategy employed in 1993–1994 (Figure 2). Although the flashing was still in place, there was considerable evidence (observations of

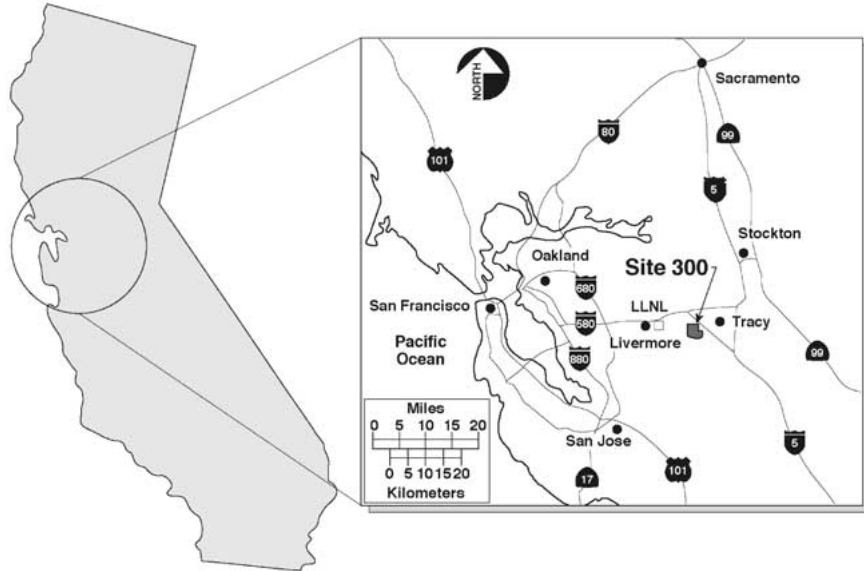


Figure 1. Location of Site 300 in California.

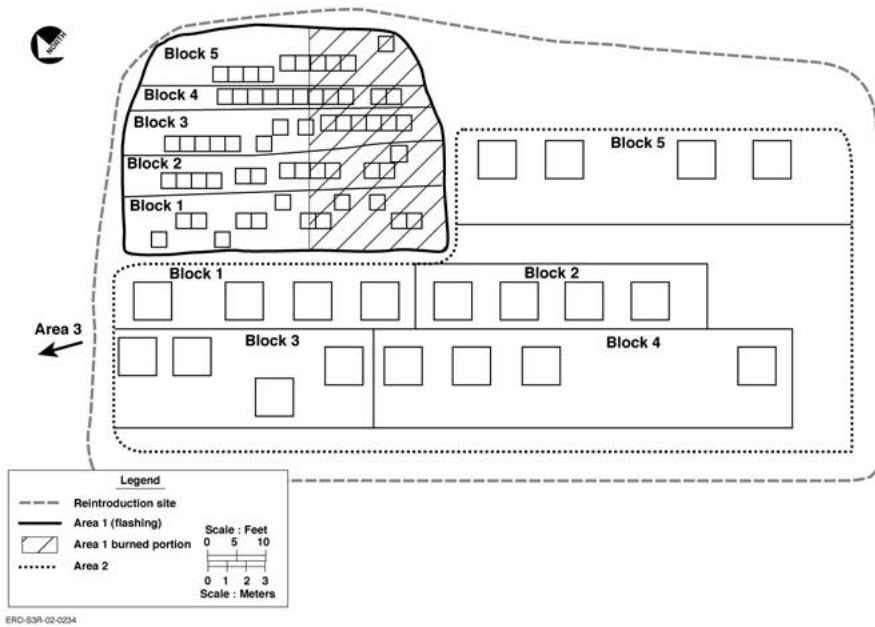


Figure 2. Layout of experiment, showing area burned within Area 1 and the block design of Area 2.

snakes and freshly dug burrows in the plots) that it was no longer effective. Area 1 consisted of five blocks of 10–14 plots measuring 80 cm × 80 cm. Area 2 was an area directly adjacent to the flashing to the west and north within the population reintroduction area. Area 2 consisted of five blocks composed of four plots, each measuring 2 m × 2 m.

