

# Seed predation has the potential to drive a rare plant to extinction

Helen M. Kurkjian<sup>1\*</sup>, Sydney K. Carothers<sup>2</sup> and Erik S. Jules<sup>2</sup>

<sup>1</sup>Department of Integrative Biology, University of California, 1005 Valley Life Sciences Bldg #3140, Berkeley, CA 94720, USA; and <sup>2</sup>Department of Biological Sciences, Humboldt State University, Arcata, CA 95521, USA

## Summary

1. Pre-dispersal seed predation is sometimes considered unlikely to dramatically affect plant population growth because plants are generally expected to produce more seeds than there are safe sites for germination. *Lupinus constancei* is a rare herb of limited distribution, with fewer than 400 reproductive individuals restricted to a single square kilometre of north-western California, USA. In addition to the vulnerability resulting from its extremely small population size, *L. constancei* faces heavy seed predation by small mammals.

2. As a stop-gap measure to prevent population decline, managers began covering a large number of the reproductive plants with herbivory exclosures in 2003, but the population-level effects of seed predation and the effectiveness of this caging treatment were unknown. We used 10 years of demographic data to compare the population dynamics of plants inside herbivory exclosures with those sustaining ambient rodent seed predation.

3. We found that the stochastic population growth rate would be robust without seed predation ( $\lambda_s = 1.17$ ), but without continued human intervention (i.e. use of exclosures), the current rate of predation would result in a decline towards extinction ( $\lambda_s = 0.92$ ).

4. After our study concluded, high mortality due to two extreme winter droughts followed by a wildland fire reduced the number of reproductive plants to  $\sim 103$ , making extinction of *L. constancei* more likely.

5. *Synthesis and applications.* The prevalence of consumer-driven population decline is largely unknown, but this study demonstrates that pre-dispersal seed predation by rodents can have powerful population-level effects, and represents one set of conditions under which consumer pressure has the potential to drive plant extinction. However, with continued management to limit the effects of seed predation in the short-term and investigation into the ultimate drivers of this high seed predation rate in the long term, the Lassics lupine population could be restored to a robust rate of growth.

**Key-words:** granivory, herbivory, legume, *Lupinus constancei*, matrix model, population viability analysis, rodent, seed predation, small mammal

## Introduction

While the effects of herbivory on individual plant survivorship, growth and fecundity have been well studied in many taxa (Belsky 1986; Mutikainen & Delph 1996), how those fitness effects translate into altered population growth is not as well understood. Plant life history, herbivore feeding guild and surrounding habitat type are all believed to mediate the strength of these population-level effects (Crawley 1989; Silvertown *et al.* 1993; Maron & Kauffman 2006). However, the prevalence of conditions

that might cause plant population growth to be limited by the activity of primary consumers rather than resource availability is largely unknown (Maron & Crone 2006).

Seed predation is a class of herbivory sometimes considered unlikely to dramatically affect plant population growth, because plants are generally expected to produce more seeds than there are safe sites for germination (Crawley 1989). But while this supposition has been supported in some systems, a review by Maron & Crone (2006) found that seed predation affects population growth as often as damage to other plant parts. The same review also contradicted the widely-held assumption that herbivory by mammals has more important

\*Correspondence author. E-mail: helen.kurkjian@berkeley.edu

population-level effects than that by insects, finding no consistent pattern between the groups.

There is scant evidence that pre-dispersal mammalian seed predation has population-level effects unique amongst those of other types of herbivory, but this may be due to the infrequency with which it is observed. Because seed predation is most commonly caused by insects (Kolb, Ehrlén & Eriksson 2007), and mammalian seed predation most commonly occurs post-dispersal (Maron & Crone 2006; Maron & Kauffman 2006; Bricker & Maron 2012), this lack of evidence may indicate that such an interaction is uncommon rather than unimportant. Indeed, Dangremond, Pardini & Knight (2010) found strong population-level effects of pre-dispersal mammalian seed predation, although they were not extreme enough to cause population decline. Given the wide range in strength of population-level effects of other types of herbivory across plant species (Maron & Crone 2006), weak effects of mammalian seed predation in some plant species should not be considered indicative of similarly weak effects in other species. Furthermore, where there are strong effects, the management interventions required to address pre-dispersal mammalian seed predation could be very different from those needed to prevent damage by insects or to dispersed seeds or other plant organs.

Here, we used a 10-year monitoring data set to test the hypothesis that seed predation by rodents plays a significant role in driving the population dynamics of a rare long-lived perennial with a persistent seed bank. The only known population of *Lupinus constancei* was, until summer of 2015, comprised of approximately 400 reproductive individuals restricted to a single square kilometre. There is some evidence that rare plants have weaker dispersal abilities, lower reproductive investments and are less able to compete with other plants or resist their natural enemies than their more common relatives (Kunin & Gaston 1993; Harrison 2013). A study of a rare *Astragalus* species found that it underwent significantly higher pre-dispersal insect seed predation than two of its more common sympatric congeners, suggesting that seed predation could be a driver of its rarity (Combs, Lambert & Reichard 2013). Given its extremely restricted geographical distribution and small absolute population size, quantification of a similar effect of seed predation in *Lupinus constancei* could be crucial to its conservation. Indeed, a large, rapid die-off of ~75% of reproductive *L. constancei* plants was observed in early summer of 2015, presumably because of extreme drought conditions throughout California. This die-off was followed by a wildland fire (the Lassic Fire of summer 2015), which burned a small portion of high density lupine habitat, and the mortality due to the fire is yet unknown. Ten years of *Lupinus constancei* demographic data allowed us to resolve species-specific conservation questions while providing a case study of circumstances under which consumer pressure can be an important driver of population growth and rarity.

