

SMALL MAMMAL AND INVERTEBRATE SEED PREDATION  
ON FIVE FUNCTIONALLY IMPORTANT SOUTH SOUND PRAIRIE PLANTS

by  
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## ABSTRACT

### Small Mammal and Invertebrate Seed Predation on Five Functionally Important South Sound Prairie Plants

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Low native plant establishment rates are a common challenge for prairie restoration land managers in western Washington. The reasons for these low establishment rates are still unknown. This study used exclusion cages to test if small mammals and invertebrates predate on seed from five functionally important plants with less than 5% establishment rates: *Balsamorhiza deltoidea*, *Dichanthelium oligosanthes*, *Armeria maritima*, *Viola adunca*, *Erigeron speciosus*. Additionally, three other factors were tested to see their influence on predation: seed size, edge effect, and timing. Five recently burned south Sound prairies were studied, each with three 50 meter transects including three plots along a gradient from the burn edge to the burn interior. Each plot contained four subplots (treatments): Insect entry, small mammal entry, complete exclusion, and no exclusion (total subplots= 180). Each treatment contained a seed dish with 20 seeds of each species (total seeds/dish= 100). These seeds were counted after 24 hours, 48 hours and one week to determine predation. Findings showed a clear preference by small mammals for larger sized seed (*B. deltoidea*, *D. oligosanthes*, and *V. adunca*). Insect predation was not observed for any species. Furthermore, no evidence of an edge effect influencing predation was found, and the majority of seed predation by small mammals was observed at the one week count. These findings suggest that attempting to mitigate seed losses from small mammals could positively influence seedling establishment rates for *B. deltoidea*, *D. oligosanthes*, and *V. adunca* in south Sound prairies.

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## **Introduction**

The prairies south of the Puget Sound in Washington state are some of the most endangered ecosystems in the United States (Noss & Scott, 1995). A startling 97% of this landscape has been lost since European colonization (Crawford & Hall, 1997). These quickly dwindling landscapes are important hotspots of biodiversity, with an impressive amount of floral and faunal diversity not seen in the surrounding forests. This diversity also includes many rare, endemic and endangered species, all of which are completely dependent on the health of this ecosystem (Dunwiddie & Bakker, 2011). Multiple drivers are responsible for this loss of prairie habitat. Euro-American colonization of the area approximately 200 years ago led to prairie landscape loss from agricultural and urban development, fire suppression, forest encroachment, and the spread of non-native and invasive species. Currently, an additional concern is how projected climate change will affect the south Sound prairie ecosystem.

These unique landscapes offer many justifications for their restoration and preservation. Ecologically, prairies perform important ecosystem services such as: providing a wide assortment of nectar and food resources for pollinators, sustaining habitat for rare and endangered species, creating buffers from wildfires and flooding, and are efficient water users with drought-tolerant plants that release less water through evapotranspiration than forests (Bachelet et al., 2011). Additionally, they offer a way to help mitigate climate change. Not only are they a drought and fire-tolerant landscape in a future projected to have hotter and drier summers (Crawford & Hall, 1997), they also store a surprising amount of carbon, even after fire, because most prairie plants have their growing structures protected underground. Grasslands also have higher albedo, reflecting

more light into the atmosphere than forests, leading to a cooling effect (Bachelet et al., 2011).

Besides their ecological value, these prairies hold important cultural significance worth considering in their preservation. South Sound prairies were important to local indigenous tribes, who maintained this open landscape through fire and harvests as a means to sustain a wide variety of useful plants as well as to make hunting and traveling easier (Dunwiddie & Bakker, 2011; Storm & Shebitz, 2006). There is great interest in reviving cultural harvests across these cultural ecosystems to support food sovereignty and security for indigenous peoples. Early Euro-American settlers also made extensive use of these prairies, finding the wide-open spaces the perfect place to begin building a life in the south Sound (Storm & Shebitz, 2006).

Many state, federal and non-governmental organizations are working on preserving and restoring this rapidly disappearing habitat. Restoration of a long-degraded ecosystem is not without its challenges, however. Decades of non-native species dominating these prairies has severely depleted the native seedbank, replacing it with an exotic-dominated seedbank (Holl et al., 2014). This legacy of non-native seed means that simple removal of invasive and exotic plants is not enough to bring back native species. Active planting and seeding of native species is needed to re-establish native flora. Unfortunately, so far many of these techniques have resulted in low establishment rates for native species (Hamman, Smith, & Bakker, 2015; Krock, 2016). Many factors likely play into these low establishment rates, yet few have been studied. The primary focus of this thesis is looking at one of these likely elements: seed predation by small mammals and invertebrates.

## South Sound Prairies Historical Background

The few prairies in the south Sound we see today are historical relics shaped from glacial outwash caused by the slow retreat of a large glacier, the Puget Lobe, around 16,700 years ago (Pringle, 2016). This outwash left soils that were well-drained with high gravel and sand content unique to the area (Spanaway and Nisqually soil series) (Lang, 1961). After this glacial retreat, the climate in western Washington was much hotter and drier than today (Foster & Shaff, 2003). During this period is when current native prairie plants, well adapted to these harsh conditions, began to establish (Whitlock, 1992).

There are hundreds of native plants found in south Sound prairies (Storm & Shebitz, 2006). The hallmark species of this landscape are the bunchgrasses (mainly Roemer's fescue (*Festuca roemerii*)), which grow in "bunches" instead of forming dense mats across the prairies. This growth form is important because it leaves patches of bare ground, allowing for the colonization of herbaceous forb species that cannot compete with mat-forming grasses (Figure 1) (Chappell & Crawford, 1997). These herbaceous species include many perennial and annual wildflowers, most commonly



Figure 1: Glacial Heritage Preserve (a prairie south of Olympia, WA) in early spring (Image credit: The Nature Conservancy)

camas (*Camassia quamash*), western buttercup (*Ranunculus occidentalis*), Oregon sunshine (*Eriophyllum lanatum*), and various lupines (*Lupinus* spp.) to name a few. Woody species are rare on the prairie, but a few shrubs (for example, serviceberry (*Amelanchier alnifolia*)) and sparsely dispersed trees such as Garry oak (*Quercus garryana*) make an occasional appearance.

Once these native species were established, frequent occurrences of drought and fire prevented conifer forests from invading the prairies (Crawford & Hall, 1997). Once the climate gradually started to cool and resemble more of what we would recognize today, local indigenous tribes intentionally introduced fire to keep out the ever-encroaching Douglas-fir (*Pseudotsuga menziesii*) forest. Native people burned the prairies to maintain plants not found in the surrounding forests used for food, medicine, and fiber. These expansive open grasslands also drew large game animals, like deer and elk, out of the forest to graze, making them easier to hunt. Additionally, open space made land easier to navigate, and offered safety by increased visibility (Storm & Shebitz, 2006).

Thousands of years of intentional management of the south Sound prairies by indigenous peoples preserved this landscape well before the arrival of Euro-Americans in the mid-1800s. The wide-open prairies in the Pacific Northwest must have shined like a gem to early settlers in the middle of the tangle of dense, dark old growth forests that required significant effort to clear for early homesteads and farms. However, many early pioneers struggled in their efforts to grow crops in these well-drained gravelly soils with low fertility (Crawford & Hall, 1997). South Sound prairie plants were adapted to these low-nutrient droughty conditions, but European crops were not. Colonists found the best

use for this landscape to be pastureland, and that is what much of it became (Easterly, Salstrom, & Chappell, 2005). These early settlers were not approving of the intentional fires being set to clear land that now had wooden structures and livestock on it, and quickly put an end to the most important tool in prairie preservation: fire (Hamman, Dunwiddie, Nuckols, & McKinley, 2011). Bachelet et al. (2011) identify the major factors in the rapid loss of prairie landscape as follows: active fire suppression and the transition of prairie into agricultural, grazing, and urban landscapes, followed closely by the introduction of invasive and non-native species (both accidental and intentional).

Invasive and non-native species, now dominate the majority of the south Sound prairie landscape and make up the bulk of the seedbank (Dennehy et al., 2011; Holl et al., 2014). Many of these species thrive in highly disturbed areas. They offer a form of competition that native prairie flora has not evolved to cope with. Additionally, invasive species like Scotch broom (*Cytisus scoparius*), a woody, nitrogen-fixing shrub, alter the vegetative structure of the prairies from bunchgrass and herb dominated to shrub dominated, as well as modify the soil chemistry and microbial communities to be unfavorable to native species (Haubensak & Parker, 2004). Other frequently observed invasive species include common lawn weeds such as hairy cat's ear (*Hypochaeris radicata*) and common sorrel (*Rumex acetosa*). Pasture grasses such as tall oatgrass (*Arrhenatherum elatius*) and colonial bentgrass (*Agrostis capillaris*) are widely prevalent, and likely intentionally introduced for livestock grazing (Chappell, 2006). Additionally, native Douglas-fir trees have been slowly colonizing the open prairie since the onset of fire exclusion, beginning the conversion of prairie to forest (Storm & Shebitz, 2006).

## **Current Restoration Practices**

Common prairie restoration protocol generally proceeds with the following order: spring grass-specific herbicide application, late-summer or fall prescribed burning to kill living exotic vegetation and consume the dead, thick thatch and moss layer (Hamman et al., 2011; Stanley, Dunwiddie, & Kaye, 2011), post-burn broad spectrum herbicide application to kill the quickly returning invasive plants, and finally native seeding and planting to reintroduce lacking native species. Seeding after burning and herbicide gives native species the best shot at germination, eliminating most of their competition and increasing the opportunity for seed-to-soil contact. It also, however, likely leaves the seed exposed and vulnerable to predation (Applestein, Bakker, Delvin, & Hamman, 2018; Hamman et al., 2015). This brings us to the focus of this thesis: the presence of seed predation on seed sown for restoration purposes. Land managers frequently suspect predation of native seed after it is sown, but until now no studies have evaluated the amount of seed lost to predation on south Sound prairies.

Having the ability to quantify where, when, and what may be consuming sown seed in the south Sound prairies could have valuable management implications. For instance, many predation studies have shown that the majority of seed predation by small mammals happens under vegetative cover because they are less exposed to predators of their own (Kollmann & Buschor, 2003; Mills, 1996). If this is also true for the prairie landscape, a mitigation technique could be to avoid sowing seed with a high likelihood of predation close to the edges of prairies. Sowing seed where it is least likely to get eaten could improve germination rates of existing seed, therefore being more cost effective. Additionally, if the seed of a species has an extremely high likelihood of getting eaten,

seeding may not be the best restoration tactic for that species, and alternatives, such as plug planting, might be necessary.

## **Research Questions and Hypotheses**

The main research question for this thesis is: Do small mammals or invertebrates prey on seed from five species commonly used for restoration in the south Sound prairies: deltoid balsamroot (*Balsamorhiza deltoidea*), panic grass (*Dichanthelium oligosanthos*), thrift seapink (*Armeria maritima*), hookedspur violet (*Viola adunca*) and aspen fleabane (*Erigeron speciosus*)?

These species were chosen because they have very low field establishment rates (less than 5%) (Hamman et al., 2015; Krock, 2016). Additionally, these species hold important roles in the prairie ecosystem and have been identified by prairie conservation partners as important plants for increasing seed production. *A. maritima* and *B. deltoidea* are nectar plants for the endangered Taylor's checkerspot butterfly (*Euphydryas editha taylori*). *E. speciosus* is an important late-season nectar source for many pollinators after most flowering plants have senesced. *V. adunca* is an oviposition host for the state candidate Valley Silverspot butterfly (*Speyeria zerene*) and a nectar plant for the state-endangered Mardon skipper (*Polites mardon*). *D. oligosanthos* is an important short-statured bunch grass that helps maintain the overall prairie habitat structure.

If predation is found, I wanted to know if it followed any patterns. Specifically:

- 1) *Does seed size influence the amount and source of predation?*
- 2) *Does distance from the edge of a burn unit affect the amount of predation?*
- 3) *In what timeframe after seeding is this predation occurring?*

My hypotheses are as follows:

1. *Predation is occurring by small mammals and insects, and the larger seed will be predated more than smaller seeds. Small mammals will likely prey on B.*

*deltoidea, A. maritima, D. oligosanthos, and V. adunca because of their size.*

Following the Optimal Diet Theory (ODT), foragers will seek to obtain resources that will give them the most calories for the least amount of energy expended (Kelrick, Macmahon, Parmenter, & Sisson, 1986). This would suggest that small mammals would select the largest and most appetizing seed and ignore smaller seeds.

2. *Invertebrates are more likely to prey on E. speciosus and V. adunca because they are small enough for ants to carry back to their colony.*

Invertebrates, especially ants, are limited in the size of seed they can carry, so they may be attracted to the smaller seeds. *E. speciosus*, the smallest of the seeds in this study, could easily be carried by ants.

3. *Small mammal predation will be most prevalent near the edges of burn units.*

Findings in other studies show that rodents feed almost exclusively under vegetative cover (Howe & Brown, 2000; Kollmann & Buschor, 2003).

Additionally, the edges of habitats experience higher levels of predation (Kollmann & Buschor, 2003). Since a recently burned prairie is very exposed and lacking in vegetative cover, I think it is unlikely small mammals will risk foraging in the open near the burn interior.

4. *Invertebrate predation will not show a preference for edges or the interior of the burn unit.*

Previous studies have found either no preference or a preference for foraging in the open for invertebrates (Herrera & Pellmyr, 2009).

