Cover crop seed preference of four common weed seed predators

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Abstract

Invertebrate seed predators (ISPs) are an important component of agroecosystems that help regulate weed populations. Previous research has shown that ISPs’ seed preference depends on the plant and ISP species. Although numerous studies have quantified weed seed losses from ISPs, limited research has been conducted on the potential for ISPs to consume cover crop seeds. Cover crops are sometimes broadcast seeded, and because seeds are left on the soil surface, they are susceptible to ISPs. We hypothesized that (1) ISPs will consume cover crop seeds to the same extent as weed seeds, (2) seed preference will vary by plant and ISP species, and (3) seed consumption will be influenced by seed morphology and nutritional characteristics. We conducted seed preference trials with four common ISPs [Pennsylvania dingy ground beetle (Harpalus pensylvanicus), common black ground beetle (Pterostichus melanarius), Allard’s ground cricket (Allonemobius allardi) and fall field cricket (Gryllus pennsylvanicus)] in laboratory no choice and choice feeding assays. We compared seed preference of ten commonly used cover crop species [barley (Hordeum vulgare), annual ryegrass (Lolium multiflorum), pearl millet (Pennisetum glaucum), forage radish (Raphanus sativus), cereal rye (Secale cereale), white mustard (Sinapis alba), crimson clover (Trifolium incarnatum), red clover (Trifolium pratense), triticale (×Triticosecale) and hairy vetch (Vicia villosa)] and three weed species [velvetleaf (Abutilon theophrasti), common ragweed (Ambrosia artemisiifolia) and giant foxtail (Setaria faberi)]. All four ISPs readily consumed cover crop seeds (P < 0.05), but cover crops with hard seed coats and seed hulls such as hairy vetch and barley were less preferred. Our results suggest that farmers should select cover crop species that are avoided by ISPs if they plan on broadcasting the seed, such as with aerial interseeding.

Introduction

Invertebrate seed predators (ISPs) such as carabid beetles (Coleoptera: Carabidae) and crickets (Orthoptera: Gryllidae) are key drivers of weed seed destruction (Westerman et al., 2003; Kulkarni et al., 2015a) and the subsequent reduction of weed emergence (White et al., 2007; Kulkarni et al., 2015b). ISPs can consume seeds before seed dispersal (pre-dispersal predation) or once the seeds have been shed and are on the soil surface (post-dispersal). Multiple generalist seed predators contribute to post-dispersal predation, which is a form of biological control that can reduce weed populations (Crawley, 1992). Previous research has shown that landscape context (e.g., proximity to field edge) and farm-management practices (e.g., reduced tillage practices) both influence ISP activity density and weed seed predation rates (Trichard et al., 2013; Petit et al., 2017).

In addition to field research, laboratory feeding assays have been used to determine weed seed preference by ISPs, and results determined in the laboratory often translate directly to field preference (Honek et al., 2006; Petit et al., 2014; Ward et al., 2014). In general, constraints such as ISP body size and mouthpart strength determine which seeds can be consumed (Honek et al., 2007; Lundgren, 2009). Several species of carabid beetles such as Amara aenea DeGeer (Ward et al., 2011), Anisodactylus sanctae crucis Fabricius (White et al., 2007), Harpalus affinis Schrankl (Honek et al., 2006) and crickets such as Gryllus pennsylvanicus Burmeister (Carmona et al., 1999) and Teleogryllus emma Ohmachi and Matsuura (Ichihara et al., 2012) have been evaluated for seed preference. However, the Pennsylvania dingy ground beetle (Harpalus pensylvanicus DeGeer) has been the model ISP species for seed preference work. Lundgren and Rosentrater (2007) found H. pensylvanicus preferred species with small, dense seeds with hard seed coats [e.g., redroot pigweed (Amaranthus retroflexus L.), mass ∼0.33 mg; seed coat strength ∼47.81 MPa] compared with large seeds [e.g., ivyleaf morning glory (Ipomoea hederacea L.); mass ∼24.65 mg; seed coat strength ∼3.95 MPa]. Ward et al. (2014) found H. pensylvanicus consumed 71% of presented giant
foxtail (Setaria faberi Herrm.) seeds compared with <1% of velvetleaf (Abutilon theophrasti Medik) seeds.

