POPULATION DYNAMICS AND SEED FEEDING TENDENCIES OF FIELD CRICKETS (GRYLLIDAE*)* IN WILD BLUEBERRY FIELDS

by

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DEDICATION PAGE

To my younger self.

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ABSTRACT

Weeds are a major limiting factor in commercial wild blueberry production and the need for economical viable management techniques continues to be of vital importance. *Gryllus pennsylvanicus* (Gryllidae), are post-dispersal seed consumers, common in wild blueberry fields. To understand the potential of *G. pennsylvanicus* as a biological control agent, this study examined their spatial and temporal population dynamics and seed feeding tendencies of weed seeds commonly found in wild blueberry fields. Laboratory and field studies were conducted during the summer-fall season of 2019 in wild blueberry fields. Field experiments revealed *G. pennsylvanicus* was active for 14 weeks, peaking in mid-August, coinciding with the seed rain of economically destructive weeds. The spatial population dynamics of *G. pennsylvanicus* did not change with increasing distance from field edge and did not migrate in or out of the field throughout their active period. Laboratory no-choice feeding studies revealed *G. pennsylvanicus* consumes a variety of seeds (0.057 – 1.9 mg). An average of 449 hair fescue seeds, per cricket, over 120 hours were consumed with an estimated final constant feeding rate of 65.5 seeds per day. These findings suggest that post-dispersal weed seed consumption by *G. pennsylvanicus* in wild blueberry fields, when used in conjunction with an integrated weed management plan, may influence weed emergence providing a valuable and sustainable ecological service. The results of this study coupled with insecticide toxicity assays will prove critical in the understanding of natural enemies' contributions in wild blueberry cropping systems.

LIST OF ABBREVIATIONS USED

P	P-value
SE	Standard error
R^2	Coefficient of determination
S	Standard error of the regression
h	Hour
m	Meter
m^{-2}	Per square meter
cm	Centimeter
L	Liter
mL	Milliliter
mg	Milligram
°C	Degrees Celsius
%	Percent

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CHAPTER 1: INTRODUCTION

1.1 Nova Scotia Wild Blueberry Industry

Wild blueberries (*Vaccinium angustifolium* Aiton, syn. ‘lowbush’ blueberry) (Ericaceae) are native to northeastern North America where they are one of the most important agricultural commodities (Robichaud 2006; Sutton 1993). Over 55 000 ha of wild blueberries are in commercial production in Canada with an average 5-year farm gate value of $86.7 million per year (Statistics Canada 2020). This plant is a small deciduous shrub that can reproduce through secondary seed dispersal from birds or mammals (Vander Kloet 1978), but mainly reproduces clonally through an extensive underground rhizome system (Bell 1950). Wild blueberries thrive in a wide range of conditions but predominately occur in well-drained soils with a pH of 4-5 (Hall et al. 1964; Jensen & Yarborough 2004). Commercially managed wild blueberry fields are typically established from native stands on deforested or abandoned agricultural land (Hall 1959). These fields are generally managed on a two-year cycle using no-till practices (Agriculture and Agri-Food Canada 2012). The cycle is initiated by pruning plants to ground level through mowing or burning following harvest to encourage vegetative growth from rhizomes and flower bud development during the non-bearing year (Glass et al. 2005; Jensen & Yarborough 2004). This is followed by the bearing year in which blueberry plants bloom, are pollinated, and produce berries. Fields are then pruned again following harvest to restart the two-year production cycle, or prepared for an additional bearing year which is referred to as double-cropping (Eaton & Nams 2006; Jordan & Eaton 1995). Double cropping, however, can result in a slower growth rate and decreased crop productivity in the second year. This is due to limited available resources compared to the first crop and is therefore not a common practice (Jordan & Eaton 1995). Although a range of pests can damage wild blueberries, weeds continue to be a major production challenge due to the lack of tillage and crop rotation associated with the perennial monoculture of wild blueberry production.

1.2 Weed Management in Wild Blueberry Fields

One of the major factors impacting the productivity and management of wild blueberries is weeds (Hall 1959; Jensen & Specht 2002; Kennedy et al. 2010; Yarborough 2004). A weed is generally defined as a plant that causes problems or adversely affects the growth of a desired plant and is persistent within that system (Vallotton 1999). With weeds present, the blueberry plant is subjected to competition for light, moisture, nutrients, and space and restriction of these critical resources has the potential to lead to lower berry quality (Jensen & Specht 2002), yields (Yarborough & Bhowmik 1988), and above all, reduced income (Yarborough et al. 1986). Further, many weeds may harbour blueberry pathogens and insect pests such as the blueberry maggot (*Rhagoletis mendax* Curran; McCully et al. 1991) while other weeds may inhibit the spread of wild blueberries into bare areas (Yarborough & Bhowmik 1988). Some weeds also clog the wild blueberry harvester head which in turn reduces harvester efficiency (Jensen & Specht 2002). However, when weeds are properly managed, a two-fold increase in yield has been observed (Yarborough 2004; Yarborough et al. 1986; Yarborough & Bhowmik 1988).

The weed flora of wild blueberry fields is diverse with over 100 weed species documented in weed surveys in the early 1980’s in Nova Scotia (McCully et al. 1991). Traditionally, the weed flora of wild blueberry fields was dominated by herbaceous and woody perennials that rely on rhizomes for persistence and spread in blueberry fields (Jensen & Yarborough 2004). Between 1984-1985 and 2001-2002, the number of weed species found in lowbush blueberry fields in Nova Scotia nearly doubled to more than 200 species (Jensen & Yarborough 2004). Additionally, Jensen & Yarborough (2004) noted a distinct trend towards an increase in weed species that rely on seeds for establishment and spread, with a doubling of annual broadleaf weeds along with the first identification of annual grass species found in lowbush blueberry fields in Nova Scotia in the early 2000's. Additional annual weed problems have since been documented (Lyu et al. 2021; White & Webb 2017), as has the importance of secondary seed dispersal (Boyd & White 2009) and seedling recruitment in populations of problematic weeds such as red sorrel (*Rumex acetosella* L.) and hair fescue (*Festuca filiformis* Pourr) (White et al. 2015b; White 2018). There has also been a decline in the use of thermal pruning methods that can damage weed seeds (White & Boyd 2016), which has been shown to contribute to species shifts (Penney et al. 2008).

Herbicides are effective in suppressing weeds in wild blueberry fields, but there are limitations associated with heavy reliance on herbicides for weed management. The heavy reliance on herbicides such as hexazinone, for example, has led to subsequent selection for resistant (Li et al. 2014) or tolerant species (Yarborough & Bhowmik 1988) which has inherently expanded the number of herbicide-resistant weeds and limited available weed control tactics. The use of pesticides can also pose adverse environmental risks throughout nontarget spray drift and persistent chemical residue (Boyetchko et al. 2009; Pimentel et al. 2005), which has resulted in deregistration of atrazine for weed control in wild blueberry (Anonymous 2003). Moreover, herbicide costs have increased, placing financial strain on growers which can further limit management options they are willing to adopt (Schnitkey & Sellars 2016). Although herbicides will likely remain an integral component of wild blueberry weed management, loss of herbicide availability due to resistance, environmental concerns, or other reasons demonstrate a growing need for an integrated pest management (IPM) system that works to manage weeds at a sustainable economic level.

1.3 Integrated Weed Management in Wild Blueberry Fields

IPM is the practice of combining pest control strategies to minimize pests in an economically effective and environmentally sound way (FAO 2020). The development of a true IPM program requires the use of alternatives to pesticides, such as preventative, mechanical, cultural, and biological controls (Jensen & Yarborough 2004). Preventative approaches are possible in wild blueberry, with most emphasis in this area on cleaning of machinery to prevent secondary seed dispersal (Boyd & White 2009). Mechanical control is difficult in wild blueberry due to lack of tillage, though mechanical mowing of weeds that grow taller than blueberry plants is possible (Jensen & Yarborough 2004; Kinsman 1993). Cultural control of weeds is limited to biennial mowing or burning (Yarborough 2011), the management of grasses to inhibit broadleaf weeds in bare areas (Anonymous 2017), and the use of sulfur to acidify soil, making soil conditions more favorable to blueberry growth rather than weed growth (Drummond et al. 2009; Eaton & Nams 2006). While effective for some species, this latter approach has not been widely adopted due to the large amount of sulfur required to acidify soil (Drummond et al. 2009) and the high costs of this input (Drummond et al. 2012). Biological weed control on the other hand has been investigated in wild blueberry and, while suffering from some limitations in effectiveness (Cutler et al. 2016; MacEachern-Balodis et al. 2017), remains a potentially underutilized and underappreciated form of weed control in this crop.

Biological weed control consists of organisms (natural enemies) that reduce the population of a weed species, contributing to ecological conservation and agricultural sustainability (Kenis et al. 2019; O'Rourke et al. 2006; Waage et al. 1988). It is an overarching term composed of different methods that vary on how the organisms are promoted and/or introduced within the system. The introduction of a natural enemy to an area requiring pest control involves the implementation of classical, augmentative, or grazing animal approaches. These methods require humans to introduce the natural enemy into the system. In contrast, conservation biological control works to safeguard or modify an environment to promote favorable conditions for the existing natural enemies. Through competition, diseases, parasitism, and predation, natural enemies can help suppress pest populations to acceptable levels and avoid otherwise inevitable pest outbreaks (Pimentel et al. 1992).

The term 'biological control' was coined by Smith (1919) and has increased substantially in acceptance and popularity over the past few decades within the agricultural community (Kenis et al. 2019). However, the notion of biological control is not a recent one. The first known practice of this dates back to 324 BCE in China, where predaceous ants (*Oecophylla smaragdina* Fabricius) were successfully used to supress populations of leaf feeding pests on citrus plants (Huang & Yang 1987; Ignacimuthu & Jayaraj 2005). Today, the practice of biological control via insects has become widely adopted and was assessed at a net value of $5.5 billion in the United States alone (Naranjo et al. 2015). From 1900 to 2012 there have been 1555 intentional releases of

468 different natural enemies against 175 target weed species in 48 plants families throughout 90 countries (Hoffmann et al. 2020). Of these cases, over two thirds of the target weed species received some level of control showcasing their capability and effectiveness.

A growing number of studies have demonstrated the capability of insects to influence weed populations through post dispersal seed consumption (Lundgren 2009; Lundgren & Rosentrater 2007; Marino et al. 1997; Menalled et al. 2000; Rand et al. 2006). For example, Ichihara et al. (2012) found that as the density of field cricket *Teleogryllus emma* increased, the proportion of Italian ryegrass (*Lolium multiflorum*) seedling emergence decreased from >90% with no crickets present to <5% with eight crickets present. Additionally, a study by O'Rourke (2006) revealed that the cricket species *Gryllus pennsylvanicus* and *Allonemobius allardi* were the primary seed consumers of giant foxtail (*Setaria faberi*) seeds within maize and soybean and explained up to 66% of the variation in seed removal.

Although the opportunity to develop effective biological control strategies exists, knowledge of the spatial and temporal occurrence of natural enemies is required. For instance, food resources or habitat refuge are sometimes known to dictate when and where natural enemies will reside within a given system (Cutler et al. 2012; Landis et al. 2000; Lundgren 2009). Additionally, morphological and physiological traits can influence an insect's ability and willingness to consume different weed seeds. How capable an insect is at manipulating a seed and the ability to break/remove the seed coat and extract the nutritional content from the seed can all determine what weed seeds may be consumed (Lundgren 2009). Therefore, understanding the natural enemy's population dynamics throughout their active season as well as understanding their feeding tendencies will undoubtedly play a role in determining what weed species they are likely to consume and where weed suppression could occur within a field.

Given the recent shifts in the weed flora of wild blueberry fields and the increasing knowledge of seedling recruitment by important perennial weeds (Jensen & Yarborough 2004), there is a growing need to consider seed-based control mechanisms as components of IPM programs in wild blueberry fields. Wild blueberry fields are not tilled and weed seedbanks therefore remain very shallow (White 2018), similar to that reported in other no-till cropping systems (Cardina et al. 2002; Yenish et al. 1992). The no-till practice and availability of seeds on or near the soil surface enables organisms to easily access and consume these seeds (Cutler et al. 2016; White 2018), leading to the possibility of weed seed predation as a form of weed biocontrol in wild blueberry fields. Nonetheless, the ability to foresee the ecological benefits these insects may provide in agricultural settings is somewhat constricted. Field crickets (Orthoptera: Gryllidae) for example, are recognized as natural enemies. They are found in various agricultural systems and have an affinity for post-dispersal weed seed predation (Carmona et al. 1999; Cutler et al. 2016; Lundgren & Rosentrater 2007; O'Rourke et al. 2006; van der Laat et al. 2015). However, the extent to which these beneficial insects consume particular weed seeds is not fully understood (Cutler et al. 2016; Lundgren 2009).

In summary, to understand how natural enemies may influence weed populations in cropping systems such as wild blueberry, the beneficial insect's natural population must first be assessed and their potential to consume weed seeds estimated. After this is determined, growers can use that knowledge to implement habitat management practices that may promote the beneficial insect's population to encourage weed seed suppression.

1.4 Gryllidae as Natural Enemies

Approximately 900 species of crickets (Gryllidae: Orthoptera) have a cosmopolitan distribution and are identifiable by their enlarged hind jumping legs, three tarsal segments and long cerci (Alexander 1968; Dossey et al. 2016). The fall field cricket, *Gryllus pennsylvanicus* Burmeister, is found in temperate zones throughout northeastern North America and is among the most well distributed cricket in the region (Carmona et al. 1999; Lundgren 2009; O'Rourke et al. 2006). In Nova Scotia, *G. pennsylvanicus* is the only field cricket recorded to date (Alexander 1957; Klymko et al. 2019; Piers 1918). This relatively gregarious cricket is commonly found in non-forested, stable habitats such as crop fields, pastures, weedy areas, roadsides, and various grassy habitats (Carmona et al. 1999; French et al. 1986; McAlpine & Smith 2010; Piers 1918; Vickery 1961). As an oviparous, hemimetabolic insect, their one-year life cycle begins in the egg stage prior to hatching into a nymph that passes through 8-9 instars over approximately 70 days (Jobin 1961). This begins with a mature female *G. pennsylvanicus* depositing her eggs under plant debris or loose soil in late summer or early autumn, where the eggs enter an obligatory diapause. As an adaptation to the long and severe winters *G. pennsylvanicus* must endure, a cold period of approximately 90 days followed by warming temperatures is required to terminate diapause, safeguarding them in their egg form (Bigelow 1962; Harrison 1979; Rakshpal 1962). Throughout June and July, the crickets hatch and develop as nymphs, become adults by the end of summer and remain active until late October with one generation per year (Carmona et al. 1999; McAlpine & Smith 2010; Piers 1918; Rakshpal 1962; Vickery 1961).