### *Plot design*

Twenty-five 9 cm long galvanized nails were pressed into the soil surface in a 5 × 5 grid. Nail heads were flush with the surrounding soil and spaced 5 cm apart over a 0.04 m<sup>2</sup> area. A single nutlet was affixed to each nail head with double-stick tape. The nutlet/nail grid was placed in the center of each plot. *Amsinckia grandiflora* plants can be highly variable in size: a single reproductive plant can be 20–150 cm in height and have 1–30 branches (Carlsen et al. 2001). A plant can produce a few to thousands of nutlets. In most years, plants occur at medium to low densities and produce fewer than 25 nutlets per plant (Carlsen et al. 2001). Thus, the density of seeds used in this experiment was not an unreasonable proxy for actual seed densities that may occur naturally due to reproduction and dispersal.

Plots were not used more than once in the same year. Nails and nutlets were removed at the end of each trial. Bird-exclusion plots were netted with 2 cm mesh polypropylene net fixed to the ground along each plot edge and supported 30–100 cm above the plot.

### *Manipulations*

On 11 June 1998, half of Area 1 was burned (Figure 2). On 15 July, five replicate nutlet/nail grids (one in each block) were set out for each treatment combination: netted/burned, netted/unburned, open/burned, open/unburned. Plots were observed at weeks 1, 2 and 4.

Two rounds of experiments were conducted in 1999, 2000, and 2001. Round 1 of 1999 was set out on 26 April at the time of natural *A. grandiflora* senescence. Five replicates in Area 1 (one in each block) were placed in each treatment/cover type: netted/disturbed (burned previous year), netted/unburned, open/disturbed (burned previous year), open/unburned. Observations were made weekly for 5 weeks. Burns were conducted on 28 June and another trial was set out that day. Two observations were made in the first week and then once per week in the second and third weeks.

The goal of the 2000 trials was to determine the effect of rodent trapping within the *A. grandiflora* population. Five replicate plots were established in open/unburned locations in each of three areas, Area 1 and 2 (with one replicate per block), which were to be trapped, and a control area (Area 3) outside the population and 10 m east of the flashing. Round 1 of 2000 was installed on 1 May 2000. No burns took place in 2000 and no netting was installed. Two observations were made

per week for a 3-week period. At the end of round 1, lethal snap traps were installed in Areas 1 and 2. The traps were installed in a grid where traps were spaced 5 m apart. Traps were baited each morning (Monday through Thursday) and checked the following morning. On 5 June 2000, the traps were removed and round 2 of the experiment was installed in different plots in the same treatment areas. Observations were made twice per week for 3 weeks.

In 2001, 10 plots were established in open/unburned locations: five in Area 1 and five in Area 2 (one in each block) for round 1. Round 1 was begun on 27 April 2001 and plots were checked twice in the first week and then weekly for a total of 3 weeks. For round 2, after a selective burn of three of the four plots in each block in Area 2, 10 plots were established on 20 July 2001 in Area 2 only. Five plots were located in unburned plots, and five plots were located in burned plots. Plots were checked twice weekly for a total of 3 weeks. On 3 August, all burned plots were restocked with nutlets, an additional plot was added, and three out of the six burned plots were netted. Unburned plots had not experienced much granivory over the 2 weeks and were allowed to remain. Plots were checked twice per week for 2 weeks.

In 2002, round 1 pre-burn plots were set out on 8 May consisting of five plots in Area 1 and 10 plots in Area 2 (five disturbed and five unburned). Plots were checked twice in the first week and then weekly for a total of 3 weeks. One plot per block was burned in Area 2 on 20 June. Round 2 post-burn plots were set out on 1 July, consisting of five open/unburned plots in each of Areas 1 and 2 and five open/burned plots in Area 2. Plots were checked twice in the first week and then weekly for a total of 3 weeks.

#### *Data analysis*

Final predation percentages were not normally distributed and were compared among treatments using Kruskal–Wallis, a nonparametric ANOVA, in the NPAR1WAY procedure in SAS (SAS 1990). We used  $\alpha = 0.05$  for within-year, among-treatment tests of difference. Areas 1 and 2 were kept separate in the analysis because of the possibility that the flashing still limited rodent granivore density and movement. Unplanned pairwise comparisons among years were performed using the Mann–Whitney U test. Since rounds of the experiment were of variable length, data were truncated at the 3-week mark, and the cumulative predation percentage at that point was used as the final predation amount. Because data were only collected at weeks 2 and 4 in 1998, an average of these two percentages was used to estimate predation at the end of week 3. The final predation percentage in the burned plots of 2001 was used, even though that trial lasted only 2 weeks. Alpha for interyear comparisons was adjusted for multiple comparisons by the Bonferroni correction, resulting in an overall  $\alpha$  of 0.005. For each trial, power analysis (Pearson and Hartley 1953) was conducted to calculate  $\beta$ , the probability of detecting a nonzero treatment effect, when  $\alpha$  was held at 0.05.

