

FEEDING BEHAVIOUR, DISPERSAL, AND COMMUNITY DYNAMICS OF  
CARABIDAE FOUND IN NOVA SCOTIA LOWBUSH BLUEBERRY FIELDS

by

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## **DEDICATION PAGE**

I dedicate this thesis to both my Brazilian and Canadian families, without whom none of this would have been possible.

Thank you for everything.

Obrigado por tudo.

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## ABSTRACT

Carabidae can be important pest control agents in many agricultural systems, and research on lowbush blueberry carabid communities is underdeveloped. In laboratory no-choice test experiments, I showed that *Pterostichus mutus* (Say) and *Poecilus lucublandus* (Say) did not feed on weed seeds commonly found in lowbush blueberry fields. I also did two field experiments that explored different aspects of Carabidae ecology. In the first, I measured the diversity and abundance of Carabidae in lowbush blueberry fields with respect to time and distance from field edge by setting up traps in a straight line from the surrounding forest edge to the center of 6 vegetative fields. I showed that carabid diversity did not change with distance from field edge over this summer season, but abundance increased linearly. In the second, I investigated *Harpalus rufipes* (De Geer) dispersal by measuring how far individuals may move over time by setting up a series of concentric circles and releasing marked individuals in the center. I developed a theoretical framework that estimates how many marked individuals are in the area based on number of beetles detected and probability of detection. I found that *H. rufipes* moved on average 5.38 (95% CI = 2.46 to 8.30), 14.47 (95% CI = 8.57 to 20.37), and 20.73 (95% CI = 8.98 to 32.48) m at 5, 29, and 53 hours respectively. These values are relatively close to that of other Carabidae and give us insight on how fast the population of *H. rufipes* may disperse in vegetative lowbush blueberry fields. The theoretical framework I developed provides methodological refinements for Carabidae dispersal research.



## LIST OF ABBREVIATIONS AND SYMBOLS USED

#	number
d.f.	degrees of freedom
P	P-value
F	F-value
se	standard error
CI	confidence interval
R <sup>2</sup>	coefficient of determination
r	Pearson's correlation coefficient
h	hour
m	meter
cm	centimeter
L	liter
mL	milliliter
°C	degrees Celsius
v:v	volume to volume
CRW	correlated random walk
GLM	general linear model
MDT	mean distance traveled
IPM	integrated pest management

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## **CHAPTER 1: INTRODUCTION**

### **1.1 Integrated Pest Management and Natural Enemies' Importance to Agriculture**

Some of the biggest challenges farmers face are pests such as weeds, animals, and pathogens, damage from which can reduce crop yields by 34, 18, and 16% respectively (Oerke 2006). Since 1960, the average yield of many crops has increased linearly in relation to pesticide sales, at least doubling in amount, which shows how effective crop protection practices have been at maximizing the output of agriculture (Oerke 2006). However, these improvements can come at a cost. There are many potential unintended effects of pesticides that may cause harm to the environment and humans (Betarbet et al. 2000; Hayes et al. 2006; Doublet et al. 2015; Zhang et al. 2016). Due to these potential unintended risks, alternative pest control methods that help reduce our reliance on pesticides are highly sought after.

Combining pest control strategies and practices to minimize pesticide use is called Integrated Pest Management (IPM) (FAO 2018). A popular component of IPM is biological control, which is the use of natural enemies to help suppress pest populations. These are organisms that through predation, parasitism, disease causing, or competition for resources, keep pest populations in check. One of the main roles of natural enemies is to prolong the period between pest outbreaks, a population ecology phenomenon called the “natural enemy ravine” (Southwood and Comins 1976). Biological control provides ecosystem services in all biomes valued at \$572/ha globally, and insects alone provide a net benefit of \$5.5 billion in the United States for attacking native pests of crops (Naranjo et al. 2015). There are three types of biological control: classical, augmentative, and conservation.

One of the aspects of conservation biological control consists of modifying the agricultural landscape to allow existing populations of native or introduced natural enemies to thrive, thus increasing their abundance and pest suppression activity (Naranjo et al. 2015). The effects existing natural enemies have on suppressing pest populations are often not noticed until disturbances occur that decrease their populations. For instance, when broad-spectrum insecticides that affect natural enemies are applied, the time it takes for pest species to reappear decreases, and outbreaks of secondary pests are promoted (Stern et al. 1959). In turn, when their populations are boosted through habitat

enhancement, there are measurable increases in the pest suppression services they provide. For instance, by boosting Carabidae (Coleoptera) diversity through habitat enhancement, farmers may see increased weed seed consumption by these beetles, which can be an important factor in controlling weed populations in agricultural fields (Fournier and Loreau 1999; Honěk et al. 2009; Gaines and Gratton 2010).

## **1.2 Carabidae as Natural Enemies**

There are 86 tribes and over 40,000 described species of Carabidae, also known as ground beetles, making them one of the most species-rich beetle families (Erwin 1985; Lövei and Sunderland 1996). In Canada, most species are either introduced from Europe, or are native members of genera such as *Harpalus* and *Pterostichus* (Lövei and Sunderland 1996), which are also common in Europe. Eggs, sometimes placed inside chambers in the ground, hatch into campodeiform larvae (well-developed legs, antennae, and a flattened body) that generally have three instar stages before pupating in a specially constructed chamber in the soil (Lövei and Sunderland 1996). The development from egg to adult takes on average less than one year, though under harsh environmental conditions, it can take up to four years. Beetles usually reproduce only once before dying, and adults from several species have been kept in the laboratory for up to four years (Lövei and Sunderland 1996). Ground beetles have a wide variety of food sources that range from plant material, such as seeds (Kulkarni et al. 2015), to other invertebrates (Hering and Plachter 1997; Renkema et al. 2014). Some species mainly eat seeds and plant material (phytophagous), while others mainly eat other insects (carnivorous), though many are omnivorous (Kulkarni et al. 2015; Lövei and Sunderland 1996).

Carabids are present in vast numbers within many agricultural systems and readily contribute to pest control by acting as natural enemies. For example, Chambers et al. (1983) demonstrated that presence of carabids in winter wheat fields can reduce local aphid populations six-fold relative to a control treatment in a three-year study. Carabidae species, along with some Staphylinidae, are amongst the most important predators of the cabbage root fly, with the carabids readily feeding on the fly's eggs (Coaker and Williams 1963). The carabid beetle *Notomus gravis* (Chaudoir) has been shown to help suppress the population of an exotic pest slug in Australian canola fields (Nash et al. 2008). Field and laboratory investigations showed that the ground beetles *Pterostichus melanarius*

(Illiger) and *Platynus dorsalis* (Pontoppidan) caused a decrease of 81% in the adult emergence of the wheat gall midge *Sitodiplosis mosellana* (Gehin) (Basedow 1973, as cited in Kromp 1999). The ground beetle *Harpalus rufipes* (De Geer) readily consumes both weed seeds and insect pests in lowbush blueberry fields in Eastern Canada (Renkema et al. 2013; Cutler et al. 2016). In a field study, 84-89% of dandelion seeds were destroyed by ground beetles after seed dispersal (Honěk and Martinkova 2005). These, amongst other examples, showcase the potential of carabid beetles for biological control of a range of pest species.

When trying to incorporate carabid beetles into IPM, it is important to consider their abundance and diversity within fields. For instance, high carabid diversity and abundance has been linked with increased weed seed predation in many cropping systems such as potato fields, and crop rotation systems of corn-soybean-winter wheat (Menalled et al. 2007; Gaines and Gratton 2010). It has also been linked with a significant decrease in aphid numbers within cereal crop fields in Sweden, more so than high abundance of aphid specific predators (Ekbohm and Wikteliuss 1985). Therefore, maintaining a diverse and abundant carabid community is desirable to those who wish to conserve these beetles in their fields. These two measures vary in agricultural fields due to several factors, many of which are within the farmer's control. For instance, no-till farming practices can provide higher carabid abundance than regular tillage practices (House 1989). Even though carabid diversity has been shown to not necessarily differ between organic and conventional farms, abundance may be over three times greater in organic systems (Shah et al. 2003). Lee et al. (2001) found that planting refuge strips for carabids within agricultural fields not only increased the existing carabid population, but allowed for stronger carabid populations to re-appear after major disturbances, such as pesticide applications, in comparison to disturbed fields without strips. These and other factors can be managed to help boost local carabid communities, which will ultimately benefit farmers and the industry. There are, however, factors which may be more difficult to control. For instance, Maisonhaute et al. (2010) found that landscape structures such as woodlands, pastures, roads, and other crops up to 500 m away from the collection sites, can have a greater impact on carabid diversity and abundance than local environment

factors. Therefore, IPM strategies should also try to incorporate factors which exist at a larger scale to maximize the benefits carabids may bring.

### **1.3 The Lowbush Blueberry Industry and its Scarcity of Carabidae Studies**

Lowbush blueberry (*Vaccinium angustifolium* Ait.) is an important Canadian crop native to eastern North America (Hall et al. 1979; Prior et al. 1998). In 2017, the combined farm gate value of highbush and lowbush blueberries was of approximately \$204 million, being the largest fruit crops by area in Canada at a combined 196,026 acres (Statistics Canada 2017a; Statistics Canada 2017b). Lowbush blueberry seeds are spread primarily in the wild in the droppings of birds and mammals (Vander Kloet 1978). Commercial fields develop from native stands on deforested or abandoned agricultural land, and are comprised of numerous variable clones which spread through underground rhizomes (Hall 1959; Hall et al. 1979; Hepler and Yarborough 1991). Commercial lowbush blueberry generally has a production cycle of two years, though some fields are managed in a three-year cycle through the use of double cropping (Jordan and Eaton 1995). Plants are pruned to near ground level by either burning or flail mowing to stimulate new shoot production in the first, or “vegetative”, year. The plants bloom and produce fruit in the second, or “crop”, year, with the potential to re-crop the field in the third year if a suitable yield can be obtained by double cropping (Jordan and Eaton 1995; Jensen and Yarborough 2004). Lowbush blueberry grows in acidic soils, with a pH of 4-5 (Hall et al. 1964). Soils with high percentage of stone or gravel provide the most favorable conditions for seedling emergence, growth, and development (Jackson et al. 1972). *Vaccinium* species have organs capable of vegetative reproduction 25 cm below the ground, which makes them resistant to fires (Flinn and Wein 1977). There are many insect pests and weeds that inhabit a blueberry field. Farmers rely on various tactics to control these pests, with pesticides being the preferred approach (Drummond and Groden 2000; Jensen and Yarborough 2004).

Carabidae have seldom been studied within this system, with only a handful of publications focusing on the topic. Cutler et al. (2012) were the only ones to study Carabidae ecology within blueberry fields, while the other studies focused on carabid laboratory feeding assays and gut content analysis (Renkema et al. 2013; Renkema et al. 2014; Cutler et al. 2016). Cutler et al. (2012) compiled a list of the most abundant species

occurring in both vegetative and crop fields over a period of two years, giving insight on carabid population dynamics in this system. They found that blueberry fields are mainly dominated by *H. rufipes*, an omnivorous species that feeds on both blueberry weed seeds and insect pests (Renkema et al. 2013; Cutler et al. 2016). Six species comprised 83.5% of all captures, suggesting that ecosystem services are mainly provided by a select group of individuals.

Cutler et al. (2012) measured how the carabid community changed with distance from the field edge, an important variable in population dynamics (Rand et al. 2006), and found that overall carabid abundance did not change, but diversity decreased with an increase in distance from the edge. Unfortunately, they only went 50 m away from the edge, which might not be enough to show a universal trend considering there are fields in Nova Scotia which can be 400 m across (J Slack – personal communication). Generally, increasing distance from field edges has positive relationships with overall carabid abundance and negative relationships with carabid diversity and richness in other agricultural systems. For instance, Bedford and Usher (1994) found that carabid richness was significantly greater in the edge zone of a farm-woodland transect than in the field. Fournier and Loreau (1999) found that carabid species diversity in an experimental farmland significantly decreased with increasing distance from newly planted hedges. Anjum-Zubair et al. (2010) found that carabid richness was higher in the edge of winter wheat fields than in their center, but that abundance was greater at the center than at the edges, and many others found similar trends in other agricultural systems (Thomas and Marshall 1999; Haysom et al. 2004; Koivula et al. 2004). Thus, a more detailed experiment studying the effect of edge distance on carabid communities within lowbush blueberry fields could reveal similar trends.

Two of the most abundant species found by Cutler et al. (2012), *Pterostichus mutus* (Say) and *Poecilus lucublandus* (Say), or some members of these same genera, though generally classified as predators, can readily consume weed seeds, thus aiding in weed control. For instance, O'Rourke et al. (2006) found that *P. lucublandus* consumed almost as many *Panicum miliaceum* (L.) seeds as known seed eaters such as the field cricket *Gryllus pennsylvanicus* (B.). Lundgren et al. (2013) found that *P. lucublandus* and *Poecilus versicolor* (Sturm) readily fed on dandelion (*Taraxacum officinale* W.) seeds,



though they did not have the largest consumption rate. Kulkarni et al. (2016) found that *P. melanarius* and *P. lucublandus* readily fed on a variety of brassicaceous weed seeds, though the latter consumed more than the former. Since *P. mutus* and *P. lucublandus* coexist with overwintering seeds of common lowbush blueberry weeds in vegetative fields (Darbyshire and Cayouette 1989; Hoeg and Burgess 2000; Cutler et al. 2012; White 2018), the question of whether they aid in lowbush blueberry weed control remains unanswered.

Carabids actively search for prey, thus knowledge on how they disperse is invaluable for IPM strategies. Since *H. rufipes* was the most abundant species found by Cutler et al. (2012), it would be valuable to understand how they disperse within lowbush blueberry fields, for they are likely the ones doing much of the ecosystem services. Few studies have tried to understand how *H. rufipes* moves within agricultural systems (Zhang et al. 1997; Kujawa et al. 2006), and some have limitations in methodology. Overall, carabid beetles seem to disperse relatively small distances per day. For instance, tiger beetles can travel at a rate of 6.81 m/day, while individual *Carabus ullrichii* can travel from 1.69 to 13.43 m/day on average (Horgan and Chávez 2004; Růžičková and Veselý 2016). Carabids move in what is called a “correlated random walk”, where at each step they take, the turning angle is independent of the previous turning angle, there is no cross-correlation between moving directions and turning angles, and successive step lengths are not auto-correlated (Kareiva and Shigesada 1983). They can diverge from this random walk in the presence of prey or other stimuli (Wallin and Ekblom 1994). Therefore, populations of *H. rufipes* in a field may cover a lot of area given the randomness in their movement, and an experiment measuring individual displacement may give us a better idea of these beetle’s “homing range” in lowbush blueberry fields.

