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Sources of Variability in Agronomic Weed Seed Predation: Time, Space, Habitat, and Hyperpredation

Sonja K. Birthisel

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SOURCES OF VARIABILITY IN AGRONOMIC WEED SEED

PREDATION: TIME, SPACE, HABITAT,

AND HYPERPREDATION

By

Sonja K. Birthisel

B.A. Luther College, 2010

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Ecology and Environmental Science)

The Graduate School

The University of Maine

December 2013

Advisory Committee:

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By Sonja K. Birthisel

Thesis Advisor: Dr. Eric R. Gallandt

An Abstract of the Thesis Presented
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Weed seed predation is an ecosystem service that benefits farmers by decreasing seedbank inputs, thereby reducing weed pressure in subsequent growing seasons. Seed predation can be considerable, but is highly variable. Sources of variability may include time, space, habitat, and trophic interactions such as hyperpredation. Two experiments were conducted to measure the impacts of these sources of variability on weed seed predation rates in Maine mixed vegetable agroecosystems.

Chapter One of this thesis describes a series of landscape-level field experiments conducted to quantify the effects of time, space, and habitat on seed predation rates. Seed assays, with and without vertebrate exclosures, were used to measure seed predation at spatially explicit sample sites across crop and non-crop habitats on a 'typical' Maine organic mixed vegetable farm. Total and invertebrate seed predation averaged 8% and 3% day⁻¹, respectively. Motion-sensing wildlife

cameras indicated that vertebrate seed predators included small mammals and birds. Pitfall trapping data indicated that one species of carabid, *Harpalus rufipes*, was highly dominant, comprising 66% of invertebrate seed predators captured within crop fields. Correlogram analysis showed that seed predation was randomly distributed in space. Based on linear mixed effects models, time and habitat were highly significant drivers of seed predation. Total seed predation varied between years of study, and both total and invertebrate seed predation decreased from August to October with winter's approach. Total seed predation was greater in crop and riparian forest habitats than in mowed grass, meadow, or softwood forest. Generally, invertebrate seed predation was greatest at sites with moderate habitat complexity, while habitat type was the chief biotic determinant of vertebrate seed predation rates. In this study system, time and habitat were more important regulators of seed predation than was space.

Chapter Two describes an experiment conducted to measure hyperpredation of *H. rufipes* and explore its effects on the weed seedbank. *H. rufipes* prefer sites with vegetative cover to fallow sites, preference speculated to be driven by predator avoidance behavior. To test this hypothesis, 'hyperpredation assays' were developed, in which live *H. rufipes* prey were presented to higher-order predators. Field trials were conducted to determine foremost if *H. rufipes* was subject to predation, and secondly, whether a) vegetative cover affords *H. rufipes* protection from hyperpredators, and b) high hyperpredation rates correspond with decreased invertebrate seed predation rates. Hyperpredation was 2.8% per day. Motion-

sensing cameras indicated that *H. rufipes*' predators included birds and small mammals. Neither a relationship between hyperpredation and vegetative treatment, nor an empirical relationship between hyperpredation and invertebrate seed predation were found. However, a simulation model predicted that hyperpredation at the rate observed could increase seedbank inputs by more than 17% annually. Additionally, complex habitats supported higher rates of hyperpredation than did simple habitats.

THESIS ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Sonja K. Birthisel, I affirm that this manuscript is the final and accepted thesis. Signatures of all committee members are on file with the Graduate School at the University of Maine, 42 Stodder Hall, Orono, Maine.

Eric R. Gallandt, Associate Professor of Weed Ecology and Management DATE

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CHAPTER ONE:
TIME AND HABITAT ARE MORE IMPORTANT REGULATORS OF
WEED SEED PREDATION THAN SPACE IN A MAINE
MIXED VEGETABLE AGROECOSYSTEM

1.1 Introduction

Postdispersal weed seed predation is a significant source of weed mortality in agroecosystems (Gallandt 2006). By decreasing seedbank inputs, seed predators provide a valuable ecosystem service that may reduce the long-term weed pressure experienced by farmers. As part of a multi-tactic ecologically based weed management strategy (Liebman and Gallandt 1997; Gallandt 2006; Mirsky et al. 2010; Bohan et al. 2011), seed predation may reduce the need for herbicide application in conventional farming systems (Westerman et al. 2005), and mechanical weed control in organic systems (Liebman and Davis 2009), mitigating the negative environmental impacts of these practices.

Common seed predators in temperate agroecosystems include mice and other small mammals, birds, and invertebrates including ants, crickets, and carabid beetles. Seed predation can be substantial, but is highly variable. In a multi-year University of Maine study, E.R. Gallandt and colleagues compared spring germinable weed seedbanks of uncovered soil and soil covered with wire mesh to exclude all seed predators fall through spring. There was a 42% reduction in germinable weed seeds due to predation one year, but no significant reduction three other years of

study (E.R. Gallandt unpublished data). Because these experiments were conducted in different fields each year, some located near forest edges and others in more open terrain, spatial and habitat effects in addition to temporal effects may have contributed to the observed inter-annual variability. Indeed, other studies indicate that space, time, and habitat may all be important drivers of seed predation rates.

Weed communities are spatially aggregated (i.e. patchily distributed) across agricultural landscapes (Alignier and Petit 2012). It is therefore expected that seed predation is aggregated also, since vertebrate seed predators respond numerically to seed density (Hulme and Borelli 1999; Robinson and Sutherland 1999; Butler et al. 2010; Baraibar et al. 2012) as may some ants (Beckers et al. 1989; Crist and MacMahon 1992) and carabids (Bohan et al. 2011; but see Baraibar et al. 2012). Many studies have qualitatively described seed predation as patchily distributed (reviewed in Hulme and Kollmann 2005; Jacob et al. 2006); however, this presumed spatial aggregation has not been quantified, nor have the effects of space and habitat been separated in any studies of which we are aware. Several studies have tested the effect of distance from field edge on seed predation, but offer mixed results: distance from field edge may increase (Saska et al. 2008), decrease (Jacob et al. 2006), or have no effect (Booman et al. 2009) on seed predation rates. Studies to quantify the overarching spatial patterns of seed predation across agricultural landscapes are needed to expand existing knowledge and make sense of these conflicting findings.

Multi-year studies often report inter-annual variation in seed predation rates (Willson and Whelan 1990; Cardina et al. 1996; Meiners et al. 2000; Booman et al. 2009). Mechanisms contributing to this variability may include cyclic (Elias et al. 2006) or otherwise variable (den Boer and van Dijk 1994) population dynamics of seed predators; differential activity of seed predators due to temperature (Honek 1997; Azcárate et al. 2007; Davis and Raghu 2010); and hit-or-miss visitation by migrating birds (Vardanis et al. 2011; Hurlbert and Liang 2012). In temperate agroecosystems, intra-annual variation in seed predation is also widely reported. Seed predation is typically low in winter and spring (Cardina et al. 1996; Saska 2008), increases to a peak in mid to late summer (Westerman, Wes, et al. 2003; Honek et al. 2006; Jacob et al. 2006) and decreases throughout the fall (Willson and Whelan 1990; Davis and Raghu 2010).

Habitat affects seed predators and seed predation rates across multiple spatial scales. At the field scale, small mammals (Kelt et al. 2004) and carabids (Shearin et al. 2008; Norbury et al. 2009; Diehl et al. 2012) typically prefer microhabitats that provide vegetative cover. These preferences may be due to predator avoidance behavior (Kelt et al. 2004; Birthisel et al. in press), or because vegetation provides a favorable microclimate (Magura et al. 2001; Diehl et al. 2012). Conversely, ants may preferentially forage in open areas (Hulme 1997). Overall, vertebrate and invertebrate seed predation within agricultural fields is positively correlated with vegetative cover (reviewed in Meiss et al. 2010; but see Jacob et al. 2006)

Less is known about the factors affecting seed predation at the landscape scale, but habitat complexity is thought to be an important driver. Complex habitats are typically desirable to small mammals (Meiners and LoGiudice 2003; reviewed in Denno et al. 2005), and may support high carabid abundances (Vanbergen et al. 2010). Similarly, many birds require forest or other non-crop habitat for nesting (Rising 1996). Seed predation rates can be higher in non-crop habitat than in nearby crop fields (Holmes and Froud-Williams 2005; Gaines and Gratton 2010); however, avian seed predators may preferentially forage within crop habitat (Holmes and Froud-Williams 2005). In a study of seed predation within and around 28 winter cereal fields located in contrasting landscape contexts, Trichard et al. (2013) found that more complex habitats supported higher seed predation rates.

Existing literature has established that space, time, and habitat may be important drivers of seed predation rates. However, no prior studies of which we are aware have examined these factors simultaneously. This study employed a landscape-level time series of spatially explicit seed predation assays to do precisely that. Experiments were conducted in October 2011, and in August, September, and October 2012. This timing coincided with peak seed rain in our system. Specific hypotheses, based on the rationales described above, were as follows:

1. Sites with high seed predation rates will be spatially aggregated.
2. Within season, seed predation will decrease throughout the fall.
3. There will be inter-annual variation in seed predation rates.
4. Seed predation will be greatest in complex, densely vegetated habitats.

1.2 Methods

1.2.1 Study System

Research was conducted at Peacemeal Farm in Dixmont, ME (**Figure 1.1a**). Peacemeal is a certified organic diversified vegetable farm, consisting of 4.9 ha of arable fields interspersed with mowed grass strips and areas of un-mowed meadowland. Fields are bordered to the West by a softwood-dominated mixed forest, and to the East by a stream surrounded by hardwood-dominated riparian forest. Soils are primarily loamy sands with 3-5% organic matter. The average germinable weed seed density in Peacemeal soils was 12,000 seeds m⁻² in 2010 (Gallandt unpublished data) In its diversity of non-crop habitat features, Peacemeal is representative of many small-scale Northern New England mixed vegetable farms.

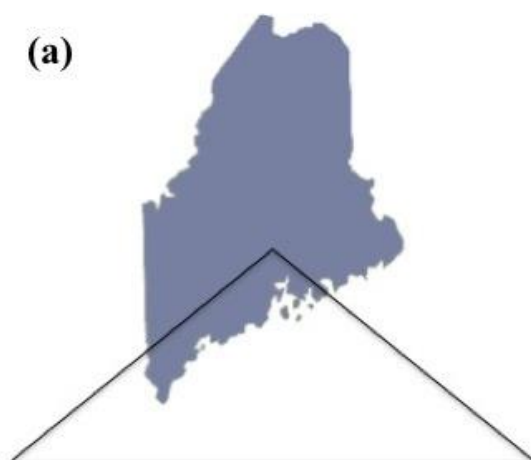
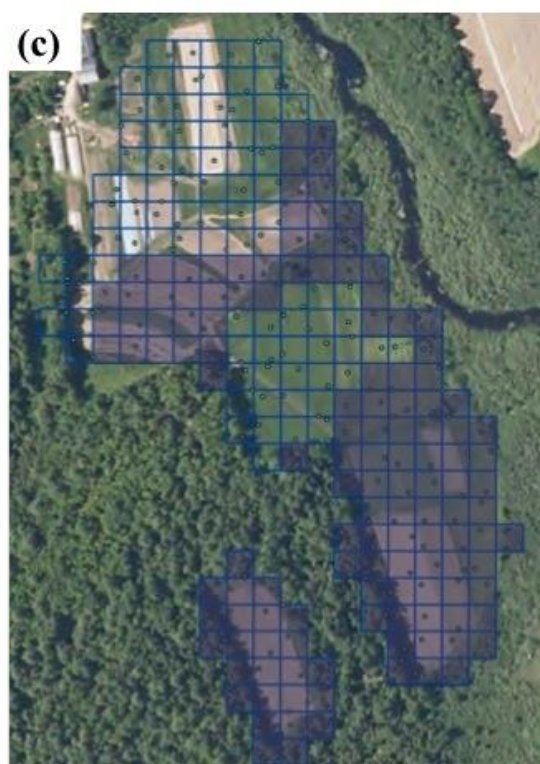


Figure 1.1: Maps showing location of Peacemeal Farm within the state of Maine **(a)**; sampling scheme: 20m grid overlay, with one randomly chosen sample site in each cell **(b)**; and reduced sample scheme: sampled sites are highlighted in lilac **(c)**.