Sometimes considered crop pests due to their abundance and occasional crop damage (Beirne 1971; Byers & Barratt 1991; Rogers et al. 1985), field crickets are mainly considered beneficial insects (Carmona et al. 1999; O'Rourke et al. 2006). Despite their known presence in wild blueberry fields and weed seed eating tendencies, the spatial and temporal dynamics of cricket populations in these systems is largely understudied. Cutler et al. (2016) measured weed seed removal rates by granivorous insects, including *G. pennsylvanicus* and concluded that overall, each distance from field edge (1, 15 and 50 m) did not have a significant effect on the number of weed seeds removed by granivores. However, this study included seed removal by all insects present in wild blueberry fields and did not isolate seed removal rates by *G. pennsylvanicus* specifically. Additionally, data was only collected up to 50 m from the forest edge, which may not be a comprehensive assessment of what occurs in the middle of larger fields.

While predominantly herbivorous, *G. pennsylvanicus* also exhibits omnivorous behaviour, consuming dead and living insects, broadleaf plant leaves, grasses, and seeds (Burgess & Hinks 1987; Carmona et al. 1999). The few published studies (Carmona et al. 1999; Cutler et al. 2016; Lundgren & Rosentrater 2007; White et al. 2007) concluded that in a laboratory setting, *G. pennsylvanicus* readily accepted and consumed weed seeds. They are specifically known to feed on seeds of common agronomic weeds such as common ragweed (*Ambrosia artemisiifolia* L.) and velvetleaf (*Abutilon theophrasti* Medic) (Carmona et al. 1999) and on seeds of common weed species in wild blueberry fields, such as red sorrel *(Rumex acetosella*) and hair fescue (*Festuca filiformis* Sibth;

Cutler et al. 2016). This inherent consumption of weed seeds showcases their potential for contributing to an integrated approach to weed management in no-till agroecosystems such as wild blueberry fields. However, few species of weed seeds were studied and the rate at which they consume these seeds was only recorded in one study over 24 hours (White et al. 2007). Further studies are necessary to fully understand the potential of the field cricket to consume current prominent weed seeds, supporting future integrated weed management programs in wild blueberry production systems.

1.5 Research Objectives and Hypothesis

The first objective of this research was to determine the time of year *G. pennsylvanicus* was present and their abundance with relation to distance from the field edge in vegetative wild blueberry fields. It was hypothesized that populations of *G. pennsylvanicus* would peak in late summer and early autumn (Alexander 1957) and that distances from field edge (-10, 0, 10, 50, 100 m) would not have an effect on their abundance. This is due to other researchers demonstrating that the occurrence and weed seed recovery by various invertebrates showed no effect of distance from field edge (Cutler et al. 2012, 2016; Ichihara et al. 2014; Westerman et al. 2003).

The second objective of this research was to determine which weed seeds *G. pennsylvanicus* was willing and able to consume by exposing them to weed seeds found in wild blueberry fields in a controlled laboratory setting. It was hypothesized that collected *G. pennsylvanicus* would consume all provided seeds. This is due to research suggesting that seed destruction by *G. pennsylvanicus* is statistically unrelated to different seed traits such as the size and toughness of the seed (Lundgren & Rosentrater 2007). It was also hypothesized that after starving *G. pennsylvanicus* for 48 hours, their initial rate of granivory would be high and then would slow over to a more constant rate, due to satiation (Honek et al. 2003; Loureiro 2018). These studies collectively highlight the potential of *G. pennsylvanicus* to contribute to weed management in wild blueberry fields.

CHAPTER 2: SPATIAL AND TEMPORAL POPULATION DYNAMICS OF *GRYLLUS PENNSYLVANICUS* IN WILD BLUEBERRY FIELDS

2.1 Introduction

Knowledge of natural enemy spatial and temporal population dynamics is required to guide use of these enemies as part of an overall integrated weed management plan. While granivorous insects may exhibit higher abundance of seed removal near field margins (Landis et al. 2000; Rand et al. 2006), this is not always the case as results vary for different species. Some granivorous insects are habitat generalists and their abundance or seed removal is variable in space (Cutler et al. 2016; Ichihara et al. 2014; Marino et al. 1997; Westerman et al. 2003). Some species prefer to congregate within forests or near forest edges (Magura 2002) while others are more common in the innermost portions of agricultural fields (Cutler et al. 2012; Jones et al. 2016; Loureiro 2018). Different species are also active during different times of the year (Loureiro et al. 2020). Therefore, when and where these species reside within a field can inherently affect their ability to contribute towards biological weed control.

The purpose of this study was to examine how captures of *G. pennsylvanicus* vary as a function of (1) date of sampling, and (2) increasing distance from wild blueberry field edges. It was predicted that the population of *G. pennsylvanicus* would peak in August-September in Nova Scotia wild blueberry fields, given that is what is found in other agro-ecosystems (Carmona et al. 1999; O'Rourke et al. 2006). It was also predicted that the number of *G. pennsylvanicus* would not change with increasing distance from field edge, given they are generally homogenously distributed throughout stable, no-till cropland (Alexander 1957; Ballman et al. 2017; Brust & House 1988; Carmona et al. 1999; Cutler et al. 2016; Jones et al. 2014, 2016; Piers 1918).

2.2 Materials and Methods

2.2.1 Cricket collection and experimental layout

Five non-bearing year wild blueberry fields at least 200 m wide from forest edge (mixed-wood forest) to field center were selected within central Nova Scotia (Table 1).

Table 1: Field names and locations used to analyze *Gryllus pennsylvanicus* captures.

Field	Coordinates
5 Houses	45°24'33.4"N 63°43'32.5"W
Cattle Market	45°21'54.7"N 63°12'48.0"W
Baseline	45°29'05.4"N 63°32'42.6"W
Highland Village	45°24'19.5"N 63°40'07.2"W
Camden	45°18'16.1"N 63°10'27.3"W

Only non-bearing year fields were used in this study as bearing versus non-bearing year fields do not affect weed seed removal by invertebrates (Cutler et al. 2016) and we wanted to minimize damage to fruit-bearing plants. Field crickets were collected using pitfall traps (Greenslade 1964) that were placed in each field beginning in June. Pitfall trapping is a method commonly used to collect surface-active invertebrates and is proven to be an effective way of capturing *G. pennsylvanicus* (Carmona et al. 1999). A single trap was set up in the shape of an equilateral triangle, with sides 100 cm in length (Figure 1). Two 473 mL clear plastic cups (9 cm diameter) were placed in the ground at each corner with the rim flush with the soil surface. A double-cup system was implemented so that the inner cup could be lifted out for easy removal of specimens while the outer cup remained in the ground. A 15 x 15 x 0.5 cm piece of plywood with nails in the corners as support were placed over each pair of cups as a rain cover (Cutler et al. 2012; Greenslade 1964; Laub et al. 2009).

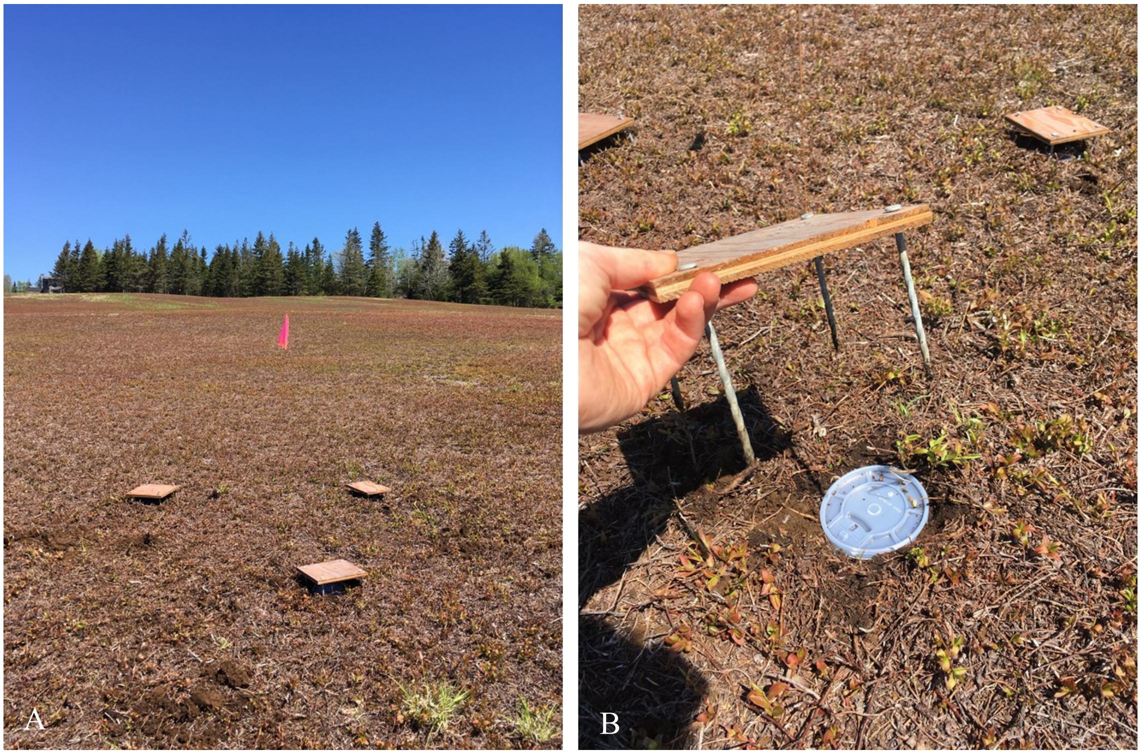

Figure 1. Pitfall trap in a non-bearing year wild blueberry field to record captures of *Gryllus pennsylvanicus.* Pitfall trap (A) and removed rain cover showing sealed catchment cup with rim flush with the soil surface (B).

To determine how cricket captures differ over time and distance from field edge, pitfall traps were placed along a single transect at -10, 0, 10, 50, and 100 m in each field, with 0 m being the edge between the forest and field. The contents of the three cups at each trap were combined to represent a single sample on each sampling date. Traps were activated for 72 h every week between 20 June and 17 October. Contents of the cups were checked after 72 h. The number of *G. pennsylvanicus* (all life stages) at each trap was recorded and then transferred to a plastic container for transport back to the laboratory for further studies. All bycatch was released back into the field and plastic lids were fitted over each cup between collection periods.

2.3 Data analyses

The effects of sampling date and distance from field edge on *G. pennsylvanicus* captures was determined using a mixed model ANOVA in Minitab 19 Statistical Software (Pennsylvania State University). Sampling date and distance were considered fixed effects in the analysis and field locations were considered random blocking effects. Effects were considered significant at $\alpha = 0.05$. Means separation, where necessary, was conducted using Fisher's least significant difference (LSD) as this test better compensates for the high degree of experimental error present in field studies (Montgomery 2017). Nonnormal data were transformed using $\log(y+1)$ to satisfy ANOVA assumptions and all presented means are a result of the back transformation.

2.4 Results

A total of 261 *G. pennsylvanicus* were collected. Five camel crickets (Rhaphidophoridae) were also captured but were omitted from the study.

Distance from field edge significantly affected *G. pennsylvanicus* captures ($P < 0.001$). No *G. pennsylvanicus* were captured at the -10 m distance (i.e. into the forest) and two on average were collected at the field edge (0 m). In contrast, 18, 15 and 17 individuals on average were collected at 10, 50 and 100 m respectively from the field edge over the entire sampling period

Sampling date significantly affected *G. pennsylvanicus* captures ($P < 0.001$). There were no captures prior to 4 July (Figure 3). Captures began to increase, peaking on 9 Aug, declining sharply in mid-August, and thereafter gradually decreasing until the final captures on 10 Oct. Inter-site variability of cricket captures was high at their peak on 9 Aug with 0 captured in the Camden field and 41 captured in the 5 Houses field. There was no sampling date by distance interaction ($P = 0.15$), indicating that the effect of distance on captures did not change over time.

Field site significantly affected *G. pennsylvanicus* captures (Table 2). There were approximately two and half times as many *G. pennsylvanicus* captured per day in the 5 Houses field compared to the field with the second most captures. There was no significant difference between captures at any of the other sampled fields.

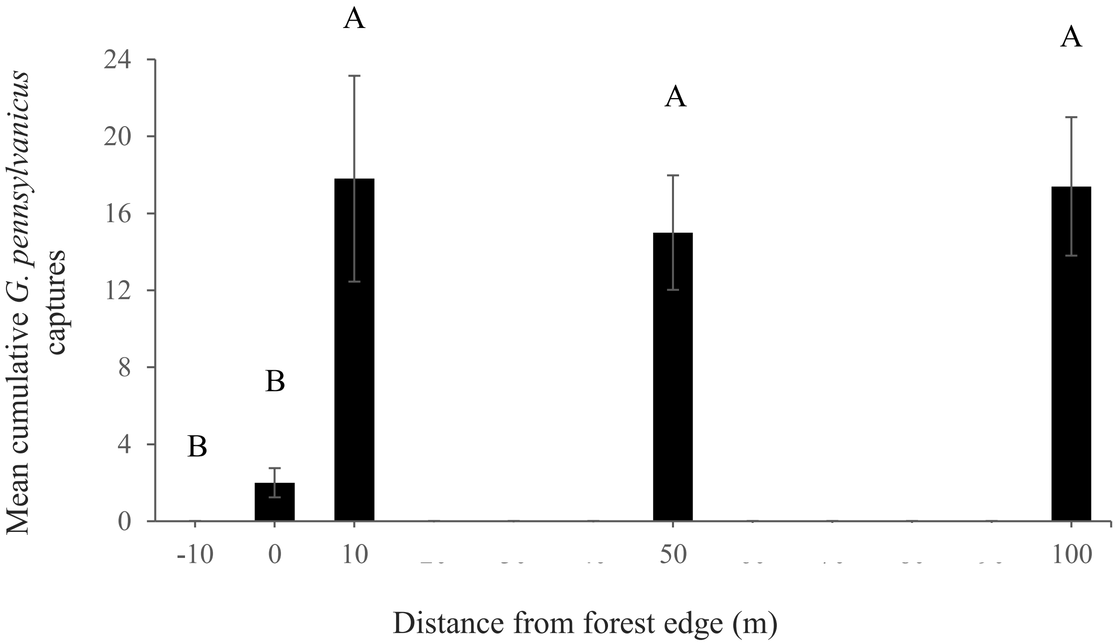

Figure 2: Mean (± SEM) cumulative nymph and adult *Gryllus pennsylvanicus* captures at different distances from the forest edge of non-bearing year wild blueberry fields. *Gryllus pennsylvanicus* collected once a week from 4 Jul – 10 Oct 2019. Values represent the mean of all fields ($n = 5$) ± 1 SEM. Values with different letters are significantly different ($P < 0.05$, Fisher's test).