#### **1.4 Research Objectives and Hypotheses**

Pesticides are amongst the most effective pest control strategies, and they have contributed to a large increase in crop production around the world (Oerke 2006). There are, however, side effects to the use of these chemicals, and these come in the form of environmental damage and health hazards to people (Doublet et al. 2015; Zhang et al. 2016). To minimize our reliance on pesticides, IPM strategies that involve tactics such as

biological control are being adopted all over the world (Naranjo et al. 2015). Natural enemies are organisms which help control pest populations through predation, parasitism, or competition for resources, and their main role is to increase the amount of time between pest outbreaks (Southwood and Comins 1976). Carabidae are abundant natural enemies in many agricultural systems, and knowledge of their basic biology and ecology is essential to efficiently implement IPM strategies involving them (Ekbom and Wiktelius 1985; Fournier and Loreau 1999; Kulkarni et al. 2015). The lowbush blueberry industry is an important sector of the Canadian economy (AAFC 2015), and currently there is a scarcity of Carabidae studies within this system. I had three research objectives, aimed at filling gaps in both the blueberry and overall Carabidae literature, which involved questions of community ecology, feeding tendencies and dispersal of carabid beetles in lowbush blueberry.

My first objective was to test the weed seed eating ability of the abundant *P. mutus* and *P. lucublandus* by exposing them to common lowbush blueberry weed seeds in the laboratory. These experiments shed light on these beetles' potential to contribute to weed control in lowbush blueberry fields. I predicted that they would feed on the weed seeds given that there's an abundance of beetles and an apparent lack of abundance of anything else they might eat in the early vegetative blueberry fields.

My second objective was to study the abundance and diversity of carabid genera with relation to distance from the field edge in very large lowbush blueberry fields (at least 200 m across from all sides), as well as with time. I predicted distance from field edge would have a positive relationship with overall carabid abundance and a negative relationship with carabid diversity, given that is the most predominant trend in other agricultural and forestry systems. I also predicted that time would have a positive relationship with abundance, while causing diversity to decrease. This is because researchers have found that *H. rufipes* significantly outnumbers other species in blueberry fields when they are active, which happens later in the summer (Cutler et al. 2012). This spike in population would cause my predicted effects on overall carabid abundance and diversity.

My third objective was to study the dispersal of *H. rufipes* in lowbush blueberry fields by using mark-recapture techniques. I predicted that the beetles would disperse

farther than the  $\approx 10$  m/day suggested by Zhang et al. (1997), since I found an unfortunate weakness in their methodology which I corrected for.

## **CHAPTER 2: *POECILUS LUCUBLANDUS* AND *PTEROSTICHUS MUTUS* (COLEOPTERA: CARABIDAE) DO NOT FEED ON HAIR FESCUE (*FESTUCA FILIFORMIS*), RED SORREL (*RUMEX ACETOSELLA*), AND POVERTY OATGRASS (*DANTHONIA SPICATA*) SEEDS**

### **2.1 Introduction**

Lowbush blueberry (*Vaccinium angustifolium* Ait.) is an important Canadian crop native to eastern North America (Hall et al. 1979; Prior et al. 1998). Commercial fields are developed from natural stands occurring on abandoned farmland or cleared woodland (Hall 1959) and are managed in a two-year production cycle. Plants are pruned to ground level by mowing or burning to stimulate new growth in the first, or vegetative year, and flowering, fruit set, and harvest occur in the second, or crop year. At the end of the crop year, farmers mow or burn their fields, which forces it to re-enter the vegetative stage in the following year (Blatt et al. 1972). In 2017, the combined farm gate value of highbush (*Vaccinium corymbosum* L.) and lowbush blueberries was approximately \$204 million, making blueberry the largest fruit crop by area in Canada at a combined 196,026 acres (Statistics Canada 2017a; Statistics Canada 2017b).

There are around 120 species of weeds that inhabit blueberry fields, including woody and herbaceous weeds, as well as grasses, rushes, and sedges (McCully et al. 1991), though since the introduction of the broad spectrum herbicide hexazinone (Velpar) in the early 1980's, there has been an increase in the number of weed species that rely on seed for dispersal and establishment (Jensen and Yarborough 2004). Weeds reduce crop yields by up to 34%, which is higher than losses due to animals and pathogens (18% and 16% respectively) (Oerke 2006). In Eastern Canada, weeds have caused up to \$372 million worth of crop losses in 58 different commodities (Swanton et al. 1993). Though outdated, this figure illustrates potential crop losses due to weeds. Lowbush blueberry is prone to yield loss from competing weed species such as red sorrel (*Rumex acetosella* L.), hair fescue (*Festuca filiformis* Pourret), and poverty oatgrass (*Danthonia spicata* L.), which can dominate fields (Jensen and Sampson – unpublished data). Other weeds such as bracken fern (*Pteridium aquilinum* L.) and dogbane (*Apocynum androsaemifolium* L.) can cause 36 kg/ha and 41 kg/ha of yield loss for every percent increase in weed cover (Yarborough and Marra 1997). Machinery such as harvesters have been shown to move

weed seeds around the field, facilitating the spread of weeds that rely on seeds for establishment (Boyd and White 2009). This, coupled with the shift in the weed flora to favour these seed spreading weeds, accentuates the importance of weed seed research, and this importance is reflected by the number of recent publications on the topic (White and Boyd 2016; White et al. 2017; White 2018; White and Webb 2018).

Herbicides have been the primary method of weed control for lowbush blueberry growers for more than 50 years (Jensen and Yarborough 2004), with a range of selective and non-selective herbicides for pre and/or post emergence use. Selection for herbicide-resistant biotypes of weeds, however, is limiting efficacy of these tools in many cropping systems (Heap 2014), including lowbush blueberry. Biotypes of red sorrel resistant to hexazinone have been identified (Li et al. 2014), and grasses such as poverty oatgrass and fescues are also resistant, or suspected to be resistant, to hexazinone and other commonly used herbicides in lowbush blueberry (Burgess 2002; Jensen and Yarborough 2004; Zhang et al. 2018). Issues associated with this resistance, combined with a global push to reduce pesticide use in agriculture, are driving an interest in the pursuit of other methods of pest management. Post-dispersal weed seed consumption can serve as a critical factor determining the population dynamics of weeds in agroecosystems (Andersen 1989) and may serve as an important form of biological weed control in cropping systems. In such systems, both vertebrates (e.g., rodents, birds), and invertebrates (mainly insects) contribute to the post dispersal consumption of weed seeds (Westerman et al. 2003; Heggenstaller et al. 2006; Honěk et al. 2009).

The Carabidae are one of the most diverse beetle families, with over 40,000 described species (Erwin 1985; Lövei and Sunderland 1996). They are important natural enemies, helping suppress pest populations in many agricultural systems (Edwards et al. 1979; Westerman et al. 2003; O'Neal et al. 2005; Honěk et al. 2009). Carabids are well known for being weed seed predators (Honěk et al. 2003; Kulkarni et al. 2015). In a field study for instance, 84-89% of dandelion seeds were destroyed by ground beetles after seed dispersal (Honěk and Martinkova 2005). Bohan et al. (2011) found that carabids significantly regulated weed seed banks in spring maize and winter oilseed rape. This means not only that carabids eat seeds on the soil surface, but they also eat seeds in the soil, which further increases their potential as weed seed predators. Carabids have been

studied in lowbush blueberry fields in both vegetative and crop years, and many of the species found inhabiting the fields are seed eaters (Cutler et al. 2012).

In early spring, *Poecilus lucublandus* (Say) and *Pterostichus mutus* (Say) are among the more prominent carabid species in vegetative lowbush blueberry fields (Cutler et al. 2012). Around the same time, overwintering seeds of many weeds can be found in fields and many of them can still germinate after this period of dormancy (Darbyshire and Cayouette 1989; Hoeg and Burgess 2000; White 2018). Therefore, it is of interest to know whether these predominant beetles consume overwintering seeds. *Poecilus lucublandus* has been shown to consume brassicaceous weed seeds in laboratory no-choice experiments, even though it is usually described as carnivorous (Cutler et al. 2012; Kulkarni et al. 2016). Kulkarni et al. (2016) also found that *Pterostichus melanarius* (Illiger), a species of the same genus as *P. mutus*, consumes brassicaceous seeds despite being described as carnivorous (Cutler et al. 2012). Therefore, it is not unreasonable to suspect that *P. mutus* may also contribute to weed control.

The objective of this study was to determine whether *P. lucublandus* and *P. mutus* consume seeds of weeds commonly found in lowbush blueberry fields. I predicted that they would consume the seeds, given that they (or at least members of the same genus) have been shown to consume seeds of other weed species (O'Rourke et al. 2006; Lundgren et al. 2013; Kulkarni et al. 2016).

## **2.2 Materials and Methods**

In summary, I did two feeding laboratory experiments with beetles collected from lowbush blueberry fields. In the first, I tested whether *P. lucublandus* and *P. mutus* ate hair fescue and poverty oatgrass seeds. In the second experiment, I added *Harpalus rufipes* (De Geer) as a positive control since it eats weed seeds and replaced poverty oatgrass with red sorrel due to a shortage of poverty oatgrass seeds. In this experiment, I also measured *H. rufipes* seed consumption over time.

### **2.2.1 Beetle collection and experimental designs**

From early to mid-July 2016, I collected *P. lucublandus*, *P. mutus*, and *H. rufipes* from two lowbush blueberry fields in Debert (45°25'12"N; 063°30'41"W) and Portapique (45°24'22"N; 063°40'06"W), Nova Scotia, using pitfall traps (Greenslade 1964). I brought

them back to the laboratory inside clear 1 L plastic containers, and then transferred them to sealable plastic cups (120 mL) containing 50:50 v:v moistened peat and play sand mixture. Beetles were fed cat food (Whiskas™) until they were needed for the experiments (Cutler et al. 2016). All beetles were collected within two weeks of the start of an experiment, and starved 60 hours prior to the experiment to standardize their hunger level (Lang and Gsödl 2001). For the first experiment, I collected hair fescue and poverty oatgrass seeds from the ground at the two fields using a hand vacuum (Shark® 12 volt hand vac). Contents were emptied into several 1 L plastic containers in the field and brought to the laboratory for separation of seeds from soil.

For the second experiment, hair fescue and red sorrel seeds were obtained from Dr. Scott White, who collected them from Nova Scotia lowbush blueberry fields in the summer of 2015. The reason for the switch in weed species and seed origin was a shortage of over wintering poverty oatgrass seeds in my soil samples.

The first experiment was a randomized 2x2 factorial design, where the factors were beetle species (*P. mutus*, *P. lucubandus*) and weed species (hair fescue, poverty oatgrass) with 10 replicates of each factorial combination. The second experiment was a randomized 3x2 factorial design, where the factors were beetle species (*P. lucublandus*, *P. mutus*, *H. rufipes*) and weed species (hair fescue, red sorrel). I added *H. rufipes* to this experiment as a positive control since it is known to feed on blueberry weed seeds as well as other seeds (Harrison and Gallandt 2012; Cutler et al. 2016). In this case, there was an uneven number of replicates for each of the factorial combinations due to a shortage in the populations of *P. lucublandus* and *P. mutus* in the field. There were 10 replicates for each of the combinations involving *H. rufipes*, while there were 8 replicates for both *P. lucublandus* vs. red sorrel and for *P. mutus* vs. hair fescue, and 7 replicates for the remaining two combinations. I placed a single beetle inside a glass Petri plate (diameter = 9 cm, depth = 2 cm) containing 30 seeds of one weed species and a cotton wick saturated with water. When needed, I resupplied seeds to the beetles until the experiment was over. Consumed seeds were counted as seeds missing from the Petri plate plus seeds where only the seed husk was left behind, indicating the endosperm was consumed.

### 2.2.2 Data collection

For the first experiment, I reported the mean cumulative number of seeds consumed (whole seed plus endosperm only) at the end of 144 hours for each treatment combination. The cumulative number of consumed seeds were determined 2, 8, 12, 24, 36, 48, 60, 72, 96, and 144 hours after the start of the experiment. In the second experiment, I reported the mean cumulative number of seeds consumed (whole seed plus endosperm only) at 2, 6, 18, 30, 42, 54, and 68 hours after the start of the experiment, which is also when data were collected.

### 2.2.3 Statistical analysis

In the 2x2 factorial design, I only measured the mean number of seeds eaten at the end of the experiment and calculated the standard error. I analyzed the 3x2 factorial design, which involved combinations between three beetle species and seeds from two weed species, by fitting a general linear model (GLM) with a quasipoisson error distribution to the data. This error distribution is used when there is overdispersion, causing the variance to be higher than the mean (Crawley 2013). Then, I extracted the ANOVA table from that model using the “glm()” and “aov()” functions in R 3.5.0 (R Core Team 2017). To analyze the feeding of *H. rufipes* over time, I fitted a Michaelis-Menten model to the data (Bates and Watts 1988). In terms of my study, this model is

$$y_i = \frac{x_i \theta_1}{x_i + \theta_2} + \varepsilon_i$$

Where  $y_i$  = Mean cumulative number of seeds eaten of weed species  $i$

$x_i$  = Time of exposure to seeds of weed species  $i$

$\theta_1$  = The value of  $y_i$  at which the model asymptotes

$\theta_2$  = The value of  $x_i$  when  $y_i = \frac{\theta_1}{2}$

$\varepsilon_i$  = The error term

With this model, we can estimate the initial feeding rate of the beetles, which is essentially a measure of how hungry they are at the start of the experiment. To find it, we simply take the derivative of the model (this will show the change in slope over time) and make  $x_i = 0$ . This gives us  $K_{0i} = \frac{\theta_1}{\theta_2}$ , where  $K_{0i}$  is the feeding rate at time = 0 on seeds of weed species  $i$ . The model, however, needs to be modified if we wish to find the final



feeding rate of beetles. Since the model asymptotes, it means when time =  $\infty$ , the rate of change (feeding rate in this case) is 0. A rate of 0 is biologically meaningless given that the beetles will always feed, unless they die. The modified Michaelis-Menten model is

$$y_i = \frac{x_i \theta_1}{x_i + \theta_2} + K_{fi} x_i + \varepsilon_i$$

Where  $K_{fi}$  = The final consumption rate of weed species  $i$  seeds

Under this modified model, the initial feeding rate is different from the one obtained through the unmodified model. I did the nonlinear regression analyses using the “nls()” function, with the Gauss-Newton algorithm for iterations, and made all graphs using the “tidyverse” and “cowplot” packages in R 3.5.0 (Wilke 2015; R Core Team 2017; Wickham 2017).

