

**Influences of Vegetation and Seed Densities on Seed Predation of
Centaurea solstitialis and *Carduus pycnocephalus* in California**

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ABSTRACT

Invasive plants are a ubiquitous problem in many ecosystems. Conservation of small populations of native plants is heavily dependent on efforts to control the spread of invasive species, which are costly to control and can lead to rangeland degradation. Two invasive species that are particularly rampant in California annual grasslands are yellow starthistle (*Centaurea solstitialis*) and Italian thistle (*Carduus pycnocephalus*). For management strategies for combating the spread of these invasive thistles, studies have shown that seed predation limits new plant recruitment and abundance. Weevils, small mammals, and birds are active in seed predation in the two thistles. However, the specific effects of vegetation and seed densities on seed predation have not been widely explored. In my study, I tested for the possible effects of varying vegetation and seed densities on seed predation levels in *C. pycnocephalus* and *C. solstitialis*. I also ran an exclusion experiment to discern which type of seed predator had the highest seed predation levels on the thistle seeds. As a result of my experiment, I found that only varied seed level yielded significant results in affecting seed predation levels. For the exclosures, I found that birds had the highest levels of seed predation. Compared to the weevils that exhibited 60-100% seed removal, birds were not as effective and only removed 20-40%. Further study into native seed predators would not be unwarranted, and may help management strategies incorporate more comprehensive approaches towards controlling the spread of invasive species.

KEYWORDS

Carduus pycnocephalus, *Centaurea solstitialis*, rangeland ecology, seed predation, density dependence, California annual grasslands

INTRODUCTION

Invasive plants are a ubiquitous problem in many ecosystems. Conservation of small populations of native plants is heavily dependent on efforts to control the spread of invasive species, which are costly to control and can lead to rangeland degradation (DiTomaso et al. 2006). Problems with invasive species are particularly prominent in California grasslands, which are dominated by invasive annual species. Native flora is rare in most California grasslands, and the negative effect of competition with invasive annuals makes coexistence difficult if not impossible due to invasive species' rapid propagation and consequent monopolization of resources (Evans et al. 1979).

Two invasive species that are particularly rampant in California are yellow starthistle (*Centaurea solstitialis*) and Italian thistle (*Carduus pycnocephalus*). Both are invasive thistles that pose a threat to grassland ecosystem stability across much of California (Evans et al. 1979, DiTomaso et al. 2006). Yellow starthistle was introduced to California around 1849 through seed contamination of imported Chilean alfalfa seeds (DiTomaso et al. 2006). By 1958, yellow starthistle had invaded over one million acres of California grasslands (DiTomaso et al. 2006). Italian thistle invasion occurred later, growing widespread to the point of large economic impacts by 1974 (Dunn 1976). The use of biological control agents (particularly weevils and other arthropods) to combat yellow starthistle began in North America in 1985 (Wilson 2003). Similar biological control tactics for Italian thistle began in 1969 (Kok 1998). The effect of native seed predators on these thistles has not been widely explored as a control option for these rampantly spread thistles. The theory of competitive exclusion describes the situation well; the invasive thistles establish themselves in an area and produce large numbers of seeds, allowing their population to increase exponentially and eventually overwhelm the native population of grasses (Palmbad 1968). Many types of counter management strategies (manual, chemical, biological) can be used to combat the propagation of the thistles (DiTomaso et al. 2006). However, what effect seed predation might have on the recruitment and spread of invasive species remains poorly understood for most species in California annual grasslands, as well as for other ecosystems (Orrock et al. 2006, Bricker et al. 2010).

Studies have shown that seed predation limits plant recruitment and abundance (Orrock et al. 2006, Bricker et al. 2010). The distribution and outcomes of interspecific plant competition are

thought to be directly influenced by small mammal seed predation (Borchert and Jaine 1978), which can negatively impact the amount of new seedlings recruited into the population (Louda et al. 1990). This suggests that areas with high seed production density have more interspecific plant competition and seed predation (Borchert and Jaine 1978, Louda et al. 1990). In particular, plant density is known to influence seed predator behavior, and is important because invasive species often grow in dense patches (Hulme and Hunt 1999). Density-responsive seed predators will consume seeds and seedlings in an area until the plant population has been reduced to the extent that is no longer beneficial to stay in the area (Janzen 1970). Vegetation provides cover for seed predators, while high seed density means the possibility for higher efficiency in terms of how many seeds the predator could be able to procure from one area (Janzen 1971, Bricker et al. 2010). If seed predators respond strongly to patch density by favoring certain conditions, the control they exert over seed availability will depend greatly on the patch size and density (Janzen 1970). Patches have relatively discrete spatial patterns that can be customized within the parameters of a study system, in other words, patches can be of different shapes and sizes depending on what parameters are convenient or useful for individual studies (Pickett and White 1985). Although ambiguous, the definition of a "patch" is always relative to the system in which it is situated (Pickett and White 1985). Understanding how various seed predators react to densities of vegetation will further our knowledge of invasive species spread dynamics. This will also inform our understanding of the distribution patterns of plants, both native and invasive, within a community.

Although studies have investigated the various relationships that affect recruitment of plants, the specific effects of vegetation and seed densities on seed predation have not been widely explored. While much research has gone into understanding the establishment and impacts of invasive species, the effects of seed predators on invasive recruitment has received far less attention. It is also important to discover more about the specific seed predators (such as mammals, birds, and arthropods) and their behavior relative to seed predation. This may reveal more about seed predation patterns and the impact of these patterns on invasive recruitment. If seed predation impacts invasive recruitment negatively, such knowledge would aide in more comprehensive management of invasive plants, and consequently aide the conservation of native plants. Currently, few studies have investigated how vegetation and seed density affects seed predation of invasive species, particularly invasive thistles. To explore this gap, I will study yellow starthistle and the

Italian thistle. In addition to the investigation into the effects of bird, mammal, and weevil seed predation, determining how each factor (vegetation density, seed density, and seed predation) relates to the other factors will ultimately aid ecosystem managers in creating more effective and comprehensive management strategies against invasive species recruitment for California grassland ecosystems.