First, we used stochastic vital rate-based matrix models to determine whether the population was growing, stable, or declining and to estimate the probability that the species will go extinct in a relatively short time period (i.e. the next 50 years). These analyses were performed in a framework of comparative management scenarios, to adjust for the inherent uncertainty of model projection focused solely on long-term prediction (Brook *et al.* 2000; Fieberg & Ellner 2000). In addition, we used sensitivity and elasticity analyses and life table response experiments (LTRE) to determine which life-history stages and vital rates have the greatest effect on the population growth rate. Finally, we used a regression LTRE to assess the effect of seed predation on the population growth rate, enabling us to both evaluate the importance of pre-dispersal seed predation in this system and to make explicit management recommendations.

## Materials and methods

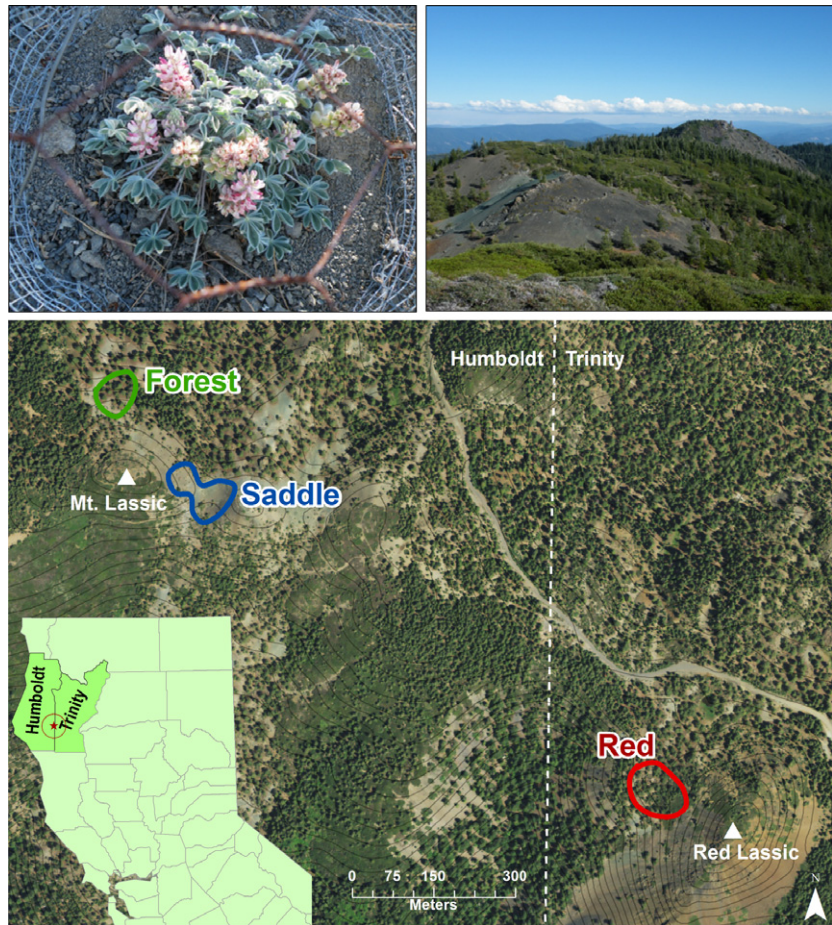
### SPECIES DESCRIPTION & STUDY SITE

*Lupinus constancei* (T.W. Nelson & J.P. Nelson, the Lassics lupine) is a rare herb whose population of <400 reproductive individuals (Carothers 2008a) is restricted to a single square kilometre in northern California, USA (Nelson & Nelson 1983; Fig. 1). The circumscribed range of this species makes it extremely vulnerable to both catastrophic disturbance and slower successional changes that might otherwise be mitigated by larger spatial distributions. In 2003, following reports that predators had removed nearly all seeds from immature *L. constancei* fruits in previous years, a federal interagency group of biologists began a programme of covering a portion of reproductive individuals with herbivory exclosures (cages) made of 1–3 cm wire mesh, which are capable of excluding most birds and mammals, but not insects (Fig. 1). This was a stop-gap measure to stem perceived population decline, and its effectiveness had not been evaluated. Camera trapping and seed surrogacy experiments later demonstrated that the principal seed predators were deer mice *Peromyscus* spp., chipmunks *Tamias* spp. and the California ground squirrel *Otospermophilus beecheyi* (Cate 2016).

*Lupinus constancei* is a polycarpic, herbaceous perennial with a branched, woody caudex and a basal rosette which rarely exceeds 30 cm in diameter (Fig. 1). As early as late May, reproductive individuals bear one to 15 inflorescences of 10–60 pink and white flowers. Each legume can eventually mature 1–5 seeds in July or August. Seeds often exhibit physical dormancy (Baskin & Baskin 1998) and form a persistent seed bank, though precisely how long seeds can survive in the soil is unknown.