## Results

### *Effects of cover and treatment on granivory*

No differences were found among treatments within the trials of 1998 and 1999. Burning and excluding birds had no effect on seed predation in these 2 years. Table 1 shows the final predation percentage for each treatment. In 1998, mean granivory ranged from 51 to 75%. In 1999, seed predators were more effective at exploiting the plots, resulting in predation between 77 and 99%. In round 2 nearly all the nutlets were eaten. The post burn trial of 1998 had the highest power of all trials, with a  $\beta$  equal to 0.82. Differences among treatments would probably have been detected if they were present in this round.

Granivory in 2000 was low compared to 1998 and 1999. In 2000, the flashed area (Area 1) experienced less predation in round 1 ( $p = 0.014$ ), but did not differ from the other two areas in round 2, after the trapping was performed ( $p > 0.1$ ). Granivory ranged from 14 to 68% in 2000. In round 2, the trapped and untrapped treatments were not different from each other ( $p > 0.1$ ). Only a single rodent was caught in Area 2 during the 2-week trapping period of 2000. This is in contrast with trapping results in 1993 and 1994 when dozens of rodents had been trapped over a smaller area of that hillside using the same methods (J. Woollett, personal communication). The difference among areas pre-trapping could have been due to the single rodent found, and the fact that few rodents were caught may indicate a low-density year for rodents on that hillside. Experimental power in 2000 was somewhat low, with the probability of detecting a nonzero treatment effect equal to 0.7 in the pre-burn trial and 0.65 in the post-burn trial (Table 1).

In 2001, granivory rates were low in unburned areas but higher in burned areas. Burned, bird excluded plots had less granivory than open burned plots. Before the burn in 2001, the flashed area (Area 1) did not experience significantly different granivory from that in the unflashed area (Area 2,  $p > 0.6$ ). Predation was very low at 11% (Table 1). After the burn in Area 2, high predation levels returned, with 87% seed loss in the burned area within the first 2 weeks. The restocked plots did not experience statistically different ( $p > 0.2$ ) granivory to the original ones, so the two 2-week periods were combined. Burned areas that had been netted experienced granivory (37%) similar to that of open, unburned areas (47%,  $p > 0.2$ ). Burned, open areas had 87% granivory in 2001, which was significantly greater than the other two treatment/covers ( $p = 0.0016$ ). Our probability of detecting treatment differences in this round was very low ( $\beta = 0.38$ ) in this trial.

Patterns of predation in 2002 were similar to those in 2001, with low predation rates in the preburn round (21–45%). Granivory rates in Areas 1 and 2 were not significantly different. Predation in open, unburned areas remained low after the burn, but every single seed in open, burned plots was eaten (Table 1). After the burn, granivory rates between the open, unburned plots Areas 1 and 2 were significantly different ( $p = 0.04$ ). Granivory was greater in Area 2, which was more similar to the burned areas. Again, the power in 2002 was somewhat low, with only a 50% chance of detecting treatment differences (Table 1).

Table 1. Final predation percentages by treatment: 1998–2002. Italics indicate significant difference ( $p < 0.05$ ) between areas for open, unburned plots. Calculated  $\beta$  (power within round to detect nonzero treatment effect,  $\alpha = 0.05$ ) is shown.