Objectives

The objectives for my research project were: 1) I used a manipulative enclosure experiment to identify which taxonomic groups out of mammals, birds, and arthropods (specifically weevils) are contributing most strongly to the predation of thistle seeds within the experiment. 2) I compared the seed predation rates of weevils and the other seed predators to determine which seed predators are the most effective at consumption/removal of the thistle seeds. 3) Finally, I investigated if vegetation density and seed density of the thistles affect seed predator foraging behavior within the chosen experimental plots.

Hypotheses

I hypothesize that seed predators will favor areas with high vegetation and high seed density because those areas provide ample cover and large amounts of seeds. Alternative hypotheses that suggest vegetation and seed density are not the main influencing factors include: areas with low vegetation and low seed densities are favored, areas with high vegetation and low seed densities are favored, or areas with low vegetation and high seed densities are favored. Additionally, it is possible that only one factor will have an effect, or neither will have any effect. In regards to which taxonomic group contributes most strongly to the predation of seeds, I hypothesize that birds will play the largest role. Mammals may also have a significant impact on thistle recruitment through seed predation. I believe that weevils will also have a significant presence and impact in the study, as they are already used as biocontrol agents for thistle management.

METHODS

Density dependence study system description

I conducted this research at the Sierra Foothills Research and Extension Center (SFREC) in Browns Valley, CA (39.25113 N, 121.313132 W). SFREC is composed of 5,720 acres of undeveloped woodland-brush foothills. I worked within an existing research area situated in a dry annual rangeland ecosystem. The research area is composed of randomly selected plots 1x1 m², each containing either yellow starthistle (*Centaurea solstitialis*) or Italian thistle (*Carduus pycnocephalus*) seeds and/or plants (vegetation) (Figure 1).



Figure 1. Map of the Campbell site. The low vegetation plots used were in the red outlined areas. High vegetation Italian thistle plots were located in the area labeled "Existing fenced enclosure". High vegetation yellow starthistle plots were located in a separate site down the road. (Source: E. Spotswood)

To test the influence of density on seed predation, I varied the densities of both vegetation and seeds. I tested all possible combinations of vegetation and seed densities for my treatments: low vegetation/low seed, low vegetation/high seed, high vegetation/high seed, and high vegetation/low seed. I also established five 'Control' plots for each species with the following treatment: petri dishes with seeds (~250 seeds) in patches with no thistles to determine whether seed predators use the presence of plants to visually locate foraging locations.

To characterize my patches, I designated as low-density vegetation those patches that contain 30% or less thistle by species composition, whereas high density patches are those that contain 60% or more. Percent species composition was used since it was simple to determine, and the percentages within the chosen patches generally could be categorized into below 30% or above 60%. I replicated each density level 20 times resulting in 20 high density and 20 low density plots per species for 40 total plots per species. Within each vegetation density level, I assigned half of the 20 plots to receive low seed density treatment (10 seeds), and half as high seed density treatment (~500 seeds by weight). For each species I had 10 replicates of every treatment combination. I replicated treatments for both species for a total of 80 experimentally manipulated plots (40 plots per species with two species of thistle).

I ran the experiment from May 2013 to August 2013, peak thistle seed production season. I visited the site every two weeks during that time, with a final sixth visit in early October. For my seed density treatments, I placed the seeds on petri dishes. My seeds were mixed with residual chaff and plant litter from the extraction and sifting process. Thistle heads were crushed open, allowing for the seeds to be loosened enough to be sifted out from the majority of the plant material. However, since I could not pick out the seeds from the remaining plant material due to time constraints, I used the finely sifted seed mixture. Some of the seed I used was left over from my mentor's experiment. Additional seeds were extracted from thistle heads picked during initial site canvassing at SFREC. During each field visit, I recorded the number of seeds removed from low-density plots. I noted removal for high seed density plots as "no change" if the petri dish was undisturbed, and collected and replaced the seeds if the dish was disturbed. The high density seed petri dishes developed a crust-like surface due to exposure to morning dew followed by hot sun (Figure 2).

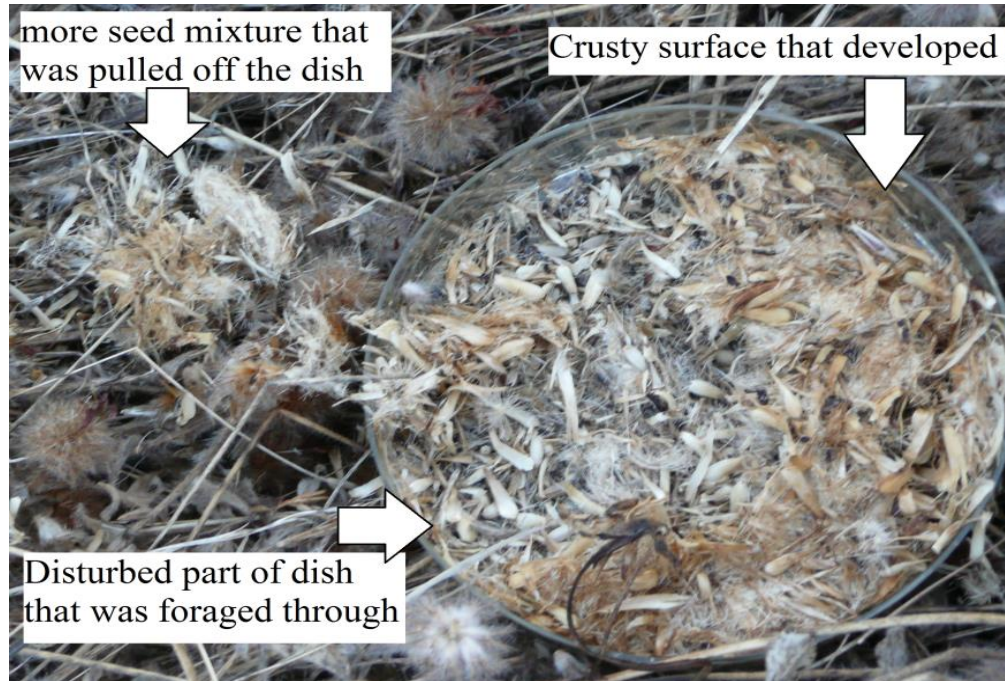


Figure 2. Example of "disturbed" high seed density plate. The crusted surface made it fairly easy to tell if anything had disturbed the dish to forage.