1.2.2 Sample Sites

Using ArcMap®, a 20m grid was placed over 8.5 ha of crop and non-crop habitat. Within each cell the latitude/longitude coordinates of one sample site were randomly selected, for a total of 240 sites (**Figure 1.1b**). Sites were located in five distinct habitat types: crop, softwood forest ecotone, riparian forest ecotone, mowed grass, and meadow. In the field, a Trimble GeoExplorer GPS unit was used to locate sites. Some of the original 240 sites were eliminated either because they were impractically far into forested habitats, or because sampling would have interfered with farm operations. In October 2011, 213 sites were sampled; in August 2012, 217 sites. A subset of 132 sites was sampled in September and October 2012 (**Figure 1.1c**). This subset preserved an even distribution of sites from each non-crop habitat type.

At each site, habitat type and visual estimates of average vegetation height and percent ground cover were recorded. Presence/absence of plant residue and recent disturbance (defined as mowing or tillage within the past two weeks) were recorded also. Additionally, in 2012 a Decagon AccuPAR LP-80 ceptometer was used to quantify leaf area index (LAI).

1.2.3 Seed Predation Measurements

Seed predation was estimated using seed assays (Brust and House 1988; Gallandt et al. 2005). Assays were constructed from inverted 100x15 mm Petri dish bottoms, covered with Grafix Double Tack mounting film. Weed seeds were

adhered to the film: 50 *Setaria lutescens* (yellow foxtail) + 50 *Amaranthus retroflexus* (redroot pigweed), for a total of 100 seeds per assay. *S. lutescens* seeds were collected from Peacemeal, and Rogers Farm in Stillwater, ME, cleaned with a seed blower, and counted with a Seedburo™ 801 Count-A-Pak automatic seed counter. *A. retroflexus* seeds were purchased from Herbiseed, Twyford, England, and counted by hand. To prevent seed predators from sticking to the film, local soil was sprinkled over assays upon installation in 2011. To eliminate between-site variability introduced by using local soil, fine sand was sprinkled over assays prior to installation in 2012. In neither year did this thin layer of soil or sand obscure seeds from view.

Two seed assays were installed at each site, at least 2 m from other site features. Each assay was installed such that the surface of the assay was flush with the surrounding soil surface. One seed assay per site was left uncovered to estimate total seed predation, the other covered with a vertebrate exclosure constructed from 1 cm galvanized mesh hardware cloth to estimate invertebrate seed predation. To estimate seed loss to abiotic factors, control seed assays, covered with 1 mm mesh exclosures designed to exclude all seed predators, were located at a randomly chosen 10% of sites per experiment.

In 2011, seed assays were installed October 6-7 and collected October 12. In 2012, seed assays were in the field August 22-25, September 23-27, and October 22-26. Upon collection, the remaining seeds were counted by hand. Percent daily seed

predation was calculated using a modified form of Abbott's (1945) correction formula:

$$\% \text{ daily seed predation} = \frac{S_i * C - S_f}{S_i * C * d} * 100 \quad \text{Equation 1.1}$$

in which S_i was the initial number of seeds, S_f the final number of seeds, C the proportion of seeds retained on control seed assays, and d the number of field exposure days. Vertebrate seed predation was estimated by subtracting invertebrate seed predation from total seed predation.

1.2.4 Photo Documentation of Seed Predators

To document visitation of sites by vertebrate seed predators, Reconyx PM75 (monochrome), Reconyx PC85 (color), and Bushnell 119436C (color) wildlife cameras were set to motion-capture, and posted on fence posts aimed at a subset of seed assays in each habitat type. Eight to ten total cameras were posted during each sample period.

1.2.5 Invertebrate Activity-Density

Invertebrate activity-density was measured concurrently with seed predation using pitfall 'kill' traps. Traps were fabricated from recycled 500 mL soda bottles, the tops of which were cut off and inverted to form funnels into the traps. Traps were installed flush with the soil surface. A specimen cup containing 40 mL RV propylene glycol was placed under the funnel in each trap.

Upon collection, pitfall contents were strained, and frozen until identification. Carabids were identified to genus, other specimens to coarse arthropod groups.

1.2.6 Temperature Logging

HOBO Pendant® Temperature/Light Data Loggers (8K) were installed 6" above the soil surface, covered by a shield, at six sites in different habitat types and regions of the farm. Temperature was logged every 30 minutes for the duration each experiment.

1.2.7 Statistical Analyses

To assess the degree of spatial autocorrelation in the seed predation data, correlogram analyses were performed. Latitude-longitude site coordinates were converted to UTM using Earth Point (Earth Point 2013). Correlograms were created using the 'spatial' package (Venables and Ripley 2002) in R (R-Development Core 2011), as described by Crawley (2013). Separate correlograms were created using total and invertebrate seed predation data from each sample date in which the full sample scheme was utilized (October 2011 and August 2012; **Figure 1.1b**). Because only weak spatial autocorrelation was detected in these analyses (**Figure 1.2**), the effects of space were excluded from subsequent statistical modeling analyses.

To determine the effects of time, habitat, seed species, and their interactions on seed predation, two pairs of comprehensive linear mixed effects (LME) models were constructed using the 'nlme' package (Pinheiro et al. 2013) in R.

The first pair of models, designed to describe inter-annual patterns in seed predation, utilized data from the October 2011 and October 2012 sample dates only. The response variables total and invertebrate seed predation, respectively, were square root transformed to improve normality of residuals. Each response was fit with a maximal model consisting of site as a random effect, and fixed effects: year, seed species, habitat type, vegetation height, ground cover, disturbance, residue, and all possible interaction terms. Models were fit using the maximum likelihood method to allow for model comparison during simplification. Simplification was accomplished by step-wise deletion of non-significant terms (Crawley 2013) until minimal adequate inter-annual models (hereafter referred to as $INTER_{Total}$ and $INTER_{Invert}$) were obtained.

The second pair of models, designed to describe intra-annual patterns in total and invertebrate seed predation, utilized data from the three 2012 sample dates only. These models were fit as described above, with the following exceptions: month was substituted for year, and LAI and its interaction terms were included as additional fixed effects. Simplification to obtain minimal adequate models ($INTRA_{Total}$ and $INTRA_{Invert}$) was carried out as previously described.

Model assumptions of constant variance and normality of residuals were assessed by visually inspecting plots of standardized residuals vs. fitted values, and quantiles of standard normal vs. residuals. $\text{INTRA}_{\text{Total}}$ and $\text{INTRA}_{\text{Invert}}$ adhered to these assumptions; $\text{INTER}_{\text{Total}}$ and $\text{INTER}_{\text{Invert}}$ displayed non-normality of residuals. Monte-Carlo simulations performed using the 'pgirmess' package (Giraudoux 2013) in R with 1000 permutations were therefore used to verify significance of and obtain *P*-values for terms retained in $\text{INTER}_{\text{Total}}$ and $\text{INTER}_{\text{Invert}}$.

Pearson's correlation tests performed in R were used to test if activity-density of granivorous invertebrates significantly affected seed predation. Pitfall catch numbers were correlated with residuals of the four LME models. Using residuals controlled for the effects of time and habitat on correlations, allowing description of variance in the data that was not captured by the LME models.

1.3 Results

Total seed predation, as measured by seed removal from open assays, averaged 8% day⁻¹ across time points and habitats. Invertebrate seed predation was 3% day⁻¹, vertebrate seed predation 5% day⁻¹.

1.3.1 Spatial Effects

Correlogram analysis of the seed predation data showed weak positive autocorrelation, indicating weak spatial aggregation of similar seed predation rates,

at distances less than 25 m (**Figure 1.2**). There was no autocorrelation, indicating that seed predation was random distributed in space, at greater distances.

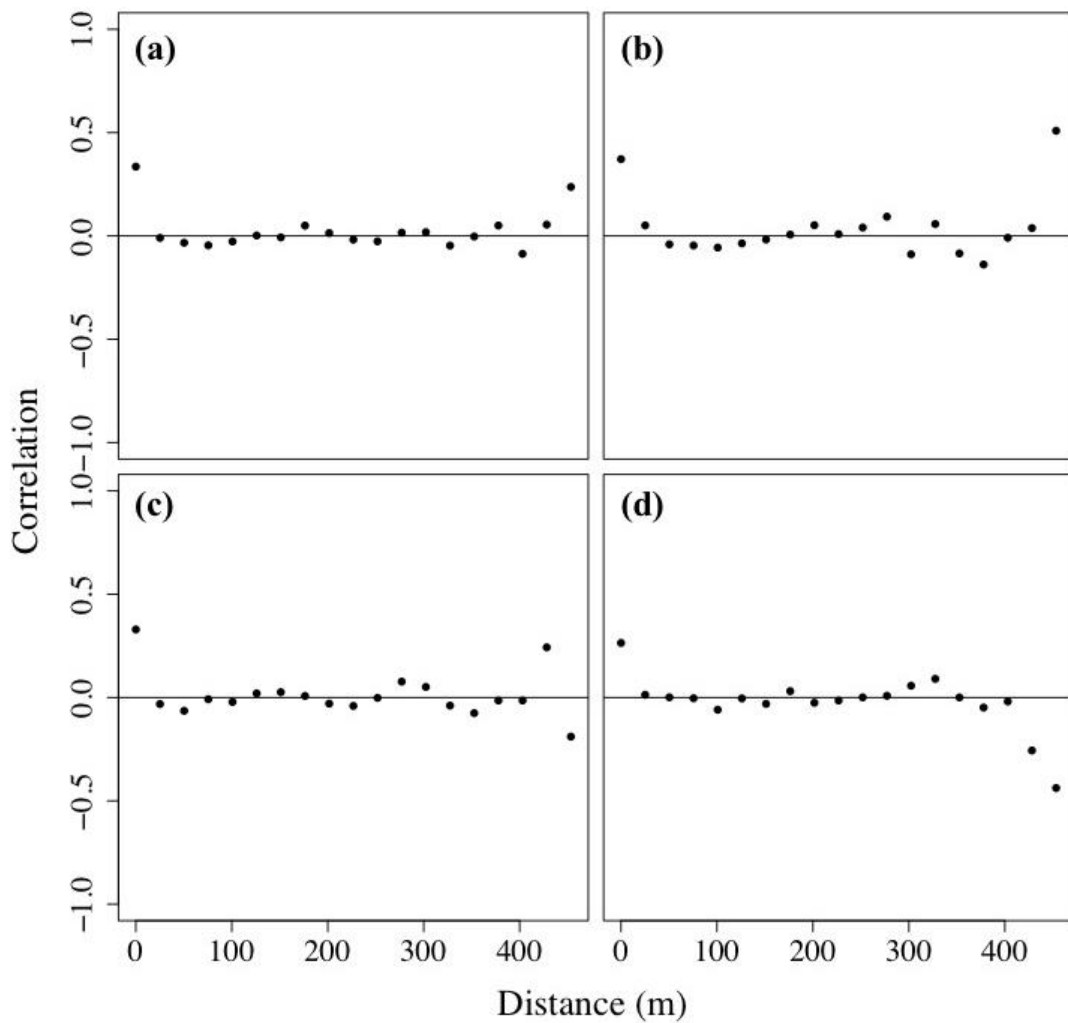


Figure 1.2: Seed predation correlograms: August 2012 total **(a)**, August 2012 invertebrate **(b)**, October 2011 total **(c)**, and October 2011 invertebrate **(d)**.