### MONITORING

*Lupinus constancei* is monitored jointly by the US Forest Service, California Native Plant Society and US Fish and Wildlife Service. Permanent monitoring transects were established at three sites, positioned to capture as much of the population as possible: the 'Red' site was established in 2001 on the north side of Red Lassic, under a closed Jeffrey pine *Pinus jeffreyi* forest canopy, the 'Saddle' site in 2002 between the two peaks of Mount Lassic,



**Fig. 1.** Lassics lupine beginning to fruit inside herbivory exclosure (top left). View from Mount Lassic main peak eastward towards Saddle and secondary peak, Red Lassic in right background (top right). Full extent of Lassics lupine range, with monitoring sites outlined in blue, green and red. Inset: northern California, USA (bottom).

under very little canopy, and the 'Forest' site in 2005 downslope of the Saddle within the forest boundary. Representatives of every *L. constancei* life-history stage were marked along each transect. Three times per year, in approximately June, July and August, each marked individual was re-visited and its stage class, rosette diameter, amount of herbivory sustained and its source, and number of inflorescences were recorded. Stage classes were defined by life history: seed, seedling, vegetative adult, reproductive adult, and dormant adult. Individuals were classed as dormant if they were observed alive after one or more years unobserved. Between 2001 and 2011, 6242 total observations were made of 940 individuals.

#### SEED EXPERIMENTS

In 2010 and 2011, we marked a haphazardly chosen subset of caged ( $n = 57$  in 2010,  $n = 35$  in 2011) and uncaged ( $n = 64$  in 2010,  $n = 34$  in 2011) plants. We covered all inflorescences on a portion ( $n = 41$  in 2010,  $n = 19$  in 2011) of the marked caged plants with plastic mesh bags after pollination and before fruit maturation, in order to collect and count the seeds produced. For each plant, we also measured morphometric (number of inflorescences, number of leaves, rosette diameter) and microsite (slope, aspect, litter depth, proximity to forest and chaparral edges) characteristics. To detect any size bias in selection of plants to cage or bag, we performed *t*-tests comparing the rosette diameter and number of inflorescences of caged and uncaged plants and bagged and unbaggaged caged plants.

We performed a linear regression using number of seeds per reproductive plant as the response and number of inflorescences as the predictor. Because all reproductive individuals produced seeds, we forced the model through the origin. We estimated the model parameters using the 2010 data and tested them using the 2011 data. We then used the model to estimate the number of seeds produced by reproductive plants in years for which number of inflorescences but not number of seeds was measured (see Fig. S1, Supporting Information).

To estimate the effect of seed predation on fertility, we calculated the number of seeds matured by each uncaged plant as a proportion of the number of seeds it would be expected to produce in the absence of seed predation (calculated using the regression equation described above). Approximately 2% of estimated seed production escaped predation in 2010 and 5% in 2011. Because seed predation in 2011 was judged to be unusually light by the agency biologists who have worked with *L. constancei* for the past decade, we chose to use that year's seed predation rate as a conservative estimate of the rate sustained by uncaged individuals.

We used data from seed burial experiments to calculate seed survival rates. In 2008, five mesh bags containing ten seeds and 5 mL of soil each were buried at seven plots in the Saddle site. In 2009, 2010 and 2011, one bag was pulled up from each site, the number of germinants was counted, and intact seeds were tested for viability using a 1% solution of tetrazolium chloride (Carothers 2008b). We performed a linear regression with number live (germinated or viable but ungerminated) seeds in year  $t + 1$  as



the response and number live seeds in year  $t$  as the predictor, and used the slope coefficient and variance estimates as the mean and variance of seed bank survivorship ( $s_1$ ). Finally, because seeds in the burial experiment were contained in mesh bags and could not emerge from the soil, and the 'germination rate' used in our model must be an estimate of the rate at which seeds become established seedlings with the possibility of being counted in the following year's census, germinants from the seed burial experiment could not be used to calculate the germination rate. We therefore used a series of seed grid experiments to calculate seed germination rates. In 2005, 435 seeds were sown in 27 grids at known locations across the Saddle and Red sites and the number of germinants was recorded at these locations for the following 6 years. Seven similar plots were sown in 2008 and 2009 with 24 seeds each. We subtracted the mean proportion of seeds germinated across these plots from one to calculate the probability that seeds in the seed bank do not germinate ( $g_{11}$ ). Methods used to estimate each vital rate can be found in Table S1.

#### POPULATION PROJECTIONS

We projected *L. constancei* population size using the equation  $N_{i,t+1} = A * N_{i,t}$ , where  $N_{i,t}$  is a vector of population size at site  $i$  and time  $t$  and  $A$  is the  $5 \times 5$  stage-structured, vital rate-based matrix in Table 1 (top). Each growth ( $g_{ij}$ ) and survival ( $s_j$ ) rate for the seedling, vegetative and reproductive classes was drawn from an appropriate beta distribution, with a mean and variance (Table 1, bottom) calculated from annual transitions and corrected for sampling variation (Kendall 1998; Morris & Doak 2002; Stubben & Milligan 2007). The growth rates of the dormant class were drawn according to the same procedure, but survival of the dormant class ( $s_5$ ) was drawn from the vegetative class

survival distribution, because there was insufficient information to build an appropriate dormant survivorship distribution. Fertility rates ( $f_j$ ) were drawn from stretched beta distributions with mean, variance, minimum and maximum computed from the individual seed production estimates discussed above and were corrected for sampling bias (Engen & Islam 1998). Vital rate parameters were calculated separately for each site.