Though the material properties of seeds play a large role in determining seed preference, nutrient regulation has been proposed as another major factor of insect food selectivity (Behmer, 2009). When multiple food sources are available, insects select those that optimize ratios of macronutrients such as lipids, carbohydrates and proteins. These nutrient ratios determine the health, development and evolutionary fitness of individual insects (Simpson et al., 2015). Jensen et al. (2012) determined that the predatory carabid Anchomenus dorsalis (Pontoppidan) selected food to optimize a lipid-to-protein ratio of 0.36, which maximized the number of eggs a female could lay. Likewise, Harrison et al. (2014) found that spring field crickets (Gryllus velletis Alexander and Bigelow) consume food sources that give a protein-to-carbohydrate ratio of 1 to 4.1 for males and 1 to 2.3 for females. Previous research has also shown how insects can maintain their required nutrient ratios by switching between nutritionally suboptimal but complementary foods (Behmer, 2009).

Laboratory seed preference of ISPs is generally studied in no choice and choice trials, but quantified in many different ways. In no choice trials, seed from a single plant species is offered to a captive insect, whereas seed from multiple plant species is offered in choice trials. In no choice trials, Lundgren and Rosentrater (2007) presented 0.25 g of seed for each plant species they tested, whereas Ward et al. (2014) presented nine seeds regardless of seed size. In their choice trials, Honek et al. (2007) presented 15 seeds of large-seeded species [e.g., great burdock (Arctium lappa L.)] and 30 seeds of small-seeded species [e.g., common lambsquarters (Chenopodium album L.)], while Ward et al. (2014) standardized by seed number in their choice trials and offered three seeds each of velvetleaf, giant foxtail and common lambsquarters. Quantifying consumed seeds is also variable among researchers. Some authors consider a seed consumed when >50% has been destroyed (e.g., Honek et al., 2007), and others consider a seed consumed if the seed coat is cracked and part of the endosperm is damaged (e.g., Carmona et al., 1999). Although methods vary in the literature, most ISP research has focused on assessing the ecosystem service of weed seed destruction and characterizing ISP ecology (Kulkarni et al., 2015a).

Relatively little research has been conducted on the negative effects of weed seed predators such as carabid beetles and crickets on crop seeds. One group of crops for which seed predation might be particularly relevant is cover crops. Cover crops are increasingly used in the USA to improve soil health, suppress weeds and provide other ecosystem services (Singer, 2008; Schipanski et al., 2014; SARE, 2016; Wayman et al., 2016). In the Northeast USA, a large portion, if not most, of the land that is covered is cropped in a crop rotation with corn and soybean and the cover crops are seeded after corn and soybean are harvested in the fall. However, cover crops are also used extensively in small grain, forage and specialty crop production. For example, some farmers ‘frost seed’ red clover into wheat in early spring, while other farmers seed sudangrass and buckwheat in mid-summer between early and late season vegetables (Mohler and Johnson, 2009). Interseeding cover crops into corn and soybean in mid- to late summer is also becoming more popular (Belfry et al., 2016; Blanco-Canqui et al., 2017; Curran et al., 2018; Youngerman et al., 2018). In addition to drill seeding, cover crops are seeded by broadcasting with a fertilizer spreader or by aerial seeding with airplanes (Fisher et al., 2011; SARE 2016). The method used by farmers often varies with farming system (e.g., drill seeding is more common in grain production whereas broadcast seeding is more common in vegetable production) and farm type (e.g., aerial seeding is more common on larger compared with smaller farms). Seeds on the soil surface are much more likely to be consumed by ISPs (White et al., 2007; Kulkarni et al., 2015b), so cover crop seeds may be susceptible to ISP predation when they are broadcast. Wilson et al. (2014) reported losses of 48–98% of aerially seeded cover crop seeds 1 week after seeding and hypothesized that seed predators (e.g., by insects, rodents and birds) were responsible for these losses.

Beyond seed placement (e.g., in furrow covered with soil compared with on the soil surface), the level of seed predation of cover crops will likely vary depending on a number of factors including the presence of seed predators, their activity levels and their seed consumption preferences. Given that ISP seed preference is likely based on seed size and seed coat strength, cover crops that are similar to preferred weed seeds could also be consumed. The goal of this study was to assess ISP seed preference for common cover crop species, and to compare their relative preference to common weeds that are known targets of ISPs. To quantify ISP preferences, a series of no choice and choice laboratory seed preference trials were conducted. We hypothesized that (1) ISPs will consume cover crop seeds to the same extent as weed seeds, (2) seed preference will vary by plant and ISP species, and (3) seed consumption will be influenced by seed morphology and nutritional characteristics.