5. *Seed predation by small mammals and insects is occurring mostly during the first 48 hours of placement.*

Existing literature has shown that small mammals and insects are highly efficient at finding seeds shortly after placement (Brown, Grover, Davidson, & Lieberman, 1975; Hulme, 1994). This is likely because rodents rely on scent to find seeds, which decreases over time since seed dispersal (Abramsky, 1983; Kollmann & Buschor, 2003).

### **Roadmap of Thesis**

This thesis aims to explore how seed predation could affect seedling establishment in south Sound prairies. The next section is the Literature Review, which discusses prairie ecosystem loss, seed ecology, and the concept of granivory (seed predation). This review is followed by my Methods, describing the specific sites and protocols behind the study. Then, in the Results, I present the findings for my research questions. This is followed by the Discussion, where I interpret the study results and how they could affect land management decisions. Finally, the Conclusion summarizes the most important findings of this study.

# Literature Review

## Introduction

This literature review is divided into four parts. Part I introduces the Puget Sound prairies and how they fit into the larger issue of worldwide ecosystem loss. In addition, I discuss some of the common restoration challenges faced by local land managers and their common restoration methods, including the seeding of native plants. Part II covers seed survival and ecology. This includes how seeds are dispersed, how seed predation affects ecology, factors influencing seed survival, how plants defend themselves against seed predation, how planting and sowing time could affect seed survival, and how seed predators can also act as seed dispersers. Part III introduces the concepts of seed predation, Optimal Diet Theory, and how this predation varies between the two most common seed predators: rodents and ants. Additionally, I consider the leading methods for measuring seed predation: exclusion cages and live trapping. Finally, I look at granivory in specific habitats: forests, grasslands, deserts, and old fields as well as the effect of edges and habitat fragmentation on seed predation. Finally, Part IV closes with the conclusion and the relevance for south Sound prairies.

## Part 1: The South Sound Prairies and Wider Ecosystem Losses

An alarming amount of species and ecosystem loss are happening on a global scale. In response, many biologists are warning of a modern-day mass extinction (Ceballos et al., 2015). The major identified causes of this mass extinction are habitat loss, degradation, and fragmentation (Noss & Scott, 1995). There are two different types of habitat loss, the first being **quantitative loss**. Quantitative loss is what most people

think of when they imagine disappearing habitat: the clearcutting of a forest for a housing development, or the transformation of grassland into a farm. The second form can be less clear: **qualitative loss**. This type of loss happens when an ecosystem still stands, but its very structure and function are degraded. In this case, an ecosystem may appear unaffected to the untrained eye but ecological webs that tie the system together slowly unravel and the ecosystem becomes unstable (Noss & Scott, 1995). This type of ecosystem loss happens with landscape fragmentation, where historically large, continuous landscapes are broken into smaller fragments. These fragments may appear simply as smaller versions of the whole, but animal and plant populations become isolated and smaller which leave them more vulnerable to extinction (Noss & Scott, 1995). The south Sound prairies are a textbook example of both types of loss. While much of this landscape was lost to development from urban and agricultural expansion, the remaining prairies continue to be affected by the resulting fragmentation, introduction of non-native and invasive species, and conifer forest invasion, which has isolated and weakened many of the remaining populations of animals and plants (Bachelet et al., 2011; Stanley et al., 2011).

These prairies are estimated to cover less than 10% of their historical extent, with only 3% of that extent considered to be high quality (dominated by native plants) (Crawford & Hall, 1997). Despite this extreme loss of habitat, these prairies remain home to a substantial number of rare and endangered species (Table 1) when compared to surrounding landscapes (Hamman, Smith, & Bakker, 2015). These areas have been long neglected since Euro-American colonization in the 1800s. This is due to the resulting decades of fire suppression and urbanization. More recently, these prairie's importance to

biodiversity has been recognized, and restoring them has become a priority for several organizations in order to preserve and expand habitat for endangered species.

**Table 1: Rare Species of South Sound Prairies and Associated Edge Habitats**

<b>Common Name</b>	<b>Scientific Name</b>	<b>Conservation Status</b>
<b>Plants</b>		
Columbian whitetop aster	<i>Sericocarpus rigidus</i>	ST
Golden Indian paintbrush	<i>Castilleja levisecta</i>	FE
Hall’s aster	<i>Symphyotrichum hallii</i>	ST
Small flowered trillium	<i>Trillium albidum</i> ssp. <i>parviflorum</i>	SS
Torrey’s pea	<i>Lathyrus torreyi</i>	ST
Virgate checkerbloom	<i>Sidalcea virgata</i>	ST
<b>Insects</b>		
Mardon skipper	<i>Polites mardon</i>	SE/FC
Puget blue	<i>Plebejus icarioides blackmorei</i>	SC
Taylor’s checkerspot	<i>Euphydryas editha taylori</i>	FE
Valley silver spot	<i>Speyeria zerene</i>	SC
<b>Vertebrates</b>		
Oregon spotted frog	<i>Rana pretiosa</i>	FT
Oregon vesper sparrow	<i>Poocetes gramineus affinis</i>	SC
Purple martin	<i>Progne subis</i>	SC
Sharp-tailed snake	<i>Contia tenuis</i>	SC
Slender-billed white-breasted nuthatch	<i>Sitta carolinensis aculeata</i>	SC
Streaked horned lark	<i>Eremophila alpestris strigata</i>	FT
Western bluebird	<i>Sialia mexicana</i>	SGCN
Western grey squirrel	<i>Sciurus griseus</i>	SC
Western pocket gopher	<i>Thomomys mazama</i>	FT
Western pond turtle	<i>Clemmys marmorata</i>	SE

Table 6: FE = federally endangered, FT = federally threatened, FC = federal candidate, SE = state endangered, ST = state threatened, SS = state sensitive, SC = state candidate, SGCN = species of greatest conservation need

## **The Endangered Species Act in Prairie Preservation**

The goal of the Endangered Species Act of 1973 (ESA) is to “protect and recover imperiled species and the ecosystems on which they depend” (U.S. Fish & Wildlife Service, 2013). Any plant or animal species can be listed as **endangered** (in danger of becoming extinct) or **threatened** (expected to become endangered). In addition to prohibiting the harvesting, hunting, or harming of species listed under the ESA, species’ identified habitats are also protected. These listings make it possible to fund prairie restoration projects in areas deemed as critical habitat, as well as preserving this habitat from development (U.S. Fish & Wildlife Service, 2013).

## **Non-native and Invasive Species on the South Sound Prairies**

As mentioned above, one of the leading drivers of habitat loss in the south Sound prairies is the noticeable increase in non-native and invasive species following Euro-American colonization in the mid-1800s (Dennehy et al., 2011). Invasive plants aggressively colonize disturbed areas and find glacial outwash prairies prime habitat. They can reach the prairies many ways, but several of them are suspected to have been intentionally introduced through historical land-use changes. For example, early settlers likely introduced the common non-native pasture grasses still present today for livestock grazing. Additionally, many non-native fruit trees and ornamental plants remain legacies from past homesteads (Hamman, Dunwiddie, Nuckols, & McKinley, 2011). Invasive species are also commonly introduced unintentionally. These species can establish after being transported a variety of ways (contaminated feed or hay for livestock, vehicles, wildlife, water flow, wind, etc.). Whatever their method of arrival, the presence of so many non-native species is concerning. Any non-native species on south Sound prairies

is occupying space that could be filled by a native species. This is important because native species provide a large number of ecosystem services that the native fauna has evolved over long periods of time to use, and when they are missing the whole ecosystem suffers (Dennehy et al., 2011).

Some invasive species, such as Scotch broom (*Cytisus scoparius*), which is prolific throughout the south Sound prairies, can alter the soil chemistry to favor invasive species over native species (Rook, Fischer, Seyferth, Kirsch, & LeRoy, 2011). In addition, particularly prolific invasive plants can change the habitat structure and/or species diversity of the prairie, sometimes nearly forming a monoculture. In the case of dense, decades-old Scotch broom stands, the habitat structure has changed from low statured bunch grass-dominated to shrub-dominated, which is not the proper habitat for the sensitive species that we are hoping to increase (Dennehy et al., 2011). Another example is reed canary grass (*Phalaris arundinacea*), a tall invasive pasture grass that forms monocultural stands with thatch so dense almost no other native species can compete (Kilbride, Paveglio, Kilbride, & Paveglio, 1999). One of the consequences of the increase in non-native and invasive plant abundance is an immense loss of native plant species diversity (Dunwiddie & Bakker, 2011; Krock, 2016). This substantial reduction of native plant species is connected to the loss of various animal species including butterflies and birds (Altman, 2011). Another result of the domination of non-native species on the prairies is a change in the fire ecology that the prairies have been adapted to for thousands of years (Hamman et al., 2011). This is a classic example of qualitative ecosystem loss, as described above.

As mentioned in the introduction, when invasive species begin to dominate the

landscape they also tend to dominate the seedbank (Holl et al., 2014). Therefore, the simple removal of invasive species is not enough to restore the native ecosystem. The prairies must be actively restored and supplemented with native seed to have a chance at recovery and to provide habitat for threatened and endangered species. Consequently, knowing how to get the most out of this seed is important for organizations operating on limited resources; and understanding how various factors (for example, seeding method, sowing rate, or seed predation) – affect seed germination and establishment is needed for efficient and effective restoration (Applestein et al., 2018).

### **Restoration Challenges in South Puget Sound Prairies**

A considerable amount of labor and money goes into the restoration of the south Puget Sound prairies. An important part of this restoration is the seeding of native plants. This seeding is done both by hand and by heavy machinery. Broadcast seeding is the most common method, in which seed is scattered over large areas. This is usually done by tractor and is sometimes followed by light tillage to increase the seed's contact with soil (Applestein et al., 2018; Hamman et al., 2015). This seeding allows native vegetation to get a head start on common invasive plants that often fill the vacant space left behind after major restoration activities such as burning and herbicide. The native seed that is applied to the prairies comes either from wild harvest or is cultivated on the Center for Natural Lands Management (CNLM)'s various seed farms (Krock, 2016). Both methods require a lot of infrastructure, maintenance, time, and funding to function.

The standard timing of seeding is the fall after prescribed burning, which usually happens in mid-late summer and is highly weather dependent. Seeding after burning allows the most seed/soil contact and has been shown to increase seedling germination on

the prairies (Maret & Wilson, 2005; Stanley et al., 2011). Besides seeding, another common technique is planting plugs (living plants). Both methods offer positives and negatives; but direct seeding tends to be much more cost-effective and can cover a larger amount of land with less labor (Dunwiddie & Bakker, 2011; Krock, 2016).

Even though seeding holds great potential for increasing native vegetation, so far it has resulted in very low germination rates ranging from 1-10% (Hamman et al., 2015; Krock, 2016). Other grassland sites have shown similarly low establishment rates, including the coastal prairies of California (Holl et al., 2014). Even accounting for sterile seed and other factors, these rates are surprisingly low. It is likely that a combination of factors is responsible for the low germination rates, and that some of these factors are species dependent.

The potential factors affecting seed germination include, but are certainly not limited to climatic conditions, microsite variation, competition from established plants, soil factors, seed predation, water, and nutrient availability, pathogens, and seeding techniques (Applestein et al., 2018; Bakker, Wilson, Christian, & Li, 2003; Fenner, 2000; Krock, 2016). Few attempts to quantify these potential factors have been made, even though studying them could greatly increase the germination rate of seedlings delivered. It is important to note that because of their rarity, there is very little known on the proper planting techniques for many of these native species, so it is expected that there will be a large learning curve in understanding the best methods for successful establishment.

### **Planting Time / Seed Sowing Time**

Early summer-fall is when native south Puget Sound species naturally disperse their seeds. The seed used for restoration must be collected, cleaned, cured, mixed, and

applied to the prairies. These tasks usually result in sowing seeds later than natural dispersal time (Krock, 2016). This seed is also applied after summer burns since that has resulted in higher germination rates (more seed/soil contact) and this process gives native species a chance to compete with invasive plants (Hamman et al., 2015; Stanley et al., 2011).

## **Part II: Seed Ecology**

### **Seed Dispersal**

Three fates await dispersed seed: Germination, death, or entering the seedbank. The most common fate of a seed is death (Clark & Wilson, 2003; Fenner, 2000), and the most common causes of death are herbivory, drought, and pathogen attack (Moles & Westoby, 2004). Most plants prepare for this inevitable loss by producing a large amount of seed (Fenner, 2000). What happens to an individual seed after dispersal from its parent plant is challenging to study and quantify in the natural environment, which is why few studies have attempted to do so. A large portion of seed death is thought to be caused by predation from insects or animals, but this predation is species and location-dependent (Clark & Wilson, 2003).

Many factors outside of seed predation contribute to high rates of seed death. Even before a seed is formed there are challenges. For instance, lack of pollination, lack of adequate resources for development, or poor genetics (Fenner, 1985). Seeds that make it past this stage and are successfully dispersed face even more obstacles to germinate: they could be desiccated, buried too deep or not deep enough, have improper access to light, become exposed to various diseases, and even suffer from competition with fellow

seedlings (Fenner, 1985; Moles & Westoby, 2004). In short, seeds must overcome an overwhelming number of hazards to germinate.

### **Seed Predators or Seed Dispersers?**

As mentioned above, seed predation can shape ecosystems. Sometimes seed predators can unintentionally act as seed dispersers. If the seed is not eaten on site, it is often transferred to caches, which are sometimes forgotten (Janzen, 1971). These caches can allow plants to expand their range beyond their dispersal ability and colonize new areas. However, it is important to note that seed survival rates from caches are low (Herrera & Pellmyr, 2009).