We projected the population size of each site individually and all sites together 50 years in the future. The projection of all sites used a multi-site matrix that incorporated between-site correlations but no movement of seeds between sites, an assumption supported by site topography and genetic analyses (Wilson & Hipkins 2004). All projections incorporated within-year vital rate correlations and auto- and cross-correlations for one time step and were performed under three seed predation scenarios. In these scenarios, fertility was adjusted to reflect the effects of possible management regimes. In the 'all caged' scenario, all reproductive individuals were projected to produce the number seeds expected in the absence of seed predation, while in the 'all uncaged' scenario, that fertility was reduced by 95%. The third scenario assumed that same proportion of individuals would be caged as in previous years (30% of reproductive individuals caged at the Saddle, 50% Forest, and 100% Red) and adjusted fertility accordingly. Demographic stochasticity was simulated using Monte Carlo methods for any stage class with less than 50 members at a given time step.

We performed 500 sets of 1000 runs for each projection, using a quasi-extinction threshold (i.e. number of individuals below which the population is believed to be unable to recover) of 10 adult (vegetative and reproductive) plants or 30 seeds for the whole species and three adults or 10 seeds at a single site. The cumulative probability of quasi-extinction was calculated by

**Table 1.** Top, projection matrix ( $s_j$ : probability of survival of class  $j$ ;  $s_{ss}$ : survival of seedlings over the summer;  $g_{ij}$ : probability of transition from class  $j$  to class  $i$ ;  $g_{>j}$ : probability of transition from class  $j$  to any class  $i$  or greater;  $f_j$ : mean number of seeds produced by class  $j$ ). Bottom, mean vital rates ( $\pm$ variance) at all sites

	Seed	Seedling	Vegetative	Reproductive	Dormant
Seed	$s_1 * g_{11}$	0	0	$f_4 * s_1 * g_{11}$	0
Seedling	$s_1 * (1 - g_{11})$	0	0	$f_4 * (1 - g_{11}) * s_1^{(9/12)} * s_{ss}$	0
Vegetative	0	$s_2 * (1 - g_{>42})$	$s_3 * (1 - g_{>43})$	$s_4 * (1 - g_{>44})$	$s_5 * (1 - g_{>45})$
Reproductive	0	$s_2 * g_{>42}$	$s_3 * (g_{>43} - g_{>53})$	$s_4 * (g_{>44} - g_{>54})$	$s_5 * (g_{>45} - g_{>55})$
Dormant	0	0	$s_3 * g_{>53}$	$s_4 * g_{>54}$	$s_5 * g_{>55}$

	Saddle		Forest		Red
	Caged	Uncaged	Caged	Uncaged	All Caged
$s_{ss}$	0.65 $\pm$ 0.01	0.65 $\pm$ 0.01	0.65 $\pm$ 0.08	0.65 $\pm$ 0.08	0.72 $\pm$ <0.01
$s_1$	0.70 $\pm$ 0.05	0.70 $\pm$ 0.05	0.70 $\pm$ 0.05	0.70 $\pm$ 0.05	0.70 $\pm$ 0.05
$s_2$	0.44 $\pm$ 0.04	0.44 $\pm$ 0.04	0.44 $\pm$ 0.08	0.44 $\pm$ 0.08	0.47 $\pm$ 0.02
$s_3$	0.63 $\pm$ 0.02	0.63 $\pm$ 0.02	0.77 $\pm$ <0.01	0.77 $\pm$ <0.01	0.60 $\pm$ 0.02
$s_4$	0.85 $\pm$ <0.01	0.78 $\pm$ <0.01	0.87 $\pm$ <0.01	0.87 $\pm$ <0.01	0.79 $\pm$ 0.03
$f_4$	45.0 $\pm$ 124.9	2.25 $\pm$ 0.31	24.3 $\pm$ 1.01	1.21 $\pm$ <0.01	32.5 $\pm$ 64.2
$g_{11}$	0.94 $\pm$ 0.01	0.94 $\pm$ 0.01	0.94 $\pm$ 0.01	0.94 $\pm$ 0.01	0.94 $\pm$ 0.01
$g_{>42}$	0.18 $\pm$ 0.04	0.18 $\pm$ 0.04	0.07 $\pm$ <0.01	0.07 $\pm$ <0.01	0.02 $\pm$ <0.01
$g_{>43}$	0.52 $\pm$ 0.02	0.52 $\pm$ 0.02	0.28 $\pm$ <0.01	0.28 $\pm$ <0.01	0.29 $\pm$ <0.01
$g_{>44}$	0.92 $\pm$ <0.01	0.74 $\pm$ 0.01	0.70 $\pm$ 0.04	0.70 $\pm$ 0.04	0.72 $\pm$ 0.01
$g_{>45}$	0.72 $\pm$ 0.04	0.72 $\pm$ 0.04	0.50 $\pm$ <0.01	0.50 $\pm$ <0.01	0.89 $\pm$ 0.02
$g_{>53}$	0.06 $\pm$ <0.01	0.06 $\pm$ <0.01	0.05 $\pm$ <0.01	0.05 $\pm$ <0.01	0.02 $\pm$ <0.01
$g_{>54}$	0.03 $\pm$ <0.01	0.05 $\pm$ <0.01	0.01 $\pm$ <0.01	0.01 $\pm$ <0.01	0.01 $\pm$ <0.01
$g_{>55}$	0.50 $\pm$ 0.10	0.50 $\pm$ 0.10	0.42 $\pm$ 0.01	0.42 $\pm$ 0.01	0.67 $\pm$ 0.11

tallying the number of runs in which the population fell below the quasi-extinction threshold at that time step or before. A mean stochastic population growth rate ( $\lambda_s$ ) for each scenario was calculated from all runs, using the formula  $\lambda_s = (N_{50}/N_0)^{(1/50)}$ , where  $N_{50}$  is the population size at time step 50 and  $N_0$  is the starting population size. Finally, to ascertain how sensitive the model was to individual parameter changes, we calculated the sensitivity (the change in  $\lambda$  resulting from a change to single matrix element) and elasticity (sensitivity scaled for meaningful comparison) of the model to each of the matrix elements at each site.