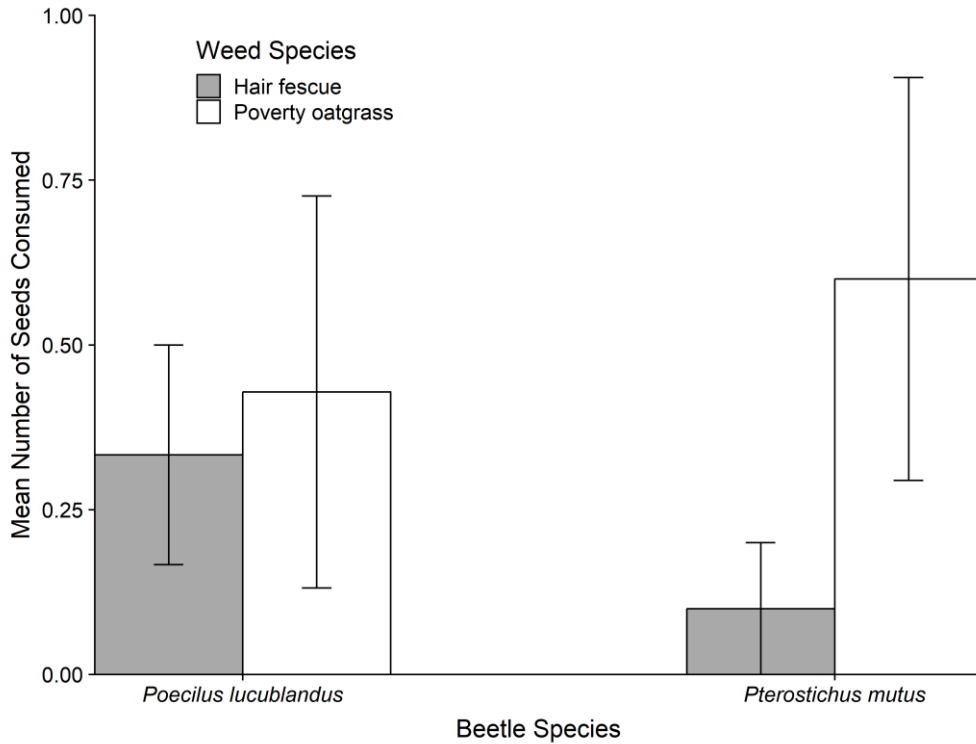
## 2.3 Results

The amount of seeds consumed by *P. lucublandus* and *P. mutus* in the 2x2 experiment was biologically insignificant. After being starved for 60 hours, the mean cumulative number of seeds consumed of both weed species by both beetle species was < 1 after 144 hours of exposure (Figure 2.1). It was therefore unnecessary to do any statistical tests for comparisons on these data.

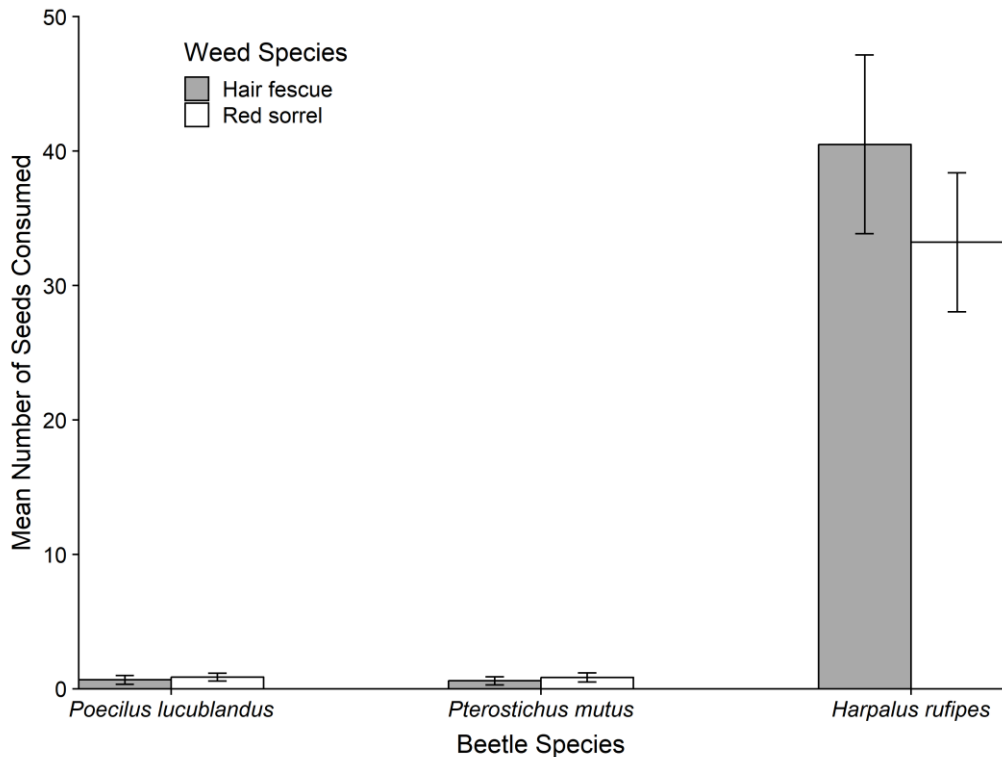
In the 3x2 experiment, the “beetle species” factor alone was significant (treatment d.f. = 2, error d.f. = 44, F = 57.6, P < 0.001). The amount of seeds consumed by *P. lucublandus* and *P. mutus* was again biologically insignificant, though *H. rufipes* readily fed on the seeds (Figure 2.2). *Harpalus rufipes* consumed both seeds equally after 68 hours since there was no interaction between beetle and weed species (P = 0.55).

Over time, *H. rufipes* slowed its feeding rate, moving towards a constant rate (Figure 2.3). The initial feeding rate of *H. rufipes* on hair fescue seeds ( $K_{0i}$ ) was 1.24 seeds/hour, while for red sorrel it was 1.3 seeds/hour. The estimated final constant feeding rate on fescue seeds by *H. rufipes* was 0.4 seeds/hour. I could not estimate the final feeding rate of *H. rufipes* on red sorrel seeds because the parameter estimate was not significant in the nonlinear regression analysis. The model parameter estimates for hair fescue seed feeding by *H. rufipes* were:  $\theta_1 = 76.73$  (se = 11.51) and  $\theta_2 = 61.50$  (se = 16.18), with convergence happening after 7 iterations. The model parameter estimates for

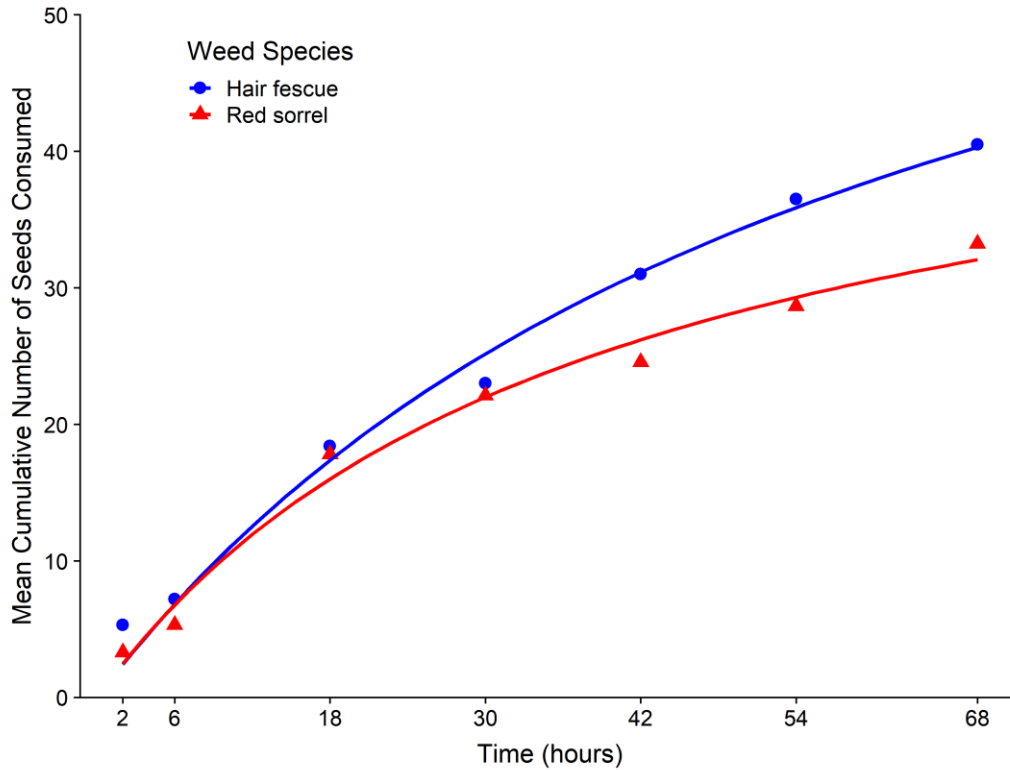
red sorrel seed feeding by *H. rufipes* were:  $\theta_1 = 50.18$  (se = 5.56) and  $\theta_2 = 38.47$  (se = 9.02), with convergence happening after 6 iterations. These parameter estimates imply that *H. rufipes* slows its consumption of red sorrel seeds before hair fescue.



**Figure 2.1** Mean number of hair fescue (*Festuca filiformis*) and poverty oatgrass (*Danthonia spicata*) seeds consumed by the ground beetles *Poecilus lucublandus* and *Pterostichus mutus* after 144 hours in a laboratory no-choice experiment. Beetles were starved for 60 hours prior to the start of the experiment. Bars represent standard error of the mean. The amount of seeds consumed was not biologically significant ( $< 1$ ).



**Figure 2.2** Mean number of hair fescue (*Festuca filiformis*) and red sorrel (*Rumex acetosella*) seeds consumed by the ground beetles *Poecilus lucublandus*, *Pterostichus mutus*, and *Harpalus rufipes* after 68 hours in a laboratory no-choice experiment. Beetles were starved for 60 hours prior to the start of the experiment. Bars represent standard error of the mean. The amount of seeds consumed by *P. lucublandus* and *P. mutus* was not biologically significant ( $< 1$ ), whereas the positive control species, *H. rufipes*, readily consumed seeds of both weed species ( $P < 0.001$ ). There was no interaction between weed seed species and beetle species, implying that *H. rufipes* consumed equal amounts of both seed types.



**Figure 2.3** Mean cumulative number of hair fescue (*Festuca filiformis*) and red sorrel (*Rumex acetosella*) seeds consumed by the ground beetle *Harpalus rufipes* over 68 hours in a laboratory no-choice experiment fitted with Michaelis-Menten model of the form  $y_i = \frac{x_i\theta_1}{x_i+\theta_2} + \varepsilon_i$ . The initial feeding rate of *H. rufipes* on hair fescue seeds ( $K_{0i}$ ) was 1.24 seeds/hour, while for red sorrel it was 1.3 seeds/hour. The estimated final constant feeding rate on fescue seeds by *H. rufipes* ( $K_{fi}$ ) was 0.4 seeds/hour, which I found by fitting a modified Michaelis-Menten model. The same parameter estimate for red sorrel feeding was not significant.

## 2.4 Discussion

The prediction that the beetles would consume the seeds was not supported by my results. In the first experiment, *P. lucublandus* and *P. mutus* consumed on average less than one seed of either weed species after 144 hours of exposure. Coupled with the results of the second experiment, where they also consumed less than one seed on average after 68 hours, it is concluded that these beetle species do not participate in post dispersal consumption of hair fescue, poverty oatgrass, and red sorrel seeds in lowbush blueberry fields. They may still feed on seeds from other common weed species of lowbush blueberry, given that they (or members of the same genus) have been shown to consume seeds in other systems. O'Rourke et al. (2006) found that *P. lucublandus* and *Poecilus*

*chalcites* (Say) preferred de-hulled seeds of *Panicum miliaceum* (L.) over seeds from common weeds found in various midwestern United States field crops. Lundgren et al. (2013) found that *P. lucublandus*, *Poecilus versicolor* (Sturm), and *Pterostichus permundus* (Say) consumed  $6.67 \pm 4.54$ ,  $16.67$ , and  $22.45 \pm 7.56$  *Taraxacum officinale* (W.) seeds per day, though they did not have the highest consumption rates out of all the species studied. Kulkarni et al. (2016) found that *P. lucublandus* consumed the most amount of brassicaceous seeds out of all four carabid species tested in a choice test. De-hulled seeds are softer than hulled seeds, and dandelion seeds are actually achenes (single-seeded fruits) that in many cases contain very large embryos (Tweney and Mogie 1999). It could have been the case that hair fescue, poverty oatgrass, and red sorrel seeds were too tough for the beetles, and softer weed seeds in blueberry fields might be consumed by them. As such, additional research with seeds of other weed species might be warranted. Both *P. lucublandus* and *P. mutus* are, however, generally described as carnivores (Cutler et al. 2012), which may limit potential for these species to contribute to weed seed consumption. The simultaneous presence of hunting spiders in the same area (Collins et al. 1996) is an indicator that there might be other insects in the vegetative field during early spring, and these could be what these carabid species are after. Both species feed on insect pests of lowbush blueberry, including the blueberry spanworm (*Itame argillacearia* Packard) (Lepidoptera: Geometridae) and the blueberry flea beetle (*Altica sylvia* Malloch) (Coleoptera: Chrysomelidae) (Renkema et al. 2013; Renkema et al. 2014). Both pests temporarily coincide with the beetles in crop and vegetative fields, even though these pest come up later in the season within vegetative fields (Renkema et al. 2013; Renkema et al. 2014).

*Harpalus rufipes* readily consumed both red sorrel and hair fescue seeds, eating on average more than 30 seeds of each weed species. This is not surprising due to the well-known weed seed feeding habits of this carabid species, including previous records of them feeding on weed seeds common to lowbush blueberry fields (Luff 1980; Jørgensen and Toft 1997; Cutler et al. 2016). *Harpalus rufipes*' final feeding rate of both weed species is lower than the initial feeding rate, and this deacceleration is likely due to satiation of the beetles (Honěk et al. 2003). It takes about 48 hours for insect prey to be completely digested by some carabid species (Renkema et al. 2014), and it is not unlikely

seeds take a similar time to be digested, even though plant material digestion is dictated by the beetle's gut bacterial community (Lundgren and Lehman 2010). The switch from a changing feeding rate to a constant one is probably due to an equilibrium between a constant supply of food and the insect body's nutritional needs.