Materials and methods

Laboratory experiments

Ten cover crop species and three weed species were used to test seed preference of four weed seed predators (Table 1). These plant species were selected because: (1) the cover crop species are used by farmers and the weed species commonly occur in cropping systems in the Northeast, and (2) they vary in several key seed traits including weight, size, compressive yield strength and oil and protein content. Weed seeds were collected from the Musgrave Research Farm in Aurora, NY (42°73′N, 76°63′W) in the fall of 2015 and kept in cold storage for the winter. Cover crop seeds were purchased from several seed companies including King’s ArgiSeeds (Lancaster, PA, USA) and Lakeview Organic Grain (Penn Yan, NY, USA). Germination of cover crop and weed seeds was tested prior to the preference trial to verify their viability, and all plant species had at least 60% germination. Dry seeds were used in all trials. Because size can influence seed viability in some species (Stanton, 1984), which may affect ISP preference (Ward et al., 2014), within-species seed sizes were kept as similar as possible through visual inspection and careful seed selection for each experiment.

Four species of ISPs, including two carabid beetles and two crickets, were selected for the preference trials (Table 2). These four species are common throughout agricultural fields in the Northeast USA during most of the growing season, and are relatively easy to trap (Carmona et al., 1999; O’Rourke et al., 2006; Ward et al., 2014). Beetles were collected with dry pitfall traps from Caldwell Field at Cornell University in Ithaca, NY (42°45′ N, 76°46′W) during the summer of 2016. Caldwell Field is a fragmented habitat with meadow, woodland and diverse cropping system ecozones. Pitfall traps were made of 9-cm diameter nested plastic cups placed in the ground with the top flush with the soil. Pitfall traps were checked and reset each day. A butterfly net was
used to capture *A. allardi*, and *G. pennsylvanicus* were captured by hand. Specimens were brought back to the laboratory and their identification was verified using several sources: Bousquet et al. (2010), Lindroth (1969) and Vickery and Kevan (1986).

Specimens were sorted into 10 by 15 cm clear plastic deli containers with a moist paper towel and small holes in the top of each container lid to allow air exchange. No more than ten insects were placed in a large plastic tub with a lid to maintain darkness, and the tub was stored in a refrigerator at 5°C. The duration of starvation used in this research (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003). The duration of starvation used in this study (i.e., 4 days) was within the range reported in the literature (Honek et al., 2003).

No choice preference trials were used to determine the proportion of seeds consumed when seed from a single species was offered to the insect. No choice trials occurred in 15-cm diameter Petri dishes (VWR International, Radnor, PA, USA). A 35 by 20 cm section of a dry paper towel lined the wider half of the Petri dish, and then 26 randomly distributed, undamaged seeds, a wetted cotton ball atop a 2.5 cm² piece of plastic and a single insect were placed onto the paper towel. The narrower half of the Petri dish was quickly replaced. The excess paper towel was folded over the outside of the narrower half of the Petri dish to reduce light exposure and disturbance to the insect. All no choice Petri dishes were kept in the laboratory at ambient temperatures and daylight conditions (Table 2). Petri dishes were kept out of direct sunlight.

Beetles and crickets were also used in choice trials where seeds of all tested plant species were offered to the insect at the same time. Choice preference trials were prepared using the same methods as the no choice trials above, except that two seeds of each species were randomly distributed in each Petri dish (total 26 seeds per dish). The number of replicate trials varied by ISP and plant species based on the number of insects that were captured (Table 3). In all trials, seed consumption was quantified by counting the number of whole undamaged seeds that remained after 120 h and subtracting that number from the total number of seeds offered (i.e., 26).

### Statistical analyses

All analyses were performed with R version 3.2.2 (R Core Team 2015). Data from no choice and choice trials were analyzed separately. Preference for individual plant species and seed type (weed vs cover crop) was compared within each of the four ISPs. In a separate analysis, preference for individual plant species was also compared across the four ISPs.

**No choice trials**

No choice ISP seed preference was assessed with generalized linear mixed models. Seed consumption was converted into a vector, using the `cbind` function of the number of seeds damaged and total seeds given, and analyzed using the binomial distribution with a logit link. Models were initially assessed with the glmer function.
A mixed-model analysis of variance (ANOVA) (Wald $\chi^2$ test) was first used to determine the differences ($P \leq 0.05$) in the mean probability of seed consumption between weed seeds and cover crop seeds. For this planned contrast, seed type (cover crop or weed) was the fixed effect and plant species nested in container identification nested in collection date was used as a random effect.

The arithmetic mean of the proportion of seeds destroyed for each plant species was presented in bar charts. Two separate models were used to determine the differences ($P \leq 0.05$) in the mean probability of seed consumption. One model tested for differences across plant species within each of the four ISPs. Another model tested for differences across ISPs within each of the 13 plant species. Least square means (package lsmeans) was used to test for differences in both models. Similar means were grouped using the cld function (package lsmeans) with Bonferroni correction. Groups with larger means were interpreted to have a greater probability of being consumed. In cases where the mean probability of seed consumption was either 0 or 1 and had a variance of 0, the seed was removed from the analysis and assigned a letter of lowest or highest rank, respectively, independent of the cld groupings. All tests were conducted on the logit scale.