Year, round, and treatment	Median (%)	Mean (%)	Variance (%)	Evenness (%)	Localization (%)	<i>n</i>
1998, post-burn ( $\beta = 0.82$ )						
Net, burned	48	51	3.2	100	20	5
Net, unburned	74	63	4.8	100	40	5
Open, burned	60	59	4.0	100	20	5
Open, unburned	79	75	0.6	100	60	5
1999, pre-burn* ( $\beta = 0.76$ )						
Net, disturbed	96	96	0.1	100	100	5
Net, unburned	96	91	1.2	100	80	5
Open, disturbed	96	91	1.2	100	100	5
Open, unburned	84	77	2.1	100	60	5
1999, post-burn <sup>+</sup> ( $\beta = 0.65$ )						
Net, burned	100	97	0.1	100	100	5
Net, unburned	100	99	0.0	100	100	5
Open, burned	100	99	0.0	100	100	5
Open, unburned	96	96	0.2	100	100	5
2000, pre-trapping ( $\beta = 0.70$ )						
Area 1	14	14	0.5	80	0	5
Area 2	72	49	7.9	100	40	5
Area 3 (control)	44	68	4.3	100	20	5
2000, post-trapping ( $\beta = 0.65$ )						
Area 1 (no rodents caught)	33	30	0.7	100	0	5
Area 2 (single rodent caught)	48	24	2.9	100	20	5
Area 3 (control)	25	47	10.6	80	0	5
2001, pre-burn ( $\beta = 0.70$ )						
Open, unburned (Area 1)	8	11	0.6	40	0	5
Open, unburned (Area 2)	8	11	1.2	40	0	5
2001, post-burn Area 2 only ( $\beta = 0.38$ )						
Net, burned	50	37	10.3	67	0	3
<b>Open, burned**</b>	<b>84</b>	<b>87</b>	<b>1.2</b>	<b>100</b>	<b>75</b>	<b>8</b>
Open, unburned	61	47	7.6	100	0	5
2002 pre-burn ( $\beta = 0.50$ )						
Open, unburned (Area 1)	20	21	0.02	80	0	5
Open, unburned (Area 2)	29	45	0.20	80	30	10
2002 post-burn ( $\beta = 0.50$ )						
Open, unburned (Area 1)	20	21	0.01	100	0	5
Open, unburned (Area 2)	56	58	0.09	100	60	10
<b>Open, burned (Area 2)**</b>	<b>100</b>	<b>100</b>	<b>0</b>	<b>100</b>	<b>100</b>	<b>5</b>

<sup>+</sup>\*Different symbols indicate rounds significantly different within year,  $p < 0.01$ .

\*\*Treatment significantly different ( $p < 0.05$ ) from other treatments within trial.

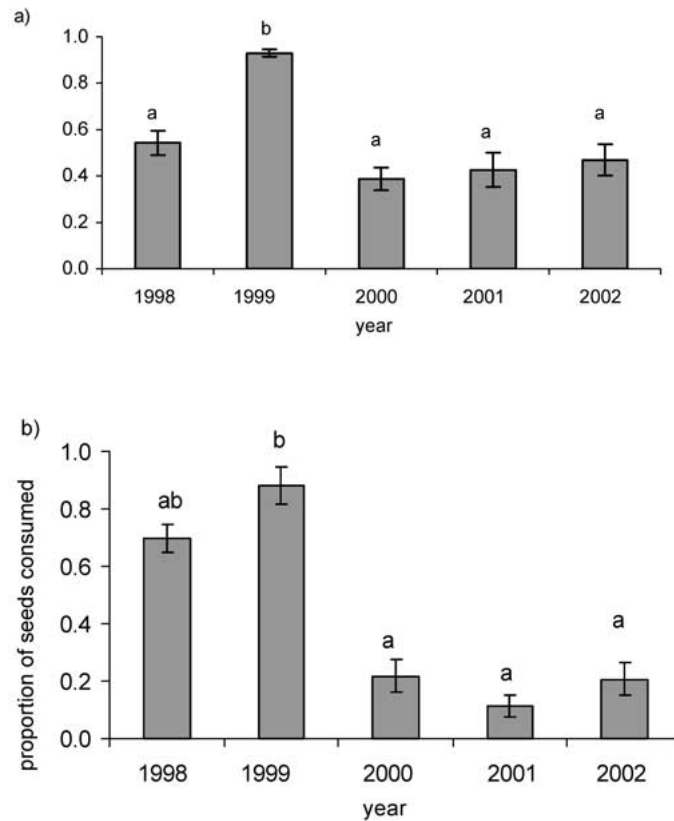


Figure 3. Mean granivory rates by year. (a) All treatments and areas combined, (b) open, unburned plots in Area 1 only. Bars represent one standard deviation. Different letters indicate significant differences (Bonferroni correction),  $p < 0.005$ .

One would expect the largest burn areas to have the greatest influence on rodent activity and smallest burn areas to have smallest influence on rodent activity. However, in 2001 when the largest area was burned (all of Area 2 except the control plots), the reduction in rodent granivory in the burned areas was small and not significant. The variation in burn areas in this experiment (five  $4 \text{ m}^2$  plots in 2002,  $94 \text{ m}^2$  in 2001, and  $17 \text{ m}^2$  in 1998–1999) was not large enough to demonstrate this effect and hence is unlikely to have confounded our experiment.