Small mammals' preference for larger seed can give smaller seeded species a chance to germinate where they otherwise would not be able to compete. In this sense, seed predation can enhance diversity (Herrera & Pellmyr, 2009). A great example of this is from a study by Brown & Heske (1990) whose removal of seed-eating rodents from a desert ecosystem led to a loss in biodiversity. Similarly, seed-eating rodents in temperate grasslands have been shown to slow tree invasion because they prefer large tree seeds (Myster & Pickett, 2019).

Understandably, immobile plants would adapt to using mobile animals as dispersal agents. Vertebrates are familiar seed dispersers through eating fruit, accidental ingestion, or having the seed attach itself to the outside of the animal (Herrera & Pellmyr, 2009). Ants are common seed dispersers as well, and many plants encourage their seeds to be harvested by ants. These seeds have an appetizing outer coating of lipids, called **elaiosomes**, designed to be eaten by ants while leaving the rest of the seed intact (Bartow,

2014). The remaining seed is usually discarded, potentially in an area where it could germinate (Herrera & Pellmyr, 2009).

### **Seed Predation's Effect on Plant Ecology**

Seed predation can alter how plants are distributed across the landscape (Kollmann & Buschor, 2003; Mittelbach & Gross, 1984). When plant recruitment is **seed limited**, the plant is not producing enough seed, or its distribution is patchy. In this case, seed predation would have an impact on this species' already limited distribution.

Another situation where seed predation could influence plant recruitment is when plants have no vegetative reproduction and/or their seed bank is depleted (Kollmann & Buschor, 2003). When a plant is **microsite limited**, the competition with other species as well as the parent plant is so high that dispersed seed is likely to die anyway, therefore predation has little impact (Fenner, 2000). In general, plant recruitment is much more likely to be limited by microsite availability than seed production. Ecosystems that are often seed limited are those that have abundant recruitment space, such in the desert and other semi-arid environments (Fenner, 2000). The rare prairies of Oregon, Washington, and California have been identified as being seed limited for native species (Holl et al., 2014; Maret & Wilson, 2005; Stanley et al., 2011), suggesting that seed predation could negatively impact these ecosystems.

Many studies have shown that both insects and rodents can have an impact on seed survivorship as well as acting as a driver for the species composition of an area. For instance, rodents' fondness of large seeds can give smaller seeded species an advantage spatially (Heithaus, 1981). Over time, seed predation drives seed evolution (Herrera & Pellmyr, 2009). Rodents' preference for eating seed under the cover of vegetation, where

plants tend to drop most of their seed, reduces the amount of seed under the parent plant. This allows the majority of regeneration to occur farther away from the parent plant and reduces the competition for resources (Janzen, 1971).

### **Plant Defenses**

Due to their attractiveness to potential predators, many plants invest a lot of energy in protecting their seeds. This can include physical and chemical defenses such as toxins, protective coatings, shells, and varying size (very large or very small seeds rule out specific types of predators). Often, the larger and more nutrient-dense seed is, the more likely it has some sort of defense mechanism (Howe & Brown, 2000). Additionally, plants can also adapt to predation over time by changing when they flower and produce seed. Another method seen in many tree species is **masting**, where trees produce massive amounts of seed some years but not others. This method prevents predators from adapting to this irregular food source and guarantees some survival of seed (Fenner, 1985).

## **Part III: Granivory**

### **Introduction: Granivory**

When animals feed exclusively or mainly on seeds they are referred to as **granivores**. These animals can shape the ecosystems they live in by the selective nature of their diets. Most ecosystems experience high rates of seed predation, and losses of over 50% of seed produced are not uncommon (Herrera & Pellmyr, 2009). To account for these immense losses from predation and other seed mortality, plants must produce a generous quantity of seed to be successful (Fenner, 2000). Seed predators act as a driver for natural selection, pushing plants to adapt to this pressure (Kollmann & Buschor, 2003). This section of the literature review will focus on the topic of seed predation and

the role it plays in ecosystems.

Seed predation has been found to have a noticeable effect on plant abundance and distribution in various ecosystems including forests, deserts, grasslands, and shrub-steppe. In ecosystems where food is extremely limited for herbivores, such as in deserts, seeds are often the most concentrated nutrient source available, offering more calories for their size than roots, stems, or leaves can provide (Fenner, 1985). This makes seeds a highly desirable food source for animals in these harsh environments.

Most seed is eaten pre-dispersal (while the seed is still on the plant, where it is highly concentrated) rather than post-dispersal (Herrera & Pellmyr, 2009). Dispersed seed is more likely to be eaten in areas with high amounts of vegetation cover, especially if it is dispersed in concentrated groups (for example, large amounts of seed dropped below a parent plant) and if it is left exposed on the soil surface, rather than buried (Kollmann & Buschor, 2003; Mittelbach & Gross, 1984). Therefore, dispersed seed has the best chance of survival if it is in an area with little vegetation cover, is dispersed far from other seeds and the parent plant, and is buried (Hulme, 1994).

### **Optimal Diet Theory**

Many of the foraging patterns we see follow the Optimal Diet Theory (ODT). The ODT states that foragers utilize prey based on what will give them the most amount of caloric input for the least amount of energy spent foraging. Additionally, if more valuable prey appears in the environment, foragers will use that instead of lesser valued prey (Kelrick, Macmahon, Parmenter, & Sisson, 1986; Sih & Christensen, 2001). In this case, larger seeds offer more nutrition per seed but may be too large to carry for insects, whereas small seeds offer little energy but are easier to transport (Brown et al., 1975). In

agreement with ODT, several studies have shown that rodents prefer and harvest larger seeds first if given a choice (Abramsky, 1983). This theory usually holds true for seed predation, but not always. Since seeds are such a highly valuable food, many plants have evolved ways to deter seed predators. These deterrents can come in the form of toxins, protective seed coatings, and protective shells (Herrera & Pellmyr, 2009). For rodents to consume seeds with high levels of defenses, they must expend more energy, which is often not worth the reward. Therefore, when offered an array of seeds rodents will choose the largest, and if they make other choices researchers should consider specific seed defenses as a possible explanation.

### **Seed Predation by Rodents**

Rodents have repeatedly been shown to heavily influence seed survival, impacting the abundance and dispersal of particular plants, and in some cases even helping to shape entire vegetative communities (Edwards & Crawley, 1999; Heithaus, 1981). Rodents predate on seed almost exclusively at night (Abramsky, 1983), and prefer to feed under the protection of vegetation (Howe & Brown, 2000; Kollmann & Buschor, 2003). More specifically, rodent seed predation is particularly high near the edges of habitats, since these areas tend to be the most densely vegetated (Kollmann & Buschor, 2003).

Overall, rodents show predictable seed preferences. In general, they prefer larger seed, per the Optimal Diet Theory (Brown & Heske, 1990; Clark & Wilson, 2003; Heithaus, 1981; Mittelbach & Gross, 1984). Additionally, meadow and prairie voles show a strong preference for dicot over monocot seeds (Howe & Brown, 2000). Likewise, they will choose seed that is less defended than seed with a high amount of

defenses (for example, toxins and hard shells) (Herrera & Pellmyr, 2009).

Rodents most commonly find seed by scent. Since a seed's scent becomes less detectable over time, the longer dispersed seed is in the environment the less likely it is to be discovered (Abramsky, 1983; Kollmann & Buschor, 2003). Additionally, the higher the concentration of seeds in an area, the stronger their scent will be, and the more likely the seeds are to be detected. Not surprisingly, burying seeds decreases their scent. However, rodents can often still find buried seed, especially if the source is concentrated enough (Heithaus, 1981). This ability separates rodents from other seed predators and is likely why they are so successful.

Once a seed source is found, a rodent's method of harvest generally involves obtaining as many of the seeds as possible at one time, indiscriminately stuffing large quantities in their mouths, and returning to their burrow (Brown et al., 1975; Heithaus, 1981). They repeatedly visit a known source of the seed until it is exhausted and they have proven to be very efficient at this process (Mittelbach & Gross, 1984). Rodents often "cache" their seeds, burying them for later use (Kollmann & Buschor, 2003). Sometimes these sizable caches turn into **larder hoards**: large amounts of the seed buried deep in the ground, which is sometimes forgotten (Herrera & Pellmyr, 2009). Rodents preying on seed frequently leave signs behind including seed shells, urine, and droppings, making them easy predators to identify in seed predation field experiments (Kollmann & Buschor, 2003).

The south Sound prairies are home to many types of rodents (Table 2). Based on habitat requirements, diet, and frequency of observation, I have identified three species that are likely predators of seed used for restoration in recently burned areas. These

species are: Deer mice (*Peromyscus maniculatus*), Townsend’s voles (*Microtus townsendii*), and Pacific jumping mice (*Zapus trinotatus*), all discussed further below.

**Table 2: Rodents found in South Sound Prairies**

Species		Diet	Seed eating
Broad footed mole	<i>Scapanus latimanus</i>	I	No
Coast mole	<i>Scapanus orarius</i>	I	No
Common porcupine *	<i>Erethizon dorsatum</i>	H	No
Creeping vole	<i>Microtus oregoni</i>	H	No
Deer mouse	<i>Peromyscus maniculatus</i>	O	Yes
Gray-tailed vole *	<i>Microtus canicaudus</i>	H	Yes
Pacific jumping mouse	<i>Zapus trinotatus</i>	O	Yes
Townsend’s mole	<i>Scapanus townsendii</i>	I	No
Townsend’s vole	<i>Microtus townsendii</i>	H	Yes
Vagrant shrew	<i>Sorex vagrans</i>	I	No
Western pocket gopher *	<i>Thomomys mazama</i>	H	No

I= insectivores, H= herbivores, O=omnivores, \* = uncommon

Deer Mice: (*Peromyscus maniculatus*):

Deer mice are widespread generalists that thrive in disturbed habitats. They are omnivores, with a diet primarily of insects and seeds. While they have a relatively small home range (0.032ha – 1.2 ha depending on food access) (Stickel, 1968), they are efficient predators of seed, with each mouse capable of caching up to three liters of seed per year (Naylor, 1994). While some seed from these forgotten caches may germinate, they often suffer from disease and intense competition due to germinating so close together (Moore, 1940).

Unlike most small mammals, deer mice are active in open habitats, not relying on

hidden pathways through vegetation like voles, or burrowing underground like pocket gophers or moles (Corn & Bury, 1991). Deer mice have been shown to respond favorably to recently burned areas, and are often the first animals to re-colonize post-burn (Baker, 1968; West, 1992). A study by Tevis (1956) found that the population of deer mice doubled after a Douglas-fir clear cut in California was burned to remove slash. Likewise, multiple studies in grasslands and prairies have found increased populations of deer mice in burned plots when compared to unburned plots (Peterson, Kaufman, & Kaufman, 1985; Schramm & Willcutts, 1983). The key for deer mice's preference for burned plots likely lies in the removal of plant litter, which exposes the soil and makes seeds easier to find (Kaufman, Kaufman, & Finck, 1988; West, 1992).

Townsend's Vole (*Microtus townsendii*):

Townsend's voles are common in grasslands and riparian areas along the western coast of North America. They prefer edge habitats near aquatic environments with thick stands of grass for burrowing (Cornely & Verts, 1988). They are herbivores, eating fresh vegetation, tubers, roots, seeds, bark, and wood. Their diets are dependent on what is available seasonally. Notably, in the late summer and fall, voles rely heavily on seeds as a nutrient-dense food source to help them prepare for winter (Taitt & Krebs, 1982; Witmer & Vercauteren, 2001). They have been known to cause damage to agricultural fields by eating the sown seed, seedlings, and root vegetables (Askham, 1990; Witmer & Vercauteren, 2001). Additionally, large populations of voles in grasslands can drastically shape species composition based on their herbivory (Sullivan & Howe, 2009). These voles also use caches but store primarily tubers and bulbs as opposed to seed (Cornely & Verts, 1988).

### Pacific Jumping Mice (*Zapus trionotatus*):

The Pacific jumping mouse is common along the western coast of North America. They require habitats with access to wet, dense vegetation, living in both forests and wet grasslands near riparian areas (Hafner, Yensen, & Kirkland, 1998; Himes & Christopher, 2013). Pacific jumping mice are omnivores, eating primarily seed. Unlike voles and deer mice, Pacific jumping mice do not cache their food (Niethammer, 1990).

While Townsend's voles and Pacific jumping mice likely have some impact on seedling establishment in the south Sound prairies, deer mice are suspected to have the greatest impact. Burning prairies enhances deer mice habitat, and seeding post-burn provides an optimal abundance of food. Both Townsend's voles and Pacific jumping mice are limited by their requirements for dense vegetation and mesic environments. This makes them unlikely to play a large role in seed predation in recently burned prairie interiors. However, they could be an additional concern in burned areas with bordering forests or riparian zones. All of these species typically have increased populations in the late summer and fall, and rely heavily on seeds for food during this time (West, 1992). This, unfortunately, coincides with when most of the seeding is conducted on south Sound prairies (Krock, 2016).

### **Seed Predation by Ants**

Ants have their own unique harvesting methods. Not surprisingly, because of their size, ants are limited by their ability to carry seeds. They prefer to gather smaller seeds and harvest them slowly but consistently, usually one at a time (Brown et al., 1975; Heithaus, 1981; Mittelbach & Gross, 1984). Like some rodents, harvester ants also stash and store seed for later use within their underground nests (Brown, Reichman, &

Davidson, 1979). For this reason, ants can act both as seed predators and as seed dispersers (Herrera & Pellmyr, 2009). Unlike rodents, ants prefer to harvest seed during the day; and are unable to find seeds that are buried (Brown et al., 1975). Ants have also been shown to cache seeds outside of their nests, often under rocks where rodents cannot get to them and the ability to germinate is severely limited (Herrera & Pellmyr, 2009). A summary of the differences and similarities of rodent and ant seed predation is shown in Table 3.