#### LIFE TABLE RESPONSE EXPERIMENTS

To better understand the effect of the caging treatment on population growth, we performed a fixed one-way life table response experiment (LTRE) on the Saddle site, which was the only site with sufficient data to perform this analysis. This method decomposes a treatment's effects on the deterministic population growth rate ( $\lambda_d$ , the dominant eigenvalue of the mean projection matrix) into the contribution from each vital rate, calculated as the product of its sensitivity and the difference between its values in caged and uncaged treatments (Caswell 2001). We also performed a regression LTRE (Caswell 2001) using the proportion of reproductive plants caged as the treatment variable. In this analysis, we assumed that caging affected only fertility and allowed uncaged plants to mature only 5% of their fruits. We calculated the deterministic population growth rate ( $\lambda_d$ ), stable stage distribution ( $w$ ) and reproductive values ( $v$ ) for each level of caging from 0% to 100%, varied in 5% increments. Finally, we determined the proportion of reproductive plants caged at which the population growth would be self-sustaining ( $\lambda = 1$ ) at each site. All analyses were conducted in R (R Development Core Team 2011).

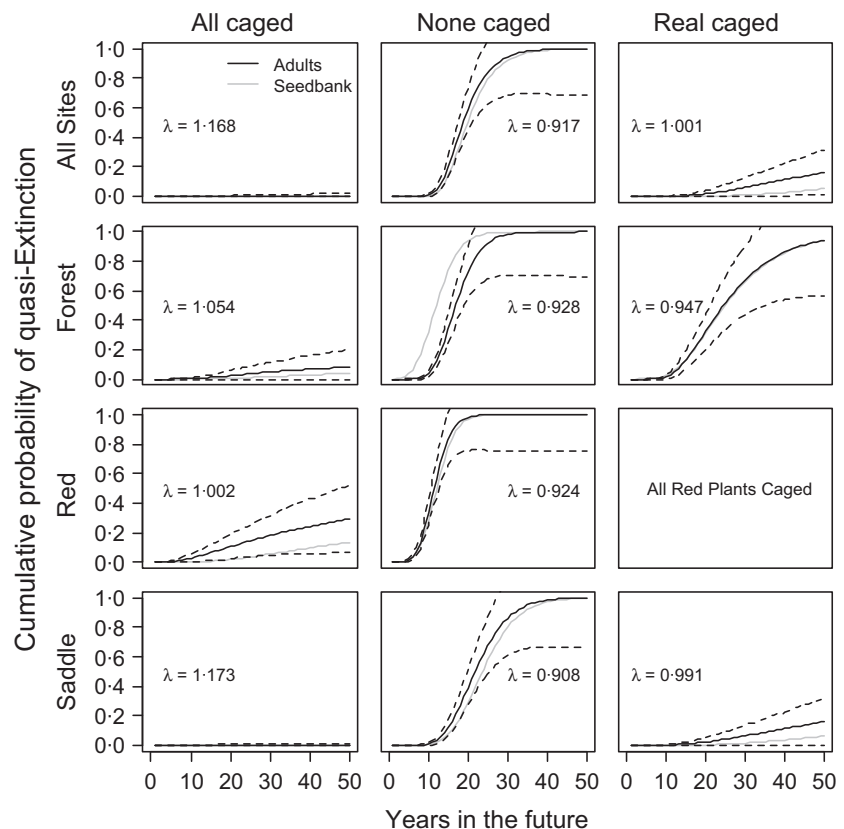
## Results

#### SEED EXPERIMENTS

There was a positive relationship between the number of seeds and the number of inflorescences produced by reproductive plants ( $R^2_{\text{adj}} = 0.8567$ , d.f. = 1,  $P < 0.001$ ), with each inflorescence adding a mean of 14.57 mature seeds to a plant's total production (see Fig. S1). All 2011 data point fits fell within the prediction intervals calculated with the model trained with the 2010 data. The  $t$ -tests revealed no size bias in caging or bagging for all plant characteristics ( $P$ -values  $> 0.26$ ), with the exception of a trend of marginally larger rosette diameter of caged plants ( $P = 0.09$ ; see Table S2). The seed burial regression slope coefficient was 0.70 ( $\pm 0.05$ ), and was used as an estimate of seed survival ( $s_1$ ; Table 1). The proportion of seeds germinated ( $0.94 \pm 0.01$ ) in the seed grid experiments were subtracted from one and used as an estimate of the proportion of ungerminated seeds ( $g_{11}$ ; Table 1).

#### POPULATION PROJECTIONS

Population projections showed that if current caging practices continue, the *L. constancei* population will remain relatively stable ( $\lambda_s = 1.001 \pm 0.003$ ), with a 0.7–31.5% probability (95% confidence interval) of quasi-extinction in the next 50 years (Fig. 2). Of the three sites, the Saddle has the best chance of persisting over the next 50 years (0.2–31.7% probability of quasi-extinction,



**Fig. 2.** Population projections under three caging scenarios. The cumulative probability of quasi-extinction for adult plants is shown in black (with 95% CI), seed bank shown in grey.