Table 1 also shows evenness, or the percent of replicates with at least three nutlets missing by the end of the trial, and localization, which is the percent of replicates with at least 75% of the nutlets missing by the end of the trial. Evenness represents the percentage of plots that were found by seed predators, while localization reflects the percentage of plots that were heavily predated. In all years evenness was fairly high, which indicated that each year seed predators were effective at locating the plots. Localization was more variable; the degree to



which granivores were able to fully exploit the plots changed among years and treatments.

Seed predation changed more due to interannual variation than due to treatments. When all treatments were combined, predation percentages in the 5 years were significantly different from each other (Figure 3a,  $p < 0.005$ ). High levels of granivory in 1999 were significantly different from the lower levels of granivory experienced in all other years. The lowest granivory level in 2000 was not significantly different from the next highest granivory level in 1998 ( $p = 0.04$ ). All other comparisons among years were not significant, with  $p$ -values well above 0.1.

When only the open, unburned plots in Area 1 are compared, the differences among the means appear to be more marked (Figure 3b).

## Discussion

We suspected that burned areas would suffer more granivory than unburned areas, because of greater visibility of the nutlets and fewer ambient seeds competing for granivore attention (Hassan and West 1986). We also hypothesized that rodents would be less likely to forage in open areas created by burning, although some rodent species are more likely to forage in open areas than other species (Reichman 1981; Price 1983; Lidicker 1989; Kollmann and Schill 1996; Howe and Brown 1999), and rodent decisions to forage in open areas may be affected by other factors (Harris 1984; Parmenter et al. 1984; Stephens and Krebs 1986). We expected that birds would be the dominant granivore of *A. grandiflora* in the burned plots. Birds forage using visual cues (Parmenter et al. 1984) and may be more effective foragers in open areas.

These hypotheses were not supported in 1998–99: granivory was no higher in open, burned plots than in netted, burned plots, and granivory was no higher in open, burned plots than in open, unburned plots. The lack of difference between netted and open plots, both before and after the burn, indicated that birds were not the primary granivores of *A. grandiflora* nutlets. While ants certainly may be responsible for some granivory of *A. grandiflora* nutlets (indeed, ants were observed actively removing nutlets from nails) due to the spatial scale of the experiment it is unlikely that ants could be responsible for the majority of the granivory occurring across all plots. Lack of difference between unburned and burned plots indicate that lack of cover was neither a significant barrier to, nor did it enhance, granivory. If rodents are the primary granivore on *A. grandiflora*, high granivory rates in burned plots in 1998–99 could be explained by high population pressure, changing rodent behavior from risk-averse to risk-prone (Stephens and Krebs 1986). It is also possible that the rodent species composition cycled over the course of the experiment as different rodent species have different foraging responses to changes in plant cover (Price and Waser 1984). Another multiyear study of rodent granivory has shown significant interyear variation in spring and summer months (Kollmann et al. 1998).

Once we determined that rodents appeared to be the most important granivore of *A. grandiflora*, we attempted trapping to reduce the rodent population and thereby reduce granivory rates. The much lower granivory experienced in 2000 and the single rodent trapped that spring may indicate that the resident rodent populations peaked in 1999 and then crashed in 2000. Population cycling has been observed in rodents of the same species and genera as are found at our site (Garsd and Howard 1982; Sexton et al. 1982; Lidicker 1989; Drost and Fellers 1991; Kesner and Linzey 1997; Ernest et al. 2000). Granivory was below 50% in the second round of 2000, and there was no difference between trapped and untrapped areas. It is possible that in absence of rodents, birds were able to consume a small number of nutlets in the unburned areas. However, if that were the case, we would expect more granivory in the unburned, open plots than in the burned netted plots. While burned/netted plots in 2001 appeared to have less granivory than unburned/open plots, this difference was not significant. The later years of this study suffered from lack of power, with the probabilities of detecting treatment effects post-burn ranging from 38 to 50%. We speculate that a difference between burned/netted plots and burned/open plots may indicate that in burned areas, birds are able to capitalize on nutlets that rodents are unable to take; however, our evidence for this is not strong.