Exclosure experiment study system description

In California grasslands, primary seed predators include small mammals and birds. I used 1x1 m² cage experiments to identify key taxonomic groups responsible for seed predation. I placed a petri dish of known intermediate density of seeds (~250) in each cage. I also used openly accessible plots that allowed entry by all seed predators as controls. I replicated these sets of exclosures five times at randomized locations around the test site for a total of 15 cages (plus 5 controls).

Small mammals

Small mammal access cages were propped up on wooden blocks to create a ~3 inch gap to allow mammal entry. The top was closed with fencing to exclude birds (Figure 3). The mesh was ~3/4 inch links.

Birds

Bird access cages were open topped with flashing to deter small mammals from climbing over the fencing. The flashing covered the holes in the mesh, creating a smooth barrier at the top of the fencing. The bottoms were firmly staked down in the ground (Figure 4).

None (all excluded)

All exclusion cages had no entrances for birds or mammals. These were similar to the



small mammal cages except they were staked down firmly to the ground.

Figure 3. Small mammal access cages. Sides and top are mesh, entirety of the cage is propped up to provide a ~3inch gap for small mammal access. All exclusion are similar except firmly staked to the ground with no gap.



Figure 4. Bird access cages. Mesh sides with an open top lined with flashing to provide access to birds while blocking mammals from climbing over. Bottom is staked firmly to ground.

Data Collection

Density dependence study system

The data that I collected and analyzed for this part of the experiment are the proportional change in seed amount (by count, estimated by seeds per gram). Low seed density plots were counted manually, while high seed density plots were estimated seed counts extrapolated from average number of seeds per gram. To quantify how much seed predation is happening at each plot, left over seeds were weighed and compared to the original amount of seeds that were placed in each plot.

Exclosure experiment study system

As for which predator is consuming the most seeds, the exclosure experiments were quantified similarly to the density manipulation experiments. Partially eaten seeds were noted and were counted as eaten. Remaining seed counts were compared to the original seed counts for each plot, and then were recorded as proportion of seeds removed compared to the original amount of seeds. Again, this allowed me to quantify the amount of seed predation occurring in the plots.

Weevil presence and seed removal

To determine if weevil presence is density dependent, I dissected randomly selected thistle heads. Weevil presence was determined if there were remaining black cocoon casings, larvae, or weevils in the thistle heads when I dissected them. The remaining number of seeds left in each thistle head was also recorded. I selected 10 thistle heads from 10 high density and 10 low density plots for each thistle species (total of 40 plots). That is, I had 100 thistle heads from high density plots per species (total 200), and 100 thistle heads from low density plots (total 200) for a grand total of 400 thistle heads.

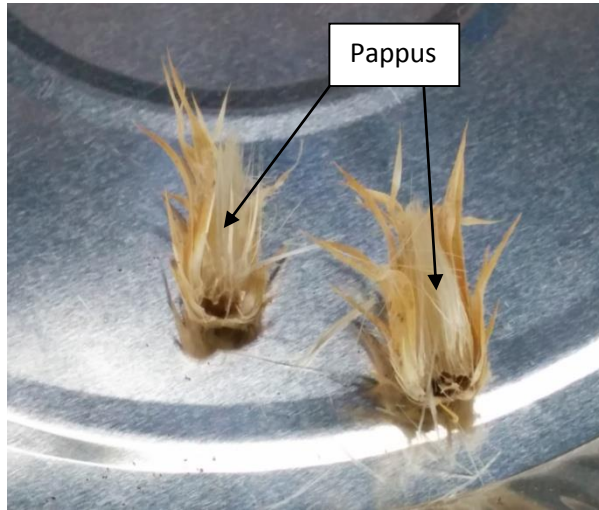


Figure 5. An example of a *Carduus pinocephalus* head with no weevil presence. Note there is no cocoon and the pappus (white) is fully intact.



Figure 6. An example of a *Carduus pinocephalus* head with weevil presence. The black hollow is the remnant of a weevil cocoon/larvae casing.

Data Analysis

All data was recorded in Microsoft Excel spreadsheets and analyzed using RStudio (Microsoft 2007, R Development Core Team 2006). Poisson regression (generalized linear model with poisson errors) was used to analyze the data due to the use of proportions in the data, as well as the data not having a normal distribution.

Exclosure experiment study system

As for the most active seed predator, I compared the proportionate amount of seeds being eaten in each type of exclosure and see which predator is eating the most seeds. The categorical variable is type of seed predator (independent variable). Numerical variables for this portion include: number of seed predators in each category (independent variable), and proportion of seed removal by count, estimated by weight (dependent on number of predators in the broad categories of mammal, bird, or arthropod). I used poisson regression (generalized linear model) to test number of seeds consumed versus each treatment (mammals, birds, all, control).

Weevil presence and seed removal

To determine weevil presence, each seed head was dissected and examined for signs of weevil predation. Such signs included: brown entry holes on the sides of the thistle head from weevil predation, black/brown sandy residue (weevil feces), black hollow casing from weevil larvae development, and finally if there were still weevils present inside the thistle seed head (DiTomaso 2006). The independent variables of the data were divided by thistle species (yellow starthistle or Italian thistle), and then by vegetation density of the plot the heads were collected from (high or low). The weevil predation rate (as a proportion) was the dependent variable. I used poisson regression to compare weevil predation rate (in proportions of 10) to vegetation density (low or high density).