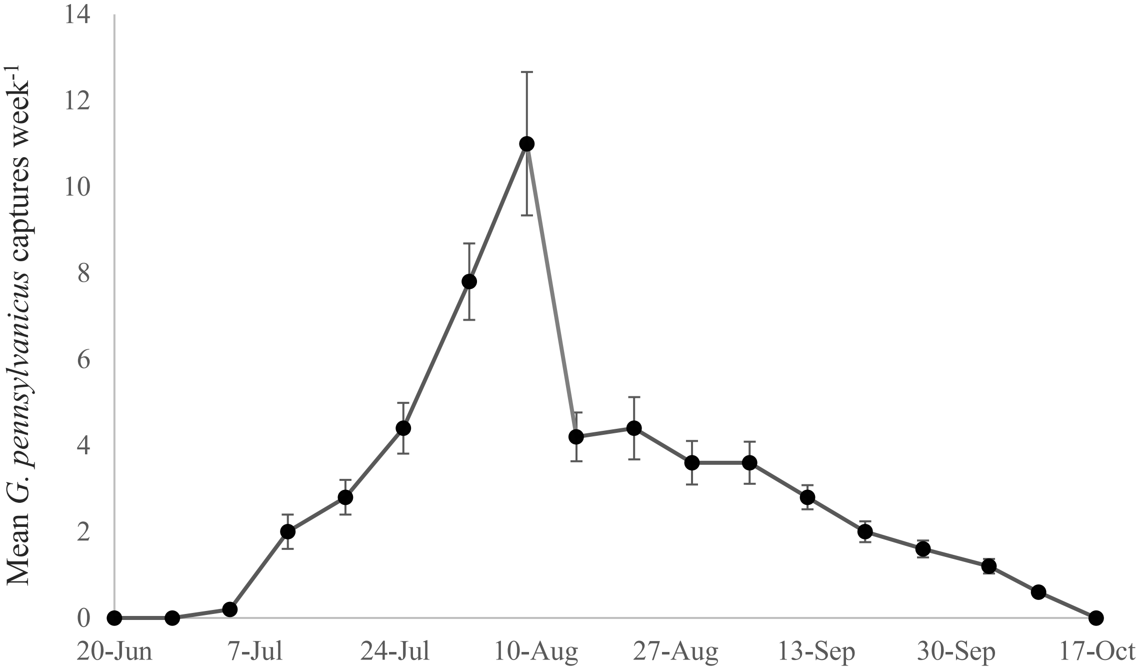

Figure 3. Mean (± SEM) weekly nymph and adult *Gryllus pennsylvanicus* captures for each sampling date in non-bearing year wild blueberry fields. *Gryllus pennsylvanicus* was collected once a week from 20 Jun – 17 Oct 2019. Means are for all sampled distances in all fields and bars represent standard error.

Table 2: Fisher's multiple means comparison of *Gryllus pennsylvanicus* captures. *Gryllus pennsylvanicus* was collected once a week from 4 Jul – 10 Oct 2019. Means (± SEM) are for all collection dates.

Field	Mean
5 Houses	9.20 ± 2.62 a
Cattle Market	3.67 ± 1.01 b
Baseline	2.20 ± 0.53 b
Highland Village	1.47 ± 0.65 b
Camden	0.87 ± 0.35 b

*Means sharing the same letter indicate no statistical difference.

2.5 Discussion

Field crickets are natural enemies in temperate agroecosystems and are generally found in stable, no-till habitats (Alexander 1957; Brust & House 1988; Carmona et al. 1999). Both field crickets (Gryllidae) and camel crickets were found in this study. Of the crickets collected, there were only five camel crickets captured and the field crickets captured were exclusively *G. pennsylvanicus.* This comes as no surprise, given they are the only field crickets recorded to date in the Maritime provinces of Canada (Klymko et al. 2019).

The first capture of *G. pennsylvanicus* was on 4 Jul, with captures peaking by 5-8 Aug and thereafter declining until the final capture on 10 Oct. These findings are consistent with early reports of *G. pennsylvanicus*' presence in July and August as nymphs to September and October as adults (Alexander 1957; Harrison 1979; Rakshpal 1962), with their peak abundance occurring in August and September. A more recent study by Cutler et al. (2016) collected *G. pennsylvanicus* in Nova Scotia wild blueberry fields using pitfall traps from August to October in 2013, also found that *G. pennsylvanicus* was active during this period. Carmona et al. (1999) observed that adult *G. pennsylvanicus* were active in Michigan between 17 Aug to 15 Oct, with the peak abundance occurring on 17 Sept. O'Rourke et al. (2006) also found *G. pennsylvanicus* peak abundance in Iowa to be in August or September.

There was a sharp decrease in the number of *G. pennsylvanicus* captured on 15 Aug compared to captures in the previous week. Growers were contacted and confirmed no insecticides were applied to the fields to account for this decrease. Additionally, no periods of abnormal temperatures or precipitation were recorded throughout the area during this time (Government of Canada 2020). A reason for the rather rapid decrease in captures may be explained by the population of *G. pennsylvanicus* reaching maturity and increased food availability. For example, Crantrall (1943) and Bigelow (1958) found that the population of *G. pennsylvanicus* matures rather rapidly in early August, peaks within approximately 10 days and persists until they are killed off naturally or by successive frosts. It is unlikely more individuals will continue to be captured after their population has maturated, as they will have all already emerged from the ground. As for the food availability element, studies have indicated that the presence of weeds can be favourable for seed consumers and thus show preference for these areas (Angelstam et al. 1987; Cromar et al. 1999; Tew et al. 2000). Given prominent weeds found in wild blueberry fields are maturing and releasing their seeds in August, and often grow in patches under field conditions (Lyu et al. 2021), *G. pennsylvanicus* may locate and remain in these food-abundant patches, thereby decreasing their movement and likelihood to be captured. These two factors in combination may be responsible for the decrease in captures following 9 Aug. This is beneficial from a grower's perspective as this would imply that the population of *G. pennsylvanicus* is concentrated in areas where weed seeds are located. That said, this in an interpretation of the findings and without measuring food availability, it is impossible to confirm this hypothesis. This could serve as the basis for a future work in *G. pennsylvanicus* population dynamics in wild blueberry fields.

Although fields were all located in central Nova Scotia and habitats surrounding wild blueberry fields are generally ecologically similar, there was variability of captures between fields for each sampling date. The number of *G. pennsylvanicus* captured on 9 Aug ranged from a low of 0 in the Camden field to a high of 41 in the 5 Houses field. The

5 Houses field had more captures on this day and significantly more captures overall. A reason for this may be due to the tendency of *G. pennsylvanicus* to inhabit grassy areas (Alexander 1957; Carmona et al. 1999; Ichihara et al. 2015). Comparative to the other fields, the 5 Houses field was observed to contain more weedy dead grass patches that may shelter and support the cricket population thereby increasing their numbers. Field edges were comprised of mixed-wood forests in all sampled fields and therefore it is unlikely that the surrounding habitat influences *G. pennsylvanicus* numbers.

The 98-day range of activity of nymph and adult crickets noted in this study lies in the cricket's physiological adaptations to their environment. *Gryllus pennsylvanicus* is found in regions where winters are long and severe, and therefore must adapt to survive these cold conditions by avoiding untimely hatching. Delaying nymph emergence in the spring for the purpose of waiting for warmer weather can result in reduced growth, leading to smaller adults with less fecundity (Pickford 1960). Early spring development can also result in mortality due to exposure to low temperatures, lack of resources, or alternative predation (Carrière et al. 1996; Pickford 1960). Though the month of May can bring favourable temperatures for nymph development, temperatures are not consistently high enough to break diapause (Carrière et al. 1996). In the same respect, temperatures may drop below 6°C in autumn, then warm again to temperatures high enough for egg development, however, a short exposure to cold and then warm conditions are not sufficient to break diapause. This life cycle trend explains why crickets are not detected until late June or early July and die off by mid-October which is in-line with the observations of this study in wild blueberry fields.

Though the nymph and adult life cycle of *G. pennsylvanicus* are only active for a few months, it is an ecologically important period as peak captures likely coincide with the presence of both insect pests and weed seeds in wild blueberry. For example, the active window of *G. pennsylvanicus* observed in this study aligns with the seed rain of problematic weeds such as hair fescue (*Festuca filiformis* Pourr.) and sheep sorrel (*Rumex acetosella* L.) (Cutler et al. 2012; White 2018; White et al. 2015a), allowing for post-dispersal weed seed feeding opportunities. Additionally, wild blueberry insect pests such as the blueberry maggot (*Rhagoletis mendax* Curran) and spotted wing drosophila (SWD; *Drosophila suzukii*) are also present in late summer (Drummond et al. 2019, 2020). This overlap is important as *G. pennsylvanicus* exhumes and consumes large numbers of pupae (Monteith 1971), including SWD (Ballman et al. 2017) and the apple maggot (*Rhagoletis pomonella*), a close relative of the blueberry maggot (Monteith 1971). Research in respect to *G. pennsylvanicus* as a biological control for blueberry maggot pupae, however, has not been conducted.

No crickets were captured 10 m into the forest, and less than ten were captured along the field edge (0 m) throughout the entire sampling period. This suggests that *G. pennsylvanicus* does not reside within the forest, nor do they favour field edges. This is not surprising as crickets are not known to inhabit forests, but instead, stable grassy areas such as crop fields (Alexander 1957; Brust & House 1988; Carmona et al. 1999). These results corroborate with previous studies where the overall abundance of particular granivorous insects was higher within the cropping system compared to the field edge (Cutler et al. 2012; Ichihara et al. 2014; Loureiro et al. 2020). The occurrence of other granivorous species in agricultural fields, however, does vary. Some granivores are found to be more abundant near the field edge (Holland et al. 1999; Kromp 1999; Saska et al. 2008), within the forest (Loureiro et al. 2020), or in some instances, no effect on their abundance with respect to field edge is observed at all (Marino et al. 1997; Westerman et al. 2003). *Gryllus pennsylvanicus* however was captured homogenously throughout the inner portions of the field up to 100 m from the forest edge. This is important since it implies that the current management practices undertaken by growers seem to be compatible with *G. pennsylvanicus* populations. As well, their uniform spatial distribution 10 – 100 m into the fields suggests that growers can expect potential biological control from *G. pennsylvanicus* throughout their fields. Given the use of agricultural equipment such as harvesters can disperse weed seeds throughout wild blueberry fields (Boyd & White 2009), the even distribution of *G. pennsylvanicus* would be advantageous for helping to destroy weed seeds.

While both distance and time influenced the number of crickets captured, there was no significant distance-time interaction. This suggests that *G. pennsylvanicus* populations are not moving in or out of the field over time but are likely overwintering in wild blueberry fields. A reason for *G. pennsylvanicus* to primarily reside in the inner portions of the field may be due to the low-lying ground cover found in wild blueberry fields and access to food sources such as weed seeds, which maybe lacking in the bordering forest. I observed *G. pennsylvanicus* running and taking refuge under dead grass and loose material within the wild blueberry fields, showcasing their preference for stable, low-lying plant covered areas. Providing insects with access to ground cover such as applying mulches or leaving crop residue in the fields may be a way to promote natural enemies. Heggenstaller et al. (2006) suggested that ground cover is well correlated with seed removal rates in cropping systems. House & Brust (1989) suggested that mulches or certain grasses may improve natural enemy shelter and overwintering habitats. Davis & Liebman (2003) found the number of *G. pennsylvanicus* to increase two-fold in wheat plots underseeded with red clover, resulting in significantly less *Setaria faberi* seeds in this treatment compared to treatments with no cover crops. Additionally, Ichihara (2015) observed crickets hiding and moving freely in the spaces between the soil surface and among the stems and leaves of crop plants, likely to avoid predators. As cover crops are not currently possible in wild blueberry systems, mulches could increase the ground cover and overwintering habitats of natural enemies such as field crickets. Given most commercial wild blueberry fields are managed in a biennial cycle, the plant debris left behind by mowing the plants close to ground level every second year may also provide a safe and stable habitat for *G. pennsylvanicus* to reside and reproduce within.

As insect pest infestations remain a challenge and post-dispersal seed consumption by crickets has been classified as a primary driver for weed seed mortality (Ichihara et al. 2014), understanding the temporal and spatial population dynamics of *G. pennsylvanicus* is one step towards understanding their potential as natural enemies. This study provides new and updated information of *G. pennsylvanicus* as well as their population dynamics in wild blueberry systems. While field edges can provide favourable habitats for some ground dwelling insects, the results from this field study show *G. pennsylvanicus* was found more often within the field and up to 100 m from the field edge. As well, *G. pennsylvanicus* was not found to migrate in or out of the field over the course of their active period. These findings suggest that *G. pennsylvanicus* overwinters in wild blueberry fields and may be homogeneously contributing to post-dispersal seed consumption in fields that are at least 200 m wide. Landscapes vary in their suitability for natural enemies, therefore, knowledge of where and when they reside within a given system is critical to understand their potential as a biological control agent. Only vegetative wild blueberry fields were sampled in this study. Although captures of *G. pennsylvanicus* in wild blueberry fields have not been compared between vegetative and fruiting fields, Cutler et al. (2012) found a greater number of carabids in vegetative crop fields. Our exclusive use of non-bearing year fields is therefore likely justified, though it is suggested that future research conducts multi-year experiments in wild blueberry systems to fully comprehend their activity throughout the biennial cycle.