*Harpalus rufipes* deaccelerated feeding on red sorrel seeds faster than hair fescue seeds, as shown by the lower model parameter estimates. The observed differences in sorrel and fescue consumption may be due to size, nutritional, or chemical differences in each seed, all of which are factors that influence granivore preference (Honěk et al. 2007; Honěk et al. 2011). Jørgensen and Toft (1997) found that *H. rufipes* thrives on a mixed seed diet, but it does not like seeds that are too hard, or seeds that have small endosperms. Cutler et al. (2016) found that *H. rufipes* ate less hair fescue seeds than red sorrel in a no-choice test. This is different from what I found, which is surprising especially since these are no-choice tests. The only substantial difference between our designs was the refrigeration of seeds prior to the experiment, something they did and I did not. That might have modified the fescue seeds in a way that made them less desirable to the beetles. Low temperatures of 13-18°C can have detrimental effects on seed nutrient content during seed development, and temperatures slightly above or below 0°C can damage seeds that are high in moisture content (Delouche 1968; Wolf et al. 1982).

The results of my experiments indicate that *P. lucublandus* and *P. mutus* do not consume significant amounts of *F. filiformis*, *R. acetosella*, or *D. spicata* seeds, which suggests they are probably feeding on other coexisting insects in vegetative lowbush blueberry fields. In accordance with the results of Cutler et al. (2016), *H. rufipes* readily feeds on common lowbush blueberry weed seeds and may contribute to weed population control through post-dispersal weed seed consumption. All three carabid species are present in crop lowbush blueberry fields, and there they coexist with insect pests, readily feeding on them (Cutler et al. 2012; Renkema et al. 2014). Therefore, maintaining strong populations of these carabid species in vegetative fields is desirable, since those will carry over into the crop year and assist with pest control. Though *H. rufipes* consumes insects as well as seeds, their larvae are purely granivorous (Hartke et al. 1998), which elevates the weed population control potential of the species.

## **CHAPTER 3: THE DIVERSITY AND ABUNDANCE OF GROUND BEETLES (COLEOPTERA: CARABIDAE) WITHIN VEGETATIVE LOWBUSH BLUEBERRY FIELDS**

### **3.1 Introduction**

Carabidae is one of the most diverse beetle families, with 86 tribes and over 40,000 described species (Erwin 1985; Lövei and Sunderland 1996). There are 290 described species in Nova Scotia, which constitutes 82% of carabid species in the Maritime Provinces (Majka et al. 2007; Neil and Majka 2008). Carabidae are important natural enemies, and help suppress pest populations in many agricultural systems (Edwards et al. 1979; Westerman et al. 2003; O’Neal et al. 2005; Honěk et al. 2009). Carabid diversity (how well distributed each species is in relation to one another) and abundance (some measure of the number of individuals) are directly related to pest control in agricultural systems. For instance, as diversity and abundance increase, so does weed seed predation (Menalled et al. 2007; Gaines and Gratton 2010). Therefore, maintaining an abundant and diverse carabid community in agricultural fields is desirable for growers who wish to reduce their reliance on pesticides, which are commonly applied in many cropping systems (Pimentel 2009).

There are several factors that can impact agricultural carabid communities. For instance, species diversity and richness (number of species in an area) decrease with an increase in distance from newly planted hedges and semi-natural habitats (Fournier and Loreau 1999; Fournier and Loreau 2001; Hendrickx et al. 2007). No-till and organic farming systems can double the diversity of carabids in comparison to conventional systems, but overall abundance can be much greater in conventional systems than in those same no-till and organic systems (Menalled et al. 2007). Insecticide applications to crops decrease abundance of carabids and change community composition, but a “refuge strip” for the beetles can act as a buffer for such effects (Lee et al. 2001). The time of year in which carabids are active can vary across species and genera (Cutler et al. 2012). In fact, a species that is most abundant one year may become uncommon in the following year, and vice versa (French and Elliott 1999).

One of the many factors that can influence the structure of a community is called the “edge effect”. This is the trend of increasing or decreasing a variety of response variables, depending on the system and time of year, many organisms show the farther

they are from habitat intersections (Rand et al. 2006). For instance, rates of predation on bird nests are higher near edges than elsewhere in the habitat (Batáry and Báldi 2004). In terms of community ecology measures, carabid species richness and diversity can be lower inside the forest than in the forest edge or its adjacent grassland (Molnár et al. 2001; Magura 2002). There are cases, however, where there is no difference in species richness between edge and inside the forest communities (Davies and Margules 1998). Some species of carabids appear in greater numbers near the edges, while others are more numerous away from the edges (Cutler et al. 2012). Field edge is therefore an appropriate explanatory variable to consider if we wish to study the community dynamics of carabid beetles.

Lowbush blueberry (*Vaccinium angustifolium* Ait.) is an important crop native to eastern North America (Hall et al. 1979; Prior et al. 1998). Commercial fields are typically managed in a two-year cycle, with a vegetative growth year and a crop year, which is the fruit setting and harvesting year. After harvesting, farmers mow or burn their fields, thereby initiating the vegetative stage in the following year (Blatt et al. 1972). Carabid communities have seldom been studied within this system, with only a handful of papers published on the topic (Cutler et al. 2012; Renkema et al. 2013; Renkema et al. 2014; Cutler et al. 2016). Cutler et al. (2012) studied the community ecology of carabids and explored edge effects on carabids, but the maximum distance from the edge used in their study was only 50 m. This is a relatively short distance considering some lowbush blueberry fields can be up to 400 m wide (J Slack – personal communication).

The goal of this study was to determine how distance from field edge and time affect the community of Carabidae and its most abundant genera within vegetative lowbush blueberry fields in one year by using regression and correlation models. I predicted distance from field edge would have a positive relationship with overall carabid abundance and a negative relationship with carabid diversity, given that is the most predominant trend in other agricultural and forestry systems. I also predicted that time would have a positive relationship with abundance, while causing diversity to decrease due to *H. rufipes* having been shown to significantly outnumber other species in blueberry fields when they are active later in the summer (Cutler et al. 2012).



## 3.2 Materials and Methods

### 3.2.1 Beetle collection, identification, and experimental layout

In the summer of 2017, I selected six vegetative lowbush blueberry fields in Nova Scotia, Canada, that were at least 200 m across from all sides. These fields were in the counties of Colchester (Webb Field, 45°24'22"N; 063°40'06"W - Kemptown Field, 45°29'59"N; 063°06'24"W - Portapique Field, 45°24'29"N; 063°43'27"W), Cumberland (Nina's Large Field, 45°34'50"N; 063°52'05"W - American Field, 45°33'35"N; 063°53'51"W), and Halifax (Wheeler Field, 45°12'30"N; 062°52'14"W). I selected only vegetative fields for this study as Cutler et al. (2012) tended to find more beetles in vegetative fields and to avoid damaging fruit bearing plants during data collection. All fields were surrounded by mixed-wood forests which had high coniferous tree density. In each of the six fields, we set up trapping sites of pitfall traps (Greenslade 1964) starting from inside the surrounding forest, and going towards the center of the field along a straight transect. Every field had trapping sites at the following distances: -10, 0, 10, 30, 50, 70, and 100 m, with the edge between forest and field being at the 0 m mark. Four of the fields (American, Nina's Large, Portapique, and Wheeler) had traps at 130 m, and Wheeler Field had traps at 160 m. Since pitfall traps measure activity-density (Greenslade 1964), all abundance measures in my study were made with activity-density data.

A trapping site consisted of three pitfall traps laid out in a triangle  $\approx$  1 m apart from one another, and rain covers at each trap made of a 6x6 inch piece of plywood with nails in the corners as supports. We activated the traps for 72 h every two weeks by removing a plastic cover from each cup and adding an  $\approx$  30% brine solution. After the 72 h activation period we separated carabids from other insects in each cup, put them in sealable bags containing some of the brine solution, and brought them to the lab for further sorting, pinning, and identification. We deactivated the traps by emptying the cups and replacing the plastic covers. I used several resources to identify beetles to the level of genus, and in some cases to species: Lindroth's keys (Lindroth 1961; Lindroth 1968), the Government of Canada's Carabidae list (Goulet and Bousquet 2014), the list of carabids captured in lowbush blueberry fields by Cutler et al. (2012), and voucher specimens in the A.D. Pickett Entomological Museum at the Dalhousie Agricultural Campus.

### 3.2.2 Statistical analyses

I did two simple linear regressions to determine whether abundance and diversity change with distance from the field edge. For diversity, I measured Simpson's Diversity's Index, which is less sensitive to rare species than other methods (Krebs 1989). For abundance, I reported the mean number of beetles caught per trapping site in 72 h. Because farther distances were present in fewer fields, giving fewer collections, this allowed values at every distance to be comparable to one another. I measured both response variables at each distance. In addition, I fitted a non-parametric Loess model to the total number of beetles captured over time since this model is a line of best fit for data that have no clear pattern (Crawley 2013).

For each of the five most abundant genera I collected, I calculated Pearson's correlation coefficient (Montgomery 2013) to determine whether there was a correlation between total number of beetles captured of each genus and time of year (date), and between mean number of beetles captured of each genus per field and distance from field edge. I did all graphs and analyses in R 3.4.4, using the "vegan", "cowplot", and "tidyverse" packages as well as base R (Oksanen et al. 2008; Wilke 2015; R Core Team 2017; Wickham 2017).

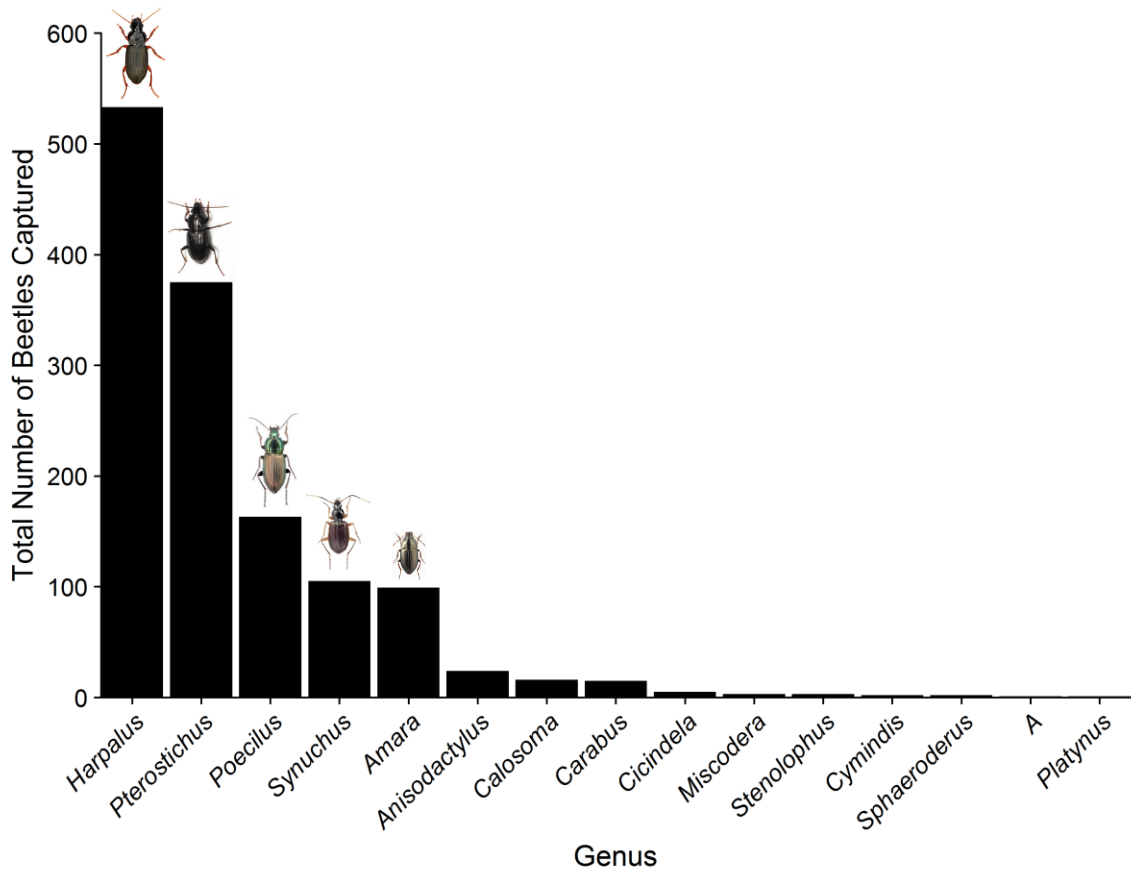
### **3.3 Results**

A total of 1347 Carabidae from 14 genera were collected, and an additional specimen was damaged and could not be identified. Over 93% of captured beetles were from the genera *Harpalus*, *Pterostichus*, *Poecilus*, *Synuchus*, and *Amara* (Figure 3.1).