Density dependence study system

Variables I analyzed include: vegetation density (independent variable), seed density (independent variable), and seed predation (dependent variable). I ran poisson regression on my data. The relationship I tested was the effect of vegetation density and seed density with seed predation as the output (using p-value <0.05 for significance).

RESULTS

Exclosure experiment

In the results of my exclosure experiment, I found that birds had the most seed predation overall (Figure 7). Mammals also had an effect, but it was markedly less than the effect of bird seed predation. The all exclusion cages should have had no proportional change, however, as we see in the graphs (Figure 7), there was a great variation in the Italian thistle “all” exclosure cages. Probable causes of this anomaly will be addressed in the Discussion section. Ultimately, it was also found that none of the seed predators had significantly different levels of seed predation (Refer to Table 1 for p-values).

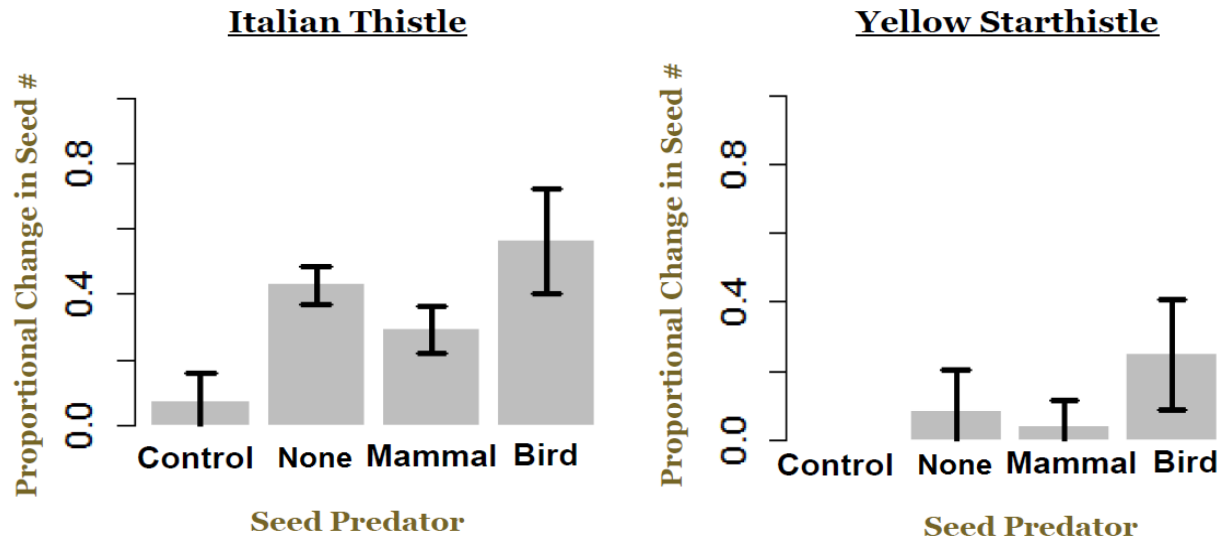


Figure 7. Enclosure experiment results: proportion of seed removal by seed predator type. Bar graph with error bar comparisons of the seed removal proportion for each seed predator, plus Controls (open plot, all predators can access) and None (no predator access, all excluded). Proportional change in seeds was calculated with (# seeds remaining) divided by (original # of seeds).

Table 1. Enclosure experiment p-values for seed predator type and proportion of seeds consumed. None of the p-values for either thistle species were found to be significant at a p-val<0.05 level. Poisson regression was used to find the p-values.

Thistle Species	Seed Predator	P-Value
Italian Thistle	Mammal	0.719
	Bird	0.783
	None	0.332
	Control (All)	0.191
Yellow Starthistle	Mammal	0.91
	Bird	0.65
	None	0.507
	Control (All)	0.38

Weevil presence and seed removal

For the weevil predation experiment results, I found that there was a significant relation between thistle density and weevil proportion density (Refer to Table 2 for p-values, refer to Figure 8 for graphs). For the relation between seed removal and vegetation density, the relationship was found significant only in Italian thistle (Refer to Table 3 for p-values, refer to Figure 9 and Figure 10 for graphs). This is further supported by the significant difference we can see in the graphs for Italian thistle and not yellow starthistle in Figure 9. The weevils that were present in the study system were *Rhinocyllus conicus*, *Larinus curtus*, and *Eustenopus villosus*, all of which are used as biocontrol agents for invasive thistles such as Italian thistle and yellow starthistle.

Table 2. P-values for weevil presence proportion per plot in relation to vegetation density of plot. *** indicates highly significant p-value at a p-val<0.05 level. P-values were calculated through use of poisson regression. Vegetation density was found to be a significant factor in both thistle species.

Thistle Species	P-Value
Italian Thistle	< 2e-16 ***
Yellow Starthistle	2.19e-05***