1.3.2 Temporal Effects

Total seed predation was greater in October 2011 than October 2012 (**Table 1.1; Figure 1.3**). Seed predation by both vertebrates and invertebrates decreased over the period August to October 2012 (**Table 1.2; Figure 1.3**). Vertebrates were responsible for the greater proportion of seed predation in all months studied.

Table 1.1: ANOVA table showing fixed effects of minimal adequate inter-annual LME models. *P*-values were obtained from Monte-Carlo simulations with 1000 permutations.

Fixed effects	INTER _{Total}			INTER _{Invert}		
	DF	F-value	<i>P</i>	DF	F-value	<i>P</i>
(Intercept)	1	294.0	0.988	1	254.8	0.924
Year	1	8.3	0.009*	1	4.5	0.443
Seed sp. ¹	1	16.2	0.000**	1	16.1	0.052
Habitat type	4	3.5	0.000**	4	5.9	0.002**
Vegetation height	1	4.1	0.006*	1	1.7	0.821
Year x habitat type				4	2.6	0.040*
Seed sp. x vegetation height				1	8.1	0.007*
Habitat type x vegetation height	4	3.7	0.006*			

**P*<0.05

***P*<0.005

¹Seed species: AMARE vs. SETLU

Table 1.2: ANOVA table showing fixed effects of minimal adequate intra-annual LME models.

Fixed effects	INTRA _{Total}			INTRA _{Invert}		
	DF	F-value	P	DF	F-value	P
(Intercept)	1	550.0	0.000**	1	471.6	0.000**
Month	2	82.3	0.000**	2	97.2	0.000**
Seed sp. ¹	1	30.3	0.000**	1	2.1	0.151
Habitat type	4	2.7	0.029*	4	5.1	0.000**
Vegetation height	1	0.1	0.784	1	0.4	0.535
LAI ²	1	0.6	0.428	1	0.5	0.491
Residue	1	3.9	0.049*	1	13.5	0.000**
Month x seed sp.	2	18.7	0.000**	2	25.7	0.000**
Month x habitat type	8	4.7	0.000**	8	11.8	0.000**
Month x vegetation height	2	3.1	0.048*			
Month x LAI	2	3.7	0.026*	2	5.4	0.005*
Seed sp. x habitat type	4	2.8	0.026*	4	3.2	0.012*
Habitat type x vegetation height	4	4.1	0.003**	4	5.4	0.000**
Habitat type x LAI				4	4.9	0.001**
Month x seed sp. x habitat type	8	2.5	0.011*	8	2.1	0.031*
Month x habitat type x vegetation height	8	3.7	0.000**	10	5.0	0.000**
Month x habitat type x LAI				8	2.6	0.009*
Habitat type x vegetation height x LAI				5	4.4	0.001**
Month x habitat type x vegetation height x LAI				10	2.7	0.003**

* $P < 0.05$

** $P < 0.005$

¹Seed species: AMARE vs. SETLU

²Leaf Area Index

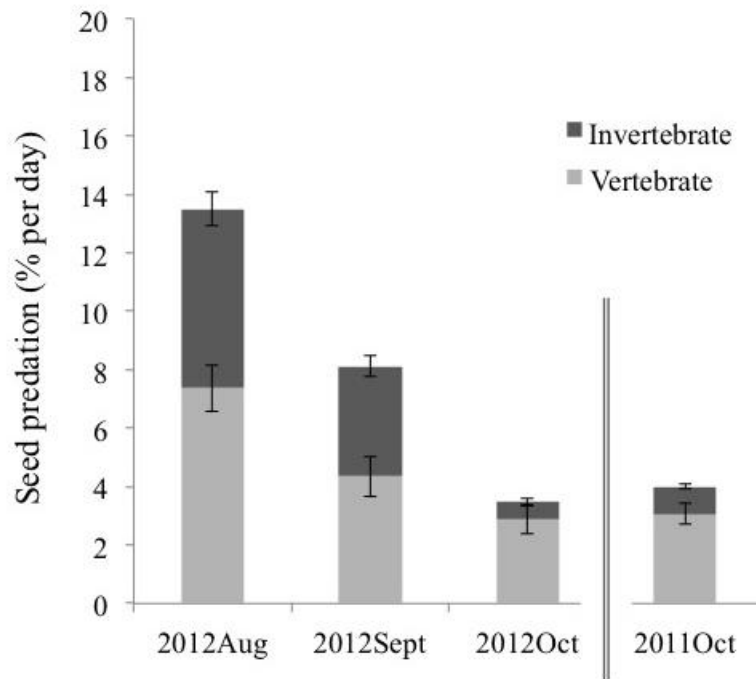


Figure 1.3: Mean (SEM) proportion of total seed predation attributable to invertebrates and vertebrates in four months of study.

1.3.3 Habitat Effects

Habitat type was a highly significant driver of seed predation (**Tables 1.1-1.2**). Across time points, total seed predation was greater in crop and riparian forest habitats than in other habitat types. These trends were driven primarily by vertebrate habitat preferences (**Figure 1.4**).

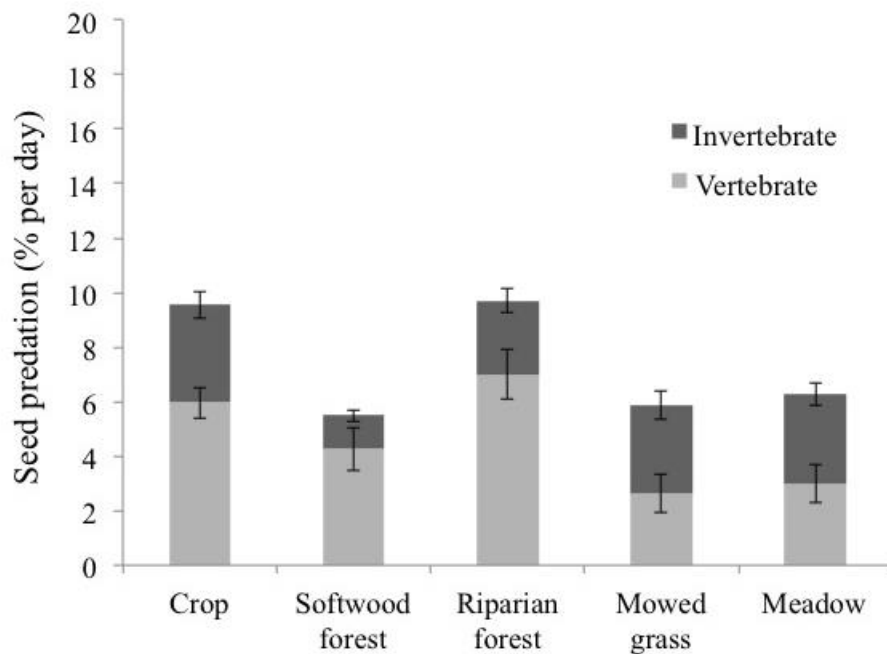


Figure 1.4: Mean (SEM) proportion of total seed predation attributable to invertebrates and vertebrates in each of five habitat types.

In 2012 (**Table 1.2**), total seed predation in crop and mowed grass habitats decreased sharply from August to September (**Figure 1.5a**). Seed predation in other habitats decreased less dramatically, as did seed predation in all habitat types from September to October 2012. In August, total seed predation was greater at sites with short vegetation (i.e. crop and mowed grass sites; **Table 1.3**); in September, total seed predation was greater at sites with taller vegetation. During the October sample dates (**Table 1.1**), total seed predation was greatest at intermediate vegetation height values of 2-4 m (**Table 1.3**).

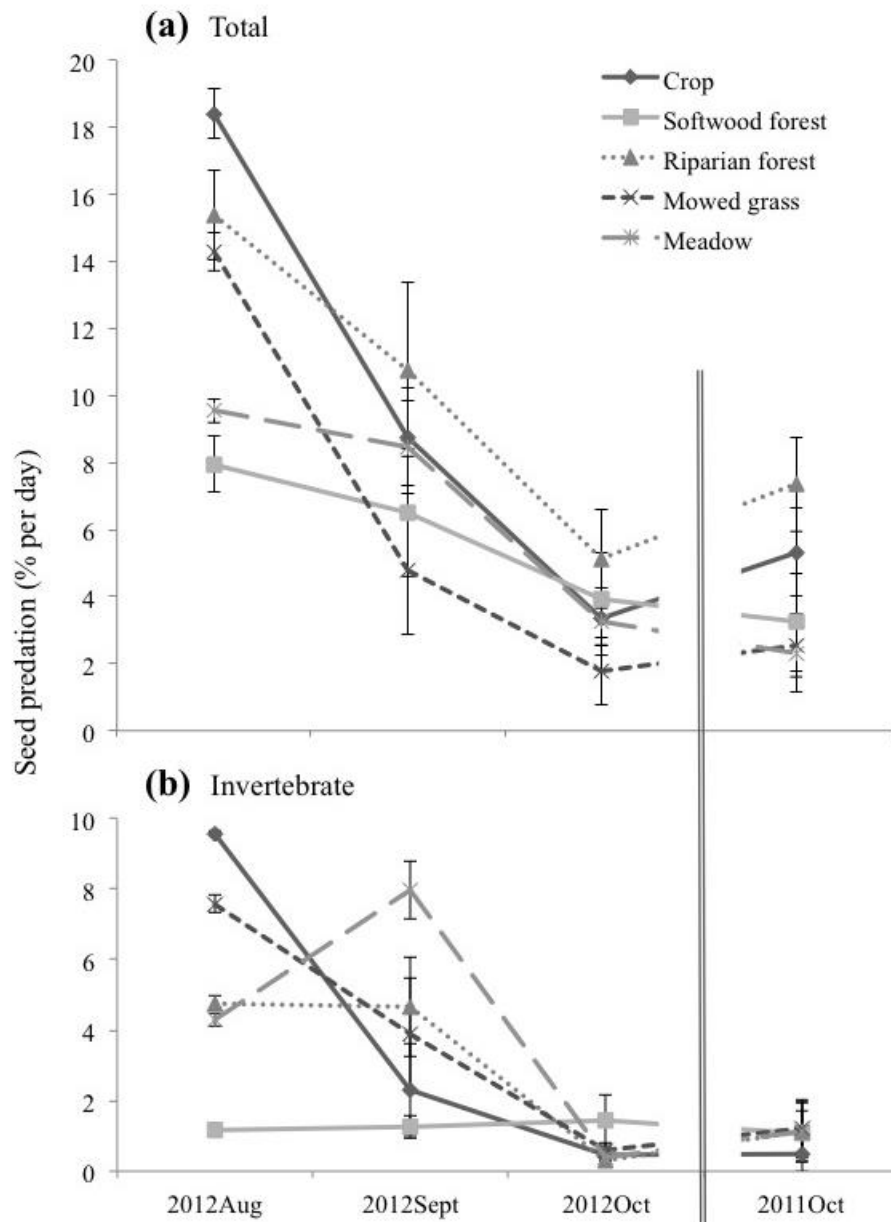


Figure 1.5: Mean (SEM) seed predation by total **(a)** and invertebrate **(b)** seed predators measured in five habitat types and at four time points.

Table 1.3: Summary of habitat attributes in each of five habitat types.

		Crop	Softwood forest	Riparian forest	Mowed grass	Meadow
	N	227	86	97	122	161
Mean±SEM	Leaf Area Index	1.7±0.1	4.9±0.3	4.8±0.3	3.6±0.2	5.2±0.2
	Ground cover (%)	52±2	86±2	90±2	98±1	100±0
	Vegetation height (m)	0.3±0.0	7.9±0.4	2.6±0.1	0.2±0.0	0.6±0.0
% of sites	Recently disturbed	25	0	0	4	0
	With residue	49	90	74	80	86

During the October sample dates (**Table 1.1**), invertebrate seed predation was low overall, but higher in forested habitats than other habitat types. Within the 2012 season (**Table 1.2**), invertebrate seed predation declined sharply in the crop habitat from August to September, but increased in the meadow (**Figure 1.5b**). In 2012, invertebrate seed predation and LAI were positively correlated in the crop habitat, but negatively correlated in the meadow and across habitat types. Total seed predation was positively correlated with LAI in September 2012 only. Presence of plant residue was negatively correlated with total and invertebrate seed predation in 2012.