**Choice trials**

Choice ISP seed consumption was first assessed with Vanderploeg and Scavia’s electivity index $E^*$ (Vanderploeg and Scavia, 1979).

This index provides an intuitive measure for assessing food preference and has been applied to many different animal systems (e.g., Averill et al., 2016; Dupuy et al., 2016).

$E^*$ is calculated as:

$$E_i^* = \frac{W_i - (1/n)}{W_i + (1/n)}$$

(1)

where $W_i$ is:

$$W_i = \frac{(r_i/p_i)}{\sum (r_i/p_i)}$$

(2)

$W_i$ is the selectivity coefficient, $n$ is the number of food species in the trial, $r_i$ is the proportion of food species $i$ consumed of all species consumed, and $p_i$ is the proportion of food species $i$ in the total food species offered. $E^*$ varies between −1 and 1. A positive $E^*$ indicates preference and a negative $E^*$ indicates avoidance; 0 $E^*$ indicates random preference.

A mixed-effect ANOVA was first used to determine the differences ($P \leq 0.05$) in the mean $E^*$ between weed seeds and cover crop seeds, using a similar planned contrast approach as with the no choice trials. Linear mixed-effect models were used to test the effect of seed species on $E^*$; statistical analyses were performed and presented as described above. Test statistics for all ANOVA results can be found in online Supplementary Material (Table S1).

**Seed traits**

Relationships between seed consumption, seed morphological and nutritional traits were tested separately for each ISP using linear regression. The seed traits were (1) mass (mg; seed weight was

| Table 2. Insects used for preference trials and temperature and light data for trial dates |
| --- |
| **Species type** | **Scientific name** | **Common name** | **Trial** | **Date range** | **Ave day** | **Temp day**<sup>a</sup> | **Temp night** |
| Carabid beetle | *Harpalus pensylvanicus* (DeGeer) | Pennsylvania dingy ground beetle | No Choice | August 21–September 27 | 14 h 30 min | 25.5 | 13.9 |
|  |  |  | Choice | August 7–August 13 | 15 h 15 min | 31.1 | 17.2 |
|  | *Pterostichus melanarius* (Illiger) | Common black ground beetle | No Choice | June 24–July 8 | 16 h 23 min | 28.3 | 14.4 |
|  |  |  | Choice | July 18–July 22 | 16 h 00 min | 30.0 | 15.0 |
| Cricket | *Allonemobius allardi* (Alexander and Thomas) | Allard’s ground cricket | No Choice | August 7–September 27 | 14 h 30 min | 25.5 | 13.9 |
|  |  |  | Choice | September 25–September 30 | 13 h 00 min | 18.3 | 13.9 |
|  | *Gryllus pennsylvanicus* (Burmeister) | Fall field cricket | No Choice | August 7–September 9 | 15 h 00 min | 26.7 | 13.9 |
|  |  |  | Choice | September 25–September 30 | 13 h 00 min | 18.3 | 13.9 |

Note: Ave day is average length of visible light for the date range. Temp day and Temp night are the average day and night temperatures (C) for the date range.

<sup>a</sup>Data are from www.wunderground.com.

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| Table 3. The number of choice and no choice replicate trials of each plant species for all ISPs. |
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| **Trial** | **Harpalus pensylvanicus** | **Pterostichus melanarius** | **Allonemobius allardi** | **Gryllus pennsylvanicus** |
| No Choice | 20 | 19 common ragweed 20 all others | 10 crimson clover 11 all others | 7 cereal rye, wild radish, velvetleaf, barley 6 all others |
| Choice | 20 | 20 | 20 | 11 |
determined as an average weight of 100 seeds divided by 100), (2) volume (mm$^3$), (3) compressive yield strength (MPa), (4) oil content (converted from % of seed weight to proportion of seed weight for analysis), (5) protein content (converted from % of seed weight to proportion of seed weight for analysis) and (6) the ratio of oil content to protein content (Table 1). The effect of each trait was analyzed individually for a total of 12 seed trait regression models for each ISP (6 traits $\times$ 2 types of trials). No choice ISP seed preference was assessed with generalized linear mixed models. Seed consumption was converted into a vector, using the cbind function of the number of seeds damaged and total seeds given, and analyzed using the binomial distribution and logit link with the glmnPQL function. Seed consumption was the response variable, seed trait was the continuous predictor fixed effect and seed species nested in container ID nested in collection date were random effects for each model. Choice ISP preference was assessed using Equation (3) with the glmmPQL function. Seed consumption was the response variable, seed trait was the continuous predictor fixed effect and seed species nested in container ID nested in collection date were random effects for each model. Choice trial intercepts and slopes are interpreted as the expected change in seed predation. The relationship between log-odds and probability is monotonic, so an increase in log-odds translates to an increase in probability. Therefore, if there is a significant positive slope associated with a no choice trait model, it will be interpreted that an increase in the magnitude of the trait (e.g., greater mass or oil content) will increase the probability of seed predation, which will indicate an increase in seed preference.