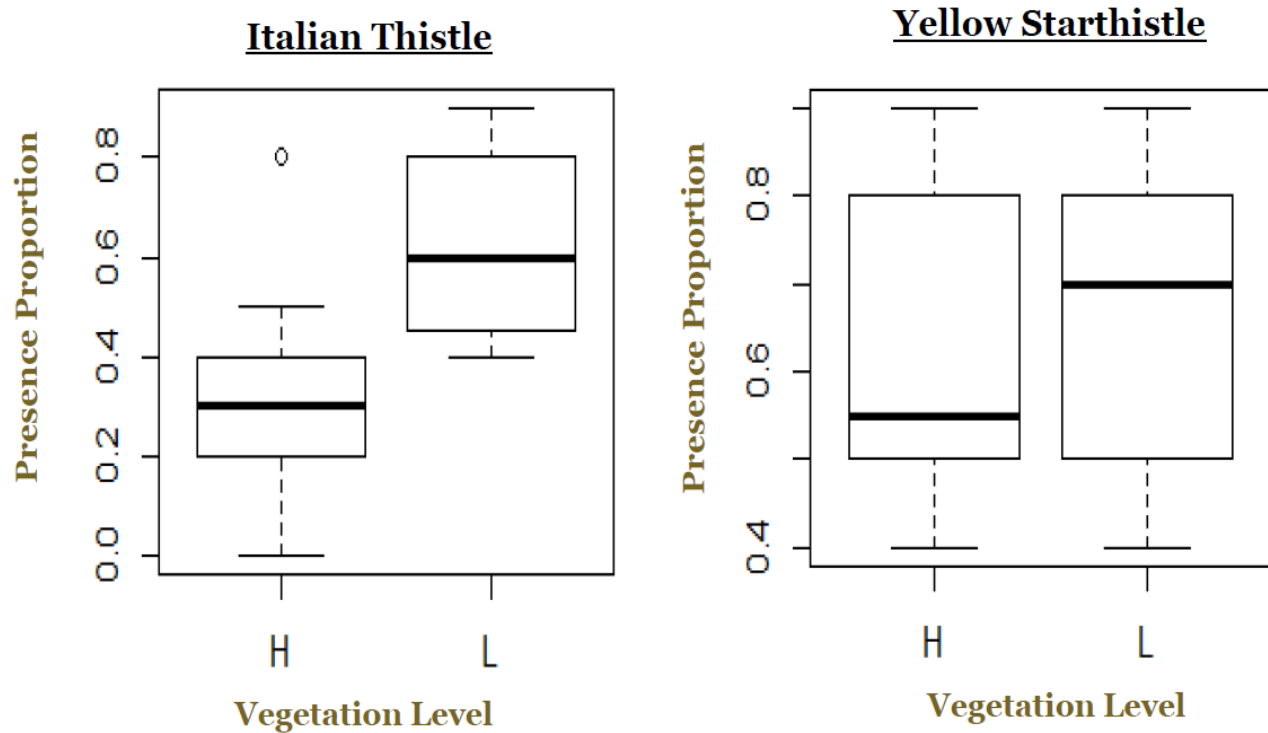


Figure 8. Presence proportion per plot in relation to vegetation density of plot. Vegetation level was either high (H) or low (L). The presence proportion was the proportion of heads that had signs of weevil presence out of 10 heads per plot. The means for the plots for both thistles can be seen to be different, suggesting that the presence of weevils is related to the vegetation density of the plot of thistles. The p-values given in Table 2 also support the statistical significance of the difference in means between vegetation levels in relation to presence proportion.

Table 3. Weevil seed removal in relation to vegetation density of plot. *** indicates highly significant p-value at a p-val<0.05 level. P-values were calculated through use of poisson regression. Vegetation density was only found to be significant factor in Italian thistle.

Thistle Species	P-Value
Italian Thistle	< 2e-16 ***
Yellow Starthistle	0.61

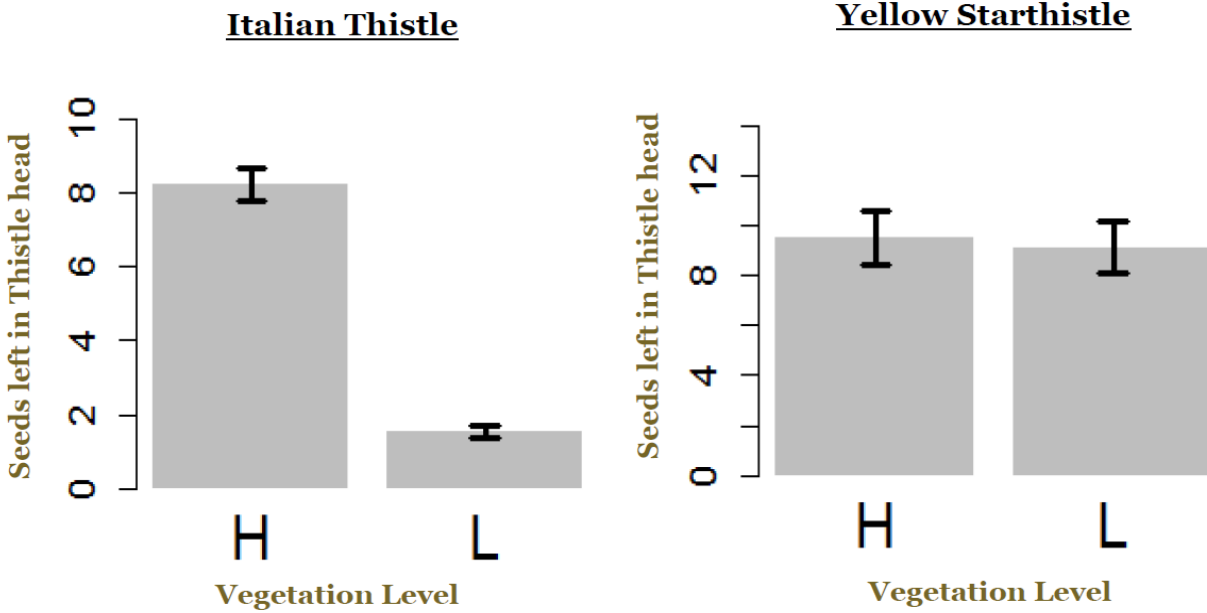


Figure 9. Thistle seeds remaining in thistle head as related to the plot’s vegetation level. Vegetation level was either high (H) or low (L). Seeds left was quantified with seed counts. As we can see, the difference in remaining seeds in Italian thistle between the two vegetation densities is easily seen as significant, while in yellow starthistle, there is no significant discernable difference.