CHAPTER 3: *GRYLLUS PENNSYLVANICUS* SEED FEEDING TENDENCIES AND FEEDING RATES OF COMMON WEED SEEDS IN WILD BLUEBERRY FIELDS

3.1 Introduction

Weed seeds are an abundant and nutritious food source for granivorous insect communities (Lundgren & Rosentrater 2007). These organisms inflict high levels of mortality among agricultural weed seeds (Brust & House 1988; Cromar et al. 1999; Davis & Liebman 2003; Gallandt et al. 2005; O'Rourke et al. 2006) and often begin consuming weeds seeds shortly after seed rains (Westerman et al. 2003b). That said, weed seeds have developed structural and chemical features to help defend themselves from granivory, which in turn influence an insect's willingness and capability to consume certain seeds. For example, Tevis (1958) found that 90% of the seeds consumed by a harvester ant (*Messor pergandei)* came from three weed species, but these weed seeds only made up 8% of the available seeds in the habitat. Tooley and Brust (2002) hypothesized that the ability of a carabid beetle to carry and transport a seed influenced what seeds would be consumed. Likewise, Brust & House (1988) found that small carabids (< 15 mm) preferred small weed seeds whereas larger carabids (> 15 mm) preferred larger weed seeds. These results highlight that granivorous insects do not readily consume all available food sources, but instead make selections based on preference as well as their morphological and physiological capabilities. Therefore, understanding the willingness and ability of a granivorous insect to consume seeds of different species can help us understand how they may influence the population dynamics of certain weed species.

Given *G. pennsylvanicus* is known to consume seeds and is active during the seed rain of some economically important weeds in wild blueberry fields (Chapter 2; Cutler et al. 2016), this species has the potential to contribute to integrated weed management through weed seed consumption. Knowledge of *G. pennsylvanicus* weed seed preference and feeding rates of common weed seeds in wild blueberry fields, however, is limited. The purpose of this study was to determine *G. pennsylvanicus* weed seed feeding preferences and feeding rates on seeds of common weed species in commercial wild blueberry fields. It was predicted that *G. pennsylvanicus* would be particularly damaging towards grass species in wild blueberry fields given their high rate of destruction towards grass seeds in other agroecosystems (Ichihara et al. 2012; Lundgren & Rosentrater 2007).

3.2 Materials and Methods

Captured *G. pennsylvanicus* were used for two no-choice feeding studies to determine (1) *G. pennsylvanicus* seed feeding preferences using seeds of the most common weed species in wild blueberry fields (Table 3), and (2) at what rate they can consume hair fescue seeds. Hair fescue seeds were chosen for this study as hair fescue is one of the most common weed species in wild blueberry fields and can reduce wild blueberry yields by >50% (Lyu et al. 2021; White 2019; Zhang et al. 2018). Seed weight was determined by counting and weighing 100 seeds in groups of 10 for each species. Figure 4 shows tested seeds ordered by increasing weight. Each of the weed species were chosen due to their prevalence in wild blueberry fields along with their potential for economic destruction and range of seed characteristics (Hughes et al. 2016; Lyu et al. 2021; McCully et al. 1991; Zhang et al. 2018).

Table 3: Weed species used in *Gryllus pennsylvanicus* no-choice feeding studies

Plant Species	**Seed weight (mg)**[a]
Narrowleaved goldenrod (*Euthamia graminifolia (L.)* Nutt.)	0.057 ± 0.005
Yellow hawkweed (*Hieracium caespitosum* Dumort.)	0.102 ± 0.009
Spreading dogbane (*Apocynum androsaemifolium* L.)	0.208 ± 0.012
Witchgrass (*Panicum capillaire* L.)	0.318 ± 0.006
Hair fescue (*Festuca filiformis* Pourr.)	0.459 ± 0.007
Sprouted hair fescue (*Festuca filiformis* Pourr.)	NA
Sheep sorrel (*Rumex acetosella* L.)	0.515 ± 0.015
Red fescue (*Festuca rubra* L.)	1.158 ± 0.019
Poverty oat grass (*Danthonia spicata* L.)	1.206 ± 0.019
Cow wheat (*Melampyrum lineare* Desr.)	1.895 ± 0.038
Goatsbeard (*Tragopogon pratensis* L.)	13.863 ± 0.233

Note: Values are the mean ± standard error.

[a] 100 seeds were weighed in groups of 10 to derive the weight of one seed for each weed species

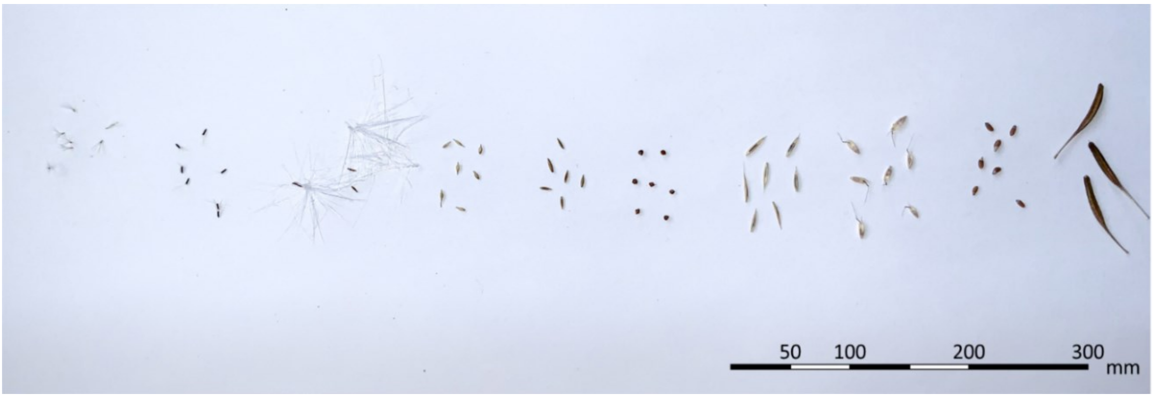

Figure 4: Tested seeds from left to right (narrowleaved goldenrod, yellow hawkweed, dogbane, witchgrass, hair fescue, sheep sorrel, red fescue, poverty oat grass, cow wheat and goatsbeard). Ordered by weight.

3.2.1 Gryllus pennsylvanicus and weed seed collection and maintenance

Adult *G. pennsylvanicus* (not sexed) for use in the feeding studies were collected in central Nova Scotia from August to mid-October in 2019 using pitfall traps (see 2.2 Materials and Methods). Captured *G. pennsylvanicus* were then transferred to the lab in sealable clear plastic 1 L containers where they were housed for a maximum of two weeks under ambient conditions. They were provided water saturated cotton wicks and fed raw carrot pieces every 24 hours until required for experiments. However, before starting the feeding rate study, food was removed 48 hours prior. In all cases, a 48-hour acclimation period was allotted to *G. pennsylvanicus* before experiment initiation (White et al. 2007) and individuals were only used for one test. Weed seeds for use in the feeding experiments were provided by Dr. Scott White or collected directly from the plants during their seed rain in 2019. Contents were held in separate brown paper bags and kept under ambient, dark conditions to avoid germination. Hair fescue seeds were placed on top of two moist filter papers in a Petri dish and sealed with Parafilm to obtain sprouted seeds. Dishes were left on the laboratory bench top until seeds had germinated and the cotyledon was approximately 2 cm long (Figure 5A).

Figure 5: Experimental set up. Sprouted hair fescue in Petri dish (A). In progress no-choice experiment (B).

3.2.2 Experimental Design

<u>No Choice Study</u>

The objective of this experiment was to determine which prominent weed seeds found in wild blueberry fields *G. pennsylvanicus* will consume. Three dates (19 Aug, 26 Sept, and 16 Oct) were used to analtyze seed consumption for each of the weed species outlined in Table 3. A single field cricket was placed in a Petri dish (diameter: 9 cm, depth: 2 cm), containing 10 seeds of a given species and a water saturated cotton wick. Petri dishes were then placed in a growth chamber at 22 ± 2°C with 65 ± 5% relative humidity in a 16:8 (L:D) photoperiod for 48 h (Cutler et al. 2016; White et al. 2007). A completely randomized block design was used, and the number of seeds consumed (whole seed or endosperm only) out of the original 10 was recorded at 48 h. There were three runs of the experiment using crickets captured on 19 Aug, 26 Sept, and 16 Oct.

Each run had four replicate plates per treatment. A limited number of crickets were captured on 6 Aug, allowing an additional preliminary run of the experiment comprising of only hair fescue, sheep sorrel, and poverty oat grass. These weeds were prioritized due to their prominence in wild blueberry fields and their impact on the industry (White 2020).

Feeding Rate Study

The objective of this study was to determine the rate at which *G. pennsylvanicus* consumes hair fescue seeds over time. Crickets were starved for 48 h before the experiment to standardize their hunger. Individual crickets were placed into Petri dishes containing 100 unsprouted hair fescue seeds and a saturated water wick. Petri dishes were placed in a growth chamber under the same conditions described above. At each time point, (1, 2, 4, 6, 12, 24, 36, 48, 60, 72, 84, 96, 108 and 120 h) the number of remaining hair fescue seeds (whole seed or endosperm only) was recorded, and the contents of each dish was replenished back to 100 hair fescue seeds per Petri dish to provide an abundant food supply during the entire experimental period. Seeds were considered consumed when missing from the Petri dish or if the endosperm was consumed and only the seed husk was left behind.

3.3 Data Analyses

Gryllus pennsylvanicus consumed all hair fescue and no goatsbeard seeds during the no-choice experiment for 19 Aug, 26 Sept and 16 Oct. Therefore, these results were not included in the analysis of variance (there was no variance with this data). Because on 6 Aug, a limited number of crickets were available for experimentation on three different weed seeds, a separate analysis was performed on only those three weed seeds as an initial experiment. This was of interest because the individuals used on 6 Aug were younger and smaller than those used later in the study which allows us to assess and compare their ability to consume seeds over their active period. Based on the phenology chart by Alexander (1968), *G. pennsylvanicus* was still in their nymph stages during the first two experimental dates (6 Aug, 19 Aug), and subsequently developed into mature adults by the last two experimental dates (26 Sept, 16 Oct). Individuals were then randomly selected for each testing date, which was representative of what was predominately present in the field at that time.

The total number of seeds consumed in the no-choice studies were compared among treatments and runs using analysis of variance (ANOVA) with the PROC MIXED procedure of SAS® Version 9.4 (SAS® Institute, Cary, NC).

Seed weight (Table 3) was fit to a linear regression against mean number of seeds consumed (x/10) using Minitab 19 Statistical Software (Pennsylvania State University). The equation was of the form:

$$y = a + bx \ [1]$$

where y = the number of seeds consumed, a = the intercept, and b = the slope of the line.

To analyze the feeding rates of *G. pennsylvanicus* over time (120-hour period), a non-linear regression model using the Power (concave) relationship in Minitab was used, demonstrating the relationship between time and seeds consumed. The equation was of the form:

$$y = \ kx^{a} \ [2]$$

where y = total number of seeds consumed over 120 hours, k = constant of variation, x = time (h), and a = a real number.

To analyze the feeding rates of *G. pennsylvanicus* after they became satiated (24 - 120 h), a linear regression model was used, demonstrating their estimated final constant feeding rate.

For all responses, the normal distribution and constant variance of the error terms were verified by examining the residuals and independence of the error terms was ensured by randomization (Montgomery 2017). While assumptions were met for all other responses, the data for the no-choice study with three sampling dates was transformed using a cube root transformation. All presented means are a result of a back transformation. All no-choice analyses were completed using the mixed procedure of SAS® followed by an LSD means separation test where necessary. Effects were considered significant at $\alpha = 0.05$.

3.4 Results

Gryllus pennsylvanicus consumed anywhere from 3 to 10 seeds of each species excluding goatsbeard over the 48 h bioassays (Figure 6). Goatsbeard seeds were presumed too large for *G. pennsylvanicus* to manipulate. In the no-choice feeding experiment including all weed seeds except hair fescue and goatsbeard (these seeds were not included because they ate all or none of the seeds), seed consumption by *G. pennsylvanicus* did not significantly vary by seed type (*P* = 0.22) but did significantly vary by date (*P* = 0.01). Average consumption on 26 Sept (8.4) and 16 Oct (9.5) was significantly greater (*P* = 0.038 and *P* = 0.0019 respectively) than that on 19 Aug (7.3), although there was no significant difference between seed consumption on 26 Sept and

16 Oct (*P* = 0.24). Seed and day interaction was not significant (*P* = 0.53). In the initial feeding study on 6 Aug, seed consumption by *G. pennsylvanicus* varied by seed type (*P* = 0.003). More hair fescue seeds (5.8 ± 1.5 SE) were consumed on average than sheep sorrel (1.8 ± 0.25 SE), and no poverty oat grass seeds were consumed.

Gryllus pennsylvanicus consumed weed seeds 0.057 – 1.9 mg. The data suggests that there is no relationship between seeds consumed and seed size (P = 0.25; $R^2 = 0.19$) based on the seeds consumed in this study (Figure 7A). When goatsbeard, a seed that was not consumed (13.9 mg), is included in the regression, there is a negative relationship between seeds consumed and seed size (P < 0.001; $R^2 = 0.92$) (Figure 7B).