Between-year factors had the strongest influence on granivory rates. When inter-season and inter-treatment data were combined, significant differences among years still occurred. Lack of variability among habitats and within years has been found in other grassland granivory systems (Hulme 1994). Other studies have found that changes in the composition and amount of vegetation can have delayed effects of one or more years on rodent population dynamics (Price and Waser 1984; Peles and Barrett 1996; Ernest et al. 2000). The lack of difference in granivory between unburned and burned areas in 1998–99 indicates that disturbances such as fire may not be important in determining within-year granivory levels, at least when overall granivory rates are high. Our results indicate that fire and bird exclusion do not consistently affect granivory when seed predation pressure is high, but in low-pressure years burned areas experience significantly higher granivory. Excluding birds may reduce granivory in burned areas in years of this type.

*A. grandiflora* sets seed in April or early May and these seeds do not germinate until November or December. How much do treatment differences in a 3–5 week period near the beginning of the dry season result in differences in numbers of germinable seed in late autumn? To examine this, we used our repeated measurements over the course of the trials to fit two models to the data for 2001, where we saw differences between the treatments and still had nutlets remaining in each treatment at the end of the trial. The first model was an s-curve, which would reflect a low predation rate at the beginning of the season as nutlets were discovered, followed by a higher predation rate as plot exploitation occurred, leading to a lower predation rate as foraging in the denuded plot became less profitable (Figure 4, Krebs and Davies 1987; Price and Correll 2001). The other model was a linear regression, which would reflect a constant granivory rate over time (Figure 4, Price and Correll 2001). These models were then used to estimate the percentage of nutlets that would remain after 160 and 200 days. Model fits were good, with

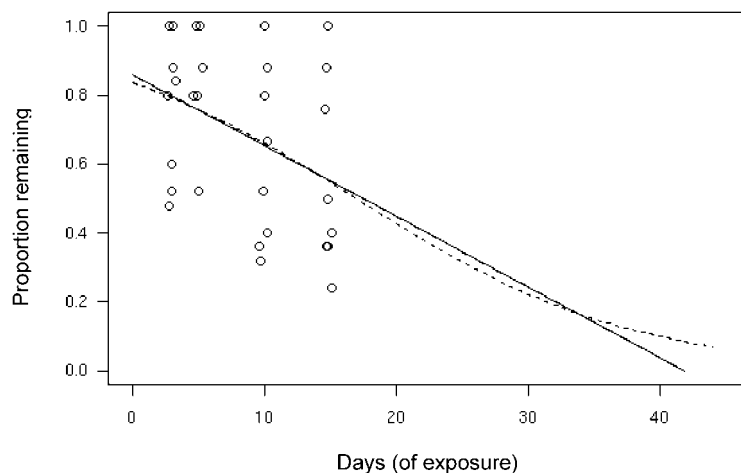


Figure 4. The s-curve (dashed line) and linear (solid line) models fit to data from unburned/open and burned/netted plots post-burn in 2001.

$R^2 = 0.44$  for the unburned and burned/netted plots combined and  $R^2 = 0.78$  for the burned/open plots. The linear model resulted in no nutlets remaining for either treatment after day 40. The s-curve model resulted in miniscule amounts of seed at the end of the dry season: burned open plots were predicted to have  $2.5 \times 10^{-8}\%$  seed left after 160 days and  $3.3 \times 10^{-10}\%$  nutlets left after 200 days. The burned/netted and unburned/open plots were predicted to have  $1.1 \times 10^{-6}\%$  nutlets left after 160 days and  $2.4 \times 10^{-8}\%$  nutlets left after 200 days. Models fit on a per plot basis to unburned, open plots post-burn in 2002 predicted seed percentages ranging from  $1.2 \times 10^{-3}\%$  to  $2.4 \times 10^{-14}\%$  ( $R^2$  for each  $> 0.9$ ) after 200 days. These plots experienced a relatively low 21–58% mean granivory over the 3-week monitoring period. In 1995 when the *A. grandiflora* population was large, we estimated a seed rain of over 95,000 nutlets (Carlsen et al. 2001). For a  $2.4 \times 10^{-8}\%$  survival to result in even two seeds, the seed rain would need to be nine times as great as it was in 1995. On the other hand, a  $1.2 \times 10^{-3}\%$  survival would have resulted in 114 seeds surviving. Clearly, *A. grandiflora* nutlets avoid granivory only rarely. If the s-curve model accurately portrays granivory occurring over the dry summer, seeds may only escape by being inaccessible. If all seed caches may be found (high evenness), it is the variance in the point at which a forager decides to leave a patch that produces the variability in seed survival. Decisions of when to stop foraging may be influenced by the profitability of a patch compared to its surrounding patches or by the foragers' population density and population-level foraging activity (Price and Correll 2001). It is entirely likely that in every year, most nutlets that can be found are eaten whether they are in burned areas or not. Other studies have also found a lack of predictability in safe-sites: no site is safe for seeds in all years and, in general, sites safe from seed predators are relatively rare (Whelan et al. 1991).