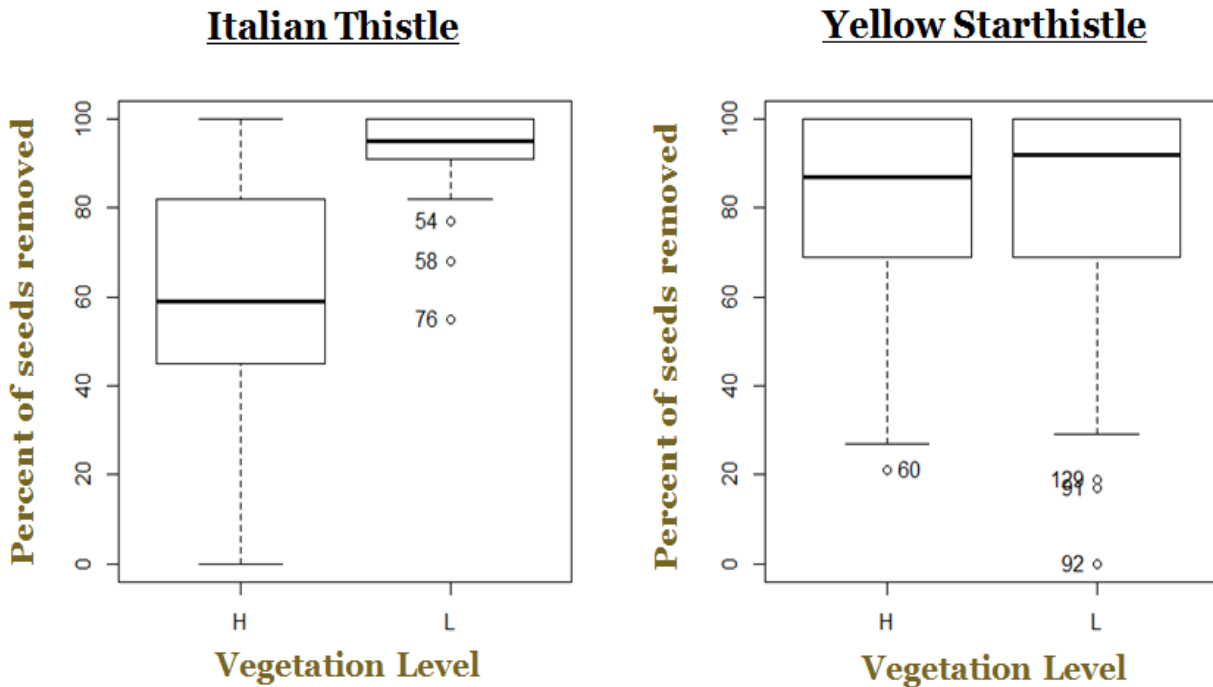


Figure 10. Proportion (transformed to percent) of seeds removed as related to the plot’s vegetation level. Vegetation level was either high (H) or low (L). Proportion of seed removal was calculated by dividing remaining seeds by the maximum amount of seeds found for each thistle species (22 for Italian thistle, 54 for yellow starthistle). As we can see, the percent of seeds removed is remarkably high throughout vegetation levels and for both species.

Density dependence study

For the total seed consumption, I found that only seed density was a significant factor, and only in Italian thistle (refer to Table 4 for p-values). In the bar graphs for vegetation and seed level and their relation to proportion of seeds removed, the difference due to variation in seed density can be seen in both thistle species, although in Italian thistle, the difference is more prominent and is statistically significant (Figure 11).

Table 4. Proportion of seeds removed as a response to vegetation and seed density. ** signifies a very significant p-value at a p-val <0.05 level. P-values were calculated through use of poisson regression. Only seed density in Italian thistle was found to be significant.

Thistle Species	Factor	P-Value
Italian Thistle	Vegetation Density	0.82669
	Seed Density	0.00801 **
Yellow Starthistle	Vegetation Density	0.49207
	Seed Density	0.12605