**Results and discussion**

**Weed seed consumption**

Seeds of common weeds species were included in the preference assays to serve as a reference and help us understand how weed seed consumption rates compare to previous studies. In general, weed seed consumption rates in our trials were similar to the rates reported from past weed seed preference trials.

**No choice trials**

Preference patterns for velvetleaf and giant foxtail seeds were consistent with previous research for *H. pennsylvanicus*, Lundgren and Rosentranter (2007), White *et al.* (2007), Ward *et al.* (2011) and Law and Gallagher (2015) found that velvetleaf was less preferred to giant foxtail. Preference of giant foxtail over common ragweed (*Ambrosia artemisiifolia* L.) for *H. pennsylvanicus* is also consistent with the literature (Law and Gallagher, 2015). No difference was observed in weed seed preference for *P. melanarius* which ate few weed seeds overall (Fig. 1). Velvetleaf was the least preferred seed for *A. allardi*, but there was no difference in preference between common ragweed and giant foxtail seeds (Fig. 1). No difference was observed in weed seed preference for *G. pensylvanicus* (Fig. 1), which may be due to the relatively low number of trials (Table 3) and thus large confidence intervals generated by the model (Nakagawa and Cuthill, 2007).

**Choice trials**

Velvetleaf was the least preferred weed species of all ISPs (Fig. 2). Although some velvetleaf seeds were eaten in the no choice trials (up to 5% with *G. pensylvanicus*), when simultaneously offered seeds from 12 other plant species, ISPs did not eat a single velvetleaf seed. Trends in weed seed preference were consistent for *H. pensylvanicus* and *A. allardi* between no choice and choice trials (Figs. 1 and 2). *Pterostichus melanarius* and *G. pennsylvanicus* preferred giant foxtail and ragweed seeds to velvetleaf (Fig. 2). Low ISP consumption rates of velvetleaf seeds have been attributed to their large size and hard coats (Carmona *et al.*, 1999; Lundgren and Rosentranter, 2007; Ward *et al.*, 2014).

**Comparing cover crop to weed seed consumption**

Cover crop seeds were readily consumed by all ISPs (Figs. 1–4). Seed type (weed vs cover crop) had no effect on the probability of seed destruction for *H. pensylvanicus* no choice ($\chi^2 = 1.6$; $P = 0.20$) and choice trials ($F = 1.09$; $P = 0.30$), *A. allardi* in no choice ($\chi^2 = 3.6$; $P = 0.06$) and choice trials ($F = 2.4$; $P = 0.16$) and *G. pensylvanicus* in no choice ($\chi^2 = 1.0$; $P = 0.30$) and choice trials ($F = 2.0$; $P = 0.06$) (lower right panels in Figs. 3 and 4). Interestingly, cover crop seeds were preferred to weed seeds for *P. melanarius* in no choice ($\chi^2 = 19.4$; $P < 0.001$) and choice trials ($F = 5.0$; $P = 0.01$) (lower right panels Figs. 3 and 4). This indicates that *P. melanarius* could be negatively impacting cropping systems where cover crops are used. Overall, the results support our hypothesis that cover crop seeds would be consumed to the same extent as weed seeds by ISPs. However, these contrasts should be interpreted with caution, as consumption patterns for ISPs were not consistent among weed species or cover crop species.

**Cover crop seed preference**

**No choice trials**

Four of the ten cover crop species were consistently the least preferred across the four ISPs (Fig. 1). Less than 45% of seeds were consumed of barley, hairy vetch, forage radish and white mustard across all ISPs (Fig. 1). We estimated barley seeds to be relatively soft (Table 2), however, a fibrous hull protected the seeds, which
might have been difficult for the ISP to chew through. The reason why consumption of hairy vetch seed was low might be a combination of its large size and hard seed coat. Honek et al. (2003) found a strong relationship between carabid body mass and the average mass of its preferred seeds \( (P < 0.001) \), three of our ISPs may be too small to adequately feed on hairy vetch. Additionally, we estimated that hairy vetch seeds would require 11.92 MPa to break, based on the values determined by Rybiński et al. (2009) for common vetch \( (Vicia sativa L.) \), a close relative of hairy vetch. This estimate is 42% higher than the estimated MPa required to break velvetleaf seeds (Lundgren and Rosentrater, 2007), and may not have been possible for ISPs to overcome. Both forage radish and white mustard are brassicas and produce glucosinolates, which are defense compounds that might deter feeding (Hopkins et al., 2009) and lower ISP preference.