Hair fescue seeds were rapidly consumed within the first 24 hours. Feeding rates of *G. pennsylvanicus* eventually slowed, and stabilized to a more linear response. The relationship for the remaining 96 hours can be described by Equation 1 ($R^2 = 99.9\%$)

$$y = 123.0 * 2.708x \qquad [1]$$

The mean cumulative number of hair fescue seeds consumed by each cricket was 449 over a 120 h period (Figure 8). Over time, *G. pennsylvanicus* slowed their feeding rate. The feeding rate over the 120 h period can be described by Equation 2 (S = 11.72).

$$y = 36.98 * x^{0.5115} \qquad [2]$$

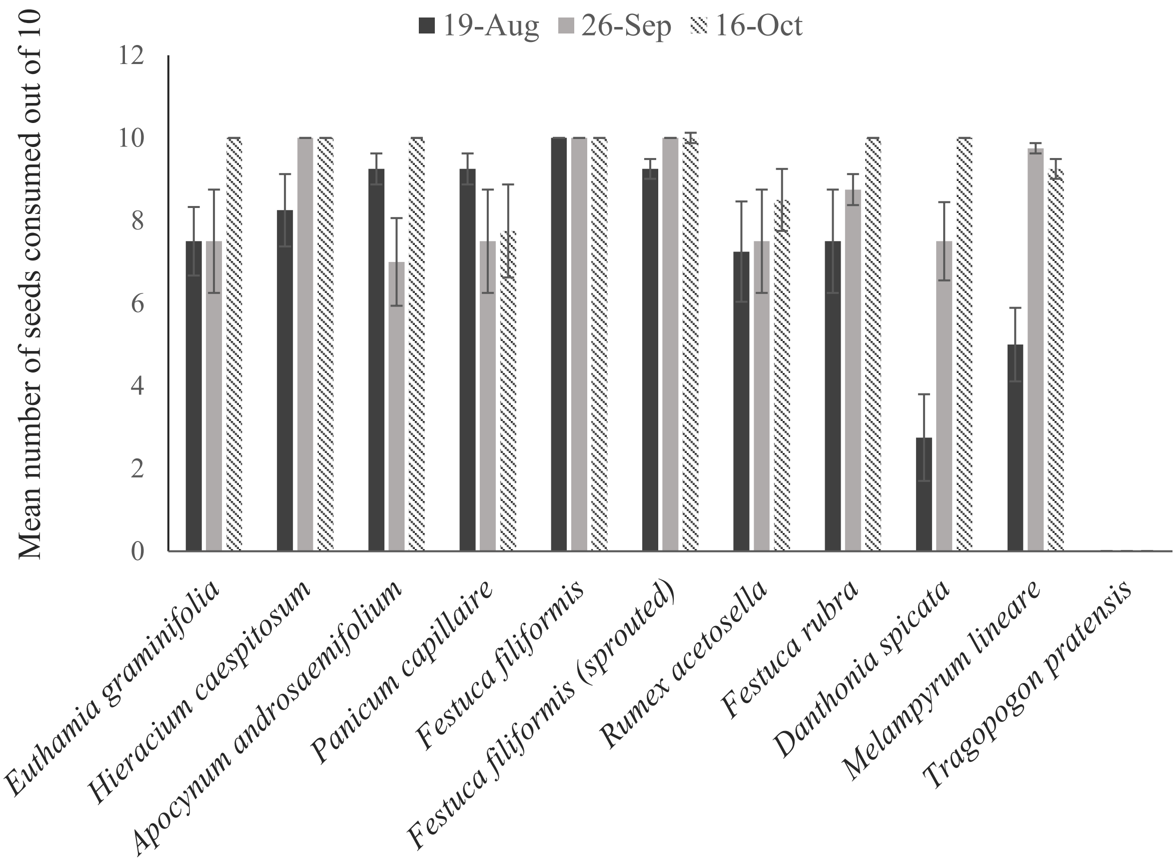

Figure 6: Mean (± SEM) number of seeds consumed (x/10) by *Gryllus pennsylvanicus* over 48 h in three laboratory no-choice feeding experiments.

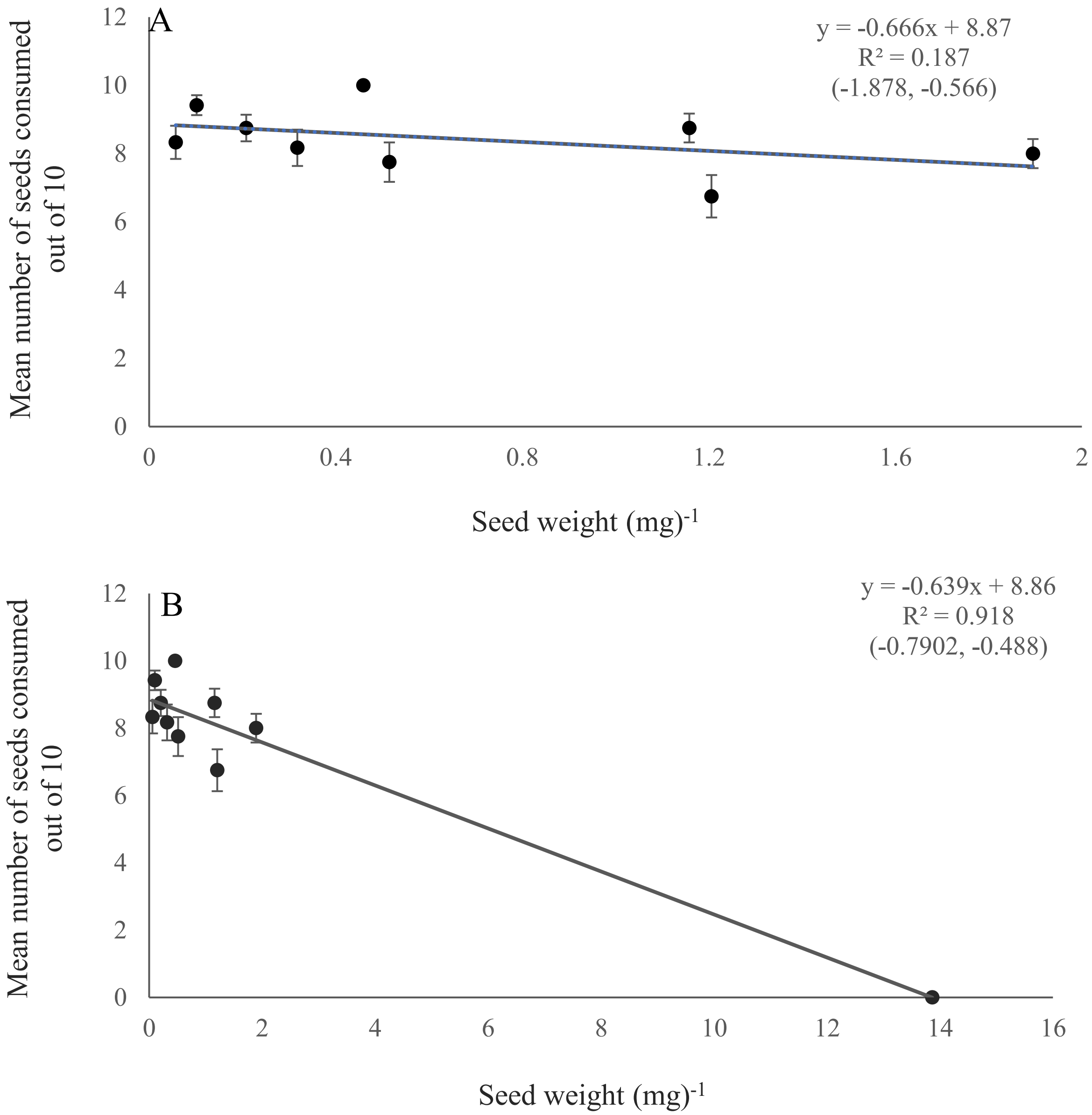

Figure 7: Mean (± SEM) consumption (x/10) of weed seeds by *Gryllus pennsylvanicus* excluding goatsbeard (A) and including goatsbeard (B) in a laboratory no-choice feeding experiment fitted against seed weight $(mg)^{-1}$ (See Table 3 for weights of each seed). Note the difference in the scales for the x-axis.

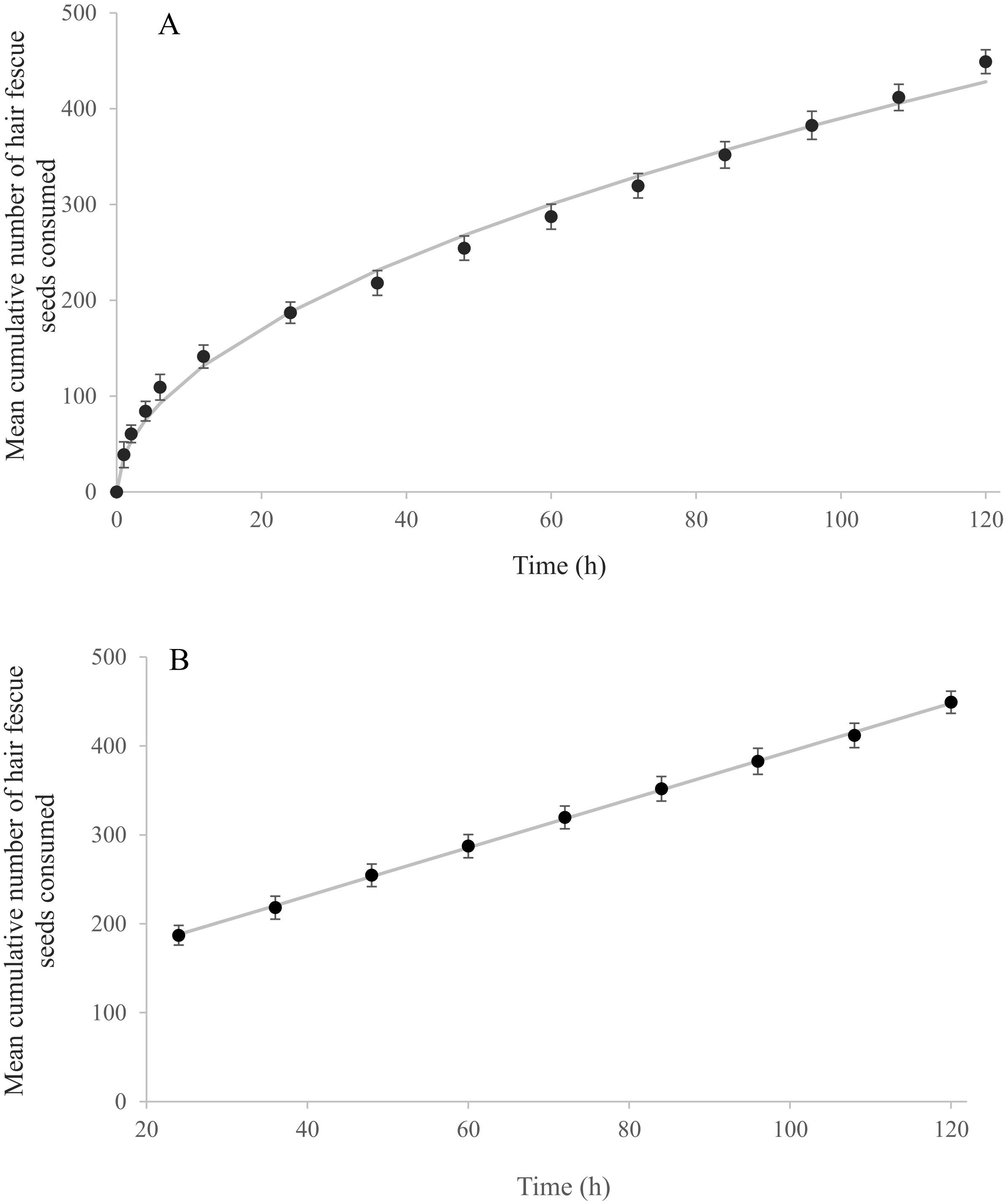

Figure 8: Mean (± SD) cumulative hair fescue seeds consumed by *Gryllus pennsylvanicus* in a laboratory no-choice feeding experiment. 0 – 120 hours fitted with a non-linear regression (power concave) $y = 36.98 * x^{0.5115}$ (A) and 24 – 120 hours fitted with a linear regression $y = 123.0 * 2.708x$ (B)

3.5 Discussion

Laboratory feeding experiments confirmed that *G. pennsylvanicus* is a consumer of weed seeds of multiple species in wild blueberry fields. In the no-choice experiment, *G. pennsylvanicus* consumed all provided hair fescue seeds and no goatsbeard seeds. *Gryllus pennsylvanicus* was observed attempting to manipulate goatsbeard seeds during the study, however it is likely that these seeds are too large or tough for *G. pennsylvanicus* to consume. For the no-choice study with all weed seeds excluding hair fescue and goatsbeard, seed type did not have a significant effect on seed consumption by *G. pennsylvanicus*. While seed types can differ in their size, hardness, allelochemicals and nutritional quality (Brust & House 1988; Carmona et al. 1999; Honek et al. 2007; Kulkarni et al. 2015; Lundgren & Rosentrater 2007), the diverse features of these particular seeds did not appear to have an effect on *G. pennsylvanicus*. Lundgren and Rosentrater (2007) also found that while *G. pennsylvanicus* was particularly damaging towards grass species, seed consumption was unrelated to volume, density and mass of the seed. For the initial no-choice feeding study on 6 Aug, *G. pennsylvanicus* consumed more hair fescue seeds than sheep sorrel, and no poverty oat grass seeds were consumed. This is likely due to the earlier sampling date where the *G. pennsylvanicus* populations consisted of nymphs compared to later in the study when they had developed into adults (Alexander 1968). For example, earlier in the season as nymphs, *G. pennsylvanicus* consumed less poverty oat grass seeds (1.2 mg^{-1}) than hair fescue seeds (0.46 mg^{-1}) but later in the season, as adults, they consumed these seeds in equal amounts. This shows that while *G. pennsylvanicus* may consume more hair fescue seeds earlier in the season, they may equally contribute towards the destruction of both weed seeds later in the season.

The number of seeds consumed by *G. pennsylvanicus* was low earlier in the year and continually increased throughout their active period. A reason for this may be due to the progression between the insect's phenological stages (i.e. pre-reproductive, reproductive, post-reproductive) (Honek et al. 2006). Spring-feeding carabids, for example, were noted to increase their food consumption in preparation for reproduction (Honek et al. 2006). Weather can also influence seed consumption. The metabolism (Neven 2000) and activity (Honek 2013) of an insect rises with increasing temperatures and therefore their demand for food is increased from spring into summer. Physiological adaptions also play a role in the number of seeds consumed over time. Insects are only capable of consuming foods that they can naturally manipulate and consume at that particular life stage, therefore seed size and strength are amongst the most influential factors in terms of dietary preferences (Lundgren 2009). For instance, size of seeds eaten often varies linearly with insect size in carabids, demonstrating that larger carabid species will generally rely on larger seeds (Honek et al. 2007). This may be the case for *G. pennsylvanicus* where on the first sampling date as nymphs, they consumed 0/10 poverty oat grass seeds whereas on the last sampling date as adults they were able to consume 10/10 of these seeds.