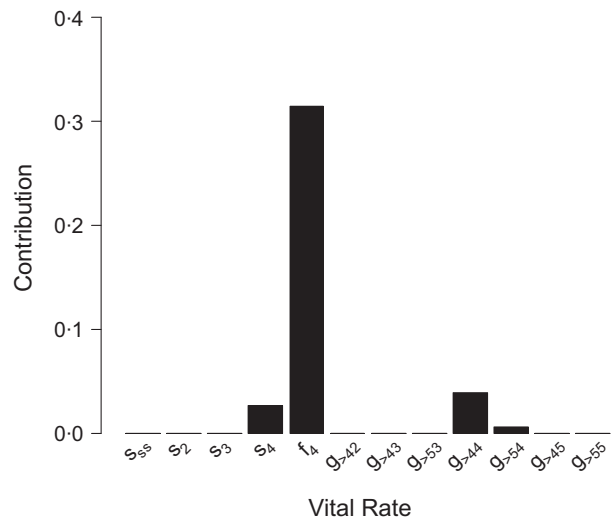
$\lambda_s = 0.991 \pm 0.003$ ), if the current practice of caging ~30% of its reproductive individuals is continued. In contrast, if all reproductive plants were left uncaged and exposed to a 95% seed predation rate, the probability of quasi-extinction in the next 50 years is 68.4–100% ( $\lambda_s = 0.917 \pm 0.001$ ) across all sites. If all reproductive plants were caged and totally protected from seed predation, the probability of quasi-extinction in the next 50 years across all sites drops to 0–1.8% ( $\lambda_s = 1.168 \pm 0.005$ ).

At all sites, the model was most sensitive to the survival and growth of the reproductive class, followed by the vegetative class or seed bank, then seedlings, and the dormant class influenced the model least (Table 2). Most between-site, within-year vital rate correlations were positive or close to zero, meaning that environmental events that depress one vital rate will likely depress others (see Fig. S2).

#### LIFE TABLE RESPONSE EXPERIMENTS

The one-way LTRE showed that the difference in fertility between caged and uncaged plants contributed almost nine times more to the effect of caging on Saddle population growth than changes in any other vital rate (Fig. 3). Survival ( $s_4$ ), stasis ( $g_{>44}$ ) and transition to dormancy ( $g_{>54}$ ) of reproductive plants all made smaller contributions to the effect of caging on population growth. The regression LTRE showed that with a greater proportion of reproductive plants caged and free from seed predation, the deterministic population growth rate ( $\lambda_d$ ) would increase at all sites (Fig. 4). Population growth would be self-sustaining when approximately 49% of Forest plants, 70% of Red plants and 21% of Saddle plants were caged.

Reproductive value ( $v$ ) and stable stage distribution ( $w$ ) also changed with caging level. Across all sites, reproductive individuals were expected to contribute the most to



**Fig. 3.** One-way life table response experiment, showing contribution to changes in the Lassics lupine population growth rate by each vital rate due to caging.

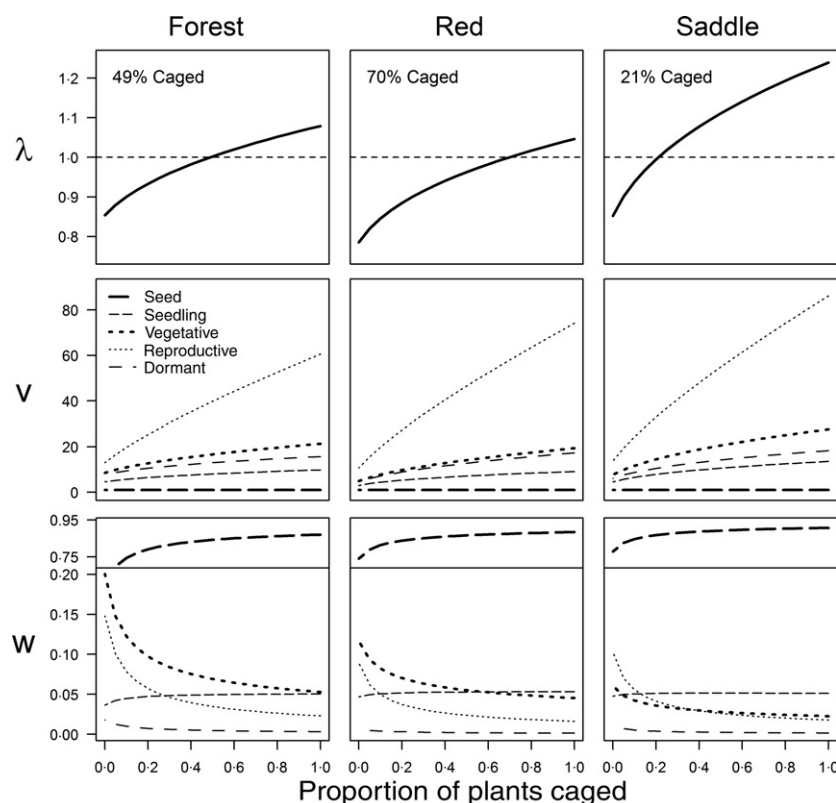
population growth over their lifetimes, followed by vegetative, dormant, seedling and seed classes. At higher predation levels, these reproductive values were greatly reduced, but maintained their order. At all sites, more than 70% of the population was in the seed class, with smaller fractions of seedlings, vegetative, reproductive and dormant individuals. When fewer plants were caged, a smaller percentage of the population was expected to reside in the seed or seedling classes, while a greater percentage would belong to vegetative, reproductive or dormant classes.