Choice trials
Cover crop seed preference results from the choice trials differed slightly from the no choice trials, indicating the availability of seed from other plant species influences ISP seed preference. Consistent with the no choice trials, hairy vetch was the least preferred cover crop species by all ISPs (Fig. 2). Interestingly, forage radish and white mustard were among the most preferred cover crop species for \( P. melanarius \) and \( G. pennsylvanicus \), respectively, suggesting that a plant species might be undesirable when it is the only species available, but preferred when other species are present (Fig. 2). In a similar preference experiment, Honek et al. (2003) found the preference of two carabid species for a reference seed was affected by what other seeds were offered. Previous research suggests that ISPs will change consumption patterns in choice and no choice trials as a result of nutrient and allelochemical interactions (Behmer, 2009). In our research, forage radish and white mustard may not have been preferred by \( P. melanarius \) and \( G. pennsylvanicus \) in no choice trials because the ISPs were ‘compromise feeding’, but preferred in choice trials because other seeds could help satisfy nutritional requirements (Behmer, 2009).

Preference of cover crops by individual invertebrate seed predators
Results from both no choice and choice trials support our hypothesis that seed predation would vary by ISP and plant species (Figs. 1–4). The results also support our hypothesis that seed predation would be influenced by morphological and nutritional traits of seeds; however, the relationship between seed traits and consumption varied by ISP and between No choice and choice trials (Table 4).

\textit{Harpalus pensylvanicus} consumed 30% of total seeds given in no choice trials and 20% of total seeds given in choice trials.
Harpalus pensylvanicus consumed giant foxtail more than all other plant species, followed by three cover crop species, annual ryegrass, pearl millet and red clover (Figs. 1 and 2). A negative relationship was observed between seed mass and the probability of seed predation in no choice \((P < 0.001)\) and choice \((P = 0.01)\) trials (Table 4). Seed protein content was also negatively related to the probability of seed predation in choice trials \((P = 0.03)\) (Table 4). Other studies have shown that \(H.\) pensylvanicus prefers small, hard seeds (Lundgren and Rosentrater, 2007), especially giant foxtail (White et al., 2007; Ward et al., 2014).

Pterostichus melanarius consumed 13% of total seeds given in no choice trials and 16% of total seeds given in choice trials. In no choice trials, pearl millet was consumed more than twice as much as any other seed species (Fig. 1). In choice trials, there was no difference in preference between pearl millet, forage radish and triticale (Fig. 2). A positive relationship was observed between seed volume and the probability of predation in no choice \((P < 0.001)\) and choice \((P = 0.001)\) trials (Table 4). A negative relationship was also observed between seed oil \((P < 0.001)\) content and the probability of predation in choice trials \((P = 0.005)\) (Table 4). Pterostichus melanarius is known as a slug predator (Symondson et al., 1996), but will consume seeds (Fawki et al., 2005) in the spring (Mauchline et al., 2005). Kulkarni et al. (2015b) found \(P.\) melanarius will consume canola seeds (Brassica napus L.). Petit et al. (2014) found \(P.\) melanarius preferred seeds of shepherd’s purse \((Capsella bursa-pastoris (L.) Medic.)\) and Canada thistle \((Cirsium arvense L.)\) more than common groundsel \((Senecio vulgaris L.)\) and dandelion \((Taraxacum officinale G.H. Weber ex Wiggers)\) and field violet \((Viola arvensis Murr.).\) In addition to our results showing that it behaved more like a pest than a beneficial organism (i.e., preferred cover crop seeds over weed seeds), seed preference of \(P.\) melanarius should be studied further because it has been introduced to North America and its range is expanding (Hajek et al., 2007).

Allonemobius allardi consumed 21% of total seeds given in no choice trials and 16% of total seeds given in choice trials. In no choice trials, \(A.\) allardi consumed common ragweed, pearl millet, cereal rye and triticale with equal preference (Fig. 1). In choice trials, triticale was the most preferred seed species, and common ragweed was rarely consumed (Fig. 2). A positive relationship was observed between seed volume and the probability of predation in no choice \((P < 0.001)\) and choice \((P = 0.001)\) trials. A negative
Table 4. Intercept and slope from logistic regression (Equations 3 and 4) and associated P-values of the effect of six seed traits on seed predation by four invertebrate seed predators in no choice (upper) and choice (lower) trials. Oil and protein content were expressed as the proportion of seed weight.