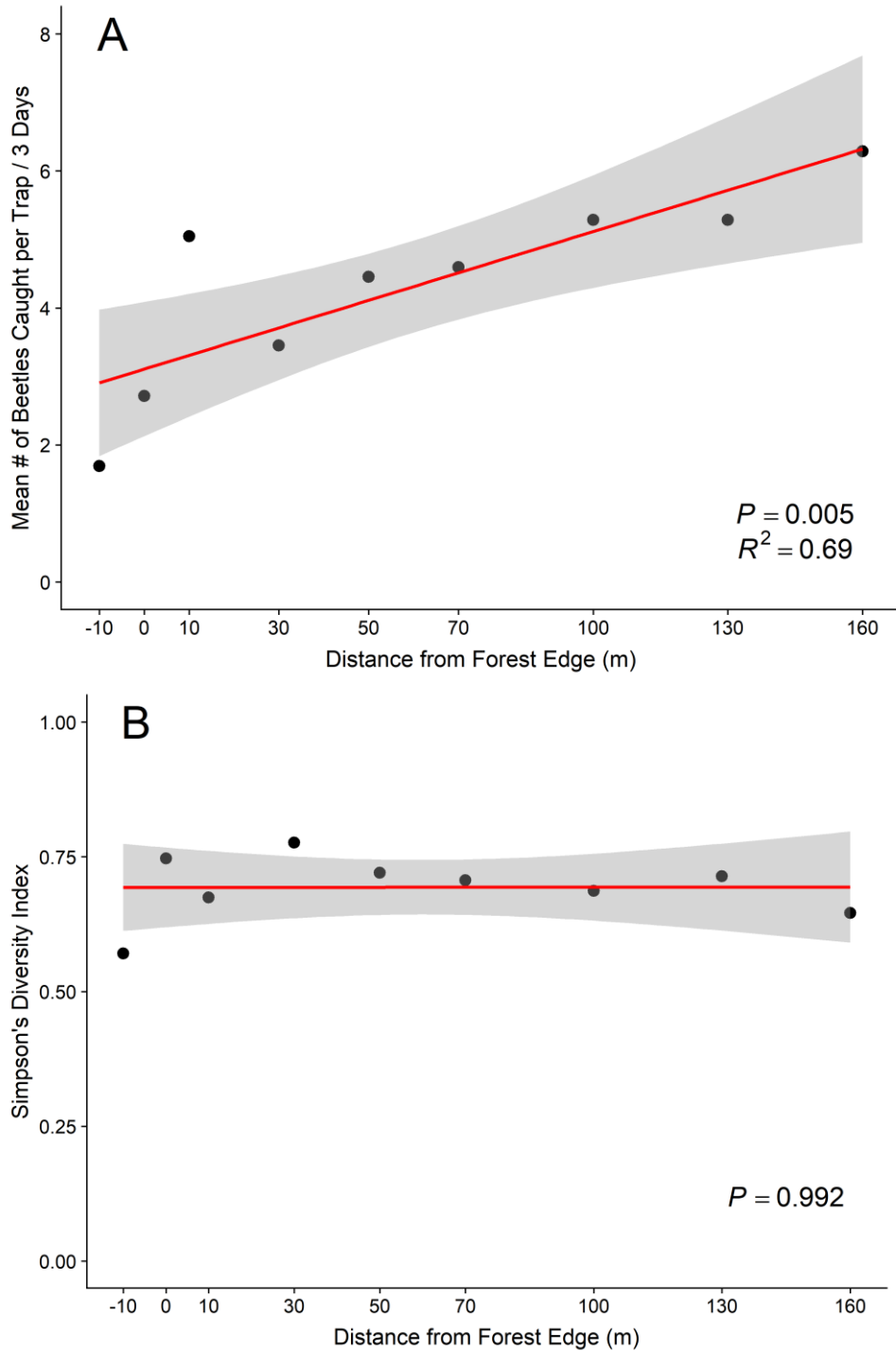
The error terms of both abundance and diversity were approximately normally distributed. There was a linear relationship between abundance (mean number of beetles captured per trap in three days) and distance from field edge ( $P = 0.005$ ;  $R^2 = 0.69$ ) (Figure 3.2A) with a predictive model of  $y = 3.11 + 0.02x$ , where  $y$  is the average number of beetles caught per trap in a three-day period and  $x$  is the distance from the field edge. This means that for every unit change in distance, abundance changes by 2%. The relationship between abundance and time (bi-weekly captures) was not linear ( $P = 0.21$ ), so these data were fitted to a non-parametric Loess model (Figure 3.3B).

There was no linear relationship between Carabidae diversity and distance from field edge ( $P = 0.992$ ) (Figure 3.2B). There was, however, a negative linear relationship between beetle diversity and time ( $P = 0.037$ ;  $R^2 = 0.61$ ) shown by the model equation  $y = 0.78 - 0.026x$ , where  $y$  is the Simpson's Diversity Index and  $x$  is the date in 2017 (bi-weekly) (Figure 3.3A). This means that every two weeks, from June 2<sup>nd</sup> to August 24<sup>th</sup>, beetle diversity decreased by 2%.

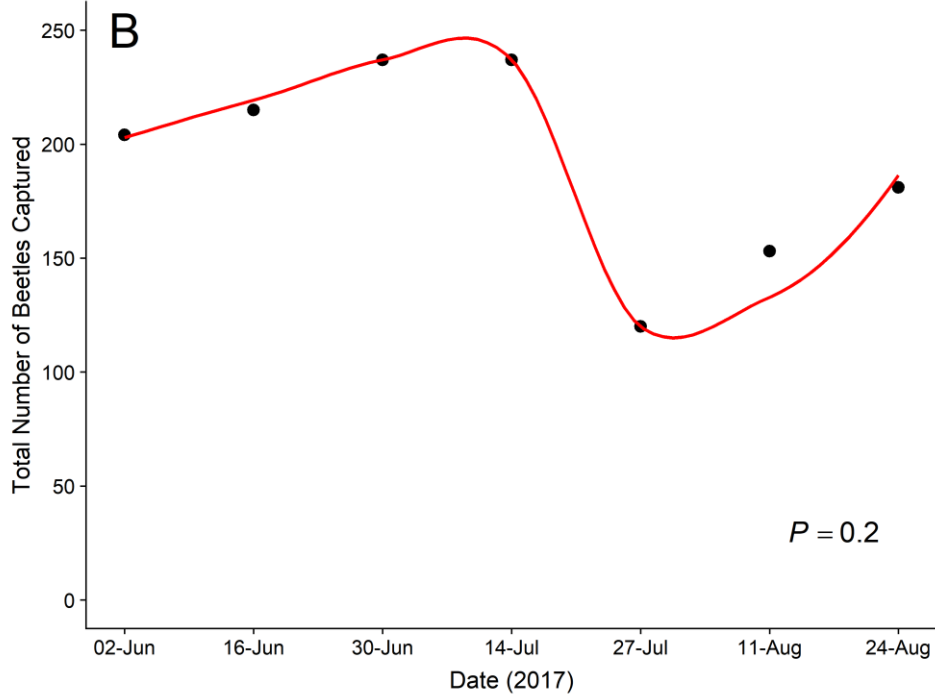
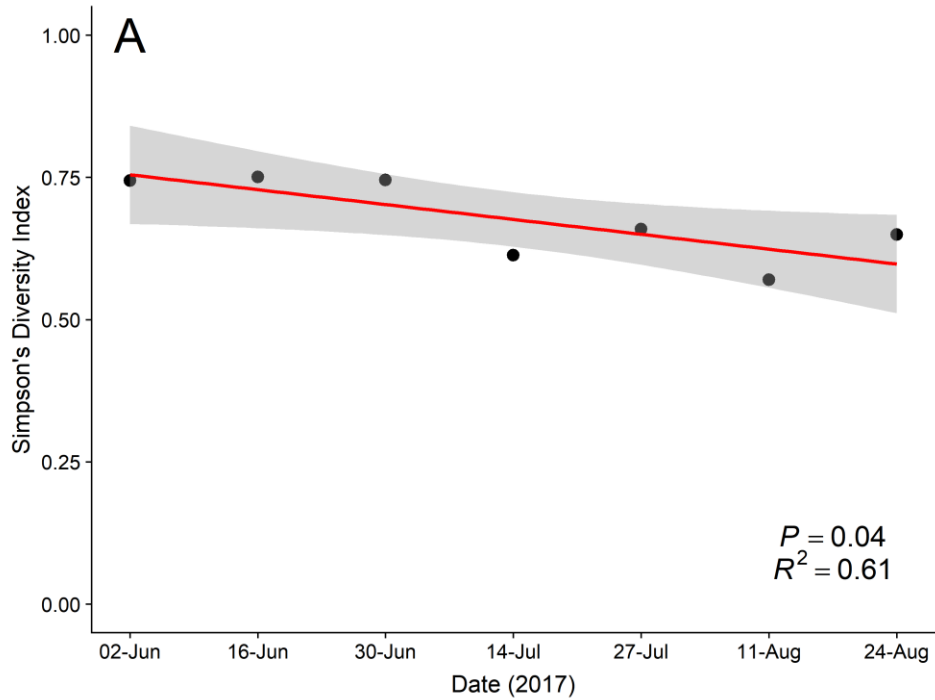
Of the five most abundant genera (Figure 3.1), *Harpalus* and *Synuchus* abundance (total number captured) increased over the course of the summer, while *Poecilus*, *Pterostichus*, and *Amara* abundance decreased (Figure 3.4A; Table 3.1). Only the abundance (mean number of beetles captured per field) of *Synuchus* decreased with distance from field edge, whereas that of the other four genera increased (Figure 3.4B; Table 3.1). Every genus was seen at least once in both the edge and field habitats. Two of the most abundant genera, *Pterostichus* and *Poecilus*, are generally described as carnivores, while the remaining three are generally described as phytophagous, though many species in each genus are omnivorous (Table 3.1).



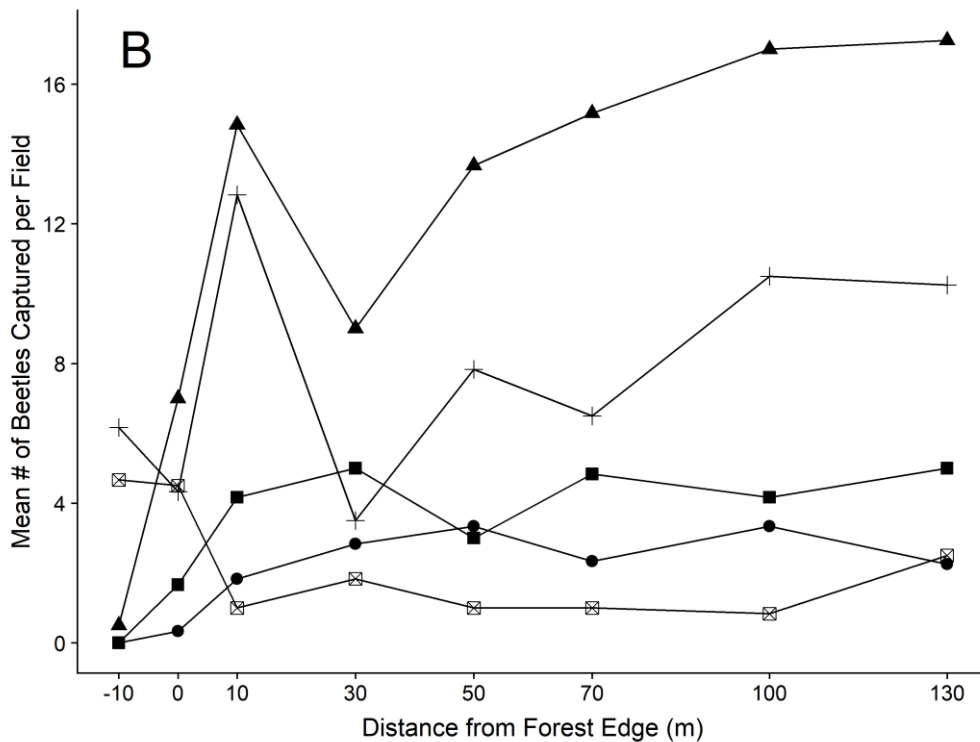
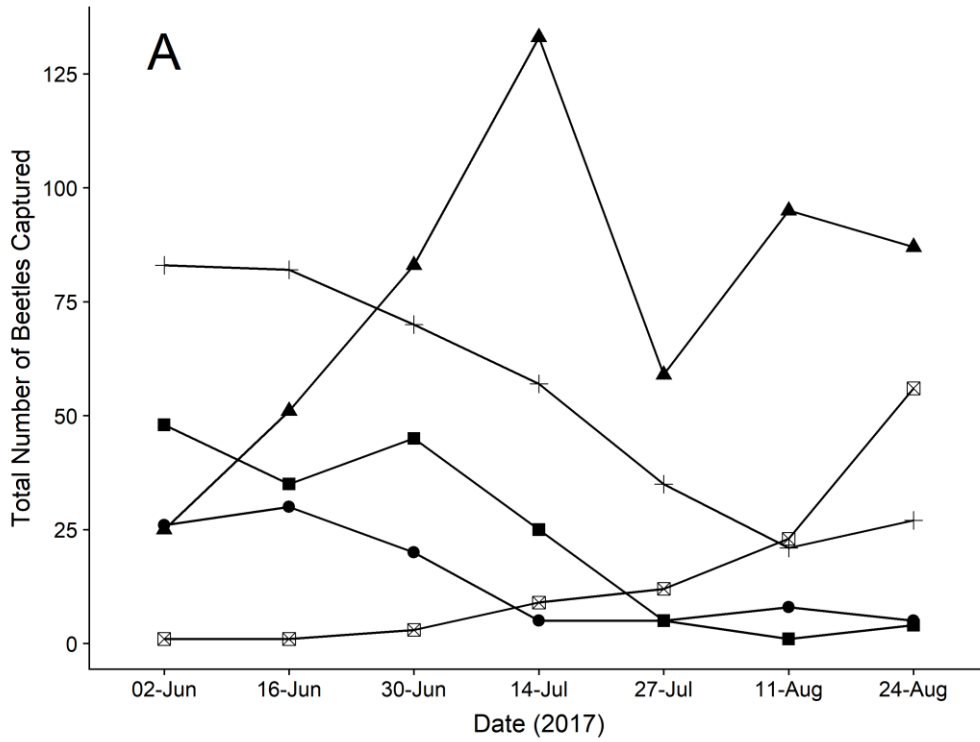
**Figure 3.1** Abundance of Carabidae genera in vegetative lowbush blueberry fields during summer 2017. *Harpalus*, *Pterostichus*, *Poecilus*, *Synuchus*, and *Amara* constituted >93% of all captures. Pictures represent predominant species of each of these genera: *Harpalus rufipes*, *Pterostichus mutus*, *Poecilus lucublandus*, *Synuchus impunctatus*, and *Amara neoscotia*. Images taken from Pinterest, Coleoptera.org.uk, bugguide.net, the Canadian Biodiversity Information Facility, and alchetron.com. Genus “A” is an unidentified specimen.



**Figure 3.2** Abundance (mean # of beetles caught per trap during seven three-day periods) (A) and diversity ( $1 - \text{Simpson's } D$ ) (B) of Carabidae genera in vegetative lowbush blueberry fields during summer 2017 vs. distance from field edge (m). Grey areas represent standard error of the model.



**Figures 3.3** Diversity (1 - Simpson's D) (A) and abundance (total number of beetles captured) (B) of Carabidae in vegetative lowbush blueberry fields every two weeks during summer 2017. The P-value refers to the test for a linear relationship between the two variables. Grey area (A) represents standard error of the model. Red line (B) is the fitted Loess line.