Gryllus pennsylvanicus readily consumed both unsprouted and sprouted hair fescue seeds. This is important as hair fescue seeds lack primary dormancy (White 2018) meaning they sprout soon after the seed rain in autumn, during which time *G. pennsylvanicus* is still active. This provides multifarious opportunities for hair fescue to be managed in both their unsprouted and sprouted form. It is clear from previous studies that granivorous insects recognize and choose specific seeds through visual, tactile, and chemical cues (Lundgren 2009). However *G. pennsylvanicus* is polyphagous, opportunistic feeders (Criddle 1925; Lundgren 2009) which likely accounts for why both hair fescue seeds and sprouts were consumed and suggests that they may consume the sprouts of other grass species as well.

Within the size range of accepted seeds (0.057 – 1.9 mg), *G. pennsylvanicus* did not show any major preference for seed types based on seed size. However, *G. pennsylvanicus* did not consume any goatsbeard seeds (13.9 mg) indicating that a negative relationship between feeding and seed size may exist that could be elucidated in future research. That said, the slopes of the two lines are similar, showing that goatsbeard does not change the relationship. While the regression between seed size and seeds consumed is not significant, the broad confidence interval demonstrates that only a huge slope would be detected. These results corroborate with other research that highlights *G. pennsylvanicus*' preference for smaller as opposed to larger seeds. For example, Carmona (1999) reported that *G. pennsylvanicus* consumed 223 redroot pigweed seeds (0.37 mg seed^{-1}) within 24 hours whereas only 8 velvetleaf seeds (0.85 mg seed^{-1}) were consumed within the same timeframe. Brust and House (1988) also reported a greater proportion of redroot pigweed seeds consumed by *G. pennsylvanicus* relative to large-seeded species such as sicklepod (*Cassia obtusifolia* L.) and jimsonweed (*Datura stramonium* L.). From these results, smaller sized seeds appear easier for *G. pennsylvanicus* to manipulate. In contrast, a large sized seed can provide greater food material per seed resulting in fewer large seeds required to satiate the granivores in respect to smaller seeds. These findings suggest that *G. pennsylvanicus* would have a greater impact on small seed species in wild blueberry fields such as hair fescue in comparison to the larger seed species such as goatsbeard.

The ability for one cricket to consume up to 449 hair fescue seeds over a 120-hour period represents an important finding in understanding their role as biological control agents in wild blueberry cropping systems. In the first 24 hours, *G. pennsylvanicus* consumed an average of 7.80 seeds h^{-1}, with a slowed rate of 2.73 seeds h^{-1} for the remaining 96 h. This reduced average feeding rate is likely due to the satiation of the crickets after gorging themselves at the start of the experiment following their 48-hour starvation period (Honek et al. 2003). Brust (1994) reported that no-tillage agroecosystems with low inputs were inhabited by *G. pennsylvanicus* at a density of 5 individuals per 2.25 m^2 or 2.2 individuals per m^2. Assuming that the same case is true in a low input, no-tillage agroecosystem such as wild blueberry fields, and considering the linear relationship that exists once the crickets are satiated, adult *G. pennsylvanicus* can consume 4469 seeds $month^{-1}$ per m^2. A one month period was selected for this calculation as this is the length of time *G. pennsylvanicus* is an adult (Alexander 1957), and the life stage of which the feeding rate was calculated for. Based on published results (White & Zhang 2020; Zhang et al. 2018), the density of hair fescue ranges from 25.4 – 47.3 tufts m^{-2} in infested fields and averages 4.41 tufts m^{-2} across all fields it occurs in (Lyu et al. 2021). Each one of those tufts is capable of producing around 2500 seeds a year (White & Kumar 2017). A high infestation of 30 tufts m^{-2} could therefore produce 75 000 seeds $year^{-1}$ while a lower infestation of 5 tufts m^{-2} could produce 12 500 seeds $year^{-1}$. The estimated final constant feeding rate of hair fescue seeds by *G. pennsylvanicus* over a one-month period would thereby result in a 6% and 36% reduction of seeds per m^2 within those plant densities, respectively. According to ecological modeling, population growth and weed densities can be significantly reduced by removing 50-86% of weed seeds from the seed bank (Firbank & Watkinson 1986; Westerman et al. 2005, 2006). For illustrative purposes using this data, an infestation of 5 hair fescue tufts per m^2 would require a cricket density of 3.1 per m^2 to remove > 50% of hair fescue seeds. While *G. pennsylvanicus* may not solely be able to reduce the population growth and density of hair fescue in wild blueberry fields, they may have important implications of the demography of this weed when combined with further weed management practices. It should be noted that the findings from this study were conducted in no-choice laboratory conditions, excluding any external factors that may occur in a field setting such as seed availability or alternative food options. Nevertheless, these results suggest that *G. pennsylvanicus* are likely to be destructive towards grass species which is beneficial for weed management in cropping systems such as wild blueberry where an increase in grass species has been detected (Jensen & Yarborough, 2004; White & Webb, 2017).

The results of this experiment conclude that *G. pennsylvanicus* can consume a variety of smaller sized weed seeds from multiple species found in wild blueberry systems, while seeds such as goatsbeard are less preferred likely due to their large size. *G. pennsylvanicus* was notably damaging towards hair fescue, consuming them in both their unsprouted and sprouted forms. This is an important finding given the seed rain of hair fescue corresponds well to the temporal population patterns of *G. pennsylvanicus* in wild blueberry fields (Cutler et al. 2016; White 2018). As well, the average consumption of seeds by *G. pennsylvanicus* continually increased throughout the season, granting an increased opportunity for the management of hair fescue and other fall-maturing weed species.

CHAPTER 4: CONCLUSIONS

4.1 Research Importance

Due to the continued growth of the global population and increased production costs, growers have been in search of sustainable methods for weed control. Although herbicides remain a significant component in weed management, they can pose negative impacts economically, environmentally, and socially. One of the most promising strategies to address this issue involves biological control, where beneficial insects consume agricultural weed seeds (Cromar et al. 1999; Gallandt et al. 2005; Menalled et al. 2000). Various studies have examined invertebrate feeding behaviours and suggest that post-dispersal seed consumption is a key factor in reducing weed populations (Brust & House, 1988; Cromar et al. 1999; Gallandt et al. 2005; Westerman et al. 2003). Given the lack of knowledge surrounding *G. pennsylvanicus* in wild blueberry fields, the intention of this research was to build onto our current understanding of this species and their potential as natural enemies in wild blueberry fields. Results from these studies highlight spatial and temporal population trends of *G. pennsylvanicus* in wild blueberry fields as well as their weed seed feeding capabilities. These findings can assist growers in developing weed management strategies that protect and promote *G. pennsylvanicus* populations.

4.2 Population dynamics

To understand how granivorous insects may contribute to biological weed control, it is imperative to first understand their community dynamics. As with many granivorous insects, the structure, diversity and ecological services of the land can influence the areas they inhabit (Balzan et al. 2016; Lundgren 2009; Schmidt et al. 2019). Increased land management such as tillage and the ubiquitous use of broad-spectrum pesticides can severely disrupt ecosystem services such as biological control via insects (Hendrickx et al. 2007; Landis et al. 2000; Lundgren 2009; Lundgren et al. 2006). Within cropping systems, different management practices such as organic and conventional farming (Döring & Kromp 2003; Jones et al. 2016; Schmidt et al. 2019) or the use of cover crops (Davis & Liebman 2003) can also alter insect communities. It is also common for the population dynamics of insects to change with distance from field edge (edge effect). This is due in part to the proximity to important alternative resources and the overwintering refuge these edge habitats provide (Bianchi et al. 2008; Cutler et al. 2012; Landis et al. 2000; Lundgren 2009; Menalled et al. 2000; Rand et al. 2006). Therefore, it is important to determine what beneficial species are present in a given system, along with their temporal and spatial population trends to assess their potential as a biological control agent. Research on insect population dynamics in and around wild blueberry fields to date have primarily focused on the blueberry maggot fly (*Rhagoletis mendax* Curran; Collins & Drummond, 2004; Drummond et al. 2020), spotted wing drosophila (SWD; *Drosophila suzukii*; Ballman et al. 2017), bees (Cutler et al. 2015), and ground beetles (Cutler et al. 2012, 2016; Loureiro et al. 2020), while the population dynamics of *G. pennsylvanicus* in wild blueberry agroecosystems have previously gone unexplored.

My study which looked at the spatial and temporal population trends of *G. pennsylvanicus* showed that this insect is active from July – October and is distributed throughout the inner-portions of fields. My study also revealed that *G. pennsylvanicus* does not migrate in or out of the field and is therefore likely overwintering in wild blueberry fields. The results of this study not only broaden our understanding of their population dynamics, but it also provides knowledge for the future conservation and promotion of this species. This is beneficial from a wild blueberry grower's perspective as the preservation of natural enemies can have a positive influence on weed seed granivory within their system. This is owing to the fact that an increase in the total number of seed consumers has been highly correlated to an increase in seed removal rates (Menalled et al. 2007). Reports also show that as the population density of *G. pennsylvanicus* increases in agro-ecosystems, weed seed emergence decreases, pointing to the potential of this insect as a biological control agent (Davis & Liebman 2003; Ichihara et al. 2014; O'Rourke et al. 2006). The findings that the population dynamics of *G. pennsylvanicus* coincides with important blueberry pests and that this insect is homogeneously distributed throughout the inner portions of the field, shows growers they can expect potential weed control throughout their fields, and not only in specific areas, giving way for high levels of post-dispersal seed consumption. Therefore, the presence of natural enemies such as *G. pennsylvanicus* in cropping systems may help reduce the number of pests and ease the reliance on herbicides, contributing towards a sustainable approach to weed management.

As insect pest infestations remain a challenge and post-dispersal seed consumption by crickets has been classified as a primary driver for weed seed mortality (Ichihara et al. 2014), understanding the temporal and spatial population dynamics of *G. pennsylvanicus* is a step towards understanding their potential as natural enemies. Although captures of *G. pennsylvanicus* in wild blueberry fields have not been compared between vegetative and fruiting fields, there have been carabid studies that target this question. Cutler et al. (2012) found a greater number of carabids in vegetative blueberry fields, however, these findings were not reciprocated the following year. Due to the uncertainty of their population dynamics between years, it is suggested that future research conducts multi-year experiments in wild blueberry systems to fully comprehend *G. pennsylvanicus* activity throughout the biennial cycle. Studies on how field management practices, such as insecticide usage, can promote the population of *G. pennsylvanicus* for augmented biological weed control, would represent a significant contribution to the field.

4.3 Feeding Tendencies

Despite the majority of weeds in wild blueberry systems being herbaceous and woody perennials (Jensen & Yarborough, 2004; Lyu, 2020), there has been a distinct trend towards weeds that rely on seeds for dispersal and establishment (Jensen & Yarborough, 2004). This is a particular cause for concern as they produce vast quantities of seeds, can be invasive, and can require the need for herbicide applications in both the sprouting and fruiting years (Jensen & Yarborough, 2004). While seedlings can be controlled through a variety of chemical and non-chemical means, destruction of weed seeds is much more challenging and generally impossible with most weed control techniques. A major exception to this is the consumption of weed seeds by natural enemies, such as *G. pennsylvanicus*. However, leverage of this ecosystem service requires a basic understanding of their seed feeding tendencies and rates.

Though feeding adaptations of granivores and defensive mechanisms of seeds can inhibit granivory, my laboratory feeding results indicated that *G. pennsylvanicus* consumed seeds from an array of weed species found in wild blueberry systems weighing 0.057 – 1.90 mg, but not seeds in excess of 13.9 mg. While seed size may be the main limiting factor in terms of consumption (Lundgren & Rosentrater, 2007), fundamental questions remain in respect to other seed characteristics. For example, seed acceptability among and within granivorous insect taxa can be dependent on a number of other factors including seed hardness (Lundgren & Rosentrater, 2007), nutritional quality (Kulkarni et al. 2015), density (Lundgren & Rosentrater, 2007), exposure (i.e. buried vs on soil surface) (White et al. 2007), and allelochemical presence (Honek et al. 2007). Therefore, it would be valuable for future research to determine the maximum consumable seed size acceptable for *G. pennsylvanicus*, as well as determine how they are influenced by these additional factors to fully understand their capabilities as seed consumers.

From nymphs into adults, *G. pennsylvanicus* increasingly consumed more weed seeds throughout their active period. They particularly showed preference for grass species such as hair fescue, which is hypothesized to be a result of their lack of defensive chemicals (Ichihara et al. 2012; Janzen, 1969; Lundgren, 2009; Lundgren & Rosentrater, 2007). Having said that, the vast number of hair fescue seeds consumed by *G. pennsylvanicus* in this study was rather surprising given biological control efforts in wild blueberries have been primarily focused on ground beetles (Cutler et al. 2012; Loureiro et al. 2019, 2020; Renkema et al. 2013, 2014). For example, Loureiro (2019) found the mean cumulative number of hair fescue seeds consumed by *P. lucublandus* and *P. mutus* to be < 1 after 144 h while the estimated final constant feeding rate by *H. rufipes* to be 0.4 seeds h^{-1}. Comparatively, the estimated final constant feeding rate by *G. pennsylvanicus* was 2.73 seeds h^{-1}. This difference in feeding rates between ground beetles and *G. pennsylvanicus* serves to suggest that future studies in biological control should also be directed towards field crickets.

Despite the weed seed consuming capabilities of *G. pennsylvanicus*, they are a polyphagous species which feed on a variety of living and dead insects, plants, grasses, and seeds (Criddle 1925). This augments their potential as biological control agents against other pests in cropping systems. For example, *G. pennsylvanicus* is reported to be a natural predator of wild blueberry insect pests such as spotted wing drosophila (SWD; *Drosophila suzukii*), which was estimated to cause $1.4 million dollars of crop damage in Maine, USA in 2012 alone (Ballman et al. 2017). It seems reasonable to assume that *G. pennsylvanicus* may also consume the blueberry maggot in the field given their congruent activity periods (Drummond et al. 2019, 2020), but this still needs to be tested. Therefore, as more pest management strategies are shifting towards a sustainable integrated approach, natural populations of granivorous insects such as *G. pennsylvanicus* should be of high consideration for growers who wish to decrease their reliance on expensive and potentially environmentally damaging pesticides.