**Table 3: Major Seed Predator Preferences**

	<b>Rodents</b>	<b>Ants</b>
<b>Seed preference</b>	Large	Small
<b>Harvest rate</b>	Fast; as many seeds as possible	Slow, one seed at a time
<b>Foraging cover</b>	Under cover	Open
<b>Foraging evidence</b>	Droppings, urine, seed hulls	Missing seed, ants in dish
<b>Foraging time</b>	Night	Day
<b>Caching</b>	Yes	Yes
<b>Find seeds by</b>	Scent	Visual cues
<b>Can find buried seeds</b>	Yes	No

### **Seed Predation by Birds**

When conditions are optimal, birds can be especially resourceful seed predators and seed dispersers (Janzen, 1971). However, they remain difficult to study, and their effects on seed survival in most environments have proven negligible. Most research that has looked at the effect of post-dispersal seed predation by birds find that they do not have a noticeable effect on plant recruitment when compared to rodents and ants (Holmes & Froud-Williams, 2005; Mares & Rosenzweig, 1978; Mittelbach & Gross, 1984). This is likely because birds require large amounts of energy, specifically in cold weather.

Average sized seeds dispersed naturally in the environment (as opposed to those seeded

in artificially large amounts for restoration or agriculture) are likely not available in concentrated or consistent enough amounts to offer enough energy for most birds to survive on (Mares & Rosenzweig, 1978).

Birds are challenging seed predators to study, and available literature on the subject is lacking. On one hand, birds can act as seed predators and seed dispersers in environments with consistent (either year-round or seasonal) access to seed (Janzen, 1971). Areas that have artificially concentrated amounts of seed, like farms, may be easy targets for granivorous birds. For example, birds are known to prey heavily on *Balsamorhiza deltoidea* seed at CNLM's seed farm (Smith, 2018). On the other hand, most research agrees that birds do not have a large effect on plant recruitment in natural ecosystems, especially when compared to rodents and ants (Mares & Rosenzweig, 1978).

There are likely flaws in some experimental designs when it comes to studying avian seed predation. Most experiments either don't have seed out for long enough for birds to become accustomed to it (seeds are usually only out for hours-weeks) or use non-native seed (Brown et al., 1979; Kelt et al., 2004; Mares & Rosenzweig, 1978; Morton, 1985). Alternatively, if bird feeding is particularly heavy in exposed trays, this would probably reflect the opportunistic behavior in response to an unnatural concentration of food and not wild behavior (Kelt et al., 2004). Birds also tend to forage seasonally, following the most abundantly available food. Therefore, the short time in which most of these experiments were conducted may not have aligned with the seasonality of when granivorous birds were present (Kelt et al., 2004). A study of avian predation in cereal fields in the UK found that while overall avian predation was low, it was at its highest (<7% removal of seed compared to 51% of non-avian predators) in the spring, while

other species had their highest seed predation in the autumn and winter (Holmes & Froud-Williams, 2005). These findings speak to the high seasonality of avian seed predation. Seed predation experiments that rely on exclusion cages may not be the most accurate, and findings of low bird granivory could be a result of study design (Morton, 1985).

In trying to interpret how birds may be taking advantage of seed sown on the south Sound prairies, we should consider a few factors. First, when burn units are seeded, seed is exposed and in larger quantities, which may make it a source worth exploiting by birds. However, this placement of seed is probably not consistent enough (done in the same time at the same place every year) for birds to become conditioned to this food source, as Kelt et al. (2004) suggests is necessary. Considering this, I think it is unlikely birds are predated large quantities of the seed used for restoration on the prairies. However, factoring in the above reasons for the shortfalls of studying birds as seed predators, this is a subject worthy of deeper investigation.

### **Other Seed Predators**

Several other animals eat seed post-dispersal, including mollusks, beetles, wasps, moths, crabs, non-rodent mammals, and even fish (Herrera & Pellmyr, 2009). These organisms are poorly studied regarding how their seed-eating effects plant populations. Many beetles, butterflies, moths, wasps, and other insects will predate on the seed during their larval or adult stages (Brown et al., 1979; Herrera & Pellmyr, 2009; Jules & Rathcke, 1999). Two studies that included mollusk seed predation as a factor found few occurrences (Hulme, 1994; Kollmann & Buschor, 2003). While these species are likely to have some influence on seed survival, their effect is highly unlikely to rival the top three

granivores (rodents, ants, and birds). Therefore, they probably have little impact on plant establishment rates (Brown et al., 1979). As with birds, it is also possible that the current methods used for measuring seed predation by these species is lacking, and therefore their impact is underestimated.

## **How Seed Predation is Measured**

### Exclusion Cages:

Most studies measuring the amount of seed predation in the field rely on exclusion cages. These cages are constructed with different sized mesh that allows or prevents access by different organisms (mainly small mammals or invertebrates) to pre-determined amounts of seed. For instance, a cage made of ¼” mesh would prevent rodent access but allow ants; and a cage with ½” mesh would allow rodents. Additional measures can be made to prevent insects from accessing a tray in the cage allowing rodent access; for example, the tray can be slightly elevated off the ground with a nail, and a protective coating can be painted on the outside of the tray with a slick surface substance such as Fluon® and/or petroleum jelly. This methodology has been replicated in several field experiments with promising results (Abramsky, 1983; Brown et al., 1975; Heithaus, 1981; Hulme, 1994; Kelrick et al., 1986; Kollmann & Buschor, 2003; Mittelbach & Gross, 1984).

### Live Trapping for Population Estimates:

Often, live trapping of small mammals is done alongside exclusion cage studies to determine rodent species and abundance in the study site (Borchert & Jain, 1978; Heithaus, 1981; Hulme, 1994; Kelrick et al., 1986; Kollmann & Buschor, 2003). This process usually involves baiting traps, checking at specific intervals, and marking the

animals caught with dye. From new captures and re-captured animals, a population density estimate can be determined. Live trapping is the most common measurement of small mammal population density, but is far from a perfect measure and relies on many assumptions of animal populations and residency that have more recently been scrutinized for their accuracy (Efford, 2004).

### **Specific Habitats**

Since there have yet to be any studies on seed predation in south Sound prairies, it is necessary to glean information from other habitats to know what to expect in this specific ecosystem. While grasslands seem like the most obvious comparison, forests are also important because many of the south Sound prairies are adjacent to conifer forests and thus may have somewhat of an edge effect with them. South Sound prairies can also be compared to desert ecosystems, with their drought tolerance and well-drained gravelly soil. Old fields (long-neglected/abandoned farm fields) are also relevant, as many of the prairies historically had agricultural practices, such as grazing.

#### Forests:

In forested ecosystems, seed predation is particularly abundant along the edges (Mills, 1996). Forest edges exposed from man-made or natural disturbances change the abiotic conditions, allowing more light penetration, exposure to wind, and more extreme temperature fluctuations (Mills, 1996). These conditions allow for an increase in understory cover, creating more space for rodents to safely feed (Kollmann & Buschor, 2003; Mills, 1996).

The effect of heavy rodent predation along forest edges has been shown in many studies. For example, a study of forest edges in Chile showed that plots that prevented

access to granivores had almost twice the amount of tree seedlings (Donoso, Grez, & Simonetti, 2003). Another study suggested the low abundance of hickory and beech trees in the Eastern U.S. was caused by the intense predation of nuts by small mammals (Janzen, 1971). In a western Oregon conifer forest adjacent to a recent clear-cut, researchers found rodents to be such efficient predators of *Trillium ovatum* seed that no new plant recruitment was found for this species within 50 meters of the forest interior. While the amount of seed predation in a given area depends on the type of seed and the type of predators that exist there, it is clear that both edges and rodents have an impact on plant diversity and abundance (Donoso et al., 2003). With increased fragmentation and deforestation worldwide, increases in seed predation could theoretically impact forest plant recruitment and change vegetative communities over time.

When compared to their edges, forest interiors are unlikely to be very affected by seed predation because they are already limited by microsite availability, mainly access to light. Basically, seed predation will not affect overall plant abundance because the likelihood of those seeds making it to a suitable site for germination is so low, they are likely to die anyway. However, some long-lived woody species in forest interiors may be negatively affected if they cannot vegetatively reproduce, have a limited seed bank, and additionally have seeds that are highly attractive to granivores (Kollmann & Buschor, 2003).

#### Desert:

When compared to most ecosystems, deserts have a noticeable lack of available food (Brown et al., 1975). In environments like this, seeds become an even more valuable food source. Seed predators in these environments are considered seed specialists

(species that only eat seed) (Mittelbach & Gross, 1984). Evidence suggests that seed availability limits granivore populations in deserts (Brown et al., 1979). Due to the lack of moisture, desert-adapted plants are highly responsive to rain events. Many desert annual plants invest in producing massive amounts of seed that can lay dormant in the soil until optimal conditions arise. Thanks to this large seed bank, granivores can rely on this food source year-round (Brown et al., 1979).

A study in an Arizona desert by Brown et al. (1975) showed that both ants and rodents were very efficient harvesters of seed but were separated by time of day. Rodents harvested seed almost exclusively at night, whereas ants harvested exclusively during the day. These foraging patterns are likely due to habits in predator avoidance. The heavy seed predation displayed in deserts shapes their floral distribution patterns. Brown & Heske (1990) showed in another Arizona desert exclusion experiment that removal of seed-eating rodents led to an ecological transition from desert to grassland over 12 years, and a reduction in overall plant diversity.

#### Grasslands and Prairies:

Grasslands often have higher seed predation by rodents and insects than other ecosystems (Borchert & Jain, 1978; Hulme, 1994). Large populations of voles can dramatically shape grasslands through their herbivory, by eating established plants and seed both pre and post dispersal (Sullivan & Howe, 2009). Since many grasslands are plagued with exotic plant invasion, reduction of the native plant seedbank from concentrated seed predation in these landscapes is common. Due to this, intense predation on native seed can have serious long-term consequences for native plant abundance in grasslands (Holl et al., 2014).

## Old Fields:

Old fields are landscapes that were historically used for agriculture but have since been abandoned. Due to their past use, they tend to be more disturbed than other landscapes and are often weedy, with grasses and herbaceous plants dominating the ecosystem. While seed predation in old fields is lower than in some other ecosystems, like deserts, it is still theorized to impact plant distribution for larger seeded species (Mittelbach & Gross, 1984). Unlike desert ecosystems, seed availability in old fields is not a year-round luxury (Brown et al., 1979), and therefore seed predators here are generalists that feed opportunistically rather than specialists (Mittelbach & Gross, 1984).

## **Part IV: Conclusion/Application to South Sound Prairies**

Low germination rates for native species on south Sound prairies are problematic for the restoration of this biologically important habitat. Many factors could play into this issue, both biotic and abiotic. This thesis aims to take what we have learned from the literature on seed predation and apply it to several difficult to establish species found in the south Sound prairies. In doing this, we can begin to quantify the impact of seed predation on low establishment rates for certain species.

The existing literature has shown that small mammals are the most likely and most destructive seed predator due to their ability to harvest many seeds at once, eating them on-site or burying them deep enough that they won't germinate (Herrera & Pellmyr, 2009). Ants have also shown to be efficient seed predators, however, they are less likely to kill a harvested seed and because of their size, they are unlikely to make a large impact on overall plant establishment (Herrera & Pellmyr, 2009). Birds and other potential seed predators have not been shown to have a notable impact on seed survival, although their

impact is likely underestimated due to challenges in study design.

Seed predators shape their environment by selecting the largest, most abundant, and most appetizing seed (Brown et al., 1975). This can be an issue in environments that are seed limited and for plants that can only reproduce by seed and have a limited seedbank. Seed predators can increase the diversity of an ecosystem by allowing small, non-competitive seeds a chance to grow in the absence of larger, more competitive seeds (Brown & Heske, 1990).

In general, habitats that have dense vegetation and/or understories tend to have the most seed predation, because in these habitats the ability to hide from predators is greater, and abundant seed is dropped below the parent plants (Kollmann & Buschor, 2003). In these ecosystems, competition for microsites and light is so high that seed predation has little impact on plant populations, as seeds are unlikely to encounter appropriate conditions for germination in the first place. Seed predators actively shape the plant populations in habitats like deserts that have sparse vegetation. In these ecosystems, seed predation is low due to a lack of seed, but the seed predators that exist there are specialists in exploiting this resource (Brown & Heske, 1990).

Since south Sound prairies are typically burned before they are seeded to increase seed to soil contact and therefore germination, they are left in a state of heavy disturbance with little vegetative cover. Considering the existing literature suggests seed predators prefer dense vegetation cover, we may not find much evidence of seed predation on these prairies. We do know from studies of south Sound prairies and similar prairies in western Oregon and California that these landscapes are seed limited and have virtually no native plant seedbank due to decades of invasive species competition (Krock, 2016; Stanley et

al., 2011). Stanley et al. (2011) found non-native plants to be so prolific on the remaining south Sound prairies that the remaining native plants could not produce enough seed to colonize open ground and compete with these exotic species. This suggests that if there is native plant seed predation on the south Sound prairies, it may harm the already tenuous native plant recruitment needed for successful restoration.