1.3.4 Seed Species Effects

Assay species was a significant driver of total seed predation rates (**Tables 1.1-1.2**). Total *S. lutescens* consumption exceeded *A. retroflexus* consumption overall, though relative consumption rates varied by month (**Figure 1.6a**), with *A. retroflexus* being consumed in equal quantities to *S. lutescens* in August. There was temporal variability in invertebrate seed preference: *A. retroflexus* was preferred in August, *S. lutescens* in September (**Figure 1.6b**). The larger-seeded *S. lutescens* was consistently preferred by vertebrate seed predators (**Figure 1.6c**).

In 2012 (**Table 1.2**), total seed predation of *S. lutescens* exceeded that of *A. retroflexus* in all habitat types except softwood forest. This preference was particularly pronounced in the riparian forest habitat in August and September. In August, total *A. retroflexus* seed predation was highest in crop and mowed grass habitats. Invertebrate consumption of *S. lutescens* was lower in crop and softwood forest habitats than in other habitat types. During the October sample dates (**Table 1.1**), predation of *A. retroflexus* was greater in tall vegetation, while there was no seed species difference in short vegetation.

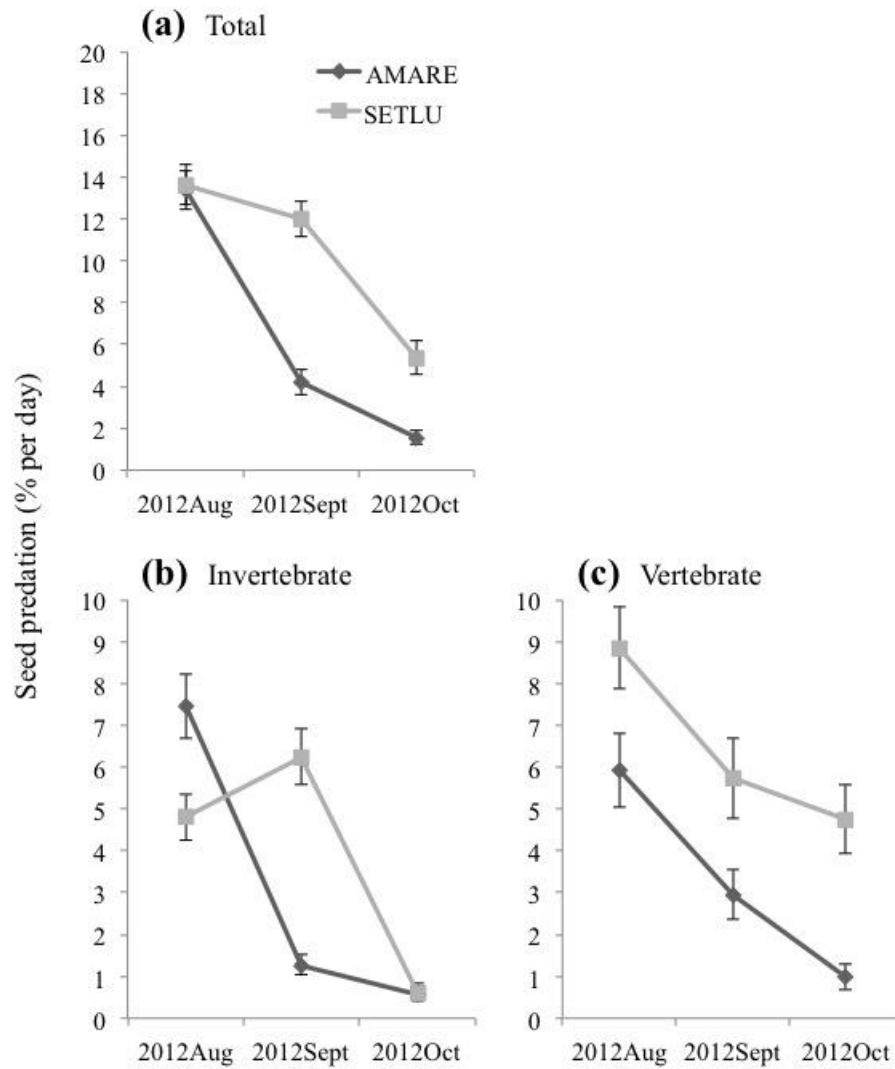


Figure 1.6: Mean (SEM) monthly seed predation of two seed species (AMARE = *A. retroflexus*; SETLU = *S. lutescens*) by total (a), invertebrate (b), and vertebrate (c) seed predators.

1.3.5 Seed Predator Community

Invertebrate seed predators captured in pitfall traps included carabid beetles (**Table 1.4**), ants, and crickets. The granivorous carabid *Harpalus rufipes* was highly dominant (**Figure 1.7**), comprising 66% of invertebrate seed predators captured within crop fields, and 39% of those captured across the landscape. *H. rufipes* activity-density was a significant driver of seed predation in 2012, explaining variation in the data beyond that captured in the LME models (**Table 1.5**).

Table 1.4: Carabid genera captured in pitfall traps.

Carabid genera
<i>Agonum</i> *
<i>Amara</i> *
<i>Anisodactylus</i> *
<i>Bembidion</i> *
<i>Calathus</i>
<i>Carabus</i>
<i>Chlaenius</i> *
<i>Cicindela</i>
<i>Clivina</i>
<i>Harpalus</i> *
<i>Poecilus</i> *
<i>Pseudamara</i>
<i>Pterostichus</i> *
<i>Spaeroderus</i>
<i>Stenolophus</i> *

*Known seed feeder (Tooley and Brust 2002; Vanbergen et al. 2010)

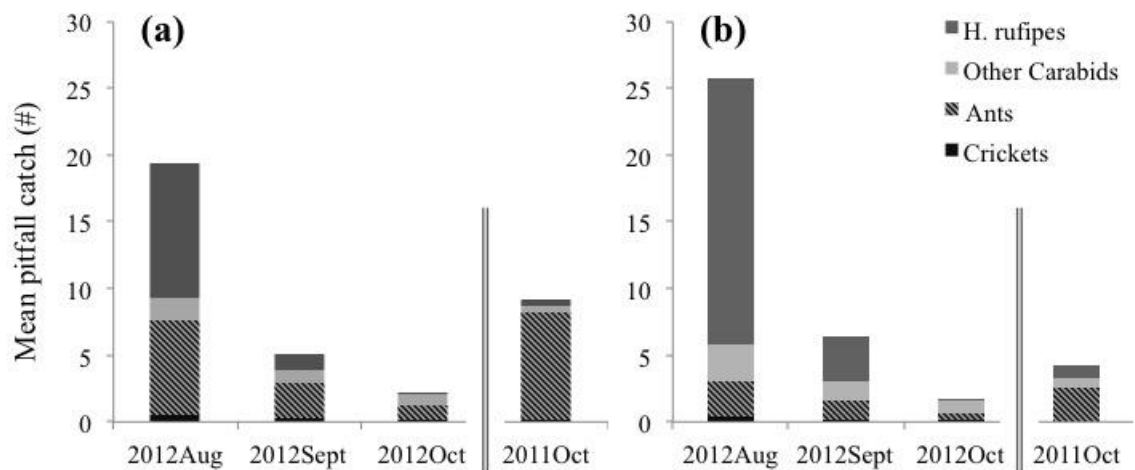


Figure 1.7: Monthly mean pitfall capture rates of granivorous invertebrates across all habitat types **(a)**, and in the crop habitat only **(b)**.

Table 1.5: Pearson's correlations between residuals of four LME models and granivorous invertebrate pitfall catches.

	INTER _{Total}		INTER _{Invert}		INTRA _{Total}		INTRA _{Invert}	
	Cor	P	Cor	P	Cor	P	Cor	P
<i>H. rufipes</i>	-0.027	0.541	-0.018	0.685	0.071	0.046*	0.106	0.003**
Other carabids	-0.045	0.317	-0.063	0.157	0.014	0.689	0.066	0.065
Ants	-0.061	0.173	0.009	0.847	0.025	0.492	0.039	0.278
Crickets	0.005	0.911	0.065	0.148	0.055	0.124	0.014	0.689

* $P < 0.05$

** $P < 0.005$

Pictures and video captured by motion-sensing wildlife cameras (**Figure 1.8**) indicated that avian seed predators included song sparrow (*Melospiza melodia*), swamp sparrow (*Melospiza georgiana*), white-throated sparrow (*Zonotrichia*

albicollis), and common yellowthroat warbler (*Geothlypis trichas*). Song and swamp sparrows were the most commonly photographed avian seed predators.

Mammalian seed predators included Eastern chipmunk (*Tamias striatus*), American red squirrel (*Tamiasciurus hudsonicus*), mice (*Peromyscus* sp.), voles (*Microtus* sp.), and rabbits (*Sylvilagus* sp.) Mice were the most commonly photographed mammalian seed predators, and the most commonly photographed vertebrate seed predators overall.

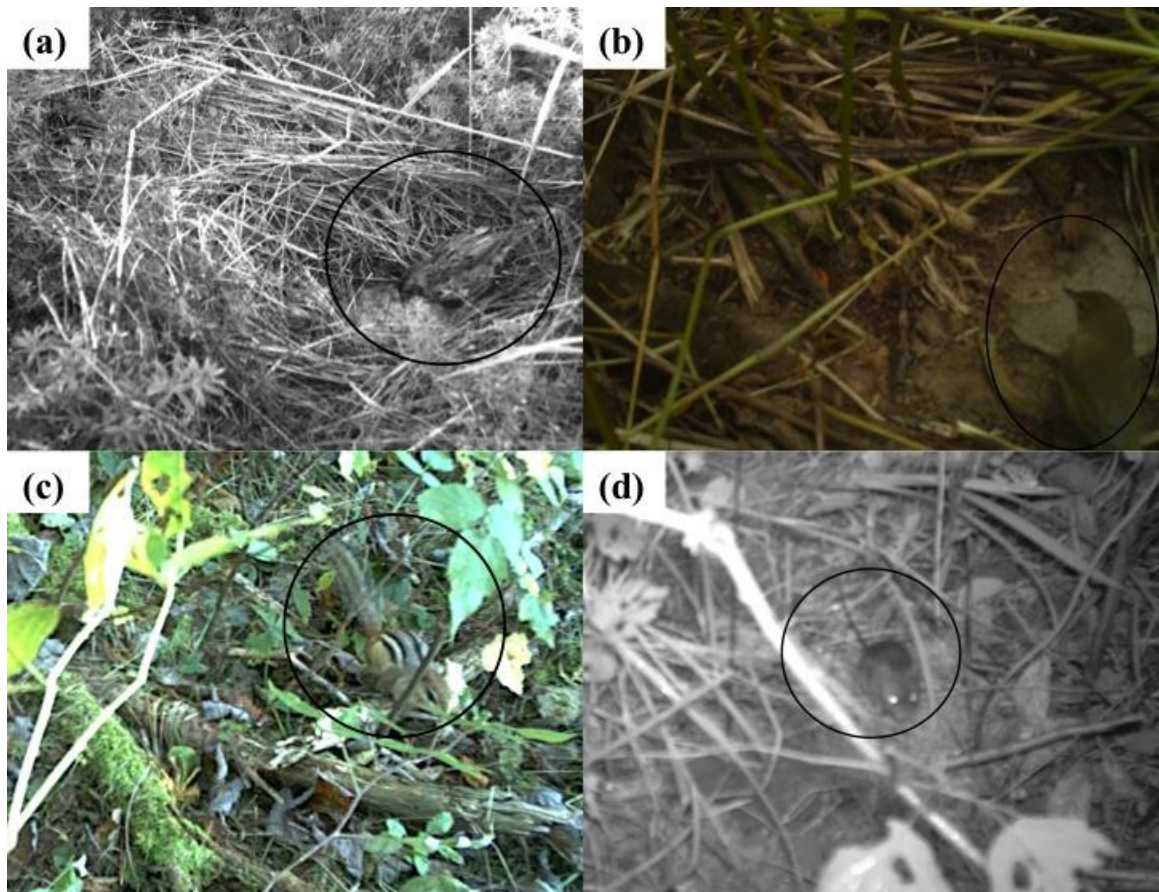


Figure 1.8: Selected photographs of vertebrate seed predators: sparrow **(a)**, common yellowthroat warbler **(b)**, Eastern chipmunk **(c)**, mouse **(d)**. Predators are circled for ease of viewing.