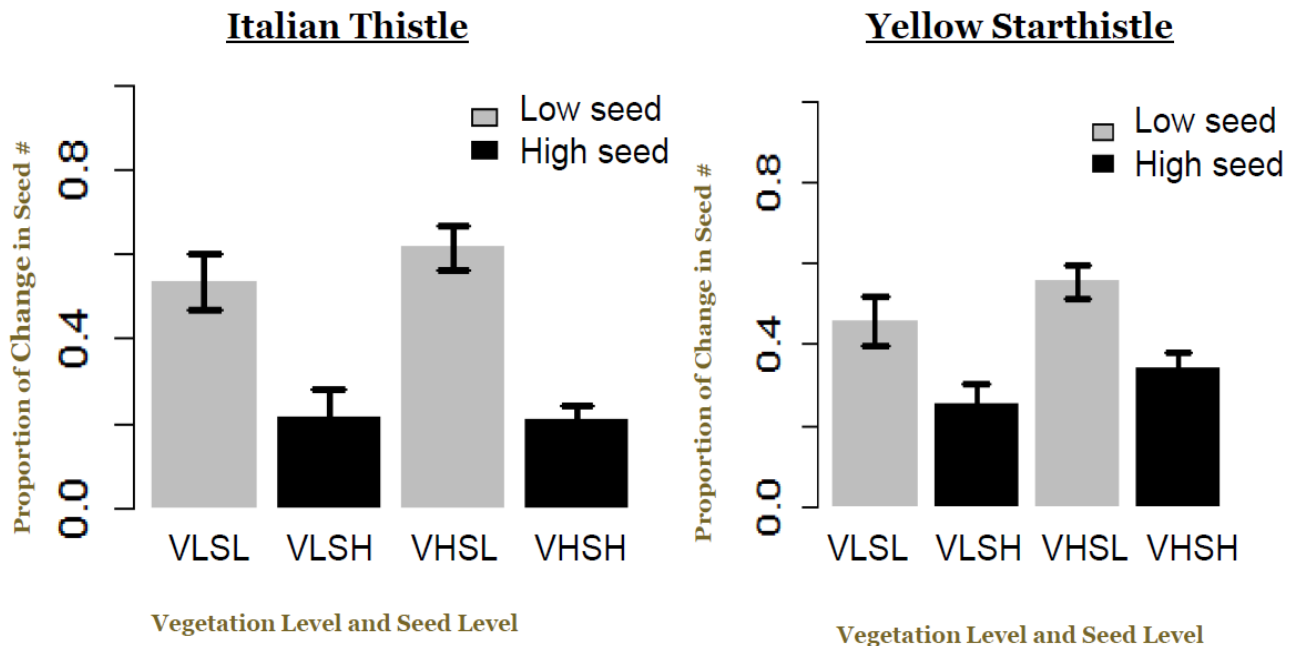


Figure 11. Proportion of seed removal in relation to vegetation level and seed level. Grey bars represent having low seed density. Black bars represent having high seed density. VL SL: low vegetation density, low seed density. VL SH: low vegetation density, high seed density. VH SL: high vegetation density, low seed density. VH SH: high vegetation density, high seed density. Proportional change in seeds was calculated with (# seeds remaining) divided by (original # of seeds).

DISCUSSION

Seed and vegetation density are factors that have been theorized to have significant impacts on seed predation patterns (Hulme and Hunt 1999). Through my experiment, I found that only seed density had a significant impact and that birds had the most seed predation activity, though it was less than weevil seed predation activity. These results are slightly contrary to my hypotheses of high densities of seed and vegetation being the most attractive patches to seed predators, though it corroborates my hypothesis that birds would have the most predation activity versus mammals. Additionally, I found that vegetation density was a statistically significant factor for weevil presence, however, for seed predation, vegetation density was only statistically significant for Italian thistle. These results show that density dependence (at least in relation to seed density) is a significant aspect that should be taken into consideration when creating comprehensive management strategies for California annual grasslands.

Exclosures

Birds had the highest levels of seed predation in this study (Figure 7). However, none of the exclosure treatments was significantly different from the rest (Table 1). Most studies done on seed predation have not found invertebrates to have particularly large impacts on seed production and plant recruitment (Zhang 1997). It is interesting to note that in the control plots, where all seed predators had access in the open plot, there is little to no seed predation activity. Perhaps this is a testament to my findings of seed density being the main factor influencing seed predators. If seed predators were only predating on the seeds set out when they chanced upon them, it could possibly explain how the open plots could have been undiscovered, while the complete exclusion plots could have possibly been infiltrated by a determined mammal. It was also interesting to note that the Italian thistle plots had higher levels of activity. This could have been a result of Italian thistle seeds being more attractive to seed predators due to their seed size being larger than that of yellow starthistle seeds, as seed size has been found to be influential (Zhang 1997). However, the exclosure activity ultimately cannot be analyzed without making some assumptions, due to lack of actual visual confirmation of seed predation (for example, through use of cameras or video). Taking that situation into account, I assumed that the all exclusion exclosures were successful and

had no seed predator activity. By using that data as a baseline for environmental factors (such as wind), we can see that even with the most activity, birds only predated on approximately 20-40% of the seeds presented. This is less than the levels of weevil predation, as discussed in the following section.

Weevil density and seed removal

There is a significant relationship between weevil presence and vegetation density in both thistle species at a $p\text{-val} < 0.05$ level (Table 2). The presence levels being higher in lower density vegetation plots could possibly be explained by the fact that in lower vegetation density plots there are fewer thistle heads present, which may mean that most heads are predated on (leading to higher proportion of presence), while in higher vegetation plots, there may be a greater number of heads available, and thus proportionally, the weevils are predated on fewer heads. Additionally, since the species of weevil found on the thistles are seed eaters (as opposed to being herbivores) (Wilson 2003), it is possible that the weevils are driven to predated on all the seeds they can find (and as a consequence are able to predate on most of the available seed heads in low vegetation density areas).

As for seed removal, my results show that the weevils remove 60-100% on average of the seeds in the thistle heads (Figure 10). This finding is not too surprising, as when the weevils lay their eggs on the thistle head, the larvae emerge and feed on the seeds (usually decimating the seeds as well as the thistle head itself at times) (Wilson 2003). Adult weevils also predate on seeds within the thistle heads (Wilson 2003). This is a much greater amount of predation as opposed to the seed predation levels of mammals and birds.

Density dependence

Seed predators were not attracted to plots based on high/low vegetation. The results showed that seed density in Italian thistle is a significant factor that may influence predation activities (Table 4). As mentioned earlier, this may have to do with forage optimization, since Italian thistle seeds are larger than those of yellow starthistle, perhaps making them more appealing (Janzen 1971). Studies have shown that seed predation limits plant recruitment and abundance (Orrock et

al. 2006, Bricker et al. 2010). Additionally, with seed predation, although this depletes the seed availability, it does not deplete the seed bank (seeds that fall to the ground and end up buried) (Zhang 1997, Joley 1992). This would suggest that even with heavy amounts of seed predation, the plants will be able to continue propagation due to remaining seed stores buried underground which are not predated as much (Louda 1990, Hulme 1999). Thus, even if current vegetation has low levels of seed remaining, new generations of plants can germinate from said remaining seeds. This may be why seed density is the more significant factor in regards to seed predation behavior. Vegetation is not always a good indicator of seed availability due to circumstances such as the patch being already cleared out of seeds by another seed predator, or the vegetation has already dispersed its seeds. If seed predators are only focused on finding stores of seeds, then foraging for seeds without taking vegetation into account would not be a folly, and could be their way of cutting out an "unnecessary" step. By using these results, management plans can be altered to reflect on-site density conditions and prime conditions to maximize impact by seed predators in the area.