| Seed trait     | H. pensylvanicus | P. melanarius | A. allardi | G. pennsylvanicus |
|----------------|------------------|---------------|------------|-------------------|
|                | Equation         | P             | Equation   | P                 | Equation | P               |
| Mass (mg)      | −0.21–0.06x      | <0.001        | −1.97–0.005x | 0.56             | −1.26–0.003x | 0.71             | 0.54–0.007x | 0.71             |
| Volume (mm³)   | −0.94–0.003x     | 0.38          | −2.31 + 0.02x | <0.001         | −1.66 + 0.01x | <0.001          | −0.32 + 0.03x | <0.001          |
| Strength (MPa) | −0.82–0.06x      | 0.08          | −2.08–0.14x | <0.001        | −0.53–0.13x    | 0.002           | 0.76–0.12x | 0.10             |
| Oil content    | −0.88–0.70x      | 0.46          | −2.48 + 1.56x | 0.10          | −1.17–1.13x    | 0.21            | 0.89–3.54x | 0.03             |
| Protein content| −0.61–1.15x      | 0.19          | −2.41 + 0.52x | 0.67          | −0.96–1.45x    | 0.15            | 0.58–0.63x | 0.78             |
| O:P            | −0.68–0.38x      | 0.08          | −1.90–0.006x | 0.98          | −1.12–0.38x    | 0.13            | 1.12–1.28x | 0.02             |
|                |                  |               |            |                   |          |                 |             |                  |
| Choice         |                  |               |            |                   |          |                 |             |                  |
| Mass (mg)      | −0.37–0.01x      | 0.01          | −0.69–0.005x | 0.44            | −0.96–0.02x   | 0.01            | −0.38–0.004x | 0.57            |
| Volume (mm³)   | −0.52–0.001x     | 0.67          | −0.82 + 0.008x | 0.02         | −1.07 + 0.02x  | 0.001           | −0.52 + 0.009x | 0.04            |
| Strength (MPa) | −0.72–0.006x     | 0.78          | −0.27–0.06x  | 0.05           | −0.74–0.02x   | 0.58            | −0.17–0.03x | 0.39             |
| Oil content    | −0.43–1.07x      | 0.06          | −0.81 + 1.7x | 0.005         | −0.49–1.23x   | 0.06            | −0.34–0.12x | 0.88             |
| Protein content| −0.22–1.48x      | 0.03          | −0.76 + 0.66x | 0.43          | −0.15–2.22x   | 0.002           | −0.40 + 0.32x | 0.74             |
| O:P            | −0.41–0.27x      | 0.06          | −0.75 + 0.26x | 0.14          | −0.50–0.29x   | 0.11            | −0.25–0.15x | 0.46             |

O:P is the oil to protein content ratio. Slopes of no choice equations can be interpreted as the increase or decrease on the log odds of a seed being consumed. Slopes of choice equations can be interpreted as the increase or decrease in the Vanderploeg and Scavia electivity index (E*) of a seed.
relationship was observed between seed strength ($P = 0.002$) and the probability of predation in no choice trials (Table 4). Greater seed mass ($P = 0.01$) and protein ($P = 0.002$) content were negatively related to the probability of predation in choice trials (Table 4). Despite being touted as an important seed predator, we are aware of no studies that have evaluated its seed preference (Lundgren, 2009). One field study correlated the activity of A. allardi with predation of giant foxtail seeds (O’Rourke et al., 2006).

Gryllus pennsylvanicus consumed 61% of total seeds given in no choice trials and 51% of total seeds given in choice trials. In the no choice trials, pearl millet, cereal rye, triticate and red clover were consumed more than velvetleaf (Fig. 1). A positive relationship was observed between seed volume and the probability of predation in no choice trials ($P < 0.001$), and in choice trials ($P = 0.04$) (Table 4). Seed oil content ($P = 0.03$) and oil-to-protein ratio ($P = 0.002$) were negatively related to the probability of predation in no choice trials (Table 4). Carmona et al. (1999) found that G. pennsylvanicus fed on seeds of different size and strength, Lundgren and Rosentrater (2007) determined seed preference to be unrelated to seed traits, and Van der Laat et al. (2015) found G. pennsylvanicus preferred smaller seeds to larger seeds.