1.4 Discussion

1.4.1 Spatial Effects

Seed predation was weakly aggregated at short distances only (less than 25 m; **Figure 1.2**). The absence of a strong spatial signature showing aggregation at greater distances was unexpected, and contradicts the conventional thinking on this topic (Hulme and Kollmann 2005). It is possible that the 20 m grid scale at which seed predation was measured was too coarse to detect a stronger small-scale spatial signature (Wiens 1989). However, this seems unlikely given the mobility of dominant seed predators in this system. Mice (Wood et al. 2010) and sparrows (Knapton and Krebs 1974) can defend territories of several hundred m², and *H. rufipes* can move up to 14 m night⁻¹ (Lys and Nentwig 1991). Additionally, field edge effects have been found at similar scales in more homogeneous landscapes (Jacob et al. 2006; Saska et al. 2008). An alternate explanation, therefore, is that the extreme degree of habitat heterogeneity (**Figure 1.1**) – and importance of habitat in regulating seed predation in this system (**Figure 1.4**) – masked the effects of space. A third explanation is that the typical pattern of seed predation across agricultural landscapes, previously assumed to be aggregated, may in fact be random. Further studies to quantitatively describe the spatial pattern of seed predation at multiple spatial scales in more homogeneous landscapes are needed to test the relative merits of these explanations.

1.4.2 Temporal Effects

Time was an important regulator of seed predation rates. Consistent with past studies (Cardina et al. 1996; Davis and Raghu 2010), within-season seed predation decreased with winter's approach (**Figure 1.3**). The less dramatic decrease in vertebrate than invertebrate seed predation corroborates Westerman et al.'s (2003) finding that seed predation by vertebrates is more constant and predictable over time than is invertebrate seed predation. The predominance of vertebrate seed predators in August 2012 was unexpected, as past studies conducted in Maine agroecosystems found that invertebrate seed predators dominate in August (Gallandt et al. 2005). Inter-annual seed predator population cycles could explain this inconsistency between studies.

Total seed predation rates varied between years, as reported in numerous studies (Willson and Whelan 1990; Cardina et al. 1996; Meiners et al. 2000; Booman et al. 2009). Seed predation was higher in October 2011 than October 2012, perhaps driven by higher average temperatures in 2011 (data not shown). A serious limitation to our understanding of seed predation, however, remains that a vast majority of studies have been conducted over one to two year time periods. Given that carabid beetle population exhibit substantial and unpredictable long-term inter-annual variation (den Boer and van Dijk 1994), and mouse and vole populations cycle with tree mast events (Elias et al. 2006), it is possible that much unexplained variation between seed predation studies could result from year

effects. We recommend longitudinal studies of greater duration to quantify long-term temporal trends in seed predation.

1.4.3 Habitat Effects

Habitat type, vegetation height, LAI, and presence of plant residue affected seed predation in complex and interacting ways (**Tables 1.1-1.2**).

Crop and riparian forest habitats supported the highest total seed predation rates, driven by high vertebrate seed predation in these habitats (**Figure 1.4**). The riparian forest may have supported vertebrate seed predation by providing a desirable breeding ground for song and swamp sparrows (Rising 1996), and a preferred foraging environment for *Peromyscus* spp. (Meiners and LoGiudice 2003). The high total seed predation rates observed in the sparsely vegetated (**Table 1.3**) crop habitat run contrary to Hypothesis 4: we expected seed predation to increase with habitat complexity. It is possible that birds, which may preferentially forage in open areas (Robinson and Sutherland 1999; Holmes and Froud-Williams 2005), were responsible for this predation. Alternatively, heavy seed rain in the crop habitat (S.K. Birthisel personal observation) may have elicited a density-dependent response in mammals (Hulme and Borelli 1999) and birds (Robinson and Sutherland 1999; Butler et al. 2010) alike. Anecdotally supporting the latter conjecture, mice comprised a majority of vertebrate seed predators captured in photographs at sites in the crop habitat.

Total seed predation in crop and mowed grass habitats decreased from August to September (**Figure 1.5a**). This was largely driven by the corresponding decrease in invertebrate seed predation (**Figure 1.5b**), which presumably resulted from the within-season decline in activity-density of invertebrate seed predators (**Figure 1.7**). The findings that total seed predation was greater at sites with short vegetation in August and sites with tall vegetation in September were corollary, as vegetation height was shortest in crop and mowed grass habitats (**Table 1.3**). The predominance of *H. rufipes* in our study system (**Figure 1.7**) is consistent with the findings of other studies conducted in Maine agroecosystems (Zhang 1993; Gallandt et al. 2005).

The increase in invertebrate seed predation in the meadow from August to September (**Figure 1.5b**) was unexpected. Seed predation may have peaked at this time due to meadow specialists with an uncharacteristically late activity peak. The positive correlation between LAI and invertebrate seed predation in September was corollary with this activity peak in the densely vegetated (**Table 1.3**) meadow. In both October sample dates, invertebrate seed predation was highest in forest ecotone habitats. The softwood and riparian forest ecotones 'buffered' against temperature extremes (data not shown), which may have allowed forest-dwelling invertebrates to remain active longer than those in more exposed habitats.

Invertebrate seed predation was positively correlated with LAI in the crop habitat, but negatively correlated with LAI in the meadow. This finding is consistent

with Navntoft et al.'s (2009) finding that seed predation rates are highest under mid levels of vegetative cover. The observed negative effect of plant residue on seed predation could have been due to decreased foraging efficacy: complex structure may hinder carabid mobility (Thomas et al. 2006; Diehl et al. 2012) and decreased the ability of invertebrates (reviewed in Denno et al. 2005) and birds (Nystrand and Granström 1997) to locate prey. Alternatively, the residue effect may simply have been a result of correlation with habitat type, as seed predation was high in the relatively low-residue crop habitats (**Figure 1.5; Table 1.3**). Supporting this latter view, Jacob et al. (2006) found no residue effect on seed predation.

1.4.4 Seed Species Effects

Consistent with past studies (Booman et al. 2009), vertebrates consistently preferred the larger-seeded *S. lutescens*. Invertebrate seed preference, however, varied across time and between habitats. Some of this variability may have resulted from the seed preferences of habitat specialists. Habitat can greatly affect carabid community structure (Magura et al. 2001; Purvis et al. 2001; Gaines and Gratton 2010), and among carabids, smaller species typically prefer smaller seeds and vice versa (Brooks et al. 2012).

1.5 Conclusions

This study is the first of which we are aware to measure seed predation at spatially explicit sites and multiple time points across a diverse agricultural landscape. Correlogram analysis indicated that, at the scale studied, space was not

an important regulator of seed predation in this system. Results of linear mixed-effects models indicated that time and habitat were highly significant drivers of seed predation. Seed predation varied between years, and decreased throughout the fall with winter's approach. Vertebrates were responsible for the majority of total seed predation, which was greater in crop and riparian forest habitats than other habitat types. Invertebrate seed predators preferred a medium degree of vegetative cover. The vertebrate results were mixed, perhaps due to divergent foraging preferences of mammals vs. birds. Based on these results, we recommend that farmers (a) delay fall tillage if seed rain has already occurred, as seed predators remain active at the soil surface well into the fall; (b) cover crop to support invertebrate seed predator communities; and (c) conserve wetland habitat to support vertebrate seed predators. We recommend that further studies be conducted to: (a) determine whether seed predation is spatially aggregated in systems where habitat heterogeneity is less potentially confounding and at smaller spatial scales; (b) measure long-term inter-annual variation in seed predation rates; and (c) parse the relative contributions of mammals and birds to vertebrate seed predation.

CHAPTER TWO:
HABITAT EFFECTS ON HYPERPREDATION OF THE SEED PREDATOR
***HARPALUS RUFIPES* AND IMPLICATIONS FOR**
WEED SEEDBANK MANAGEMENT

2.1 Introduction

Carabid beetles can provide valuable ecosystem services to farmers by preying on weed seeds (Tooley and Brust 2002) and arthropod pests (Sunderland 2002). Seed predation may benefit farmers as a component in multi-tactic ecologically based weed management approaches (Bohan et al. 2011; Gallandt 2006; Liebman and Gallandt 1997; Mirsky et al. 2010; Westerman et al. 2005). However, inter-annual seed predation rates can be highly variable (Booman et al. 2009; Meiners et al. 2000), and the factors supporting and limiting seed predation are not clearly understood.

In Maine agroecosystems, the carabid *Harpalus rufipes* DeGeer is the predominant invertebrate seed predator (Gallandt et al. 2005; Zhang et al. 1997), shown to consume up to 90% of postdispersal seeds of some species (Zhang 1993). *H. rufipes* has a clear preference for habitat that provides vegetative cover: in a mark-recapture study, *H. rufipes* were twice as likely to be re-captured in their starting plots if released in vegetated vs. fallow plots (Shearin et al. 2008). Weed seed predation, too, is positively associated with vegetative cover (reviewed in Meiss et al. 2010; but see Jacob et al. 2006). We speculated that *H. rufipes* prefers

vegetated environments because they afford protection from higher order predators (Shearin et al. 2008), which we term ‘hyperpredators.’ However, this hypothesis has not been tested. Indeed, hyperpredation of *H. rufipes* has not, to our knowledge, been documented.

Hyperpredation is “one of the least researched areas of carabidology” (Holland 2002), and what little research has been done offers mixed results. By placing beetles in individual plastic containers in an outdoor insectary, Luff (1980) estimated a low *H. rufipes* mortality rate of 8.5% month⁻¹. It is unclear from these methods, however, whether hyperpredators were able to access *H. rufipes* in the insectary, or whether this figure represents non-hyperpredation mortality only. Conversely, total carabid abundance in a shrub-steppe ecosystem was 111% higher within rodent exclosures than without after two years of study (Parmenter and Macmahon 1988). In a UK grassland system, however, a similar study found no exclosure effect on carabid abundance (Churchfield et al. 1991).

Carabid hyperpredators common in temperate agroecosystems include rodents and other small mammals (Larochelle 1975a), birds (Larochelle 1975b; Larochelle 1980), amphibians, reptiles (Larochelle 1975c), and invertebrates including members of the Araneae, Carabidae, and Formicidae (Thiele 1977). Many of these hyperpredators are omnivorous, consuming seeds in addition to invertebrate prey. The tremendous diversity of omnivorous seed feeders potentially existing within a single farmscape (Evans et al. 2011) provides the

potential for a myriad of yet-unstudied trophic interactions between and amongst seed feeding guilds.