#### Discussion

These results demonstrate that pre-dispersal seed predation by rodents has the potential to drive *L. constancei* to

**Table 2.** Estimated elasticity matrices for each site, if all plants were caged

	Seed	Seedling	Vegetative	Reproductive	Dormant
<i>Forest</i>					
Seed	0.134	0	0	0.086	0
Seedling	0.086	0	0	0.039	0
Vegetative	0	0.104	0.146	0.031	0.006
Reproductive	0	0.022	0.132	0.197	0.003
Dormant	0	0	0.008	0.001	0.004
<i>Red</i>					
Seed	0.160	0	0	0.095	0
Seedling	0.095	0	0	0.044	0
Vegetative	0	0.130	0.104	0.019	0.001
Reproductive	0	0.010	0.146	0.186	0.004
Dormant	0	0	0.003	0.001	0.003
<i>Saddle</i>					
Seed	0.126	0	0	0.112	0
Seedling	0.112	0	0	0.071	0
Vegetative	0	0.109	0.040	0.015	0.002
Reproductive	0	0.074	0.122	0.206	0.004
Dormant	0	0	0.003	0.002	0.002



**Fig. 4.** Regression life table response experiment, showing the response of *Lasiscs lupine* population growth rate ( $\lambda$ ), reproductive value ( $v$ ) and stable stage distribution ( $w$ ) at each of the three monitoring sites, across a gradient of caging of reproductive plants.

extinction. Few studies have quantified the population-level effects of this particular type of consumption. In a similar study, Dangremond, Pardini & Knight (2010) examined seed predation on a congeneric species, *Lupinus tidestromii*, and although they found strong population-level effects, no site was driven from growth to decline as a result of consumer pressure.

Several additional studies have examined the population-level effects of seed predation by rodents occurring post-dispersal (Louda, Potvin & Collinge 1990; Maron & Kauffman 2006; Davis, Tyler & Mahall 2011; Bricker & Maron 2012). For example, Davis, Tyler & Mahall (2011) found that *Quercus lobata* populations in Santa Barbara County must be protected from both post-dispersal seed predators and grazers to maintain population growth ( $\lambda > 1$ ), while Bricker & Maron (2012) found that although post-dispersal seed predation lowered the population growth rate of *Lithospermum ruderalis*, it did not cause population decline. However, as the spatial and temporal context for post-dispersal interactions can be quite different from those occurring pre-dispersal, they can be meaningfully considered discrete phenomena (Worthy, Law & Hulme 2006; Kolb, Ehrlén & Eriksson 2007). Similarly, an abundant literature exists on the population-level effects of pre-dispersal seed predation by insects, because they are the most common culprit of such consumption (Maron & Crone 2006; Kolb, Ehrlén & Eriksson 2007). Froberg & Eriksson (2003) found that pre-dispersal seed predation by moth larvae resulted in population decline ( $\lambda < 1$ ) in *Actaea spicata* in some

years, but not others. And Ehrlén (1995) found that insect seed predation had population-level effects on *Lathyrus vernus* that were not as strong as those of meristem damage by molluscs or vertebrate grazing. But while the plant population dynamics resulting from damage by rodents and insects may be similar, the management interventions needed to mitigate them are sufficiently different to justify separate attention.

Although long-lived species are often expected to be less sensitive to changes in fertility (Silvertown *et al.* 1993; Knight, Caswell & Kalisz 2009) and persistent seed banks are presumed capable of carrying a population through low production years (Louda & Potvin 1995; Maron & Crone 2006), *L. constancei* shows that these assumptions are far from universal. With the exception of the dormant class, the elasticity of the model was spread fairly evenly across vital rates, including fertility, which is unusual and provides a partial explanation of why seed predation has such a dramatic effect in this system. Also, as fewer plants are caged and the population sustains more seed predation, the stable stage distribution shifts and reproductive individuals make up proportionally more of the population. At the same time, reproductive plants decrease in reproductive value and their contribution to population growth becomes closer to that of a seed. High seed predation could lead to a *L. constancei* population with a reproductive class that is disproportionately large, but of diminished value to population growth.

The mechanics of *L. constancei* demographics, however, provide little insight into why seed predation is having

this dramatic effect now, but presumably did not in the past. Comparison of soil from areas inhabited by *L. constancei* with nearby similar areas where it does not grow found very few sites that met the plant's soil requirements and were not already occupied, suggesting that it is unlikely that *L. constancei* was more widespread in the recent past than it is now (Imper 2012). This indicates that the species current and historic ranges are comparably sized. So, if *L. constancei* has existed as a small but stable population, what caused the recent intensification of seed predation?

The answer may lie in the vegetation changes that have taken place on Mount Lassic over the past several decades. Analysis of historical photos dating as far back as the 1930s indicates that the edge of the Jeffrey pine/incense-cedar forest has moved upslope markedly on the north side of Mount Lassic, while the chaparral edge has made a similar move upslope on the south side (Carothers 2008a). Encroachment of structured vegetation may bring rodents into more frequent contact with *L. constancei*, because they are unlikely to live in unprotected bald areas (G. Falxa, pers. comm.). This hypothesis is supported by a pilot study that we conducted in 2010, in which we used transects originating in bald areas occupied by *L. constancei* and running into the surrounding vegetation (forest and chaparral) to measure removal rates of seeds placed in trays at regular intervals. We found that the seeds were removed more frequently within and just outside of the forest and chaparral boundaries than they were in bald areas (Kurkjian 2011). Based on this data, we were able to draw a provisional link between seed predation intensity and the proximity to surrounding vegetation. Studies to further quantify this relationship in *L. constancei* are currently underway, including intensive sampling of small mammal population size at known distances from lupines.