Limitations

There were varying difficulties that I came up against while doing this project. There were difficulties in identifying exactly what seed predators were present. I had originally planned to use wildlife cameras to possibly gain footage of nocturnal vertebrates, but I did not manage to get access to appropriate equipment. As for birds, I attempted in-person observations while I was on-site, but I did not observe enough birds feeding at the thistles to make and identifications of possible birds that were active within my study area. The seed predators that had the most impact on my experiment were weevils, identified from taking specimens from the field site. Another difficulty I faced was with low levels of seed predation. This may have been a result of doing my study during the summer. In SFREC, the time frame in which I did my experiment was after the peak of most seed production, especially the wild oat (*avena*) that was plentiful at the site. This may have influenced seed predator activity perhaps due to a lull in seed predation after the *avena* had finished seeding. Time constraints mostly interfered with getting more samples or having time to finely sort seeds, and other such aspects of the project that required much time. Even with the difficulties, the findings of this experiment hold implications towards invasive species management.

Broader implications

My findings provide more information towards developing improved strategies for management for yellow starthistle and Italian thistle. As the study found that only seed density seems to affect seed predator foraging behavior, the implications of this are that management strategies could focus more on seed production and dispersal rather than vegetation presence. There is also the possibility that there are other factors not addressed in my study that are affecting the rangeland system. For example, the impact of interspecies competition between grasses and thistles, or even between seed predators and how that may affect seed predation behavior. There is also the possibility of natural disinterest in invasive thistle seeds due to the fact the thistles are invasive and do not have any of their native predators present in the California grasslands (besides the introduced weevils, which are technically also invasive species). The results showing that weevils are much more active in seed predation and thistle head destruction reinforces the rationale for their use as biocontrol agents, but it is still unclear as to how to prevent the weevils from possibly decimating native thistles that may also be present. More research into native seed predators may help provide an solution to this issue. These findings are important towards being able to control the spread of invasive thistles, which is a step towards finding more effective processes to reclaiming the native California rangeland landscape.

Future directions

Two important factors in invasive propagation were investigated in this project, but there are still more avenues of inquiry that should be explored. Future avenues to be explored could include other invasive species that are problematic in California rangelands and what factors affect their propagation. Specifically, what affect seed predation has on the propagation of these other invasive species. The effect of other factors that may be influencing the system may also be explored, such as interspecies competition between plant species, or between seed predator types. As to future options related specifically to my project, replicating the enclosure experiment so as to yield more conclusive results would be helpful in further clarifying the situation in the grasslands. The more avenues that are explored related to this topic, the better managers can

understand what the best strategy is to combat the encroachment of invasive plant species, and hopefully have a positive impact on the future of native annual grasses returning to dominance in California.

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REFERENCES

- Borchert, M.I. and S.K. Jain. 1978. The effect of rodent seed predation on four species of California annual grasses. *Oecologia* (Berlin) 33: 101-113.
- Bricker, M., D. Pearson, and J. Maron. 2010. Small-mammal seed predation limits the recruitment and abundance of two perennial grassland forbs. *Ecology* 91: 85-92.
- DiTomaso, J.M., G.B. Kyser, and M.J. Pitcairn. 2006. Yellow starthistle management guide. Cal-IPC Publication 2006-03. California Invasive Plant Council: Berkeley, CA.
- Dunn, P. H. 1976. Distribution of *Carduus nutans*, *C. acanthoides*, *C. pycnocephalus*, and *C. crispus*, in the United States. *Weed Science* 24:518–524.

- Evans, R.A., J.A. Young, and R. Hawkes. 1979. Germination characteristics of Italian thistle (*Carduus pycnocephalus*) and slenderflower thistle (*Carduus tenuiflorus*). *Weed Science* 27: 327-332.
- Hulme, P.E. and T. Borelli. 1999. Variability in post-dispersal seed predation in deciduous woodland: relative importance of location, seed species, burial and density. *Plant Ecology* 145: 149-156.
- Hulme, P.E. and M.K. Hunt. 1999. Rodent post-dispersal seed predation in deciduous woodland: predator response to absolute and relative abundance of prey. *Journal of Animal Ecology* 68: 417-428.
- Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104: 501-528.
- Janzen, D.H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2: 465-492.
- Joley, D.B., D.M. Maddox, D.M. Supkoff, and A. Mayfield. 1992. Dynamics of yellow starthistle (*Centaurea solstitialis*) achenes in field and laboratory. *Weed Science* 40: 190-194.
- Kok, L.T. 1998. *Rhinocyllus conicus* (Coleoptera: Curculionidae). Cornell University Department of Entomology. <http://www.nysaes.cornell.edu/ent/biocontrol/weedfeeders/rhinocyllus_c.html>
- Louda, S.M., M.A. Potvin, and S.K. Collinge. 1990. Predispersal seed predation, postdispersal seed predation and competition in the recruitment of seedlings of a native thistle in sandhills prairie. *American Midland Naturalist* 124: 105-113.
- Microsoft. 2007. Microsoft Office Excel 2007. Microsoft, Seattle, Washinton, USA.
- Orrock, J.L., D.J. Levey, B.J. Danielson, and E.I. Damschen. 2006. Seed predation, not seed dispersal, explains the landscape-level abundance of an early-successional plant. *Journal of Ecology* 94: 838-845.
- Palmblad, I.G. 1968. Competition in experimental populations of weeds with emphasis on the regulation of population size. *Ecology*. 49:26-34.
- Pickett, S. T. A. and P. S. White. 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press. Orlando, Florida, USA.
- R Development Core Team. 2006. R version 2.8.0. R project for statistical computing, Vienna, Austria. www.r-project.org

Wilson, M.W., C. Jette, J. Connett, J.P. McCaffrey, C.B. Randall, C. Kuykendall, and L. Lake. 2003. *Biology and Biological Control of Yellow Starthistle*. U.S.D.A. Forest Health Technology Enterprise Team, USA.

Zhang, J., F.A. Drummond, M. Liebman, and A. Hartke. 1997. Insect predation of seeds and plant population dynamics. *Maine Agricultural and Forest Experiment Station Technical Bulletin 163*: 5-25.