We know of no research that has quantitatively tested the effects of carabid hyperpredation on weed seed predation. Our group conducted field experiments to document and measure hyperpredation of *H. rufipes*, and identify the responsible hyperpredators. This study sought further to quantify the effect of vegetative cover on *H. rufipes* hyperpredation, and the effect of hyperpredation on invertebrate weed seed predation. Hypotheses were as follows:

1. Hyperpredation is a source of *H. rufipes* mortality.
2. Vegetative cover affords *H. rufipes* protection from hyperpredators.
3. Hyperpredation decreases invertebrate seed predation.

2.2 Methods

2.2.1 Hyperpredation Field Experiment

Field experiments to measure hyperpredation were conducted at the University of Maine Rogers Farm in Stillwater, ME. Two 72-hour experiments were conducted, beginning on August 8 and September 10, 2012.

2.2.1.1 Sample Sites

To maximize the chance of detecting hyperpredation, sites at least 100 m distant from each other, and located in three distinct habitat types (crop, forest edge, and mowed grass) were chosen for sampling. In August, 15 sites were

sampled; in September, 12 different sites. At each site, in addition to habitat type, up to four plant taxa representing the majority of plant biomass present in a 3-m² area were recorded. A Decagon AccuPAR LP-80 ceptometer was used to quantify leaf area index (LAI). LAI readings represent an average of 5 above-canopy and 5 below-canopy readings. Visual estimates of percent ground cover, average vegetation height, presence/absence of plant residue, and presence/absence of recent disturbance (mowing or tillage within past two weeks) were recorded at each site.

2.2.1.2 Hyperpredation Assays

Hyperpredation assays were constructed using 55x43x7 cm greenhouse flats filled with soilless medium (Sun Gro Metro-Mix® 560 SUN-COIR™). Assays received one of two treatments: bare fallow or vegetated. Bare fallow assays consisted of only medium, with no further modification. Vegetated assays were seeded with 8.8 ± 0.2 g oat seeds, representing a sowing density of 280 kg ha⁻¹. Oat seedlings were grown in a greenhouse to a height of approximately 23 cm.

Five paper clips were bent into loops and inserted into the medium on each hyperpredation assay to serve as stakes to which *H. rufipes* were tethered (**Figure 2.1a**). One live *H. rufipes* was tethered to each stake, for a total of five *H. rufipes* assay⁻¹, using 2.7 kg fishing line secured behind the first pair of legs with a two-half-hitch knot (**Figure 2.1b**) and stop knot (not shown). Tether length was 10 cm (**Figure 2.1c**).

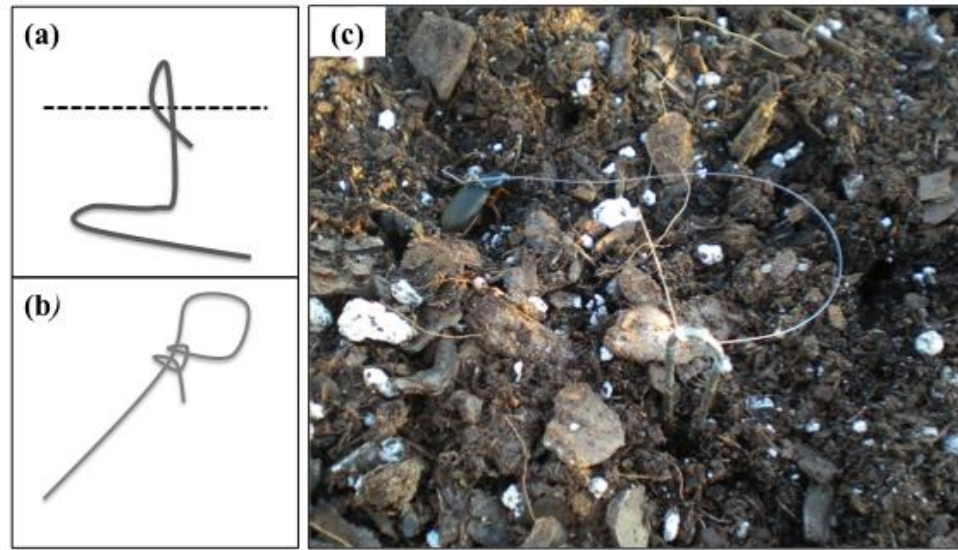


Figure 2.1: Illustration of tethering methods: location of tether stake relative to soil surface (dotted line) **(a)**, two-half-hitch knot **(b)**, tethered *H. rufipes* **(c)**.

Vegetated and fallow hyperpredation assays were presented in pairs at each site. The greenhouse flats were buried flush with the surrounding soil surface (**Figure 2.2**). At a subset of five sites, additional control hyperpredation assays were included during the September experiment. Control assays consisted of fallow assays covered with 1-mm mesh enclosure cages to exclude hyperpredators. Presence/absence of tethered *H. rufipes* was recorded at dusk and dawn to separate nocturnal from diurnal hyperpredation. Hyperpredated and dead beetles were replaced. Non-hyperpredation mortality was $9.3 \pm 1.2\%$. The majority of these losses (93%) occurred when beetles failed to burrow into the soil during the day and, presumably, desiccated.



Figure 2.2: Photo of a sample site, showing paired vegetated and fallow hyperpredation assays, and motion-sensing wildlife camera.

Percent hyperpredation was calculated using a modified form of Abbott's (1945) formula:

$$\% \text{ Hyperpredation} = \frac{H_p * C - H_r}{H_p * C} * 100 \quad \text{Equation 2.1}$$

where H_p was the number of *H. rufipes* presented on a hyperpredation assay, H_r the number of *H. rufipes* remaining at the end of the measurement period, and C the proportion of *H. rufipes* retained on control hyperpredation assays. The control

values from September were used to adjust both August and September hyperpredation values.

Eight Reconyx® and two Bucknell® wildlife cameras, set to motion-capture, were focused on tethered *H. rufipes* to capture images and video of hyperpredators (**Figure 2.2**). Carnivores or omnivores photographed during time periods coinciding with hyperpredation were considered likely hyperpredators.

2.2.1.3 Invertebrate Activity-Density

Invertebrate activity-density was measured with pitfall 'live' traps. Traps were fabricated from recycled 500 mL soda bottles, the tops of which were cut off and inverted to form funnels into the traps. Two traps were installed at each site, 2 m from hyperpredation assays, and no less than 2 m apart. Traps were checked at dawn and dusk, and the number of captured *H. rufipes*, other Carabidae, Formicidae, and Gryllidae recorded. Trapped *H. rufipes* were collected and stored at 4°C for use in subsequent trials. Other invertebrates were released at least 2 m from traps to prevent immediate re-capture.

2.2.1.4 Invertebrate Seed Predation

Invertebrate seed predation was estimated using seed assays (Brust and House 1988; Gallandt et al. 2005). Seed assays were constructed from inverted 100 x 15 mm Petri dish bottoms, covered with Grafix Double Tack mounting film. Weed seeds were gently adhered to the film: 30 *Setaria lutescens* (yellow foxtail), 30

Amaranthus retroflexus (redroot pigweed), and 30 *Dactylis glomerata* (orchard grass) seeds, for a total of 90 seeds assay⁻¹. Fine sand was sifted over the seed assays so that predators would not stick to the film. This thin layer of sand did not obscure seeds from view. *S. lutescens* seeds were collected from Rogers Farm in Stillwater, ME. *A. retroflexus* seeds were purchased from Herbiseed, Twyford, England; *D. glomerata* seeds were purchased from Seeds Trust, Inc., Littleton, CO.

Two seed assays were installed at each site, at least 2 m from any other site features. Each seed assay was installed such that the surface of the assay was flush with the surrounding soil surface. Seed assays were covered with vertebrate exclosures constructed from 1-cm hardware cloth. To estimate seed loss from abiotic factors, additional control seed assays, covered by 1-mm mesh exclosures designed to exclude all seed predators, were located at a randomly chosen subset of five sites trial⁻¹. Seed assays were exposed in the field for the duration of each 72-hour trial period.

Mean seed loss was calculated by averaging seed loss from the two seed assays at each site. Percent seed predation was calculated as (modified from Abbott 1945):

$$\% \text{ Seed predation} = \frac{S_i * C - S_f}{S_i * C} * 100 \quad \text{Equation 2.2}$$

where S_i was the initial number of seeds, S_f the final number of seeds, and C the proportion of seeds retained on control seed assays.

2.2.2 Statistical Analyses

All analyses were performed in R (R-Development Core 2011), using non-parametric tests appropriate to count data (Crawley 2013).

To test the effect of month (August, September) on hyperpredation, a 2-sample test for equality of proportions with Yates continuity correction (which reduces the error in assuming a continuous χ^2 distribution) was used. To test the effects of sample period (day, night) and vegetative treatment (bare fallow, vegetated) on hyperpredation, Pearson's χ^2 tests were used.

To test for effects of habitat variables on hyperpredation, 2- and 3-sample tests for equality of proportions with Yates continuity correction were used for categorical variables (habitat type, presence/absence of plant residue, presence/absence of disturbance), and Kendall's τ tests for continuous variables (LAI, percent ground cover, average vegetation height). Pearson's χ^2 was used to test for a sample site effect.

To test for effects of categorical variables (month, seed species) on percent seed predation, Pearson's χ^2 tests were used. Kendall's τ tests were used to test for effects of continuous variables (*H. rufipes* activity-density, hyperpredation) on seed predation, and to test for correlation between hyperpredation and *H. rufipes* activity-density.

2.2.3 Simulation Model

A simulation model was constructed in R (R-Development Core 2011) to estimate the impact of hyperpredation on the number of seeds entering the weed seedbank during August-September in temperate agroecosystems (**Appendix**). The model was comprised of three scalar functions, which calculated absolute density of *H. rufipes*, number of seeds available on the soil surface, and number of seeds entering the weed seedbank at each time step, respectively. Each simulation included 61 time steps, corresponding to the number of days in August and September, and calculated an estimate of the total number of seeds entering the seedbank over this time frame.

The absolute density of *H. rufipes* (B), or number of beetles m⁻², was a function of prior absolute density, rate of loss to hyperpredation (h), and rate of new adult emergence (n).

$$B_{t+1} = B_t - h * B_t + n * B_t \quad \text{Equation 2.3}$$

H. rufipes larvae mature into adults in late summer, emerging from metamorphosis July-August (Zhang 1993). Because carabid eggs and larvae may be subject to high mortality (Heessen 2013; Heessen and Brunsting 1981), emergence was considered the best indicator of new beetles entering the system. Negligible immigration, emigration, and mortality to sources other than hyperpredation were assumed. Given that carabid populations are thought to be relatively stable over time (Luff 1982; Thomas et al. 2001), we think these assumptions reasonable.

The number of seeds available on the soil surface (A) was a function of seed dispersal (D), seed burial rate (b), vertebrate seed predation rate (v), and per-beetle seed consumption rate (p).

$$A_{t+1} = A_t + D - b * A_t - v * A_t - p * B \quad \textbf{Equation 2.4}$$

Equation 2.4 was constructed such that *H. rufipes* seed predation, $p*B$, was not seed density dependent. This was done because invertebrate seed predators typically do not respond numerically to seed density (Baraibar et al. 2012; Marino et al. 2005; Westerman et al. 2008; but see Bohan et al. 2011). For the sake of model simplicity, the effect of seed species on *H. rufipes* seed predation (Harrison and Gallandt 2012; Zhang 1993) was assumed to be negligible. Further, seed predation by invertebrates other than *H. rufipes* was assumed to be negligible. Our pitfall trap data showed that *H. rufipes* comprised a vast majority (79%) of captured invertebrate seed feeders in this system, and we are not aware of data that would allow us to estimate a rate of invertebrate seed predation due to non-*H. rufipes* seed predators only. As a result of this last assumption, however, the model likely underestimates the total impact of invertebrate seed predators on seeds entering the seedbank.