**Figures 3.4** Abundance of *Amara* (●), *Harpalus* (▲), *Poecilus* (■), *Pterostichus* (+), and *Synuchus* (⊠) in vegetative lowbush blueberry fields during summer 2017 as a function of (A) time and (B) distances from the field edge (m). See table 3.1 for the Pearson correlation between the factors relevant to these figures.

**Table 3.1** Pearson’s correlation coefficient (r) for the five most abundant Carabidae genera in vegetative lowbush blueberry fields in Nova Scotia during summer 2017. The units used in the correlation analysis were total number of beetles captured over time (bi-weekly over the course of three months) and mean number of beetles captured per field over distance from field edge (m). Genera are arranged from most abundant (*Harpalus*) to least abundant (*Amara*).

Genus	r (vs. time)	P-value	r (vs. distance from field edge)	P-value	Primary Diet*
<i>Harpalus</i>	0.55	0.19	0.79	< 0.001	Phytophagous
<i>Pterostichus</i>	-0.96	< 0.001	0.37	0.01	Carnivorous
<i>Poecilus</i>	-0.92	0.003	0.66	0.005	Carnivorous
<i>Synuchus</i>	0.85	0.01	-0.55	< 0.001	Phytophagous
<i>Amara</i>	-0.86	0.01	0.68	< 0.001	Phytophagous

\*(Lindroth 1961; Lindroth 1968; Cutler et al. 2012)

### 3.4 Discussion

Carabid beetles are abundant natural enemies of pests in many agricultural systems including lowbush blueberry (Luff 1978; Menalled et al. 1999; Menalled et al. 2007; Cutler et al. 2012; Kulkarni et al. 2015). In my study, over 93% of captures were from genera *Harpalus*, *Pterostichus*, *Poecilus*, *Synuchus*, and *Amara*, which were also the most abundant genera found by Cutler et al. (2012), suggesting carabid communities in lowbush blueberry fields are likely well established, and relatively static. *Pterostichus*, *Poecilus*, and *Amara* dominated fields early in the season, but then were replaced by *Harpalus* and *Synuchus*, the latter later in the season. *Harpalus* increased very rapidly between June and July, but then it alone decreased dramatically during July 14-27, while the other genera stayed within the expected trends. This decrease compromised the correlation analysis between *Harpalus* abundance and time, making it non-significant due to correlation’s high sensitivity to outliers (Montgomery 2013).

*Harpalus*’ rise in population coincides with the maturing of different abundant weed seeds in lowbush blueberry fields such as red sorrel (*Rumex acetosella* L.) and hair fescue (*Festuca filiformis* Pourret) (Hoeg and Burgess 2000; White 2018). This carabid genus is generally described as “phytophagous”, eating mainly seeds and pollen, though many of its species are omnivorous (Lindroth 1961; Lindroth 1968). In fact, *Harpalus rufipes* (De Geer), the most abundant species Cutler et al. (2012) and I found, consumes



both insect pests and weed seeds of lowbush blueberry (Renkema et al. 2013; Cutler et al. 2016).

It is unclear why *Pterostichus*, *Poecilus*, and *Amara* decrease over time. Cutler et al. (2012) found the same trend for the most abundant members of the genera *Pterostichus* and *Poecilus* in lowbush blueberry fields. Certain *Pterostichus* and *Amara* species also decrease in abundance around May and June in other ecosystems (Niemelä et al. 1992). *Pterostichus* and *Poecilus* are generally described as carnivorous, including its most abundant members in blueberry fields, while *Amara* is usually phytophagous (Lindroth 1968; Cutler et al. 2012). It is possible that these three genera get out competed by the more numerous *Harpalus*, especially since *H. rufipes* is omnivorous and eats the same foods the others do (Renkema et al. 2013; Renkema et al. 2014; Cutler et al. 2016). It is more likely, however, that life history events of these taxa dictate their population dynamics.

Luff (1980) found that *H. rufipes* populations in strawberry fields increased dramatically between May and June due to female emergence, while males were present throughout the season, but only sporadically up until May. The females mated, carried eggs throughout June, July, and August, and first instar larvae were found mostly between August and September. *Pterostichus melanarius* (Illiger), an abundant member of *Pterostichus* populations in lowbush blueberry fields (Cutler et al. 2012), is known for having two abundance peaks, each around the months of May and September. The break between peaks is caused by life history events, such as egg laying and emergence of hibernated individuals (Matalin 2006). My data only captured the first peak in late May, as well as its decrease and stasis through the following summer months. Kegel (1994) found that *Poecilus* species in German rye fields are spring breeding species, peaking in population in May and early June. This is the same trend I found in *Poecilus* population numbers, suggesting similar biological events may be occurring in lowbush blueberry fields. *Amara* species tend to have overwintering larvae and be spring breeders (Hurka and Duchac 1980; Saska and Honěk 2003). This suggests adult populations would tend to be higher in the spring and early summer, which is in accordance with what I found. *Synuchus* remained inactive until mid to late July, then it appeared in greater numbers in August. This genus is mostly represented in North America by *Synuchus impunctatus*

(Say), and indeed it was the only *Synuchus* species found in the 2012 survey of lowbush blueberry carabids (Lindroth 1961; Cutler et al. 2012; Goulet and Bousquet 2014). This species is generally described as a phytophage (Cutler et al. 2012). Adults of this species generally do not appear before the end of May, likely because the larvae are the ones who hibernate, which delays the emergence of adults (Lindroth 1961).

Out of the five genera, *Synuchus* was the only one that decreased in abundance with increasing distances from the field edge, while all others increased. Cutler et al. (2012) found that phytophage abundance increased with increasing distance from field edge, but that *Synuchus* abundance did not change. This suggests that other phytophagous species may be the main contributors to weed control within lowbush blueberry fields, at least during the months in which they are most active. The differences between our results could be due to the small maximum distance used by Cutler et al. (2012), which might have made it hard for them to detect the negative trend. The forest habitat was dominated by *Pterostichus* and *Synuchus*, while virtually none of the other genera were present. This is not surprising, given these two genera are commonly found throughout the forests of North America, and *Harpalus*, *Poecilus*, and *Amara* are generally associated with cropping habitats (Niemelä and Spence 1994; Andersen 1997; Beaudry et al. 1997; Koivula et al. 1999; Taboada et al. 2004; Cutler et al. 2012).

Overall carabid abundance had a positive linear relationship with distance from field edge, being almost three times as high in the center than at the edge. Positive relations between abundance and increasing distance from field edge have been observed in other agricultural systems (Thomas and Marshall 1999; Haysom et al. 2004; Koivula et al. 2004; Anjum-Zubair et al. 2010), but it is unlikely this trend happens everywhere. For example, Cutler et al. (2012) found that trap placement had no bearing on overall carabid abundance. They only went 50 m into the field however, which might not have been enough to capture the trend. Varchola and Dunn (2001) also found no difference in carabid abundance between corn fields and the hedgerow borders, though during corn emergence abundance was higher at the edges. Carabid abundance had no linear relationship with time, and instead, we see a large drop in abundance between the 14<sup>th</sup> and the 27<sup>th</sup> of July, and then we see it rising once more. This drop in overall abundance is explained by the sudden decrease in *Harpalus* captures, which happened at the same time

interval. This, coupled with the decrease of other genera early in the season, implies that *Harpalus* species are dominant drivers in the community dynamics of carabids in vegetative lowbush blueberry fields. The knowledge of where and when Carabidae are most abundant within a field is of great importance to growers who wish to maximize these beetle's contributions to pest control. This is because abundance has direct implications on how effective insects are at providing ecosystem services, sometimes even more than species richness (Winfree et al. 2015; Manning and Cutler 2018). Therefore, those developing IPM strategies using Carabidae should take this into consideration.

Carabid diversity did not change with distance from field edge, which was unexpected since edges are well known for harboring higher diversity than other habitat areas (Bedford and Usher 1994; Andersen 1997; Magura and Tóthmérész 1997; Fournier and Loreau 1999). There are instances, however, where the edge effect does not occur. For example, Molnár et al. (2001) found that there was no difference between carabid diversity in the edge of a grassland and in its center. Interestingly, in the same study, they found a difference in diversity between that same edge and the adjacent forest. Taboada et al. (2004) found no difference between carabid diversity or abundance in edges vs. in the center of oak forests. As expected, however, they did find different species preferred different habitats. These findings indicate that the edge effect does not occur in every case, and it most likely has to do with how preferable certain habitats are to certain taxa. Cutler et al. (2012) found that species richness in lowbush blueberry fields decreased with distance from field edge. They did not measure diversity however, which means my work complements theirs. Carabid diversity decreased over time by 2% every two weeks. This negative correlation is likely explained by the increase in *Harpalus* population and by the decrease in the population of *Pterostichus*, *Poecilus*, and *Amara* over time, given that the Simpson's Diversity Index is a measure that incorporates both richness and the abundance of each species (or genus). This reinforces the idea that *Harpalus* is a key driver of carabid community dynamics within lowbush blueberry fields. Some research has been done on abundant members of this genus within lowbush blueberry systems (Renkema et al. 2013; Cutler et al. 2016), but more is needed to explore these species' full potential for pest management.

The fact that diversity measures tend to be used on species rather than genus in most studies implies that my diversity values cannot be directly compared with those that used species. This is because diversity values calculated with species tend to be higher than those calculated with genera since Simpson's Diversity Index is based on proportions (Krebs 1989). However, comparing the change in the diversity measures due to treatments in those studies to changes due to treatment in my study is still valid, given that I am comparing the change in diversity with respect to the treatment, rather than directly comparing the diversity values.

My results shed more light on the dominant genera and community dynamics of Carabidae in vegetative lowbush blueberry fields, but questions remain that have ramifications for biological control in this cropping system. I examined the Carabidae community in vegetative lowbush blueberry fields only, but the two-year cycle of commercial lowbush blueberries can have a measurable impact on its carabid community. In one of their study years, Cutler et al. (2012) found there were more carabids in vegetative than in crop fields, but the trend did not carry over into the following year. They also found more phytophagous beetles in vegetative than in crop fields in both years. Future research on this topic should consider repeating my experiments on lowbush blueberry crop fields to fully capture the community dynamics of this system, thus expanding on what both Cutler et al. (2012) and I did. Lowbush blueberry fields harbor diverse Carabidae communities, and their potential as natural enemies of insect pests and weeds cannot be undermined. Future research should study basic biology and ecology traits (e.g. dispersal, tolerance and susceptibility to insecticides) of the abundant species in this cropping system such as members of the *Harpalus*, *Pterostichus*, *Poecilus*, *Synuchus*, and *Amara* genera. It is also important to better understand factors that may drive carabid community dynamics in lowbush blueberry fields such as species life history, management practices, and strategies to boost carabid populations. This will ensure that growers are supplied with relevant information about these natural enemies, which will allow them to devise reliable integrated pest management strategies for their fields.

## **CHAPTER 4: DISPERSAL OF THE GROUND BEETLE *HARPALUS RUFIPES* (COLEOPTERA: CARABIDAE) IN A LOWBUSH BLUEBERRY FIELD**

### **4.1 Introduction**

Insect natural enemies help suppress pest populations in many agricultural systems, with their biological control services valued around \$4.5 billion in the United States (Losey and Vaughan 2006). Some natural enemies are mobile hunters (Lövei and Sunderland 1996), so it is important to understand their movement patterns and dispersal trends if we wish to maximize their contributions to pest management.

Carabidae beetles, which are important natural enemies in many cropping systems, tend to move in what is called a “correlated random walk” (CRW), where at each step they take, the turning angle is independent of the previous turning angle, there is no cross-correlation between moving directions and turning angles, and successive step lengths are not auto-correlated (Kareiva and Shigesada 1983; Lövei and Sunderland 1996; Kulkarni et al. 2015). A dispersal event which follows the principles of the CRW is known as a simple, or “passive”, diffusion. Here, the number of individuals will be normally distributed with mean at the release point and with a variance that increases linearly over time (Okubo 1980, as cited in Turchin and Thoeny 1993). This mode of dispersal is not applicable to every insect however, since there are many organisms that disperse with distributions other than Gaussian and factors other than simple diffusion that affect how animals disperse, such as presence of prey, death rates, and spatial heterogeneity (Turchin and Thoeny 1993; Wallin and Ekblom 1994; Kot et al. 1996). Considerable work has been done on mosquito dispersal, with development of a theoretical framework for calculating mean distance travelled (MDT) by marked individuals over time. This framework accounts for different probabilities of capture at different distances based on the size of the area being surveyed, as well as how many trapping sites there are in each area (Lillie et al. 1981; Muir and Kay 1998; Marini et al. 2010). There is, however, no built-in way of reporting an appropriate measure of error for the MDT.

The lowbush blueberry (*Vaccinium angustifolium* Ait.) is an important Canadian crop native to eastern North America (Hall et al. 1979; Prior et al. 1998). The commercial lowbush blueberry has a production cycle of two years. Plants are pruned to near ground

level by either burning or flail mowing to stimulate new shoot production in the first, or vegetative, year. The plants bloom and produce fruit in the second, or crop, year (Jensen and Yarborough 2004). *Harpalus rufipes* (De Geer) is an abundant natural enemy in many agricultural systems of both Europe and North America, including lowbush blueberry (Luff 1978; Cutler et al. 2012). Therefore, understanding *H. rufipes*' movement and dispersal within fields is necessary to maximize this species' potential for pest management. The question of how far *H. rufipes* travels over time in lowbush blueberry fields has never been addressed, and only few studies have measured this in other systems (Zhang et al. 1997; Kujawa et al. 2006), some with methodology limitations.

The objective of this study was to determine how far *H. rufipes* travels over time in a vegetative lowbush blueberry field with mark-recapture techniques and a newly developed theoretical framework. I predicted that beetles would move more than 10 m/day, given this estimate was derived in the literature with methods that likely underestimate how far *H. rufipes* moves.

## **4.2 Materials and Methods**

### 4.2.1 Beetle collection, marking, and maintenance

In summer 2017, I collected 225 adult *H. rufipes* from a commercial lowbush blueberry field in Debert, Nova Scotia, Canada (45°25'12"N; 63°30'41"W) with pitfall traps (Greenslade 1964). Beetles were brought back to the laboratory in 1 L plastic containers. In the lab, beetles were transferred to sealable plastic cups (120 mL) with an 80:20 (v:v) mixture of moistened peat and play sand. Beetles were fed and maintained on cat food (Whiskas™) (Cutler et al. 2016).