## Materials and Methods

### Study Location

This study was conducted from October to November 2019 on five south Sound prairie burn units. Four of the locations were on Joint Base Lewis-McCord (JBLM), located south of Tacoma, Washington (Marion Prairie, Johnson Prairie, and two sites in Upper Weir Prairie) (Figure 2). JBLM is a 35,000-hectare military base with most of its land broken up into undeveloped training areas, which are left open for military training activities and in some cases, recreation. The fifth site is at Glacial Heritage Preserve, located south of Olympia, WA (Figure 2). This property is owned by Thurston County and managed by CNLM.

Typical restoration tactics for these prairies involve sowing seed into units after they have been burned, in order to increase germination and suppress weeds (Hamman et al., 2015; Krock, 2016). All units were burned in the summer of 2019. All but one



Figure 2: Map of study locations

underwent a post-burn herbicide treatment before seeding to kill re-emerging non-native plants and most sites were seeded using a broadcast seeder before plot placement (Table 4).

**Table 4: Pre-study Burn Unit History for 2019**

<b>Training area</b>	<b>Prairie</b>	<b>Burn unit</b>	<b>Date burned</b>	<b>Seeded Y/N</b>	<b>Herbicide applied</b>
TA 21	Upper Weir	UWP 01	08/20/19	No; REF	No
TA 21	Upper Weir	UWP 03	08/20/19	Yes; FESROE	Yes: Fusilade
TA 18	Marion	MAP 02	7/30/19	Yes; Grass-forb mix	Yes: Fusilade
TA 22	Johnson	JP 03	7/31/19	Yes; Grass-forb mix	Yes: Garlon IV, Fusilade, Vastlan
N/A	Glacial Heritage	2018- B	8/8/2019	Yes	Yes: Glyphosate

Table 4: REF: Reference site. Reference sites are used as controls for habitat enhancement actions and are therefore excluded from seeding  
 FESROE: *Festuca roemerii*; native bunch grass  
 Grass-Forb mix: Seed mix including native grasses and forbs

Burn unit locations were selected based on the following factors: 1) Located in the south Sound and are under management regularly by CNLM, 2) A minimum size of 5 hectares, 3) Burned in the summer of 2019, 4) Had a “soft-line”, meaning the burn unit was not entirely surrounded by roads (gravel or hardtop) allowing a more natural edge effect to be studied, 5) Access cleared with JBLM range control as to not interfere with military training activities.

**Site Conditions**

South Puget Sound prairies are classified as grasslands with well-drained gravelly

soils lacking in substantial organic matter and fertility. Native vegetation communities in these prairies differ greatly from the more common forested landscapes in the region. They are dominated by the bunchgrass Roemer’s fescue (*Festuca roemerii*) and fire-tolerant herbaceous species, with infrequent shrubs and trees (namely the Garry Oak (*Quercus garryana*) (Crawford & Hall, 1997; Dunn, 1998). Unfortunately, in more recent times these prairies are more likely to be dominated by non-native species. If not the prevalent Scotch broom (*Cytisus scoparius*), a woody shrub that is a frequent invader of open areas in the PNW, then by hundreds of escaped pasture grasses, common weeds, and escaped ornamentals. The prairies in this study range in “quality” or abundance and diversity of native vegetation cover. A prairie is considered high quality if it has >30% native cover, <25% shrub cover, and <5% tree cover (Applestein & Hamman, 2016).

### Experimental Design

In each of the five burn units, three 51 meter transects were placed from the unburned edge into the interior of the burn unit. Along each transect, three plots were placed along a gradient from burn edge (1m), middle (26m), and interior (51m) (Figure 3). This placement of plots allowed us to determine if there is a



Figure 3: Example of how transects were placed in a burn unit (white dots symbolize individual plots: edge, middle and interior)

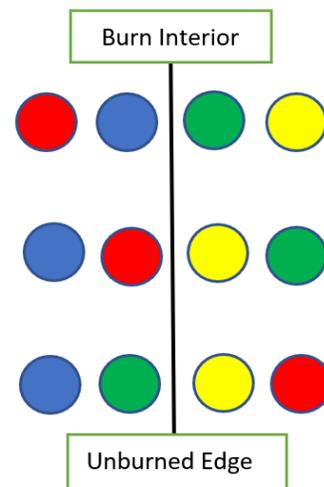


Figure 4: Example of a transect. Different colors symbolize the different types of exclusion cages (randomized)

difference in type and rate of seed predation near the edge of the unit vs. the interior, as past studies have shown (Mittelbach & Gross, 1984; Price & Brown, 1983).

Each plot contained four treatment subplots: one cage allowing invertebrate entry but excluding mammals, one allowing mammals but excluding invertebrates, one excluding both (control), and one dish that is completely open (Figure 4). Including all locations, there is a total of 180 subplots (cages) (4 subplots per plot x 3 plots per transect x 3 transects per site x 5 sites). All cages contained Petri dishes with the following seed mix: *Balsamorhiza deltoidea*, *Dichanthelium oligosanthes*, *Armeria maritima*, *Viola adunca*, *Erigeron speciosus* (one dish per cage, with 20 seeds per species for a total of 100 seeds per dish) (Figure 5). While the plots themselves were quite small (<3.5m<sup>2</sup> each), they were distributed across at least 27 hectares (minimum of 5 hectares per burn).



Figure 5: Seed mix pre-dispersal

## Materials

### Cage Construction:

All cages were constructed of wire mesh shaped into cylinders secured with zip ties

(Table 5). The top of each cage was covered with plastic rain covers. All cages were secured to the ground using fencing staples (Figure 6).

In the cages that prevented invertebrate entry, the petri dish was mounted 2cm above the ground using a nail. The outer edges of the Petri dishes were coated in Fluon® (Polytetrafluoroethylene), a liquid resin used to prevent insect entry or escape from

containers. The upper surface of the nail was also coated in petroleum jelly to further prevent access to the dishes. Any vegetation that was touching the Petri dishes was removed. In cages that allowed insect access, dishes were placed with over-hanging vegetation to allow a way for insects to enter and exit the dishes. Cage design was adapted from Mittelbach & Gross (1984) and Price & Brown (1983).

**Table 5: Cage Specifics**

Entry allowed	Entry excluded	Cage material	Opening size	Cage diameter	Cage height	Dish mounted above ground
In	SM	Hardware cloth	0.6cm	18cm	10cm	No
SM	In	Chicken wire	2.5cm	30cm	15cm	Yes
None (Control)	In & SM	Hardware cloth	0.6cm	18cm	10cm	Yes
All (Open)	None	Chicken wire	15cm	N/A	15cm	No

Table 5: In = (invertebrates), SM = (small mammal)



Figure 6: Cages in an edge plot in Upper Weir (UWP03)

Seed Selection:

The following species were selected for this study: *Balsamorhiza deltoidea*, *Dichanthelium oligosanthos*, *Armeria maritima*, *Viola adunca*, *Erigeron speciosus*. Relative seed sizes are listed in Table 6 and shown in Figure 7, with species information in Table 7. These species were selected for this study based on the following factors: 1) These species have historically been hard to establish on south Sound prairies with current seeding methods (less than 5% establishment rate) (Hamman et al., 2016), 2) Species are ecologically and functionally important in south Sound prairies, 3) Seed was available through CNLM’s seed farm and is commonly used in seed mixes for restoration. Sourcing information for the seed used in this study is listed in Table 5.



Figure 7: Relative seed sizes

**Table 6: Seed Sizes**

Species	Length	Width	# Seeds/gram
<i>Armeria maritima</i>	5mm*	2mm	426**
<i>Balsamorhiza deltoidea</i>	7mm	2mm	155
<i>Dichanthelium oligosanthos</i>	4mm	2mm	859
<i>Erigeron speciosus</i>	2mm	1mm	2857
<i>Viola adunca</i>	2mm	1mm	1124

Table 6: Seed sizes including length, width, and weight (# of seeds per gram)

\*Length includes paper calyx

\*\*Weight includes calyx

**Table 7: Species Profiles**

<b>Species</b>	<b>Code</b>	<b>Family</b>	<b>Growth Habit</b>	<b>Importance</b>
<i>Armeria maritima</i>	ARMMAR	Plumbaginaceae	F/P	TCB nectar plant
<i>Balsamorhiza deltoidea</i>	BALDEL	Asteraceae	F/P	TCB nectar plant
<i>Dichanthelium oligosanthes</i>	DICOLI	Poaceae	G/P	Short statured bunch grass that maintains prairie habitat structure
<i>Erigeron speciosus</i>	ERISPE	Asteraceae	F/P	Late season nectar source for many pollinators
<i>Viola adunca</i>	VIOADU	Violaceae	F/P	Oviposition host for Valley Silverspot; Mardon Skipper nectar plant

Growth Habit: F = Forb, G = Grass, P = Perennial  
 TCB = Taylor's checkerspot butterfly

**Table 8: Seed Sourcing**

<b>Species</b>	<b>Year packed</b>	<b>Region Collected</b>	<b>Site Collected</b>	<b>Grade</b>
ARMMAR	2013 & 2014	SOP	WB	A
BALDEL	2016	SOP	VP	A
DICOLI	2018	SOP	VP	A
ERISPE	2013	SOP	WB	A
VIOADU	2016	SOP	WCC	A

SOP = Southern Puget Prairies, WB = Websters Seed Farm (Tumwater, WA), VP = Violet Prairie Seed Farm (Tenino, WA), WCC = Washington Corrections Center (Shelton, WA)  
 Grade: A is the highest possible quality of seed

## **Field Methods**

Each petri dish was placed in the field according to the previously described design and checked after 24hrs, 48hrs and at one week for signs of predation (e.g., seed missing). Seeds were counted in each petri dish at each time point. Predation was confirmed when over 50% (10 seeds) of one or more species was missing from cages accessible to small mammals or invertebrates but not missing from the control cage. This controls against potential losses from wind, rain, or human error in counting. Other signs of predation were also noted, such as empty seed husks and the presence of rodent feces in petri dishes, which are common signs of rodent predation.

## **Statistical Analysis**

Results were analyzed using a mixed model ANOVA test on JMP statistical analysis software, conducting separate analyses for each plant species. This considered exclusion treatment type (mammal, insect, open, and control) and distance from the edge as fixed effects. Burn location and individual transects are considered random effects, with transects nested within each burn unit. This analysis allowed me to determine the statistical effects of these treatments on seed predation. Prior to running the mixed model ANOVA, each species was tested for homogeneity of variance using Levene's test. Additionally, a Tukey's HSD post-hoc test was conducted for treatment effects on each species. One-way ANOVAs were used to consider the effects of edge on all species and treatments, as well as for the timing of predation at the 24-hour, 48-hour, and one-week intervals. An alpha of 0.05 was used to determine significance for all analyses.

## Results

### Evidence of Seed Predation

My main research question asked if seed predation was occurring on south Sound prairies, and, if so, what organisms were responsible. The results of this study show that most of the seeds tested are experiencing predation by small mammals, but not insects. Across all burn units, seed dishes that were accessible to small mammals (referred to as “mammal” and “open”) were predated upon significantly more than those that were not (insect and control) for all species. (Figure 8, Table 9).

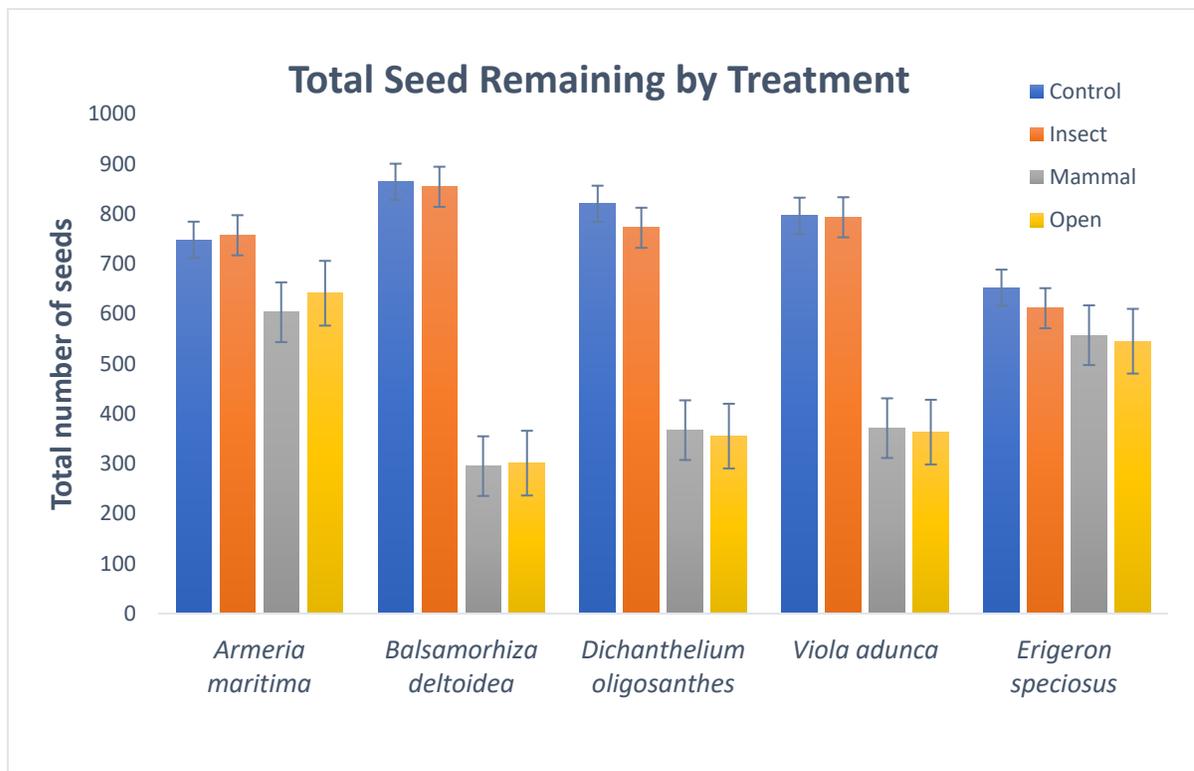


Figure 8: Total seed remaining by treatment for each species after one week of placement in the field

**Table 9: Seed Predator Exclusion Treatment for Each Species**

Species	R <sup>2</sup> Adjusted	F Ratio	DF	DF den	p-value
<i>Armeria maritima</i>	0.41	10.6	3	162	<0.0001
<i>Balsamorhiza deltoidea</i>	0.66	75.62	3	162	<0.0001
<i>Dichanthelium oligosanthes</i>	0.55	44.75	3	162	<0.0001
<i>Erigeron speciosus</i>	0.41	3.12	3	162	0.0277
<i>Viola adunca</i>	0.57	39.78	3	162	<0.0001

Table 9: Results of mixed-effects ANOVA of seed predator exclusion treatment (main effect), burn unit (random), transect (nested in burn unit) for each species



Figure 9: Seed dish pre-dispersal (left) and post-dispersal (right), showing signs of rodent predation.