The number of seeds entering the seedbank (S) was a function of seed burial rate and seeds available on the soil surface.

$$S_{t+1} = S_t + b * A_t \quad \textbf{Equation 2.5}$$

While seed burial is in reality a complex process, subject to variation caused by weather and other disturbances (Benvenuti 2007; Westerman et al. 2009), a constant seed burial rate was assumed for the sake of model simplicity.

2.2.3.1 Parameter Estimates

The model was parameterized using values from our data and the literature (Table 2.1).

Table 2.1: Variables and parameter estimates for hyperpredation simulation model.

Parameter	Variable	Estimate	Source
Seeds entering seedbank	S	0 at t_0	---
Seeds available on surface	A	0 at t_0	---
Seeds dispersed	D	111 to 2622 seeds $m^{-2} day^{-1}$	Davis and Raghu 2010
Beetle absolute density	B	0 to 20 beetles m^{-2}	Briggs 1965; Hamon et al. 1990; S.K. Birthisel
Seed burial rate	b	0.04 seeds seed $^{-1} day^{-1}$	Westerman et al. 2009
Vertebrate seed predation	v	0.066 seeds seed $^{-1} day^{-1}$	S.K. Birthisel
Seeds predated beetle $^{-1}$	p	23.3 to 38.8 seeds beetle $^{-1} day^{-1}$	Saska et al. 2010
New beetle emergence rate	n	0 to 0.04 beetles beetles $^{-1} day^{-1}$	Zhang 1993
Hyperpredation rate	h	0 to 0.042 beetles beetles $^{-1} day^{-1}$	S.K. Birthisel

Few estimates of *H. rufipes* absolute density, B , are reported in the literature. Briggs (1965) recorded densities ranging from 0.2 to 13.5 m⁻² across a UK farmscape; Hamon et al. (1990) recorded densities of 0.97 to 3.43 m⁻² in UK field beans. We think it likely, however, that *H. rufipes* absolute densities can exceed these estimates in Maine agroecosystems. In a landscape-level study conducted in Dixmont, ME in August-September 2012, our group recorded an *H. rufipes* pitfall catch rate of (mean \pm SE) 13.2 \pm 1.7 beetles trap⁻¹ 3 days⁻¹ (S.K. Birthisel unpublished data). This exceeds by more than a factor of ten the corresponding estimate of 1.1 *H. rufipes* trap⁻¹ 3 days⁻¹ extrapolated from Hamon et al. (1990). Although pitfall traps have been criticized as inexact (Lang 2000; Thomas et al. 1998), carabid absolute densities are thought to be strongly correlated with activity-density (Baars 1979; Lang 2000; Luff 1982). Thus, the high activity-densities found in Maine agroecosystems may reflect *H. rufipes* absolute densities significantly exceeding published estimates. To determine the sensitivity of seeds entering the seedbank, S , to absolute density, B , simulations were run over a range of B values from 0 to 20 beetles m⁻².

Rate of new *H. rufipes* emergence, n , was estimated from pitfall data collected in Maine potato agroecosystems by Zhang (1993). Newly emerged and total adult pitfall catch numbers were used to calculate weekly values of the proportion of adults newly emerged. These values were used to construct a vector of daily emergence rates for August-September (Appendix).

Hyperpredation rate was estimated using hyperpredation assay data. Simulations were run at values ranging from 0 to 0.042 hyperpredated beetles beetle⁻¹ day⁻¹ to determine the sensitivity of seeds entering the seedbank to h . The maximum value corresponded to 1.5 times our measured estimate of 2.8% hyperpredation.

Seed rain data from Davis and Raghu (2010, Figure 2) was used to estimate the seed dispersal parameter, D . The time frame, latitude, and weed species utilized in this study was more relevant to our system than those presented in other studies. Mean seed rain week⁻¹ was calculated, and used to construct a vector of daily seed rain values (**Appendix**).

Seed burial rate, b , was estimated from Westerman et al. (2009, Figure 5); b was calculated as mean burial day⁻¹ across surrogate seed sizes, cropping systems, and years.

Vertebrate seed predation day⁻¹, v , was estimated from seed predation data collected at Peacemeal Farm in Dixmont, ME (S.K. Birthisel unpublished data). Daily seed consumption beetle⁻¹ in August and September was estimated from Saska et al. (2010, Figure 1b) and temperature means measured during hyperpredation experiments at the Bangor Airport weather station in Bangor, ME. A vector of daily seed consumption rates beetle⁻¹ was constructed from these estimates (**Appendix**).

2.3 Results and Discussion

A daily hyperpredation rate of 2.8% was estimated (**Table 2.2**).

Hyperpredation was statistically constant across months ($\chi^2 = 0.098$, $P = 0.754$).

Thus, months are considered together in subsequent analyses unless otherwise noted. Control beetle loss was low; two total beetles went missing from control assays. Based on images from motion-sensing cameras, likely hyperpredators included mice (*Peromyscus spp.*), Eastern chipmunk (*Tamias striatus*), American red squirrel (*Tamiasciurus hudsonicus*), common raccoon (*Procyon lotor*), and red-winged blackbird (*Agelaius phoeniceus*) (**Figure 2.3**). Red-winged blackbird (Laroche 1975b), common raccoon, and several species of mice and squirrels are known carabid predators (Laroche 1975a). These results support Hypothesis 1: that hyperpredation is a source of *H. rufipes* mortality, and represent the first documentation of vertebrates likely responsible for *H. rufipes* hyperpredation.

Table 2.2: Hyperpredation of *H. rufipes* in August, September, and across months.

	N	<i>H. rufipes</i> hyperpredated (#)	Hyperpredation day ⁻¹ (%)
August	150	23	2.5
September	120	21	3.2
Total	270	44	2.8



Figure 2.3: Photos of likely hyperpredators. From top left: mouse, Eastern chipmunk, common raccoon, red-winged blackbird.

2.3.1 Day vs. Night Effect

As expected, hyperpredation was greater at night than during the day ($\chi^2 = 5.818$, $P = 0.016$) (**Figure 2.4a**), likely because *H. rufipes* are primarily night-active (Thiele 1977). The majority of likely hyperpredators captured on camera were likewise nocturnal.

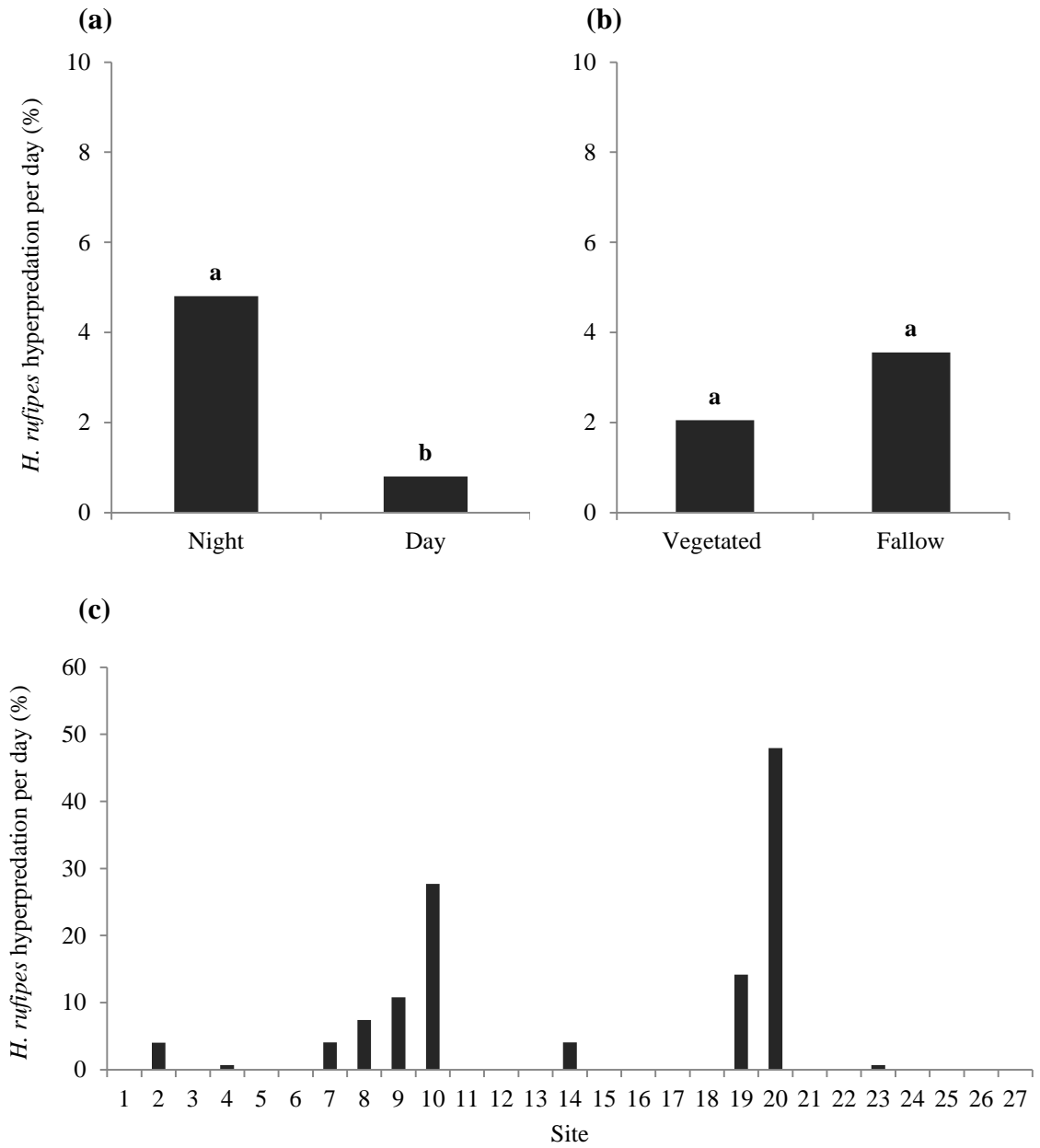


Figure 2.4: Diurnal vs. nocturnal hyperpredation **(a)**, hyperpredation in vegetated vs. fallow assays **(b)**, hyperpredation at each of 27 sample sites: sites 1-15 are from the August experiment, sites 16-27 from September **(c)**.

2.3.2 Vegetative Treatment Effect

Based on Shearin et al.'s (2008) suggestion that *H. rufipes* preference for vegetative cover may be driven by predator avoidance behavior, we expected to find higher rates of hyperpredation on fallow assays than vegetated assays (Hypothesis 2). Contrary to expectation, hyperpredation did not differ between bare fallow and vegetated assays ($\chi^2 = 0.8182$, $P = 0.366$) (**Figure 2.4b**). Failure to detect an effect may have been due to the close proximity of vegetated and fallow assays to one another (**Figure 2.2**). For instance, beetles in the bare fallow assay may have drawn hyperpredators close enough to the vegetated assay to find and prey upon those *H. rufipes* that would otherwise have been shielded from view by the vegetation. Alternatively, *H. rufipes* preference for vegetative cover may be driven by factors other than hyperpredation. For example, vegetative cover may promote a favorable microclimate (Magura et al. 2001), or provide habitat for carabid prey (Hawthorne and Hassall 1995).