The dynamics of granivory observed in this study may not be applicable to more common California grassland forbs. *A. grandiflora* produces the only seed of its size during late spring within its grassland community. The community contains many other forbs (such as *Castilleja exserta*, *Collinsia heterophylla* and *Amsinckia tessellata*) which produce smaller seeds (up to 3 mg). Voles, in particular, appear to have a preference for forb seeds over grass seeds (Howe and Brown 1999). Not only do a variety of heteromyid rodent species prefer seeds that weigh about 5 mg (Price 1983), but large-seeded forbs in old fields benefit more from seed predator removal than smaller-seeded species (Reader 1993). By restoring a section of California grassland from exotic annual grass dominated to a more diverse array of forbs and perennial grasses as we did at the reintroduction site, we may have actually attracted granivores that prefer forb seeds. Likewise, if the native *A. grandiflora* population occurs in a site of forb diversity within an exotic grass-dominated landscape, this site may also attract granivores and sustain different granivore populations than surrounding areas.

Granivory in a single year has been shown to have a significant impact on plant species diversity and community structure (Hoffman et al. 1995; Howe and Brown 1999). Our study indicates that granivory within a grassland can vary considerably between years. Species that do not maintain large seed banks are especially vulnerable in peak granivory years, and the coincidence of poor seed production with high granivory in consecutive years could have far-reaching effects on plant, particularly rare-plant, population viability. Our results indicate that factors that vary among years, such as rodent population size, may be more important than factors that vary within years, including such drastic events as burns, in determining granivory levels.

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### References

- Batzli G.O. and Pitelka F.A. 1970. Influence of meadow mouse populations on California grassland. *Ecology* 51: 1027–1039.
- Bouchert M.I. and Jain S.K. 1978. The effect of rodent seed predation on four species of California annual grasses. *Oecologia* 57: 406–411.

- Brooks M.L. 1999. Alien annual grasses and fire in the Mojave desert. *Madroño* 46: 13–19.
- Carlsen T.M., Menke J.W. and Pavlik B.M. 2000. Reducing competitive suppression of a rare annual forb by restoring native California perennial grasslands. *Restoration Ecology* 8: 18–29.
- Carlsen T.M., Espeland E.K. and Smith A.H. 2001. Rare plant restoration and monitoring at Lawrence Livermore National Laboratory Site 300. Lawrence Livermore National Laboratory, Livermore, California. UCRL-AR-142408.
- Carlsen T.M., Espeland E.K. and Pavlik B.M. 2002. Reproductive ecology and the persistence of an endangered plant. *Biodiversity and Conservation* 11: 1247–1268.
- Drost C.A. and Fellers G.M. 1991. Density cycles in an island population of deer mice, *Peromyscus maniculatus*. *Oikos* 60: 351–364.
- Ernest S.K.M., Brown J.H. and Parmenter R.R. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* 88: 470–482.
- Garsd A. and Howard W.E. 1982. Microtine population fluctuations: an ecosystem approach based on time-series analysis. *Journal of Animal Ecology* 51: 225–234.
- George M.R., Brown J.R. and Clawson W.J. 1992. Application of nonequilibrium ecology to management of Mediterranean grasslands. *Journal of Range Management* 45: 436–440.
- Gordon D.R. and Rice K.J. 1993. Competitive effects of grassland annuals on soil water and blue oak (*Quercus douglasii*) seedlings. *Ecology* 74: 68–82.
- Guerrant E.O. 1992. Genetic and demographic considerations in the sampling and reintroduction of rare plants. In: Fiedler P.L. and Jain S.K. (eds) *Conservation Biology: The Theory and Practice of Nature Conservation, Preservation and Management*. Chapman & Hall, New York, pp. 321–344.
- Harris J.H. 1984. An experimental analysis of desert rodent foraging ecology. *Ecology* 65: 1579–1584.
- Hassan M.A. and West N.E. 1986. Dynamics of soil seed pools in burned and unburned sage brush semi-deserts. *Ecology* 67: 269–272.
- Hoffmann L.A., Redente E.F. and McEwen L.C. 1995. Effects of selective seed predation by rodents on shortgrass establishment. *Ecological Applications* 5: 200–208.
- Howe H.F. and Brown J.S. 1999. Effects of birds and rodents on synthetic tallgrass communities. *Ecology* 80: 1776–1781.
- Hulme P.E. 1994. Post-dispersal seed predation in grassland: its magnitude and sources of variation. *Journal of Ecology* 82: 645–652.
- Inouye R.S., Byers G.S. and Brown J.H. 1980. Effects of predation and competition on survivorship, fecundity and community structure of desert annuals. *Ecology* 61: 1344–1351.
- Kesner M.H. and Linzey A.V. 1997. Modeling population variation in *Peromyscus leucopus*: an exploratory analysis. *Journal of Mammalogy* 78: 643–654.
- Kollmann J. and Schill H.P. 1996. Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. *Vegetatio* 125: 193–205.
- Kollmann J., Coomes D.A. and White S.M. 1998. Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. *Functional Ecology* 12: 683–690.
- Krebs J.R. and Davies N.B. 1987. *An Introduction to Behavioural Ecology*. 2nd edn. Blackwell Scientific Publications, Oxford, UK.
- Lidicker W.Z. 1989. Impacts of non-domesticated vertebrates on California grasslands. In: Huenneke L.F. and Mooney H. (eds) *Grassland Structure and Function: California Annual Grassland*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 135–150.
- Menke J. 1992. Grazing and fire management for native perennial grass restoration in California grassland. *Fremontia* 20: 22–25.
- Meyer M.D. and Schiffman P.M. 1999. Fire season and mulch reduction in a California grassland: a comparison of restoration strategies. *Madroño* 46: 25–37.
- Parmenter R.J., MacMahon J.A. and Vander Wall S.B. 1984. The measurement of granivory by desert rodents, birds and ants: a comparison of an energetics approach and a seed-dish technique. *Journal of Arid Environments* 7: 75–92.