Rodents are the assumed predator of the small mammal and open cages due to rodent feces frequently left behind in dishes that were predated upon (Figure 9). While insect and control treatments are not suspected to have experienced predation, they did

have some loss of seed. Due to the fact that there was no significant difference in the seed missing from these treatments at one week, it is unlikely that this reflects predation and more likely it reflects abiotic influences such as wind and rain, and/or human error in counting.

### **Findings by Species and Seed Size Preferences**

My second question asked if seed size influenced potential predation. Specifically, is there a preference for larger seed over smaller seed? As discussed in the Literature Review, Optimal Diet Theory (ODT) suggests that seed predators would target the largest seeds first because they offer the most calories for energy spent harvesting (Brown et al., 1979; Mittelbach & Gross, 1984). The results of this study show a preference for the larger seeded species by mammals (*B. deltoidea*, *D. oligosanthos*, and *V. adunca*) (Figure 9). Likewise, the smallest seeded species, *E. speciosus*, was the least impacted by predation, suggesting that it is an unlikely target for predation by small mammals. The exception to this rule is *A. maritima*, which is a larger seeded species that also appeared to not be targeted. It should be noted, however, that a large portion of this seed (>50%) is chaff, or the seed husk, which is likely not appealing to small mammals. Since no predation by insects was observed during this study, it is unclear if their harvesting methods would also follow ODT. Results for how individual species were affected by each treatment are discussed below.

### *Balsamorhiza deltoidea*

*B. deltoidea* was heavily influenced by treatment ( $F_{(3,162)} = 75.62, p = <0.0001$ ). Being the largest of the seeds, it is not surprising that *B. deltoidea* was favored by small mammals. The mean of remaining seeds for the mammal and open treatments was 7, with a mode of 0. This contrasts with those treatments that did not allow mammal access, with a mean of 19 and mode of 20 (Figure 8). It should be noted that being the largest seed, *B. deltoidea* was the easiest to count in the field and is likely too large to be predated on by ants. It is also the least likely to be affected by abiotic conditions such as wind or rain.

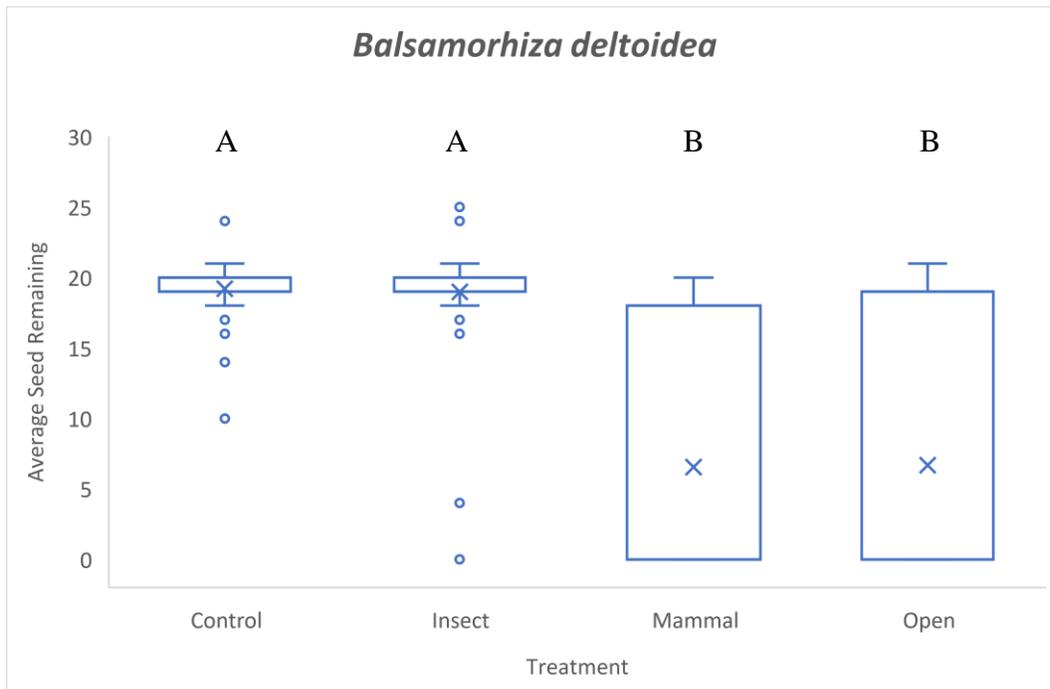


Figure 8: Box plot showing *B. deltoidea* seed remaining after one week by treatment. Different letters signify treatments that are significantly different from each other ( $\alpha = 0.05$ ).

### *Dichanthelium oligosanthes*

*D. oligosanthes* is the second largest of the seeds in this study and was highly responsive to the treatments ( $F_{(3, 162)} = 44.75, p = <0.0001$ ). Both treatments accessible to small mammals had a mean of 8 seeds remaining, with a mode of 0. This contrasts with the seeds not accessible to mammals with a mean of 18.5 and mode of 19.5. Figure 9 shows the total amount of seed remaining in the control and insect treatments compared to those in the mammal and open treatments, where there was significantly less seed remaining. This seed was also likely too large to be preyed upon by ants, and unlikely to be affected by abiotic conditions.

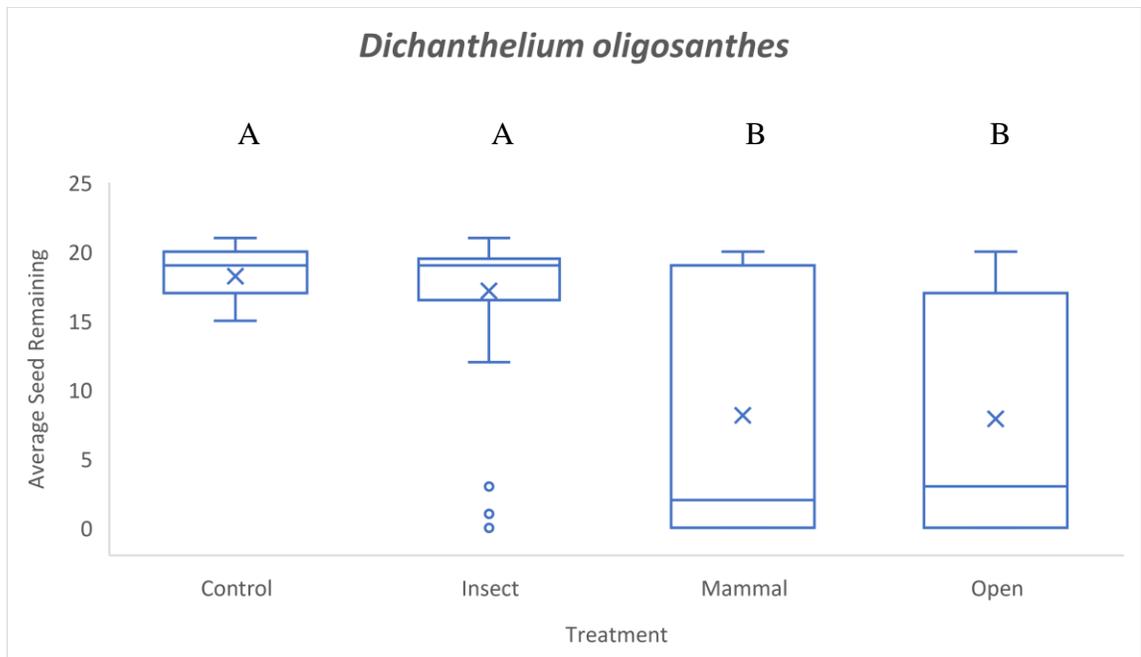


Figure 9: Box plot showing *D. oligosanthes* seed remaining after one week by treatment. Different letters signify treatments that are significantly different from each other ( $\alpha = 0.05$ ).

## *Viola adunca*

The third-largest seed, *V. adunca* followed similar patterns as *B. deltoidea* and *D. oligosanthos*, ( $F_{(3, 162)} = 39.78, p = <0.0001$ ) with the mean amount of seeds left being 8 and the mode being 0 for seeds accessible to mammals, and the numbers for non-mammal access having a mean of 18 with the mode of 19. Figure 10 shows the seed remaining in each treatment after one week, noting the contrast between the open/mammal treatments and the insect/control treatments. This seed is a known favorite amongst rodents at CNLM's seed farm, so their preference for it is not surprising. Interestingly, ants are known to distribute *Viola adunca* seed (Bartow, 2014), but the low numbers of missing seeds from the cages accessible to insects suggest they did not take advantage of these seeds.

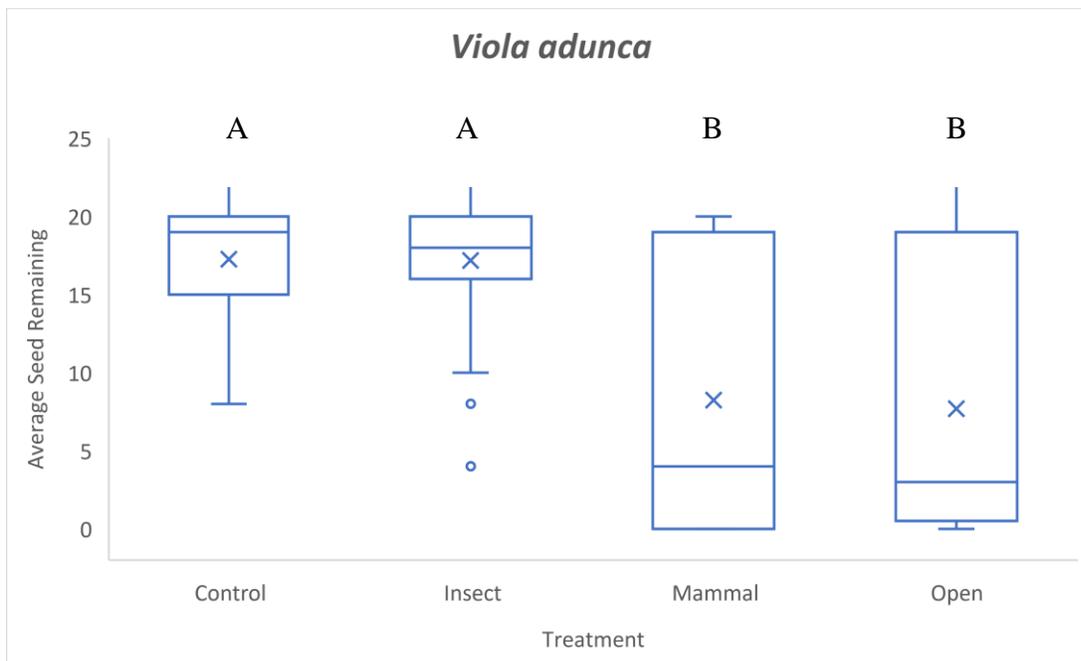


Figure 10: Box plot showing *V. adunca* seed remaining after one week by treatment. Different letters signify treatments that are significantly different from each other ( $\alpha = 0.05$ ).

### *Armeria maritima*

*A. maritima* also had significantly more seed missing from the mammal and open treatments than the control and insect ( $F_{(3, 162)} = 10.06, p = <0.0001$ ). In treatments accessible to mammals, *A. maritima* had a mean of 14.5 with a mode of 15. In treatments not accessible to mammals, *A. maritima* had a mean of 17 and a mode of 19. Figure 11 shows the total remaining seeds for each treatment, and the differences between treatments are noticeably less than the previously discussed species. A potential explanation for the greater seed loss from the mammal and open cages besides predation could be that the seeds were disturbed by mammal visitors and either stuck to the mammals themselves or were knocked out of the dish.