Distance from particular species has been demonstrated to affect seed removal rates in a number of other systems. For example, Orrock, Witter & Reichman (2008) demonstrated that proximity to *Brassica nigra* increases small mammal seed predation pressure on *Nassella pulchra*. Like other types of plant–consumer interactions, the effects of seed predation can be habitat- and context-dependent (Orrock, Holt & Baskett 2010). Maron & Kauffman (2006) demonstrated that *Lupinus arboreus* underwent significantly higher post-dispersal seed predation by mice in dune habitats than in grasslands, and that this disparity led to markedly different population-level effects. In a forest ecosystem, Kolb, Leimu & Ehrlén (2007) found that while pre-dispersal seed predation by insects on *Primula veris* increased over a gradient of canopy cover, the effects of predation on the population growth rate actually decreased over the same gradient. And Dangremond, Pardini & Knight (2010) determined that proximity to an invasive grass in a dune habitat increased

pre-dispersal seed predation by rodents on *Lupinus tide-stromii*, thereby exacerbating population decline.

An opportunity to investigate the hypothesis that encroachment of woody vegetation has caused seed predation to intensify may have been created by the Lassic Fire, which burned 7364 ha including ~1 ha of *L. constancei* habitat. Extensive pre-fire monitoring data of both small mammal and *L. constancei* populations could allow the fire to be used as a natural experiment with the potential to find a causal relationship between the two. The specific effects of fire on *L. constancei* population demographics are particularly difficult to predict, given the potential for interacting effects of fire and small mammal abundance and consumer pressure (Zwolak 2009; Litt & Steidl 2011). For example, Zwolak *et al.* (2010) found that deer mouse population size increased dramatically post-fire and that the effects of seed predation on *Pinus ponderosa* and *Pseudotsuga menziesii* seedling establishment ultimately overwhelmed the effects of the fire itself. However, the full effects of the fire on the *L. constancei* population, already at great risk of extinction due to its small absolute population size, will not be known until at least the 2016 growing season.

Another plausible explanation for the increase in seed predation on *L. constancei* is a change in higher level trophic interactions. Such trophic cascades are well documented in terrestrial systems (Schmitz, Hamback & Beckerman 2000), but because of the complexity of food webs, especially their nonlinearities in interaction strength and range of spatial scales, their effects can be difficult to predict (Estes *et al.* 2011). Many predators of deer mice (e.g. snakes, martens, foxes) have experienced population declines in California and elsewhere (Zielinski *et al.* 2005; Reading *et al.* 2010). And while we have little knowledge of their present or historic population sizes on Mount Lassic, it is possible that a reduction in large predators could have allowed the consumer population to expand and exert additional pressure on *L. constancei* population growth.

Without caging, the *L. constancei* population would decrease towards extinction as a direct result of seed predation. With a caging treatment, however, *L. constancei* could be able to maintain a higher population growth rate and lower extinction risk. It is remarkable that based on keen observation and knowledge of the system, managers were able to identify an underlying cause of population decline and counter it with perhaps the best possible response. Early identification of the role of seed predation in *L. constancei* population dynamics was likely instrumental in the prevention of a substantial reduction in population size. Nonetheless, at the current rate of caging, *L. constancei* still has a significant chance of extinction; current caging results in  $\lambda_s \approx 1$ , where the chance of reaching quasi-extinction in the next 50 years is as high as 31.5%.

Further complicating the question of population status is the fact that this model did not incorporate extreme



variability in the vital rates. While climatic conditions during the ten study years included some severe seasons, there is no reason to believe this timespan captured the most extreme conditions we might expect in the coming decades. The summer survival of *L. constancei* seedlings may be hit especially hard by climate change, as that vital rate seems to be the most closely correlated with ambient air temperature (Imper 2012). Since the model was quite sensitive to changes seedling vital rates, increased seedling mortality could have a dramatic effect on population persistence. Finally, when considering the vulnerability of *L. constancei* to extinction, the small absolute size of the population cannot be ignored. A single catastrophic event, such as the Lassic Fire, could eradicate the species en masse, but the probability of such an occurrence has not been incorporated in this model.

This study demonstrates that pre-dispersal seed predation by rodents can have powerful population-level effects, and represents one set of conditions under which consumer pressure can limit plant population size. Contrary to our expectations, the effects of seed predation in this system do not appear to be mitigated by long generation time, abundant seed production or the persistent seed bank. And because *L. constancei* has an extremely small population size and restricted geographical distribution, this strong consumer pressure has the potential to make the difference between population growth and decline and to push the species to extinction. Therefore, although the underlying causes of the timing and intensity of seed predation on the species are unresolved, this consumption by small mammals is a strong proximate driver of *L. constancei* population decline.

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## Data accessibility

*Lupinus constancei* monitoring data and R scripts used in analyses are available online in the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.mq3mq> (Kurkjian, Carothers & Jules 2016).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Fig. S1.** Linear regression of number of seeds per inflorescence.

**Fig. S2.** Correlation of vital rates between sites.

**Table S1.** Summary of data collection methods.

**Table S2.** T-test results for bias in caging and bagging.