4.4 Final Summary

From these results it can be concluded that *G. pennsylvanicus* is homogenously distributed throughout wild blueberry fields from July through to October, peaking with the seed rain of common agricultural weeds. While weed species such as goatsbeard may not be managed due to their large seed size, *G. pennsylvanicus* may play a vital role in regulating weed populations that produce smaller seeds. As Lundgren (2009) remarked about *G. pennsylvanicus*, “Given their tremendous abundance within cropland, it is almost criminal that we do not have a better handle on the feeding ecology of these insects”. Although our understanding of their seed feeding preferences in the field is still limited, we now know that these insects have the potential to contribute to the destruction of weed seeds in wild blueberry fields. It is therefore suggested that future research be conducted to improve the knowledge gap of *G. pennsylvanicus* as a natural enemy and determine how registered insecticides in wild blueberry fields impact this species. It is equally imperative that growers are educated to use this knowledge to implement any habitat management practices that may promote *G. pennsylvanicus* populations.

References

Agriculture and Agri-Food Canada. (2012). Crop profile for lowbush blueberry in Canada*, 2011* http://publications.gc.ca/collections/collection_2012/agr/A118-10-31-2012-eng.pdf

Alexander, R. D. (1957). The taxonomy of the field crickets of the Eastern United States (Orthoptera: Gryllidae: Acheta). Annals of the Entomological Society of America: **50**: 584–602

Alexander, R. D. (1968). Life cycle origins, speciation, and related phenomena in crickets. The Quarterly Review of Biology: **43**: 1–41. JSTOR

Angelstam, P., Hansson, L., & Pehrsson, S. (1987). Distribution borders of field mice Apodemus: The importance of seed abundance and landscape composition. Oikos: **50**: 123–130

Anonymous. (2003). *PACR2003-13.* Re-evaluation of atrazine. Alternative Strategies and Regulatory Affairs Division, Pest Management Regulatory Agency, Health Canada, Ottawa, ON. Catalogue No. H113-18/2003-13E-PDF. 30 pp.

Anonymous. (2017). Wild blueberry IPM weed management guide. Government of New Brunswick https://www2.gnb.ca/content/dam/gnb/Departments/10/pdf/Agriculture/WildBlueberries-BleuetsSauvages/C420-E.pdf

Ballman, E. S., Collins, J. A., & Drummond, F. A. (2017). Pupation behavior and predation on *Drosophila suzukii* (Diptera: Drosophilidae) pupae in Maine wild blueberry fields. Journal of Economic Entomology: **110**: 2308–2317

Balzan, M. V., Bocci, G., & Moonen, A.-C. (2016). Landscape complexity and field margin vegetation diversity enhance natural enemies and reduce herbivory by Lepidoptera pests on tomato crop. BioControl: **61**: 141–154

Beirne, B. (1971). Pest insects of annual crop plants in Canada. Entomological Society of Canada

Bell, H. P. (1950). Determinate growth in the blueberry. Canadian Journal of Research: **28**: 637–644

Bianchi, F. J. J. A., Goedhart, P. W., & Baveco, J. M. (2008). Enhanced pest control in cabbage crops near forest in The Netherlands. Landscape Ecology: **23**: 595–602

Bigelow, R. S. (1958). Evolution in the field cricket, *atcheta assimilis* fab. **2**: 139–151

Bigelow, R. S. (1962). Factors affecting developmental rates and diapause in field crickets. Evolution: **16**: 396–406

Boyd, N. S., & White, S. N. (2009). Impact of wild blueberry harvesters on weed seed dispersal within and between fields. Weed Science: **57**: 541–546

Boyetchko, S. M., Bailey, K. L., & De Clerck-Floate, R. A. (2009). Current biological weed control agents—Their adoption and future prospects. Prairie Soils and Crops Scientific: Perspectives for Innovative Management https://agris.fao.org/agris-search/search.do?recordID=US201301843303

Brust, G. E., & House, G. J. (1988). Weed seed destruction by arthropods and rodents in low-input soybean agroecosystems. American Journal of Alternative Agriculture: **3**: 19–25

Burgess, L., & Hinks, C. F. (1987). Predation on adults of the crucifer flea beetle, *phyllotreta cruciferae* (goeze), by the northern fall field cricket, *gryllus pennsylvanicus* burmeister (orthoptera: Gryllidae)1. The Canadian Entomologist: **119**: 495–496

Byers, R. A., & Barratt, B. I. P. (1991). Behavior of slugs, *Derocerus reticulatum* (Gastropoda: Limacidae), and crickets, *Gryllus pennsylvanicus* (Orthoptera: Gryllidae), on seedling alfalfa. Entomological News (USA)

Cantrall, I. (1943). The ecology of the Orthoptera and Dermaptera of the George Reserve, Michigan. Miscellaneous Publications of the Museum of Zoology, University of Michigan: **54**: 1–182

Cardina, J., Herms, C. P., & Doohan, D. J. (2002). Crop rotation and tillage system effects on weed seedbanks. Weed Science: **50**: 448–460

Carmona, D. M., Menalled, F. D., & Landis, D. A. (1999). Gryllus *pennsylvanicus* (Orthoptera: Gryllidae): Laboratory weed seed predation and within field activity-density. Journal of Economic Entomology: **92**: 825–829

Carrière, Y., Simons, A. M., & Roff, D. A. (1996). The effect of the timing of post-diapause egg development on survival, growth, and body size in *gryllus pennsylvanicus*. Oikos: **75**: 463–470

Criddle, N. (1925). Field crickets in Manitoba. The Canadian Entomologist: **57**: 79–84

Cromar, H. E., Murphy, S. D., & Swanton, C. J. (1999). Influence of tillage and crop residue on postdispersal predation of weed seeds. Weed Science: **47**: 184–194

Cutler, G. C., Astatkie, T., & Chahil, G. S. (2016). Weed seed granivory by carabid beetles and crickets for biological control of weeds in commercial lowbush blueberry fields. Agricultural and Forest Entomology: **18**: 390–397

Cutler, G. C., Renkema, J. M., Majka, C. G., & Sproule, J. M. (2012). Carabidae (Coleoptera) in Nova Scotia, Canada wild blueberry fields: Prospects for biological control. The Canadian Entomologist: **144**: 779–791

Davis, A. S., & Liebman, M. (2003). Cropping system effects on giant foxtail (*Setaria faberi*) demography: Green manure and tillage timing. Weed Science: **51**: 919–929. JSTOR

Döring, T. F., & Kromp, B. (2003). Which carabid species benefit from organic agriculture?—A review of comparative studies in winter cereals from Germany and Switzerland. Agriculture, Ecosystems & Environment: **98**: 153–161

Dossey, A. T., Tatum, J. T., & McGill, W. L. (2016). Chapter 5 - Modern insect-based food industry: Current Status, Insect Processing Technology, and Recommendations Moving Forward. In A. T. Dossey, J. A. Morales-Ramos, & M. G. Rojas (Eds.), *Insects as Sustainable Food Ingredients* (pp. 113–152). Academic Press

Drummond, F. A., Collins, J. A., & Bushmann, S. L. (2020). Movement of *Rhagoletis mendax* (diptera: Tephritidae) in fruit-bearing wild blueberry fields. Part II. Journal of Economic Entomology: **113**: 1323–1336

Drummond, F. A., Smagula, J., & Yarborough, D. E. (2009). Organic wild blueberry production. Maine Agricultural and Forest Experiment Station Bulletin 852

Drummond, F., Ballman, E., & Collins, J. (2019). Population dynamics of spotted wing drosophila (*Drosophila suzukii* (Matsumura)) in Maine wild blueberry (*Vaccinium angustifolium* Aiton). Insects: **10**: 205

Drummond, F., Smagula, J. M., Yarborough, D., & Annis, S. (2012). Organic lowbush blueberry research and extension in Maine. International Journal of Fruit Science: **12**: 216–231

Eaton, L. J., & Nams, V. O. (2006). Second cropping of wild blueberries—Effects of management practices. Canadian Journal of Plant Science: **86**: 1189–1195

FAO. (2020). Integrated Pest Management (IPM) http://www.fao.org/agriculture/crops/thematic-sitemap/theme/spi/scpi-home/managing-ecosystems/integrated-pest-management/en/

Firbank, L. G., & Watkinson, A. R. (1986). Modelling the population dynamics of an arable weed and its effects upon crop yield. Journal of Applied Ecology: **23**: 147–159

French, B. W., McGowan, E. J., & Backus, V. L. (1986). Spatial distribution of calling field crickets, *Gryllus pennsylvanicus* (Orthoptera: Gryllidae). The Florida Entomologist: **69**: 255–257

Gallandt, E. R., Molloy, T., Lynch, R. P., & Drummond, F. A. (2005). Effect of cover-cropping systems on invertebrate seed predation. Weed Science: **53**: 69–76

Glass, V. M., Percival, D. C., & Proctor, J. T. A. (2005). Tolerance of lowbush blueberries (Vaccinium angustifolium Ait.) to drought stress. I. Soil water and yield component analysis. Canadian Journal of Plant Science: **85**: 911–917

Government of Canada. (2020, September 17). Daily data report for August 2019. Climate - Environment and Climate Change Canada https://climate.weather.gc.ca/climate_data/daily_data_e.html?StationID=42243&timeframe=2&StartYear=1840&EndYear=2021&Day=1&Year=2019&Month=8

Greenslade, P. J. M. (1964). Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). The Journal of Animal Ecology: **33**: 301

Hall, I. V. (1959). Plant populations in blueberry stands developed from abandoned hayfields and woodlots. Ecology: **40**: 742–743

Hall, I. V, Aalders, L. E., & Townsend, L. R. (1964). The effects of soil pH on the mineral composition and growth of the lowbush blueberry. Canadian Journal of Plant Science: **44**: 433–438

Harrison, R. G. (1979). Speciation in North American field crickets: Evidence from electrophoretic comparisons. Evolution: **33**: 1009–1023

Heggenstaller, A. H., Menalled, F. D., Liebman, M., & Westerman, P. R. (2006). Seasonal patterns in post-dispersal seed predation of *Abutilon theophrasti* and *Setaria faberi* in three cropping systems. Journal of Applied Ecology: **43**: 999–1010

Hendrickx, F., Maelfait, J.-P., Wingerden, W. V., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekötter, T., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V., & Bugter, R. (2007). How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology: **44**: 340–351

Hoffmann, J. H., Moran, V. C., Zimmermann, H. G., & Impson, F. A. C. (2020). Biocontrol of a prickly pear cactus in South Africa: Reinterpreting the analogous, renowned case in Australia. Journal of Applied Ecology: **57**: 2475–2484

Holland, J., Perry, J. N., & Winder, L. (1999). The within-field spatial and temporal distribution of arthropods in winter wheat. Bulletin of Entomological Research: **89**: 499–513

Honek, A. (2013). The effect of temperature on the activity of Carabidae (Coleoptera) in a fallow field. **94**: 97–104

Honek, A., Martinkova, Z., & Jarosik, V. (2003). Ground beetles (Carabidae) as seed predators. European Journal of Entomology: **100**: 531–544

Honek, A., Martinkova, Z., Saska, P., & Pekar, S. (2007). Size and taxonomic constraints determine the seed preferences of Carabidae (Coleoptera). Basic and Applied Ecology: **8**: 343–353

Honek, A., Saska, P., & Martinkova, Z. (2006). Seasonal variation in seed predation by adult carabid beetles. Entomologia Experimentalis et Applicata: **118**: 157–162

House, G. J., & Brust, G. E. (1989). Ecology of low-input, no-tillage agroecosystems. Agriculture, Ecosystems & Environment: **27**: 331–345

Huang, H. T., & Yang, P. (1987). The Ancient Cultured Citrus Ant. BioScience: **37**: 665–671

Hughes, A., White, S. N., Boyd, N. S., Hildebrand, P., & Christopher Cutler, G. (2016). Red sorrel management and potential effect of red sorrel pollen on *Botrytis cinerea* spore germination and infection of lowbush blueberry (*Vaccinium angustifolium* Ait.) flowers. Canadian Journal of Plant Science: 590–596

Ichihara, M., Inagaki, H., Matsuno, K., Saiki, C., Mizumoto, S., Yamaguchi, S., Yamashita, M., & Sawada, H. (2014). Postdispersal weed seed predation by crickets in a rice paddy field after irrigation water recedes. Japan Agricultural Research Quarterly: **48**: 63–69

Ichihara, M., Inagaki, H., Matsuno, K., Saiki, C., Yamashita, M., & Sawada, H. (2012). Postdispersal seed predation by *Teleogryllus emma* (Orthoptera: Gryllidae) reduces the seedling emergence of a non-native grass weed, Italian ryegrass (*Lolium multiflorum*). Weed Biology and Management: **12**: 131–135

Ichihara, M., Matsuno, K., Inagaki, H., Saiki, C., Mizumoto, S., Yamaguchi, S., Yamashita, M., & Sawada, H. (2015). Creation of paddy levees to enhance the ecosystem service of weed seed predation by crickets. Landscape and Ecological Engineering: **11**: 227–233

Ignacimuthu, S., & Jayaraj, S. (2005). Sustainable insect pest management. Alpha Science Int'l Ltd.