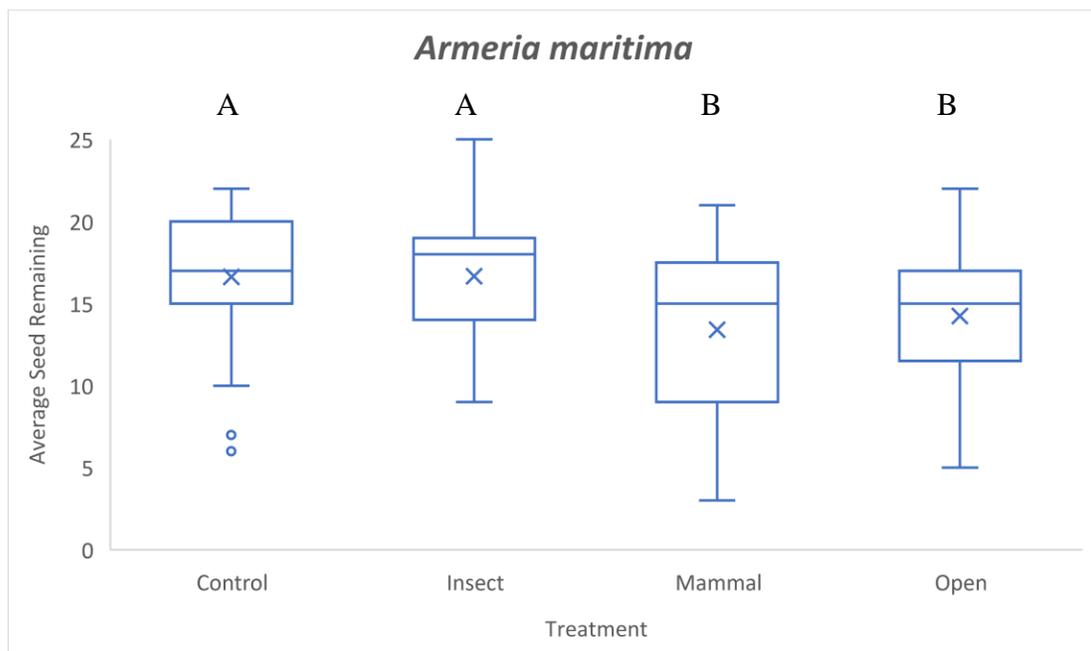


Figure 11: Box plot showing *A. maritima* seed remaining after one week by treatment. Different letters signify treatments that are significantly different from each other ( $\alpha = 0.05$ ).

## *Erigeron speciosus*

*E. speciosus* showed significant differences amongst treatments for the mixed effects ANOVA ( $F_{(3, 162)} = 3.12, p = 0.0277$ ). However, when just looking at treatment using a one way ANOVA effects were not significant ( $F_{(3, 98)} = 2.20, p = 0.0933$ ). While the Levene's test showed that these data had homogenous variance, the Shapiro-Wilk test revealed that the data were not distributed normally, regardless of any transformations. This calls into question validity of these results. For treatments accessible to mammals, *E. speciosus* had a mean of 12 seeds remaining, slightly less than the mean for treatments not accessible to mammals, 14. This species also had the largest losses of seeds overall across all treatments (Figure 8) suggesting that some other factor besides predation was responsible for seed loss. These conflicting results are likely due to the relatively small size of *E. speciosus*, which made these seeds more difficult to count in the field and more susceptible to losses from wind and rain than other species. Figure 12 shows the total remaining seeds for each treatment.

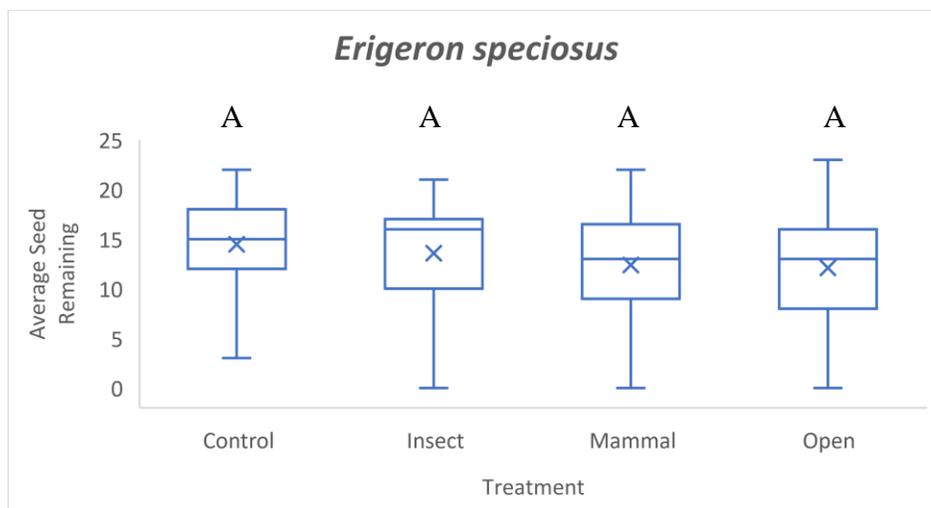


Figure 12: Box plot showing *E. speciosus* seed remaining after one week by treatment. Different letters signify treatments that are significantly different from each other ( $\alpha = 0.05$ ).

## Edge Effects

My third question asked if closer proximity to the unburned edge of a burn unit increased predation. For the burn units tested, the average seed remaining for all species in each plot had little variation. Therefore, distance from edge and transect location did not significantly impact the amount of seed predated ( $F_{(2, 897)} = 1.5, p = 0.23$ ), as shown in Figure 13. Averages per species are listed in Table 10.

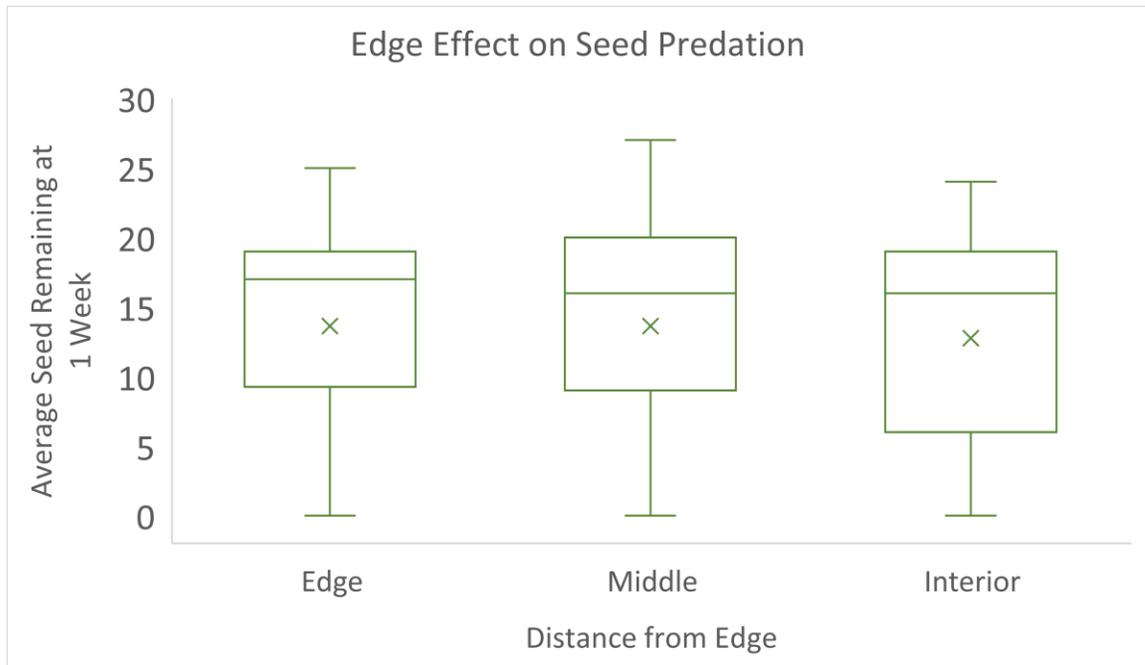


Figure 13: Edge effect on seed predation (edge= 1m, middle= 26m, interior= 51m away from edge)

**Table 10: Mean number of seeds remaining in each location after 1 week**

Species	Edge	Middle	Interior	DF	F-Ratio	p-value
ARMMAR	15.3 (0.6)	15.7 (0.6)	14.9 (0.6)	2 (177)	0.5	0.62
BALDEL	13.4 (1.2)	12.9 (1.2)	12.3 (1.2)	2 (177)	0.2	0.81
DICOLI	13.3 (1.0)	13.5 (1.0)	11.8 (1.0)	2 (177)	0.8	0.45
ERISPE	13.2 (0.7)	13.5 (0.7)	12.8 (0.7)	2 (177)	0.3	0.75
VIOADU	13.1 (1.0)	12.6 (1.0)	12.1 (1.0)	2 (177)	0.2	0.78
All Seeds	13.6 (0.4)	13.6 (0.4)	12.8 (0.4)	2 (897)	1.5	0.23

Table 10: Results of one-way ANOVA for each species: mean seeds remaining for distance from edge (edge= 1m, middle= 26m, interior= 51m) with standard error in parenthesis. DF = degrees freedom with error in parentheses.

### Timing of Predation

The final question for this project focused on when seed predation is occurring (after 24 hours, 48 hours, or one week). For all species in this study, it took small mammals longer than 48 hours to find and consume seed (Figure 14, Table 11). The three larger seeded species saw the most losses after one week (*B. deltoidea* ( $F_{(2, 537)} = 34, p = <0.0001$ ), *D. oligosanthes* ( $F_{(2, 537)} = 58, p = <0.0001$ ) and *V. adunca* ( $F_{(2, 537)} = 31, p = <0.0001$ )). The effect of time was also significant for *E. speciosus* ( $F_{(2, 537)} = 15, p = 0.0001$ ) and *A. maritima* ( $F_{(2, 537)} = 44, p = <0.0001$ ).

**Table 11: Mean Number of Seeds Remaining at Each Time Interval**

Species	24hr	48hr	1 Week	DF	F-Ratio	p-Value
ARMMAR	18.4 (0.2)	17.7 (0.2)	15.3 (0.2)	2 (573)	43.8	<0.0001
BALDEL	18.7 (0.5)	17.4 (0.5)	12.9 (0.5)	2 (537)	34.3	<0.0001
DICOLI	18.6 (0.4)	18.0 (0.4)	12.9 (0.4)	2 (537)	58	<0.0001
ERISPE	15.1 (0.3)	15.6 (0.3)	13.1 (0.3)	2 (537)	14.7	<0.0001
VIOADU	17.3 (0.5)	16.4 (0.5)	12.6 (0.5)	2 (537)	30.7	<0.0001
Species	24hr	48hr	1 Week	DF	F-Ratio	p-Value
ARMMAR	18.4 (0.2)	17.7 (0.2)	15.3 (0.2)	2 (573)	43.8	<0.0001
BALDEL	18.7 (0.5)	17.4 (0.5)	12.9 (0.5)	2 (537)	34.3	<0.0001
DICOLI	18.6 (0.4)	18.0 (0.4)	12.9 (0.4)	2 (537)	58	<0.0001
ERISPE	15.1 (0.3)	15.6 (0.3)	13.1 (0.3)	2 (537)	14.7	<0.0001
VIOADU	17.3 (0.5)	16.4 (0.5)	12.6 (0.5)	2 (537)	30.7	<0.0001

Table 11: Results of one-way ANOVA for each species: mean seeds remaining for each time interval (24hr, 48hr, and one week) with standard error in parentheses. DF = degrees freedom with error in parenthesis.

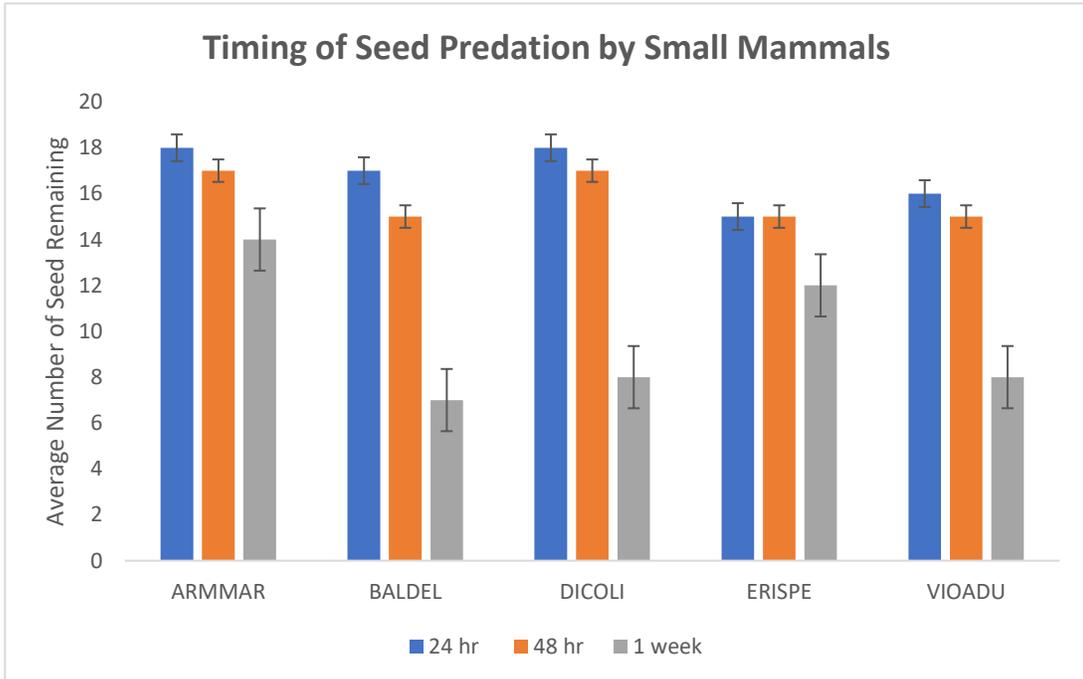


Figure 14: Seed remaining at each time interval

## Discussion

The prairies of the south Puget Sound are an important biological and cultural resource. Restoring these long-neglected landscapes is essential to the survival of many rare and endangered species. Streamlining the restoration process, in addition to making it more efficient, is essential for restoring this landscape. Part of that process is figuring out the best and most resourceful ways to use what we have access to. Considering that seed predation may be a potential factor in inhibiting that restoration, this and further research will help make the restoration process more productive.