2.3.3 Habitat Effects

Hyperpredation varied among the 27 sampled locations at Rogers Farm ($\chi^2 = 183.045$, $P = 0.000$) (**Figure 2.4c**). Hyperpredation also differed significantly between habitat types ($\chi^2 = 73.552$, $P = 0.000$), being greater in forest edge than in crop or mowed grass habitats (forest edge > crop: $\chi^2 = 63.636$, $P = 0.000$; forest edge > mowed grass: $\chi^2 = 20.260$, $P = 0.000$; crop \approx mowed grass: $\chi^2 = 0.000$, $P = 1.000$). Some of this variation may have been caused by habitat attributes. Hyperpredation was positively correlated with leaf area index ($\tau = 0.208$, $P = 0.001$), percent ground

cover ($\tau = 0.142$, $P = 0.031$), and average vegetation height ($\tau = 0.181$, $P = 0.005$). Additionally, hyperpredation was greater at sites with plant residue present than at sites without plant residue ($\chi^2 = 32.206$, $P = 0.000$), and greater at undisturbed sites than disturbed sites ($\chi^2 = 13.571$, $P = 0.000$). Leaf area index, ground cover, vegetation height, and residue are all measures of habitat complexity; similarly, disturbance most often decreases habitat complexity. These results indicate that complex habitats support higher rates of hyperpredation. This is consistent with existing literature: complex habitats and ecotones generally promote a favorable habitat for predators (Langellotto and Denno 2004; Denno et al. 2005), including many invertebrates (Thiele 1977) and small mammals (Larochelle 1975a) that may prey upon carabids.

2.3.4 Seed Predation and Pitfall Data

Mean percent seed predation was greater in August than in September (**Figure 2.5**) ($\chi^2 = 25.638$, $P = 0.000$). Seed predation was not affected by seed species in either trial period (August: $\chi^2 = 4.345$, $P = 0.114$; September: $\chi^2 = 0.005$, $P = 0.998$).

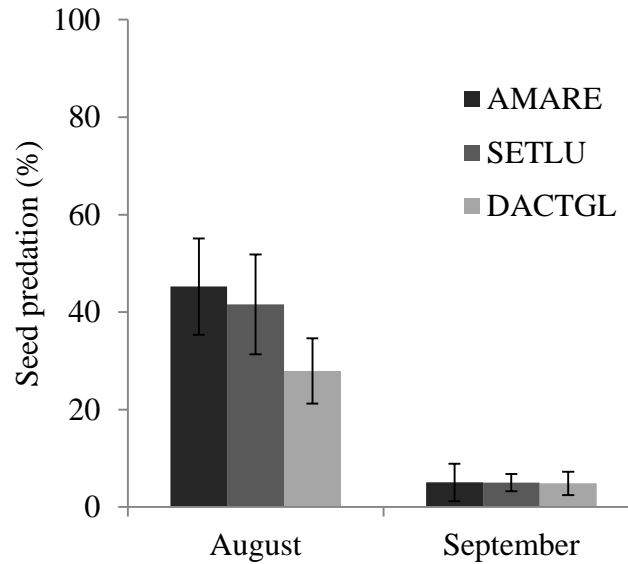


Figure 2.5: Mean (SEM) seed predation of three seed species (AMARE=*A. retroflexus*, SETLU=*S. lutescens*, DACTGL=*D. glomerata*) in August and September.

There was a strong positive correlation between seed predation and *H. rufipes* activity-density ($\tau = 0.201$, $P = 0.001$). Hypothesis 3, that hyperpredation decreases invertebrate seed predation, was not supported: there was no correlation between seed predation and number of *H. rufipes* hyperpredated ($\tau = 0.028$, $P = 0.669$). However, given the strong correlation observed between seed predation and *H. rufipes* activity-density, such a relationship may be detected with larger sample sizes. There was no relationship between hyperpredation and *H. rufipes* pitfall catch ($\tau = -0.063$, $P = 0.377$).

2.3.5 Simulation Model

We ran simulations to determine the sensitivity of seeds entering the seedbank to both *H. rufipes* absolute density and hyperpredation rate (**Figure 2.6**;

Table 2.3). If no *H. rufipes* were present in the system, hyperpredation had no impact on number of seeds entering the seedbank (estimated to be 16,000 seeds m^{-2}) (**Figure 2.6a**). When *H. rufipes* were present, number of seeds entering the seedbank increased with hyperpredation. As might be expected, however, the magnitude of the hyperpredation effect was strongly dependent on *H. rufipes* absolute density (e.g. **Figure 2.6b** vs. **Figure 2.6d**).

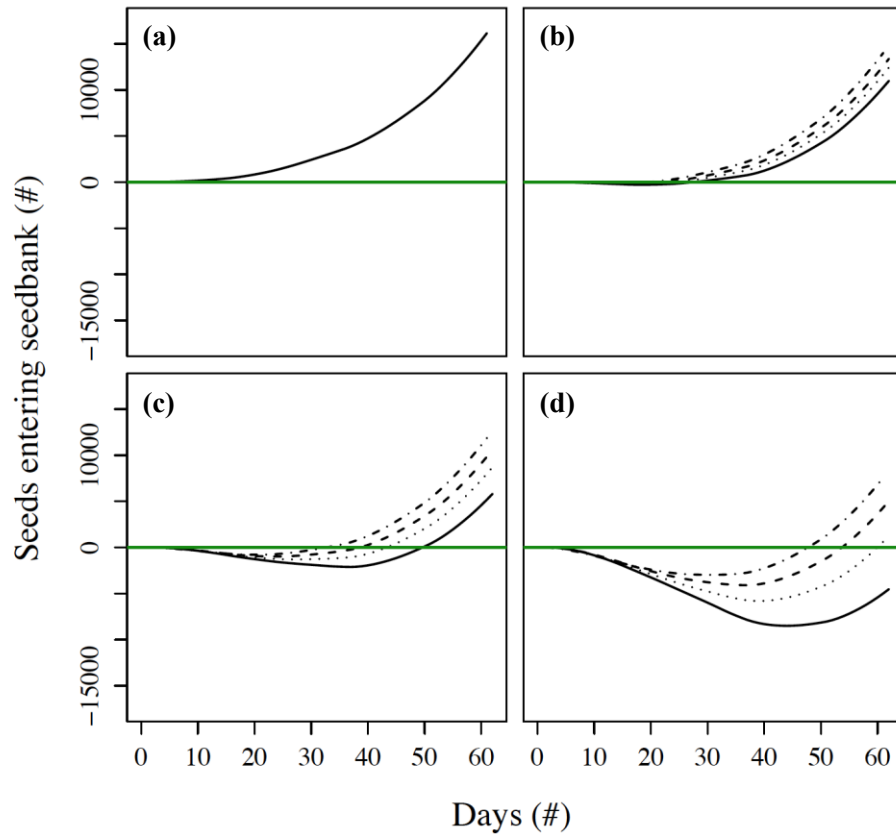


Figure 2.6: Simulations of number of seeds entering the seedbank m^{-2} at starting *H. rufipes* absolute densities of 0 **(a)**, 5 **(b)**, 10 **(c)**, and 20 **(d)** beetles m^{-2} and hyperpredation rates of 0% (—), 1.4% (···), 2.8% (---), and 4.2% (-.-) day^{-1} .

Table 2.3: Estimated number of seeds entering the seedbank m^{-2} (S) at varying beetle densities (B) and hyperpredation rates (h).

	Seeds entering the seedbank m^{-2} (S)			
	$B=5$	$B=10$	$B=15$	$B=20$
$h=0.0\%$	10,984	5,813	641	-4,530
$h=1.4\%$	12,432	8,707	4,983	1,258
$h=2.8\%$	13,376	10,596	7,816	5,036
$h=4.2\%$	14,011	11,866	9,721	7,576

As hyperpredation (h) increased, the rate of increase in seeds entering the seedbank (S) was less than proportional to the increase in h (**Table 2.3**). Thus, even a moderate hyperpredation value of $1.4\% \text{ day}^{-1}$ (half our experimental estimate) in a system with a conservative initial *H. rufipes* absolute density (B) of 5 beetles m^{-2} may cause a greater than 10% increase in number of seeds entering the seedbank. Conversely, the effect of increasing *H. rufipes* absolute density on S was more than proportional to the rate of increase (**Table 2.3**). At $h=1.4\%$, our model predicted that S would decrease by nearly tenfold if B increased by a factor of four, from 5 to 20 beetles m^{-2} . Thus, supporting large *H. rufipes* populations may provide substantial weed control benefits to farmers, even in the face of considerable hyperpredation.

2.3.6 Considerations for Future Research

It is possible that by restricting the motion of otherwise highly mobile *H. rufipes* (Zhang 1993) and presenting them via inherently unnatural assays, our methods made beetles more vulnerable to hyperpredators that they would otherwise be. Tethering seems a better reflection of natural conditions than pinning bait in place (Lundgren et al. 2007); however, further studies on the effectiveness of tethering as a means of assessing hyperpredation of mobile species such as *H. rufipes* are recommended.

This study allowed identification of likely vertebrate hyperpredators of *H. rufipes* (**Figure 2.3**). Specific invertebrate hyperpredators, however, were not identified, nor the effects of vertebrate vs. invertebrate hyperpredation separated. Davis and Raghu (2010) found invertebrate seed predation to be negatively correlated with Araneae abundance, illustrating the potential for invertebrate hyperpredators to impact seed predation. Future work to further explore the impact of predatory invertebrates on carabid communities and invertebrate seed predation rates is recommended.

The finding that hyperpredation is greater in complex habitats could have implications for work aimed at supporting carabid-mediated ecosystem services via agri-environmental schemes (Gaines and Gratton 2010). We suggest that the effects of habitat complexity on hyperpredation be more thoroughly quantified in future work.

2.4 Conclusions

This study used a 'tethering' method to provide documentation that important seed predator *H. rufipes* falls prey to hyperpredators. A model simulating the effect of hyperpredation on seeds entering the weed seedbank predicted that moderate rates of hyperpredation have the potential to substantially increase the number of weed seeds entering the seedbanks of temperate agroecosystems each fall. The results further suggest that habitat complexity is an important driver of hyperpredation rates.

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APPENDIX:

HYPERPREDATION SIMULATION MODEL R CODE

```
# Simulation model varying Harpalus rufipes density (B)
# and hyperpredation rate (h)

# Number of time steps (days in August and September)
numSteps = 61

# Initialize vectors to count time steps (t) and record seeds available (A) and seeds
# entering the seedbank (S)
t = rep(0, numSteps+1)
A = rep(0, numSteps+1)
S = rep(0, numSteps+1)

# Create vectors of daily seed dispersal (D), new H. rufipes emergence (n) and H.
# rufipes seed predation (p) values
D = c(rep(111, 7), rep(201, 7), rep(478, 7), rep(666, 7), rep(573, 7), rep(1349, 7),
      rep(1451, 7), rep(2346, 7), rep(2622, 6))
n = c(rep(0.043, 7), rep(0.015, 7), rep(0.023, 7), rep(0.01, 7), rep(0.003, 7),
      rep(0, 27))
p = c(rep(38.8, 31), rep(23.3, 31))

# Set vertebrate seed predation (v) and seed burial (b) values
v = 0.066; b = 0.04

# Prior to each simulation, manually set initial H. rufipes density (x) to 0, 5, 10, 15, or
# 20 and set trial hyperpredation rate (y) to 0, 0.014, 0.028, or 0.042.
B = rep(x, numSteps+1); h = y

# Run simulation
for (i in 1:numSteps){
  A[i+1] = A[i] + D[i] - A[i]*b - A[i]*v - p[i]*B[i]
  S[i+1] = S[i] + A[i]*b
  B[i+1] = B[i] + n[i]*B[i] - h*B[i]
  t[i+1] = t[i] + 1
}
print(B[62]); print(S[62])

# Repeat for all combinations of x and y
```

BIOGRAPHY OF THE AUTHOR

Sonja Katharine Birthisel was born in Clinton, Wisconsin in June of 1988. She grew up homeschooled in Wisconsin and Maine, and spent a great deal of time outdoors. She attended Luther College in Decorah, IA and graduated *magna cum laude* in 2010 with a Bachelor of Arts degree in Biology and a minor in Mathematics. While at Luther, she took the opportunity to study abroad in Lillehammer, Norway. She returned to Maine in 2011 and enrolled in graduate school at the University of Maine. She enjoys dancing, singing, and playing strategy board games. Sonja is a candidate for the Master of Science degree in Ecology and Environmental Science from the University of Maine in December 2013.