Jensen, K. I. N., & Specht, E. G. (2002). Response of lowbush blueberry (*Vaccinium angustifolium*) to hexazinone applied early in the fruiting year. Canadian Journal of Plant Science: **82**: 781–783

Jensen, K. I. N., & Yarborough, D. (2004). An overview of weed management in the wild lowbush blueberry—Past and present. Small Fruits Review: **3**: 229–255

Jobin, L. J. (1961). The nymphal instars of certain American species of Gryllus (Orthoptera: Gryllidae). McGill University https://escholarship.mcgill.ca/concern/theses/c821gp62t

Jones, M. S., Halteman, W. A., & Drummond, F. A. (2016). Predator- and scavenger-mediated ecosystem services determined by distance to field–forest interface in the Maine lowbush blueberry agroecosystem. Environmental Entomology: **45**: 1131–1140

Jones, M. S., Vanhanen, H., Peltola, R., & Drummond, F. (2014). A global review of arthropod-mediated ecosystem-services in Vaccinium berry agroecosystems. Terrestrial Arthropod Reviews: **7**: 41–78

Jordan, W. C., & Eaton, L. J. (1995). A comparison of first and second cropping years of Nova Scotia lowbush blueberries (*Vaccinium angustifolium*) Ait. Canadian Journal of Plant Science: **75**: 703–707

Kenis, M., Hurley, B., Colombari, F., Lawson, S., Sun, J., Wilcken, C., Weeks, R., & Sathyapala, S. (2019). Guide to the classical biological control of insect pests in planted and natural forests. FAO, UN http://www.fao.org/3/ca3677en/CA3677EN.pdf

Kennedy, K. J., Boyd, N. S., & Nams, V. O. (2010). Hexazinone and fertilizer impacts on sheep sorrel (*Rumex acetosella*) in wild blueberry. Weed Science: **58**: 317–322

Kinsman, G. (1993). The history of the lowbush blueberry industry in Nova Scotia 1950-1990. Nova Scotia Dept. of Agriculture & Marketing https://DalSpace.library.dal.ca//handle/10222/28451

Klymko, J., Catling, P., Ogden, J. B., Harding, R. W., McAlpine, D. F., Robinson, S. L., Doucet, D. A., & Adam, C. I. G. (2019). Orthoptera and allies in the Maritime provinces, Canada: New records and updated provincial checklists. The Canadian Field-Naturalist: **132**: 319

Kromp, B. (1999). Carabid beetles in sustainable agriculture: A review on pest control efficacy, cultivation impacts and enhancement. Agriculture, Ecosystems & Environment: **74**: 187–228

Kulkarni, S. S., Dosdall, L. M., & Willenborg, C. J. (2015). The role of ground beetles (Coleoptera: Carabidae) in weed seed consumption: A review. Weed Science: **63**: 355–376

Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. Annual Review of Entomology: **45**: 175–201

Laub, C., Youngman, R. R., Love, K., & Mize, T. (2009). Using pitfall traps to monitor insect activity

Li, Z., Boyd, N. S., McLean, N., & Rutherford, K. (2014). Hexazinone resistance in red sorrel (*Rumex acetosella*). Weed Science: **62**: 532–537

Littell, R. C., Henry, P. R., & Ammerman, C. B. (1998). Statistical analysis of repeated measures data using SAS procedures. Journal of Animal Science: **76**: 1216–1231

Loureiro, A. M. M. C. (2018). *Feeding behaviour, dispersal, and community dynamics of carabidae found in nova scotia lowbush blueberry fields* [Master's thesis]. Dalhousie University

Loureiro, A. M. M. C., Nams, V. O., White, S. N., & Cutler, G. C. (2020). Short-term dispersal and long-term spatial and temporal patterns of Carabidae (Coleoptera) in lowbush blueberry fields. Environmental Entomology: **49**: 572–579

Lundgren, J. G. (2009). Relationships of natural enemies and non-prey foods. Springer Science & Business Media

Lundgren, J. G., & Rosentrater, K. A. (2007). The strength of seeds and their destruction by granivorous insects. Arthropod-Plant Interactions: **1**: 93–99

Lundgren, J. G., Shaw, J. T., Zaborski, E. R., & Eastman, C. E. (2006). The influence of organic transition systems on beneficial ground-dwelling arthropods and predation of insects and weed seeds. Renewable Agriculture and Food Systems: **21**: 227–237

Lyu, H., McLean, N., McKenzie-Gopsill, A., & White, S. N. (2021). Weed Survey of Nova Scotia Lowbush Blueberry (Vaccinium Angustifolium Ait.) Fields. International Journal of Fruit Science: **0**: 1–20

MacEachern-Balodis, M. C., Boyd, N. S., White, S. N., & Cutler, G. C. (2017). Examination of dogbane beetle (Chrysochus auratus) feeding and phenology on spreading dogbane, and considerations for biological control. Arthropod-Plant Interactions: **11**: 807–814

Magura, T. (2002). Carabids and forest edge: Spatial pattern and edge effect. Forest Ecology and Management: **157**: 23–37

Marino, P. C., Gross, K. L., & Landis, D. A. (1997). Weed seed loss due to predation in Michigan maize fields. Agriculture, Ecosystems & Environment: **66**: 189–196

McAlpine, D. F., & Smith, I. M. (2010). Assessment of Species Diversity in the Atlantic Maritime Ecozone. NRC Research Press

McCully, K. V., Sampson, M. G., & Watson, A. K. (1991). Weed survey of nova scotia lowbush blueberry (*Vaccinium angustifolium*) fields. Weed Science: **39**: 180–185

Menalled, F. D., Marino, P. C., Renner, K. A., & Landis, D. A. (2000). Post-dispersal weed seed predation in Michigan crop fields as a function of agricultural landscape structure. Agriculture, Ecosystems & Environment: **77**: 193–202

Monteith, L. G. (1971). Crickets as predators of the apple maggot, *Rhagoletis pomonella* (Diptera: Tephritidae). The Canadian Entomologist: **103**: 52–58

Montgomery, D. C. (2017). *Design and Analysis of Experiments*. John Wiley & Sons

Naranjo, S. E., Ellsworth, P. C., & Frisvold, G. B. (2015). Economic value of biological control in integrated pest management of managed plant systems. Annual Review of Entomology: **60**

Neven, L. G. (2000). Physiological responses of insects to heat. Postharvest Biology and Technology: **21**: 103–111

O'Rourke, M. E., Heggenstaller, A. H., Liebman, M., & Rice, M. E. (2006). Post-dispersal weed seed predation by invertebrates in conventional and low-external-input crop rotation systems. Agriculture, Ecosystems & Environment: **116**: 280–288

Penney, B. G., McRae, K. B., & Rayment, A. F. (2008). Effect of long-term burn-pruning on the flora in a lowbush blueberry (*Vaccinium angustifolium* Ait.) stand. Canadian Journal of Plant Science: **88**: 351–362

Pickford, R. (1960). Survival, fecundity, and population growth of *melanoplus bilituratus* (Wlk.) (Orthoptera: Acrididae) in relation to date of hatching. The Canadian Entomologist: **92**: 1–10

Piers, H. (1918). The Orthoptera (cockroaches, locusts, grasshoppers and crickets) of Nova Scotia. Nova Scotia Institute of Science: **14** http://hdl.handle.net/10222/12976

Pimentel, D., Acquay, H., Biltonen, M., Rice, P., Silva, M., Nelson, J., Lipner, V., Giordano, S., Horowitz, A., & D'amore, M. (1992). Environmental and economic costs of pesticide use. BioScience: **42**: 750–760

Pimentel, D., Rodolfo, Z., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics: **52**: 273

Rakshpal, R. (1962). Diapause in the eggs of *Gryllus pennsylvanicus* Burmeister (Orthoptera: Gryllidae). Canadian Journal of Zoology: **40**: 179–194

Rand, T. A., Tylianakis, J. M., & Tscharntke, T. (2006). Spillover edge effects: The dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecology Letters: **9**: 603–614

Robichaud, M.-J. (2006). Blue skies for blueberries. Statistics Canada https://www150.statcan.gc.ca/n1/en/pub/21-004-x/21-004-x2006001-eng.pdf?st=o2Gd8y0a

Rogers, D. D., Chamblee, D. S., Mueller, J. P., & Campbell, W. V. (1985). Fall no-till seeding of alfalfa into tall fescue as influenced by time of seeding and grass and insect suppression. Agronomy Journal: **77**: 150–157

Saska, P., Van der Werf, W., Vries, E., & Westerman, P. (2008). Spatial and temporal patterns of carabid activity-density in cereals do not explain levels of weed seed predation. Bulletin of Entomological Research: **98**: 169–181

Schmidt, J. M., Whitehouse, T. S., Green, K., Krehenwinkel, H., Schmidt-Jeffris, R., & Sial, A. A. (2019). Local and landscape-scale heterogeneity shape spotted wing drosophila (Drosophila suzukii) activity and natural enemy abundance: Implications for trophic interactions. Agriculture, Ecosystems & Environment: **272**: 86–94

Schnitkey, G., & Sellars, S. (2016). Growth rates of fertilizer, pesticide, and seed costs over time. Department of Agricultural and Consumer Economics, University of Illinois at Urbana-Champaign: 1–5

Smith, H. S. (1919). On some phases of insect control by the biological method. Journal of Economic Entomology: **12**: 288–292

Statistics Canada. (2020). *Table: 32-10-0364-01.* Area, production and farm gate value of marketed fruits https://www150.statcan.gc.ca/t1/tbl1/en/cv.action?pid=3210036401

Sutton, H. J. (1993). The sweet lowbush blueberry, (*Vaccinium angustifolium*) in international trade: Technical Standards as Agricultural Trade Barriers in the Canada-United States Context. Dalhouise J. Legal Stud.: **2**: 310

Tevis, L. (1958). Interrelations between the harvester ant *Veromessor Pergandei* (Mayr) and some desert ephemerals. Ecology: **39**: 695–704

Tew, T. E., Todd, I. A., & Macdonald, D. W. (2000). Arable habitat use by wood mice (*Apodemus sylvaticus*). Journal of Zoology: **250**: 305–311

Tooley, J. A., & Brust, G. E. (2002). Weed seed predation by carabid beetles. The Agroecology of Carabid Beetles: 215–230

Vallotton, A. (1999). Weed biology and ecology. Virginia State University https://rockingham.ext.vt.edu/content/dam/rockingham_ext_vt_edu/files/horticulture/homeownerweedbiologyecology.pdf

van der Laat, R., Owen, M. D. K., Liebman, M., & Leon, R. G. (2015). Postdispersal weed seed predation and invertebrate activity density in three tillage regimes. Weed Science: **63**: 828–838

Vander Kloet, S. P. (1978). Systematics, distribution, and nomenclature of the polymorphic Vaccinium angustifolium. Rhodora: **80**: 358–376

Vickery, V. R. (1961). The Orthoptera of Nova Scotia. **25**: 28–30

Waage, J. K., Greathead, D. J., Brown, R., Paterson, R. R. M., Haskell, P. T., Cook, R. J., Krishnaiah, K., Wood, R. K. S., & Way, M. J. (1988). Biological control: Challenges and opportunities. Philosophical Transactions of the Royal Society of London. B, Biological Sciences: **318**: 111–128

Westerman, P. R., Hofman, A., Vet, L. E. M., & van der Werf, W. (2003). Relative importance of vertebrates and invertebrates in epigeaic weed seed predation in organic cereal fields. Agriculture, Ecosystems & Environment: **95**: 417–425

Westerman, P. R., Liebman, M., Heggenstaller, A. H., & Forcella, F. (2006). Integrating measurements of seed availability and removal to estimate weed seed losses due to predation. Weed Science: **54**: 566–574

Westerman, P. R., Liebman, M., Menalled, F. D., Heggenstaller, A. H., Hartzler, R. G., & Dixon, P. M. (2005). Are many little hammers effective? Velvetleaf (*Abutilon theophrasti*) population dynamics in two- and four-year crop rotation systems. Weed Science: **53**: 382–392

White, S. N. (2018). Determination of *Festuca filiformis* seedbank characteristics, seedling emergence and herbicide susceptibility to aid management in lowbush blueberry (*Vaccinium angustifolium*). Weed Research: **58**: 112–120

White, S. N. (2019). Evaluation of herbicides for hair fescue (*Festuca filiformis*) management and potential seedbank reduction in lowbush blueberry. Weed Technology: **33**: 840–846

White, S. N. (2020, March 20). *Considerations for spring weed management and weeds to watch for in 2020*. 2020 Wild Blueberry Priducers Association of Nova Scotia Winter Information Meeting, Truro, NS

White, S. N., & Boyd, N. S. (2016). Effect of dry heat, direct flame, and straw burning on seed germination of weed species found in lowbush blueberry fields. Weed Technology: **30**: 263–270

White, S. N., Boyd, N. S., & Van Acker, R. C. (2015a). Temperature thresholds and growing-degree-day models for red sorrel (*Rumex acetosella*) ramet sprouting, emergence, and flowering in wild blueberry. Weed Science: **63**: 254–263

White, S. N., Boyd, N. S., Van Acker, R. C., & Swanton, C. J. (2015b). Studies on the flowering biology of red sorrel (*Rumex acetosella*) ramets from lowbush blueberry (*Vaccinium angustifolium*) fields in Nova Scotia, Canada. Botany: **93**: 41–46

White, S. N., & Kumar, S. K. (2017). Potential role of sequential glufosinate and foramsulfuron applications for management of fescues (*Festuca* spp.) in wild blueberry. Weed Technology: **31**: 100–110

White, S. N., & Webb, C. (2017). Susceptibility of American burnweed (*Erechtities hieraciifolius*) to herbicides and clipping in wild blueberry (*Vaccinium angustifolium* Ait.). Canadian Journal of Plant Science: **98**: 147–154

White, S. N., & Zhang, L. (2020). Fall-bearing year herbicides and spring-nonbearing year foramsulfuron applications for hair fescue management in lowbush blueberry. HortTechnology: **30**: 670–676

White, S. S., Renner, K. A., Menalled, F. D., & Landis, D. A. (2007). Feeding preferences of weed seed predators and effect on weed emergence. Weed Science: **55**: 606–612

Yarborough, D. (2004). Factors contributing to the increase in productivity in the wild blueberry industry. Small Fruits Review: **3**: 33–43

Yarborough, D. (2011). Weed management in wild blueberry fields. Cooperative Extension: Maine Wild Blueberries https://extension.umaine.edu/blueberries/factsheets/weeds/236-weed-management-in-wild-blueberry-fields/

Yarborough, D., & Bhowmik, P. C. (1988). Effect of hexazinone on weed populations and on lowbush blueberries in Maine. IV International Symposium on Vaccinium Culture **241**: 344–349

Yarborough, D., Hanchar, J. J., Skinner, S. P., & Ismail, A. A. (1986). Weed response, yield, and economics of hexazinone and nitrogen use in lowbush blueberry production. Weed Science: **34**: 723–729

Yenish, J. P., Doll, J. D., & Buhler, D. D. (1992). Effects of tillage on vertical distribution and viability of weed seed in soil. Weed Science: **40**: 429–433

Zhang, L., White, S. N., Randall Olson, A., & Pruski, K. (2018). Evaluation of flazasulfuron for hair fescue (*Festuca filiformis*) suppression and wild blueberry (*Vaccinium angustifolium* Ait.) tolerance. Canadian Journal of Plant Science: **98**: 1293–1303