### Evidence of Seed Predation

This study has provided clear evidence for seed predation by small mammals for the following seeds in the field: *B. deltoidea*, *D. oligosanthos*, and *V. adunca*. Considering that small mammals are highly efficient at finding seeds, including those that have been buried (Kollmann & Buschor, 2003), this seed predation could be significantly impacting seed germination rates, as has been found in previous studies (Edwards & Crawley, 1999; Heithaus, 1981). This is likely less true for *A. maritima* and *E. speciosus*, for while they did show less seed in the mammal and open treatments, the differences were much less pronounced than the other species. The large losses of *E. speciosus* from the control cages suggest that external factors influenced these results. These species were likely not the target food for small mammals but may have been disturbed while rodents fed on other seeds. For example, they may have been knocked out of the dish or stuck to the animals themselves due to condensation. A different protocol that reduces losses from abiotic influences or physical disturbances for small seed such as *E. speciosus* would need to be used to more accurately test these assumptions.

After reviewing the literature on small mammal populations in the Puget Sound while taking into consideration habitat needs, diet, and local abundance, I believe deer mice are the main predators of seed used for restoration in south Sound prairies. This is based on their widespread nature, seed heavy diet (Naylor, 1994), and habitat preferences for areas with little to no vegetation cover and plant litter (West, 1992). Several studies have noted deer mice populations increase after fire (Peterson et al., 1985; Schramm & Willcutts, 1983; Tevis, 1956). Additionally, since rodent populations generally reach their peak in late summer and fall (West, 1992) (the same timeframe in which seeding for restoration is taking place) deer mice are likely taking advantage of this abundant food source.

The lack of insect predation, especially on seed that is known to be harvested by ants, such as *V. adunca* (Bartow, 2014) suggests that insects are not the main harvesters of seed on the prairie, or that they were not active during this time (late fall). Previous research has noted that insect activity lessens with cooler temperatures (Abramsky, 1983; Brown et al., 1975). Therefore, insect predation may increase in the spring or summer. Expanding this study over multiple seasons would be necessary to test this theory.

### **Seed Size Preferences**

These findings mostly follow what is to be expected from the Optimal Diet Theory (ODT), with species preferring larger seed because they offer more calories to energy spent harvesting. The exception to this rule was *A. maritima*, which is one of the larger seeded species that showed low predation rates. However, unlike all of the other species in this study, a large part of this seed is chaff (>50%) and therefore likely offers little nutritional value when compared to the other seeds. While in general, it is true that

ODT may not be consistent for all species, one could assume that larger seeds sown in great quantities for restoration are more likely to suffer from rodent predation due to their attractiveness and nutritional value when compared to smaller seeded species, as shown in this study and others (Brown & Heske, 1990; Clark & Wilson, 2000; Heithaus, 1981; Mittelbach & Gross, 1984).

### **Edge Effects**

The edge effect that has been observed in other studies (Jules & Rathcke, 1999; Kollmann & Buschor, 2003) was not replicated here. A potential explanation for this could be that 50 meter transects were not long enough to gauge an edge effect.

Alternatively, since this is the first study looking at this topic in south Sound prairies and small mammal populations are poorly understood in this area, these prairies may be exceptions to the rule of edges increasing rodent populations and instead, rodents are evenly distributed across the landscape. Deer mice (*Peromyscus maniculatus*), for instance, would fall into this category due to their preference for burned areas and seem likely to be the main seed predator in prairie burn units. An important factor not considered in this study is different types of edges. For example, other species of rodents such as voles and mice are likely more abundant near riparian zones and wetlands, agricultural lands, or urban and suburban areas (Cornely & Verts, 1988; Himes & Christopher, 2013; Witmer & Vercauteren, 2001). Burn units that border these types of landscapes may experience heightened seed predation along edges.

### **Timing of Predation**

The timing of seed predation ended up being an important component of this study. While most of the literature identifies heavy predation soon after placement of

seeds (less than 48 hours) (Brown et al., 1975; Hulme, 1994), in this case, most seed predation was observed at the one week counts. This has important management implications, suggesting that any mitigation techniques may need to be in place a week or longer.

### **Study Challenges**

There were many challenges during this field experiment. I initially was concerned about the stability of the cages that were going to be exposed not only to the harsh conditions of a Pacific Northwest fall, but also to curious large mammals (coyotes are notorious for tampering with equipment in the area such as flagging), and potentially human vandalism. Luckily, all but one of the 180 cages remained standing at the end of the study. The wind did not appear to be a large issue, except for the smallest species, *E. speciosus*, which proved to be a challenge to measure not only because of potential abiotic influences on seed loss but its markedly small size, making counting this species in the field difficult. I was lucky to have little rainfall during this study, except for the last week at Glacial Heritage, but the rain covers on the cages stood up well to this challenge. A condition I wasn't expecting was the daily condensation that ended up in the dishes, which made counting seeds a challenge because they stuck to each other and the dishes themselves.

### **Relevance for Land Managers**

The motivation behind this study was finding out what types of seed used for restoration in south Sound prairies are predated on in the field, and by what organisms. Knowing this information could lead to more efficient use of this seed. For instance, if large seed such as *B. deltoidea* is highly predated along the edges of burn units by

rodents, choosing to not seed this species within a given distance from the edge could save land managers money in the long term by allowing them to seed where individual species are most likely to survive. The findings of this study did not fit so cleanly into the above-projected scenario, as predation seemed to be more uniform across the burn units than responsive to edges, as discussed above. However, it did show that small mammals are highly efficient at finding concentrated sources of seed in the field and that they show a preference for larger seed over smaller seed (in most cases). This suggests that trying to mitigate this predation would be useful.

### **Potential Mitigation Methods**

The evidence in this study suggests that rodents could be playing a role in low seedling establishment rates. While a multitude of factors contribute to successful germination, this study shows that the low establishment rates for *B. deltoidea*, *D. oligosanthos*, and *V. adunca* are linked to heavy predation in the field. The following are suggestions for potential mitigation methods, using Integrated Pest Management (IPM) principles. IPM was developed to reduce increasing reliance on pesticides, allowing land managers to consider physical, chemical, biological and cultural tactics, and combinations of these tactics, in addressing pest issues in a wide range of scenarios (Duke & Powles, 2008).

#### Physical Methods:

Physical methods work by directly preventing pest access. For instance, fencing could be used in smaller, recently seeded areas to keep out rodents. While unlikely to be practical over large areas, fencing could be placed around small plots to protect seed- especially in particularly sensitive areas or areas with high predation. This study suggests

that fencing would need to be in place at least a week to be effective, and likely longer. If deer mice are the main seed predator on the prairies, fencing would need to be secured to the ground but not buried, since these rodents do not burrow (Corn & Bury, 1991). Additionally, there was no sign of rodents digging under seed cages in this study, and wire fencing with <0.6 cm openings secured to the ground with fencing staples was enough to keep rodents out. Fencing could also be an important tool along the edges of riparian zones and wetlands bordering burns, which are likely to have higher rodent populations (Cornely & Verts, 1988; Himes & Christopher, 2013; Witmer & Vercauteren, 2001). A study in an Arizona desert by Brown & Heske (1990) found that fine-meshed fencing was enough to exclude rodents, resulting in a drastic change in plant species composition over 12 years.

#### Chemical Methods:

Commercially available chemical repellents, such as concentrated predator odors like urine, have not proven to be effective over large areas in deterring seed predation. They may be useful in smaller, targeted areas, but field studies have not been conclusive for these treatments (Baldwin, Meinerz, Witmer, & Werner, 2018; Witmer & Vercauteren, 2001). Rodenticides are likely effective in reducing rodent populations but are not a viable option for this scenario for many reasons. For example, there is the potential this could negatively affect non-target organisms (Erickson & Urban, 2004), including the federally threatened Mazama pocket gopher (*Thomomys mazama*), as well as rodent predators, in some south Sound prairies.

#### Biological Methods:

Biological methods use naturally occurring predators or pathogens to reduce pest

populations. Encouraging rodent predation, especially by nighttime predators could be useful at deterring seed predation (Witmer & Vercauteren, 2001). This could include installing raptor poles and nest boxes, as well as increasing habitat for rodent-eating snakes, coyotes, foxes, weasels, skunks, and bobcats (Altman, Hayes, Janes, & Forbes, 2001). Unfortunately, encouraging predation has shown little response in rodent populations in agricultural settings (Askham, 1990; Moore, 1940; Witmer & Vercauteren, 2001). An additional concern could be that encouraging increased predation could put federally endangered *Mazama* pocket gopher populations at further risk.

#### Cultural Methods:

Cultural methods rely on making the surrounding environment less inviting for pests. Minimizing seed predator habitat is one example of a cultural method. This could include mowing surrounding areas of dense vegetation, which would reduce habitat for voles and Pacific jumping mice (Cornely & Verts, 1988; Hafner et al., 1998).

Additionally, the removal of habitat features that are preferred deer mice nesting sites such as: brush piles, stumps, logs, and rock piles could help limit deer mouse reproduction (Naylor, 1994). However, these habitat features are also important for other beneficial wildlife (Altman et al., 2001), so thorough consideration should be made before removing these features.

Cultural methods also include altering seeding techniques. For example, sowing seed that is not as desirable to rodents, burying seed so it is harder to find (Heithaus, 1981), sowing highly predated seed in less concentrated amounts, planting plugs instead of seed, sowing seed in late winter or spring when rodent populations are low (West, 1992), and using chaff or mulch to make seed harder to find (Kaufman et al., 1988).

These alterations come with tradeoffs, however. Both burying seed and planting plugs are far less economical and much more labor-intensive than broadcast seeding (Krock, 2016). Using chaff and mulch likely reduces seed-to-soil contact and access to light, making germination more difficult (Maret & Wilson, 2005; Stanley et al., 2011). Likewise, September – October has been identified by Krock (2016) as resulting in the highest germination rates. Therefore, it is up to land managers to determine if losses from seed predation are enough to justify altering current seeding techniques.

### **Further Research**

Expanding this study to be done over multiple years and through multiple seasons in conjunction with small mammal trapping would give a more robust picture of the rate of seed predation in relation to small mammal populations. It also would provide information on whether insect predation increases during the warmer parts of the year. Additionally, expanding the transect length in some of the larger burn units (25+ hectares) may generate different patterns with edge effects. In this study, the smallest burn unit (JP03) was just over 5 hectares. Arguably, this entire unit could be considered “edge”, which some studies, such as Kollmann & Buschor (2003), considered to be 50 meters or more.

Furthermore, this study could be expanded to consider other seed predators, mainly birds. While the existing literature (Brown et al., 1979; Mares & Rosenzweig, 1978; Morton, 1985) suggests that birds are unlikely to have a significant impact on native seed populations, it is worth investigating for a few reasons. First, we know that birds are an issue for CNLM’s seed farm and show a preference for larger seeds, similar to rodents (Smith, 2018). Second, because CNLM’s seeding methods distribute an

artificially large amount of seed on the ground compared to natural seed dispersal, birds could be taking advantage of this abundant food source. Third, introduced game species (ring-necked pheasant and northern bob-white) (Altman et al., 2001) are present in some south Sound prairies and could eat seed used for restoration, but this has not been observed in the field.

Other plant species worth considering that have low establishment rates identified by Krock (2016) include *Solidago simplex*, *Clarkia amoena*, *Lomatium utriculatum*, *Potentilla gracilis*, and *Sisyrinchium idahoense*. Over 150 species are grown for restoration purposes in south Sound prairies, all of which have the potential to be negatively affected by seed predators (Hamman et al., 2015).

#### **Additional Research Questions:**

- 1) What small mammals are eating seed in south Sound prairies, and how do their populations respond to burning?
- 2) Does edge type (forest, unburned prairie, riparian, agricultural, urban) influence the amount of seed predation?
- 3) Does prairie quality (percent native cover) affect the amount of predation?
- 4) Does the rate of seed predation by small mammals and/or insects change seasonally?

## Conclusion

In summary, three species were heavily predated upon by mammals in this study: *B. deltoidea*, *D. oligosanthes*, and *V. adunca*. The two other species, *A. maritima* and *E. speciosus*, also suffered losses but not as drastically as the other three. *E. speciosus* lost seed across all treatments, including the control, suggesting that it is highly susceptible to wind and other abiotic influences. These findings fall in line with the Optimal Diet Theory, which states that seed predators will consume larger seeded species first because they offer the most nutrition for the least amount of energy expended foraging (Brown et al., 1975). No plant species appeared to be influenced by insect predation, and the edge effect did not influence the amount of predation found in this study.

The main takeaway from this study for land managers on south Sound prairies is that small mammal predation is likely a substantial source of loss for larger seeded species, especially when sown in concentrated amounts. Predation is less likely an issue for smaller seeded species such as *E. speciosus*. Certain mitigation methods can be implemented to reduce the loss of these seeds by predation depending on their cost-effectiveness. This study found that predation can occur at least up to one week after seed placement, meaning that temporary mitigation measures, such as fencing, likely need to be in place for at least one week. Luckily, this fencing likely does not need to extend belowground to be effective. Further study should consider potential losses from bird predation and site factors such as surrounding vegetation, burn unit size, and surrounding habitat types and land use to see if these factors influence the amount of rodent predation.

The species in this study were chosen because they hold an important ecological function in the south Sound prairies and have historically been difficult to establish from

seed. While there are certainly numerous factors influencing the establishment of seed in the south Sound prairies, every factor studied allows us to make more informed management decisions. This permits the most efficient use of limited resources and ideally results in greater success of habitat restoration for these rare biological hotspots.

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