**Effect of invertebrate seed predator on seed consumption by plant species**

ISPs did not consume or consumed very little hairy vetch and velvetleaf seed (Figs. 3 and 4). Seed consumption by ISPs varied for all other species in the no choice trials. Gryllus pennsylvanicus consumed more seeds than the other three ISP for barley, pearl millet, cereal rye, crimson clover, red clover, triticate and common ragweed (Fig. 3). Seed consumption by H. pensylvanicus did not differ from G. pennsylvanicus for annual ryegrass or giant foxtail, and they both consumed more seed than P. melanarius and A. allardi for these two plant species (Fig. 3). Electivity index ($E^*$) by ISPs was the same for common ragweed, barley and pearl millet, but varied for all other species in choice trials (Fig. 4). $E^*$ did not differ between G. pennsylvanicus and A. allardi for triticate, which they both preferred more than either H. pensylvanicus or P. melanarius (Fig. 4). $E^*$ did not differ between G. pennsylvanicus and H. pensylvanicus for giant foxtail and red clover, which they both preferred more than either P. melanarius or A. allardi (Fig. 4). $E^*$ did not differ between G. pennsylvanicus and P. melanarius for white mustard, which they both preferred more than H. pensylvanicus or A. allardi (Fig. 4).

Differences in seed preference between ISPs can probably be explained by ISP mouthpart strength, size and feeding ecology. Members of the Harpalus genus have relatively large mandibular adductor muscles (Evans and Forsythe, 1985) and strong mandibles (Acorn and Ball, 1991), which likely enable H. pensylvanicus to easily destroy and consume small hard seeds (Lundgren and Rosentrater, 2007). Gryllus pennsylvanicus generally consumed more seeds than the other ISPs, possibly because of its relatively large size and higher caloric intake requirements compared with the other ISPs. Moreover, G. pennsylvanicus is an aggressive and territorial species that has evolved powerful mouthparts for fighting (Jang et al., 2008; Judge and Bonanno, 2008), which may also be excellent tools for seed destruction. The relatively lower predation and preference patterns of P. melanarius and A. allardi may be due to their feeding ecology. Both species are known for consuming other invertebrates and plant material (Lundgren and Harwood, 2012), so their mouthparts may not be suited to feeding exclusively on seeds.

**Experiment considerations**

In our research, we offered ISPs 26 seeds regardless of seed size or volume. Although we standardized the number of seeds, we also could have standardized the mass of seeds or the volume of seeds offered to ISP. Most ISP seed preference research has used the total seed biomass consumed to establish preference (e.g., Honek et al., 2006; Lundgren and Rosentrater 2007; Ward et al., 2014), but this metric is not used exclusively (e.g., Carmona et al., 1999; Petit et al., 2014). In our research, we used the number of seeds destroyed instead of total seed biomass consumed because it simplified the experimental process. It was noted that all insects focused their feeding near the seed embryo, and rarely consumed a whole seed before consuming a new one.

In previous seed preference research, trials have often been conducted using imbibed or wetted seeds. Dry seeds were used in our experiment because it better reflects seed conditions immediately following weed seed shed and broadcast seeding for cover crops. It is unclear if using dry seeds vs imbibed seeds will alter ISP seed preference. Research on the material properties of seeds (e.g., Bargale and Irudayaraj 1995; Babić et al., 2011) consistently shows that the force required to break a seed decreases with increasing moisture content. If the force required to break a seed determines seed predation, then preference should change when hard, unpalatable, seeds have high moisture content. However, Law and Gallagher (2015) showed that H. pensylvanicus preference trends between imbibed and dry seeds did not differ. Our analyses of the relationships between seed traits and ISP preference were limited by the fact that some trait measurements were not performed on seeds that were used for the preference tests (Table 1). Values for seed strength as well as oil and protein content were from previous literature. Nonetheless, results from these regression analyses provide useful information about the direction of the relationship (i.e., positive or negative).

**Management implications**

Although ISPs play an important role in limiting weed populations, the results from this research show that they can also be pests by consuming seeds of commonly grown cover crop species. All four ISP species that we tested readily consumed cover crop seeds in both no choice and choice preference trials. These four species are active seed predators from early summer through autumn in the Northeast region of the USA (O’Rourke et al., 2006; Hajek et al., 2007; Lundgren, 2009; Ward et al., 2014). Given the overlap in timing of cover crop seeding with peak ISP population size, ISPs are likely limiting cover crop establishment, especially when seeds are left on the soil surface. However, other granivores such as birds and mice can also reduce cover crop establishment based on field trials showing greater seed predation in open vs caged seed cards that exclude vertebrates (Youngerman et al., 2015). Future research should be conducted to further quantify the temporal patterns of ISP activity density and the extent to which ISPs are consuming cover crop seeds in crop fields. Farmers and the seed industry can use seed preference information to guide cover crop species selection, choosing species that are less likely to be consumed by ISPs for broadcast seeding. Based on our results, farmers might select hairy vetch and barley if they are concerned about seed losses to ISPs. Farmers can also reduce seed losses to ISPs by using planting equipment that
deposits seed and covers it with soil, thus reducing seed accessibility to ISPs (Kulkarni et al., 2015a), while increasing seed-to-soil contact and improving crop establishment (Fisher et al., 2011).

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