Before marking beetles, they were chilled in a freezer at -22°C for approximately 90 seconds to slow them down. After cooling, a layer of white out (Wite.Out Bic®) was applied on the elytra of each beetle with just enough product to cover its surface. When dry, we applied a layer of orange fluorescent enamel paint (Testors®) on the patch of white out. Beetles were then returned to containers until the release in the field on July 5<sup>th</sup>, 2017. During the study, the average temperature was 18.1°C, the minimum was 8.5°C and the maximum was 26.9°C (Environment Canada, <http://climate.weather.gc.ca>).

#### 4.2.2 Experimental layout

In the field, a series of seven concentric circles with radii of 1, 5, 10, 15, 20, 30, and 50 m were marked and mapped in a vegetative section of the same field from which the beetles were collected. The seven concentric circles resulted in seven concentric rings. I chose 50 m as the maximum distance based on the findings of Zhang et al. (1997), where *H. rufipes* displaced around 10 m in 24 h on average in oat and potato fields. Marked beetles were released in the center of the circles at 5 PM and were located at 10 PM using UV flashlights (UV flashlight 100 LED, Arf Pets). Beetles were located by four people in each ring within a set amount of time using a zig zag search pattern. The search time in each ring, from smallest to largest, was as follows: 5, 15, 15, 10, 10, 10, and 10 minutes. The location of every sighted beetle was marked with a red stake, and given the beetles' apparent slow movement rate, we avoided counting beetles sighted within one meter of a marked location the second time we walked around that same area to avoid double counting. The following day the number of stakes within each ring was counted. We repeated this at 29 and 53 hours after release, changing the search time in each ring to 2, 5, 10, 12, 15, 20, and 25 minutes.

#### 4.2.3 Estimating percentage of marked beetle population in each concentric ring

The probability of detecting beetles is inversely related to the area of the ring and directly related to the amount of time spent searching in the area of each ring, which can be stated in mathematical terms as follows:

$$P_i = k \frac{T_i}{A_i} \quad (1)$$

Where,  $P_i$  = Probability of detecting marked individuals in concentric ring  $i$

$k$  = Unknown constant of proportionality

$A_i$  = Area of concentric ring  $i$

$T_i$  = Total time spent searching for beetles in concentric ring  $i$

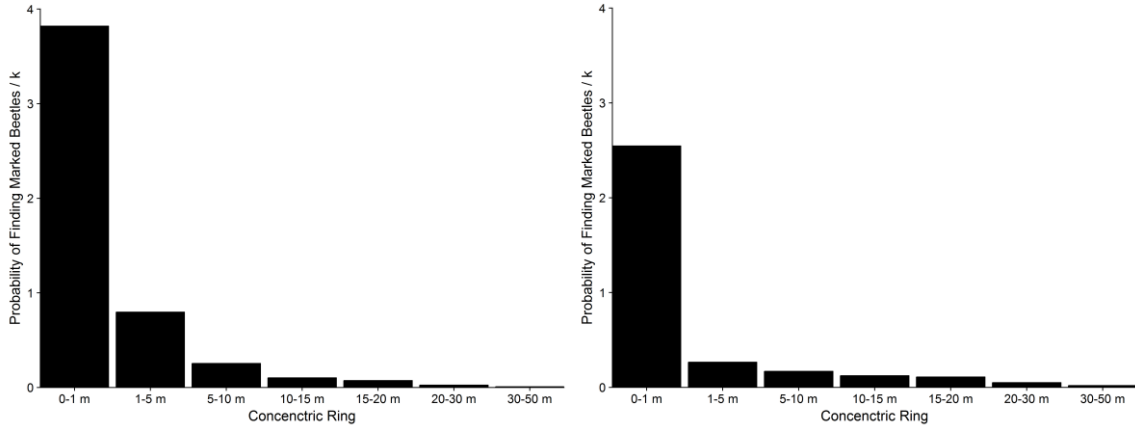
Here,  $T_i = t_i p_i$  and  $A_i = b_i - b_{i-1}$

Where,  $t_i$  = Searching time for each person in concentric ring  $i$

$p_i$  = Number of people searching in concentric ring  $i$

$b_i$  = Area of concentric circle  $i$

To better visualize the magnitude of the effect area and search time have on the probability of detection in each ring, an estimate can be obtained by dividing both sides of formula (1) by  $k$  (Figure 4.1).



**Figure 4.1** Probability of detecting marked beetles divided by the constant of proportionality for each of the concentric rings at 5 (left) and 29 (right) hours after release.

The population of marked beetles in ring  $i$  is thus expected to be inversely proportional to the probability of detecting beetles. This means that if, for example, 10 beetles are detected in each of two rings, the ring with the greatest area is expected to have a greater population of marked beetles, which can be described mathematically as:

$$Z_i = \frac{C_i}{P_i} \quad (2)$$

Where,  $Z_i$  = Expected population of marked individuals in concentric ring  $i$   
 $C_i$  = Number of detected marked individuals in concentric ring  $i$

To make the results intuitive, we can calculate  $Z_i$  as a percentage of the total population of marked beetles. This can be expressed as:

$$Y_i = \frac{Z_i}{\sum_{i=1}^n Z_i} 100 \quad (3)$$

Where,  $Y_i$  = Percentage of total marked individuals in concentric ring  $i$   
 $n$  = Total number of rings

We can then replace  $Z_i$  with the right side of equation (2) so that we get:



$$Y_i = \frac{\frac{C_i}{P_i}}{\sum_{i=1}^n \frac{C_i}{P_i}} 100 \quad (4)$$

Then, we can replace  $P_i$  with the right side of equation (1) and solve it to arrive at the final equation:

$$Y_i = \frac{\frac{C_i A_i}{T_i}}{\sum_{i=1}^n \frac{C_i A_i}{T_i}} 100 \quad (5)$$

This estimate has a multinomial distribution since the numbers of marked individuals in ring  $i$  are first calculated as a proportion, which means the probabilities of every possible outcome always sums up to 1 (Crawley 2013), and only later turned to a percentage. This proportion, which can also be used to calculate confidence intervals, can be expressed as:

$$P_{C_i} = \frac{C_i}{\sum_{i=1}^n C_i} \quad (6)$$

Where,  $P_{C_i}$  = Proportion of counted beetles in concentric ring  $i$

Combining equations (5) and (6) gives the following expression:

$$Y_i = P_{C_i} \frac{\frac{A_i}{T_i}}{\sum_{i=1}^n \frac{C_i A_i}{T_i}} \sum_{i=1}^n C_i 100 \quad (7)$$

With formula (7) we can determine the percentages and 95% confidence intervals of total marked individuals. Formula (7) also ensures that confidence intervals are adjusted for the differences in probabilities of detection. I created two functions in R that run formula (7) and give both the percentages of marked beetles in each area and the 95% multinomial confidence intervals adjusted for probability of detection. The confidence interval function integrates the “MultinomialCI” package in R 3.4.4, which uses the Sison-Graz method (Sison and Glaz 1995; Villacorta 2015; R Core Team 2017).

#### 4.2.4 Calculating mean distance traveled

Another useful measure to estimate in studies examining animal movement is mean distance traveled by marked individuals over a given time. Since I already have an

estimate of the adjusted proportion of marked individuals in a given area (formula (7) without the “100” at the end), the mean distance traveled is:

$$MDT = \sum_{i=1}^n rm_i Y_i \quad (8)$$

Where,  $MDT$  = The mean distance traveled at each time after release  
 $rm_i$  = The radius of the circle generated by dividing the area of ring  $i$  by 2 and then subtracting the area of circle  $i - 1$  from that value

Lillie et al. (1981) also derived this formula, and MDT is now a measure widely used in mosquito dispersal studies. The 95% confidence interval (CI) for each MDT estimate was generated using the bootstrapping technique (Krebs 1989) in Mathematica 11.3 (Wolfram Research 2018).

### 4.3 Results

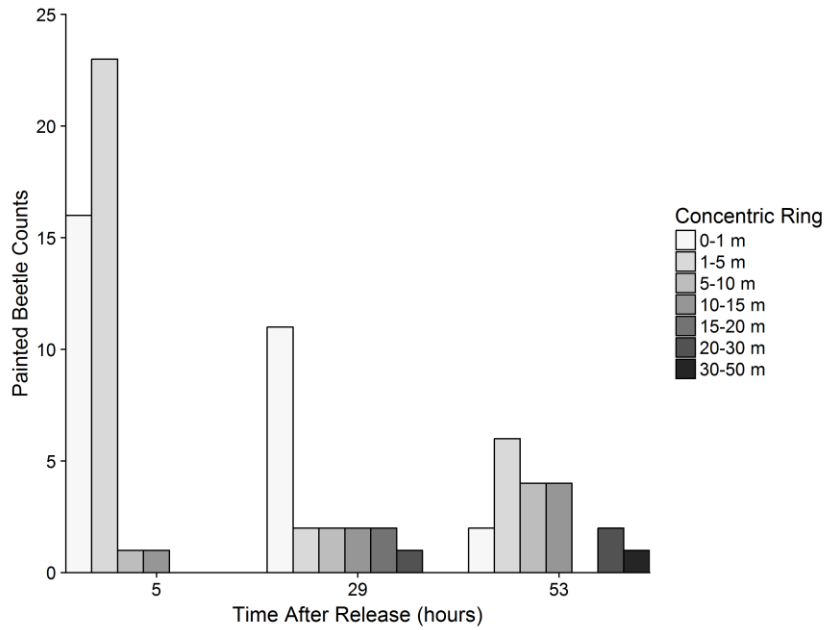
There were 41 (18.2%), 20 (8.8%), and 19 (8.4%) marked beetles detected 5, 29, and 53 hours after dispersal, respectively, and distribution of beetles at these times varied within each concentric ring (Figure 4.2). As time went on, beetles were captured at farther concentric circles, and at 53 hours, they had reached the outermost ring.

Values from Figure 4.2 were used in formula (7) to generate  $Y_i$  values and associated confidence intervals corrected for probability of capture (Figure 4.3). The  $Y_i$  values suggest that beetles moved outward at a faster pace than what the capture numbers suggest (Figure 4.2). They are, however, not very reliable due to the large confidence intervals, which increase in range as the discrepancy between area searched and number of detected beetles increases.

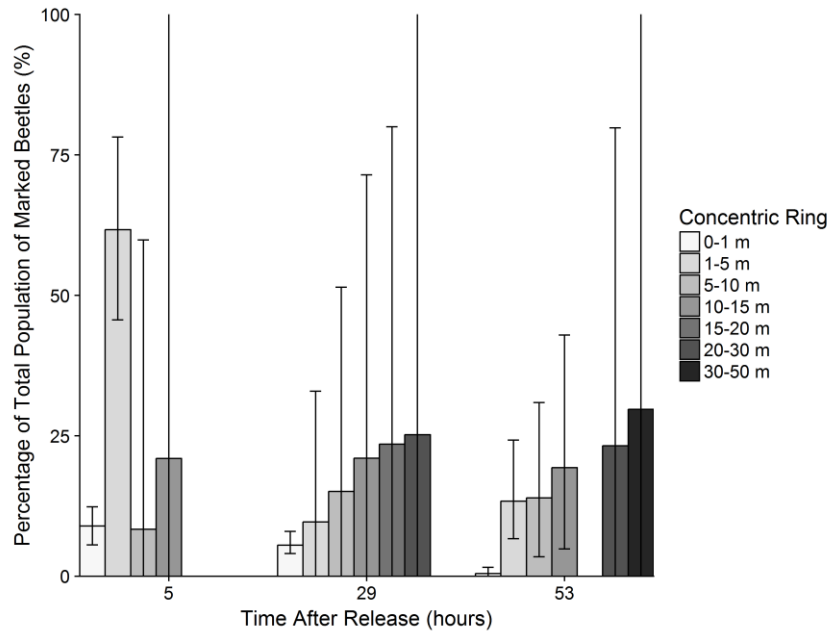
To get an idea of how increased detection numbers would affect the confidence intervals, I multiplied the number of detected beetles at each ring by 5 and used these new values in formula (7) (Figure 4.4). Though the new confidence intervals are still large, they are substantially narrower in range than the original intervals, indicating that more beetles need to be marked and released for the experiment.

Values from Figure 4.3 were used in formula (8) to generate MDT estimates for each of the three times after release (Table 4.1). *Harpalus rufipes* individuals traveled on average 5.38 (95% CI = 2.46 to 8.30), 14.47 (95% CI = 8.57 to 20.37), and 20.73 (95%

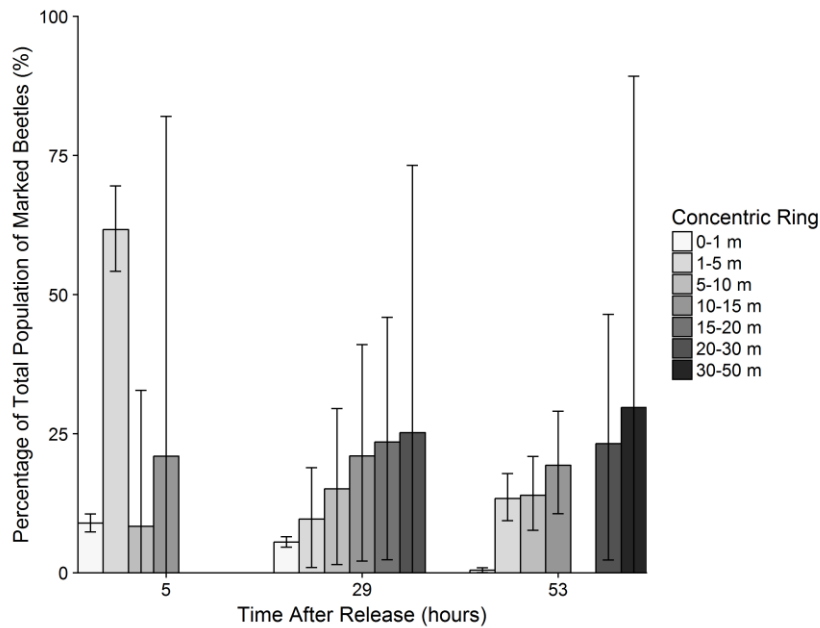
CI = 8.98 to 32.48) m at 5, 29, and 53 hours respectively. The wider confidence interval at 53 hours is a product of the lower number of beetle detections coupled with the larger area in which beetles were found at that time.



**Figure 4.2** Marked *Harpalus rufipes* counts within each of seven concentric rings of a grid (41, 20, and 19 respective count totals at each time) set up in a vegetative lowbush blueberry field in Nova Scotia in summer 2017. Time is hours after release of the beetles at the center of the rings.