- Pavlik B.M. 1995. And the beat goes on: populations of *Amsinckia grandiflora* under different management regimes. Prepared for the Endangered Plant Program, California Department of Fish and Game, Sacramento, California.
- Pavlik B.M., Nickrent D.L. and Howald A.M. 1993. The recovery of an endangered plant. I. Creating a new population of *Amsinckia grandiflora*. *Conservation Biology* 7: 510–526.
- Pearson E.S. and Hartley H.O. 1953. Charts of the power function for analysis of variance tests, derived from the non-central *F*-distribution. *Biometrika* 38: 112–130.
- Pevelan J.D. and Barrett G.W. 1996. Effects of vegetative cover on the population dynamics of meadow voles. *Journal of Mammalogy* 77: 857–869.
- Price M.V. 1983. Laboratory studies of seed size and seed species selection by heteromyid rodents. *Oecologia* 60: 259–263.
- Price M.V. and Correll R.A. 2001. Depletion of seed patches by Merriam's kangaroo rats: are GUD assumptions met? *Ecology Letters* 4: 334–343.
- Price M.V. and Waser N.M. 1984. On the relative abundance of species: postfire changes in a coastal sage scrub rodent community. *Ecology* 65: 1161–1169.
- Pulliam H.R. and Brand M.R. 1975. The production and utilization of seeds in plains grassland of southeastern Arizona. *Ecology* 56: 1158–1166.
- Reader R.J. 1993. Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology* 81: 169–175.
- Reichman O.J. 1981. Factors influencing foraging in desert rodents. In: Kamil A.C. and Sargent T.D. (eds) *Foraging Behavior*. Garland STPM, New York, pp. 195–213.
- SAS 1990. SAS/STAT<sup>®</sup> User's Guide, Version 6. 4th edn. Vol. 2. SAS Institute Inc., Cary, North Carolina, pp. 891–996.
- Sexton O.J., Douglass J.F., Bloye R.R. and Pesce A. 1982. Thirteen-fold change in population size of *Peromyscus leucopus*. *Canadian Journal of Zoology* 60: 2224–2225.
- Stephens D.W. and Krebs J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Whelan C.J., Willson M.F., Tuma C.A. and Souza-Pinto I. 1991. Spatial and temporal patterns of postdispersal seed predation. *Canadian Journal of Botany* 69: 428–436.