**Figure 4.3** Percentage of total population of marked *Harpalus rufipes* within each concentric ring at different hours after release ( $Y_i$ ) at a grid in a Nova Scotia vegetative lowbush blueberry field during summer 2017. The lines are the 95% confidence intervals (CIs) calculated on a Multinomial distribution. All values in this figure, including the CIs, incorporate the probability of detecting a marked beetle, which depends on the area searched and the total time spent searching in each area.



**Figure 4.4** Simulated percentage of total population of marked *Harpalus rufipes* within each concentric ring at different hours after release ( $Y_i$ ) at a grid in a Nova Scotia vegetative lowbush blueberry field during summer 2017. Values from figure 4.2 were multiplied by 5 to see the effect of more marked beetle detections on the range of the confidence intervals (CIs). The lines are the CIs calculated on a Multinomial distribution. All values in this figure, including the CIs, incorporate the probability of detecting a marked beetle, which depends on the area searched and the total time spent searching in each area.

**Table 4.1** Mean distance traveled (MDT) by marked *Harpalus rufipes* at various times after release starting from the center of a grid in a Nova Scotia vegetative lowbush blueberry field in summer 2017. Confidence intervals (CI) were generated using the bootstrap technique.

Time after release (hours)	MDT (meters)	95% CI
5	5.38	2.46 to 8.30
29	14.47	8.57 to 20.37
53	20.73	8.98 to 32.48

#### 4.4 Discussion

Unfortunately, the  $Y_i$  estimate confidence intervals for most concentric rings were too wide to draw meaningful conclusions about the percentages of marked beetles at each ring, except for the first ring at each time after release. If only one beetle is caught at a given ring, the  $Y_i$  estimate is useless since the confidence intervals go from 0 to over 100% (see last ring of each time after release). Given that the confidence intervals increase in range as the discrepancy between area searched and number of detected beetles increases, a possible solution is to get more people searching for beetles. Alternatively, more beetles could be released. I simulated data with capture of 5 times as many beetles in total but kept the percentages the same, which resulted in a dramatic decrease in all confidence intervals. In some dispersal studies that use mark-recapture techniques, researchers were able to mark thousands of individuals (Turchin and Thoeny 1993; Rotheray et al. 2014), which means confidence intervals generated using their data and formula (7) would likely be much narrower, with recapture rates similar to mine. Other researchers have reported proportions of marked individuals that are adjusted for probabilities of capture, but they do not report confidence intervals or any measure of variance (Lillie et al. 1981). This is unfortunate because without an appropriate measure of error, there is uncertainty with proportions that are reported. This is evident by the large confidence intervals generated with my data. My recovery rates were similar to many other studies (Zhang et al. 1997; Muir and Kay 1998; Marini et al. 2010), so it is unlikely this trend is unique to my case.

After 29 hours, *H. rufipes* displaced 14.47 (95% CI 8.57 to 20.37) m on average, which is a larger number than all estimates found by Zhang et al. (1997). They found that male and female *H. rufipes* displaced  $7.5 \pm 5.4$  m and  $9.8 \pm 5.2$  m in a potato field and  $6.3 \pm 4.7$  m and  $11.2 \pm 7.0$  m in an oat field. This is not surprising given they did not consider different probabilities of detection, which likely biased results favouring the distances with higher probability of detection, these usually being the closer distances. Kujawa et al. (2006) found that *H. rufipes* displaced on average 25 to 27 m/day in shelterbelts and 15 to 17.5 m/day in cereal fields. Their results are closer to what I found because this was a study carried over the course of 2 years with daily mark-release-recapture data, which likely generated good estimates of displacement. *Harpalus rufipes* is a nocturnal hunter

(Luff 1978), which means it has reduced dispersal during the day. Other carabids have showed similar average distances traveled. For instance, tiger beetles (Carabidae: Cicindelinae) were estimated to travel 6.81 m/day, while *Carabus ullrichii* can travel from 1.69 to 13.43 m/day (Horgan and Chávez 2004; Růžičková and Veselý 2016). These distances are relatively close amongst these beetle species, which could be due to factors such as their similar lengths (Pearson and Stemberger 1980; Harrison and Gallandt 2012; Růžičková and Veselý 2016). Mobility is crucial in determining Carabidae success as bio-control agents in agro-ecosystems, since that is how they aggregate around areas of high prey density, and how they reach habitats required for their different life history stages (Thomas et al. 1997). Since *H. rufipes* does not move very far over time by walking, populations in lowbush blueberry fields affected by disturbances could take some time to recover if new individuals move in from neighbouring fields by walking. Ground beetles are able to fly, with colonizing populations having more winged individuals than established populations (Lövei and Sunderland 1996). Therefore, *H. rufipes* may be able to replenish damaged populations faster than expected. In the lowbush blueberry industry, mowing and burning are common practices used to turn crop fields back into vegetative fields to maximize their yield (Blatt et al. 1972). Therefore, *H. rufipes* populations are likely subjected to these stresses, and a better understanding of how populations may be affected is needed if we wish to make management decisions that favour *H. rufipes*.

Even though work has been done concerning the effect of probabilities of capture on the estimates of proportion or mean distance traveled (Okubo 1980; Lillie et al. 1981; Turchin and Thoeny 1993; Miller et al. 2015), especially in the field of mosquito dispersal, some researchers of other areas were unaware or did not understand how to expand on their results. For instance, Thomas et al. (1997) remarked in their study that it was impossible to make comparisons between the movements of beetles within fields because of a decreasing probability of capture in the outer edges of their search area. Zhang et al. (1997) did not take this into account and measured how far a species of carabid traveled over time by averaging the number of recaptured individuals in each concentric circle. Rotheray et al. (2014) concluded that fewer hover flies located breeding sites at greater distances from the release spot, using a similar approach to the one used by Zhang et al. (1997). Unfortunately, their estimates are biased towards the

closer collection sites. Since these studies and others show the same trend of not taking these probabilities into account (Thomas et al. 1997; Zhang et al. 1997; Horgan and Chávez 2004; Rotheray et al. 2014), it is clear that there is a need for more awareness in this area of research. In some cases, however, computing the probabilities might not be of great consequence. For instance, describing the dispersal ability of a beetle with regards to direction can be done simply by comparing captures at different directions within the same distances (Follett et al. 1996).

My study sheds light on the nature of the dispersal of *H. rufipes*, and how it only tends to travel relatively small distances over time. This is important since that can give us an idea of how far populations may disperse over long periods of time, and how fast disturbed populations may be replenished by neighbouring populations. Future experiments should study how mowing and burning practices in lowbush blueberry fields may affect *H. rufipes* populations, and whether re-colonization is done by populations from neighbouring fields or not. Repeating my experiment with more marked beetles is desirable, since it would likely reduce confidence intervals, thereby giving us more reliable estimates of the percentages of marked individuals at each distance. Researchers studying insect dispersal should take the effects of probabilities of capture into account when estimating certain response variables. This practice is common in mosquito dispersal research but is limited in Carabidae research.



## CHAPTER 5: CONCLUSIONS

### 5.1 The Importance of My Work

The goal of this thesis research was to further our understanding of Carabidae in lowbush blueberry fields in light of their demonstrated potential as natural enemies (Lövei and Sunderland 1996; Honěk and Jarošík 2000; Kulkarni et al. 2015), and the scarcity of studies focusing on Carabidae within the lowbush blueberry system. My research findings help better define the ecological function of some abundant carabid species, reveal expected and unexpected community dynamics trends, and provide methodological refinements for dispersal studies. This information can help farmers make better IPM decisions concerning the use of Carabidae as natural enemies and help Carabidae researchers better perform dispersal studies.

### 5.2 Understanding Carabid Feeding Tendencies

To understand which species are most likely to aid in pest control, it is important that we determine what they consume within the system in question. Though certain species are known for a certain feeding habit, these generalizations do not always apply. For instance, the ground beetle *Harpalus rufipes* (De Geer) is usually described as a phytophagous species (Cutler et al. 2012), but it also consumes insect pests of lowbush blueberry which makes it omnivorous within the lowbush blueberry system (Renkema et al. 2013). Therefore, we cannot always rely on generalization to predict what certain species are doing in the system. Both *Poecilus lucublandus* (Say) and *Pterostichus mutus* (Say) can be classified as carnivorous, but there are many reported instances where they (or members of the same genus) consume plant-based foods (O'Rourke et al. 2006; Lundgren et al. 2013; Kulkarni et al. 2016). My experiments showed that *P. mutus* and *P. lucublandus* do not feed on seeds of the common lowbush blueberry weeds hair fescue (*Festuca filiformis* P.), poverty oatgrass (*Danthonia spicata* L.), and red sorrel (*Rumex acetosella* L.). My experiments also showed that *H. rufipes* readily fed on red sorrel and hair fescue in no-choice laboratory tests, at rates that are likely faster than what they would be in the field due to the presence of other food sources. My results support the descriptions of these species by Cutler et al. (2012), though those descriptions might not hold if these beetle species are offered other seed food sources. It would be valuable to

know the range of foods these beetle species feed on, considering they make up a large portion of the Carabidae fauna in lowbush blueberry fields (Cutler et al. 2012).

### 5.3 Understanding Carabid Community Dynamics

The community dynamics of a group of individuals plays a major role on how effective they are as natural enemies. The general hypothesis is that high diversity and abundance are associated with increased benefits from ecosystem services (Worm et al. 2006; Gaines and Gratton 2010; Isbell et al. 2011). This is likely because having a diverse and abundant community means there is a higher probability that community contains species that will be capable, and numerous enough, to provide whatever service is needed. For instance, Menalled et al. (2007) found that both no-till and organic systems of farming tended to have greater carabid diversity than conventional systems, but weed seed removal was two times greater in no-till systems because they had twice as many phytophagous beetles in their communities. Therefore, in a given system, it is important to identify the members of its community, who is most abundant, what their spatial and temporal trends are, and what their basic biology is. My study, which tackled community spatial and temporal trends, showed that the genera *Harpalus*, *Pterostichus*, *Poecilus*, *Synuchus*, and *Amara* dominated vegetative lowbush blueberry fields in summer 2017. Early in the season, *Pterostichus*, *Poecilus*, and *Amara* were more abundant, but they were replaced by *Harpalus* and *Synuchus* in mid to late summer. My work also showed that overall carabid abundance, proxied by measuring activity-density, significantly increased with distance from field edge, whereas diversity stayed the same. Over time, carabid diversity decreased, likely due to the large increase in population of *Harpalus* species. Overall carabid abundance was dictated by the population of *Harpalus* species, which significantly increased in early June, crashed to half its size in mid-July for unknown reasons, and then re-established itself.

Field edges are known for harbouring higher species diversity than the center of agricultural fields (Bedford and Usher 1994; Andersen 1997; Magura and Tóthmérész 1997; Fournier and Loreau 1999). What I found, even though it was concerning genus and not species, deviates from this trend, given that diversity did not change across the field. These findings should be of interest to farmers since the potential for ecosystem

services in their fields is likely comparable across their entirety, especially given that the natural enemy community has penetrated well into the field. Given my results and those found by Cutler et al. (2012), coupled with the many examples in the literature correlating high diversity and abundance with increased ecosystem services, farmers may see fewer pest outbreaks in fields with high Carabidae abundance and diversity. Therefore, it would be of interest to compare the Carabidae community of fields suffering from heavy pest infestations with those of healthy fields to know whether this prediction holds in lowbush blueberry fields. It would also be of interest to know, given the overall carabid abundance and diversity trends I found, whether they are the same within crop fields, considering that different management strategies are used in the two types of fields (Blatt et al. 1972; Jensen and Yarborough 2004). If anyone wishes to replicate this study, it would be useful to measure field patchiness, temperature of the fields throughout the study, and identify individuals to species, since these factors could have affected my results and I did not measure them.

#### **5.4 Understanding Carabid Dispersal**

Knowledge of how organisms disperse allows us to predict how they aggregate around areas of high prey density, and how they reach habitats required for their different life history stages (Thomas et al. 1997). Such knowledge is essential for the incorporation of natural enemies in IPM strategies. Carabidae is a highly successful beetle family, with over 40,000 described species, some of which are well known natural enemies in many agricultural systems (Erwin 1985; Lövei and Sunderland 1996; Kulkarni et al. 2015). Carabids move in a correlated random walk (CRW), where at each step they take, the turning angle is independent of the previous turning angle, there is no cross-correlation between moving directions and turning angles, and successive step lengths are not auto-correlated (Kareiva and Shigesada 1983). Coupled with other factors, such as presence of prey and hunger levels (Wallin and Ekblom 1994), the CRW eventually leads carabids to their food source. Many of these factors are specific to certain systems, especially spatial heterogeneity (Turchin and Thoeny 1993), which makes studying species movement within one's system imperative. *Harpalus rufipes* is an abundant species in many cropping systems, including lowbush blueberry (Cutler et al. 2012), and only few studies

have tried to quantify their movement (Zhang et al. 1997; Midtgaard 1999; Kujawa et al. 2006). My experiment showed that *H. rufipes* individuals can displace close to 15 m/day in vegetative lowbush blueberry fields, though this measure does not reflect the total distance traveled by the beetle in that time. From personal observations, I noticed that the marked *H. rufipes* did not move towards any specific direction. This re-enforces the idea that carabids move in CRW, though the results for displacement are likely a product of both the CRW and of the other factors which influence movement. To find this displacement measure, I developed a theoretical framework that corrects for the different probabilities of detecting individuals at different areas. This framework parallels the advancements made in the mosquito dispersal field (Lillie et al. 1981) and fills a gap in the Carabidae dispersal literature. It is possible to obtain better estimates of how far *H. rufipes* moves over time by releasing many more marked individuals at the beginning. It would also be of interest to see how Carabidae displacement changes with respect to prey density, such as insect pests or weeds, within blueberry fields. This would show us how quickly species such as *H. rufipes* can find prey and how long they are likely to stay in an infested area.

## **5.5 Final Summary**

We can conclude from my thesis results that Carabidae communities in vegetative lowbush blueberry are rich but dominated by only few genera. Some of the dominant species seem to not contribute to weed seed control, while others probably do. I recommend that farming practices seeking to maximize carabid numbers should consider their distribution within the fields, so that damage in the areas where they occur the most are minimized. We can also conclude that *H. rufipes* moves on average 15 m/day in vegetative lowbush blueberry fields, and that my theoretical framework provides methodological refinements for dispersal studies.

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