Research Paper

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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 predation 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 sanctaecrucis* 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 veletis* 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.*, 2015*a*).

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 cover cropped is 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 and Van Eerd, 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.*, 2015*b*), 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

Table 1. Seed trait values for species included in preference trials

Scientific name	Common name	Mass (mg)	Length (mm)	Width (mm)	Volume (mm³)	Strength (MPa)	Oil (%)	Protein (%)	O:P
Hordeum vulgare L.[a]	Barley	24.0	9.71	3.00	68.64	6.90[1]	1.30[6]	13.00[10]	0.10
Lolium multiflorum Lam.[a]	Annual ryegrass	3.1	5.28	1.40	8.13	–[b]	1.67[7]	9.50[7]	0.18
Pennisetum glaucum L.[a]	Pearl millet	5.8	3.24	1.89	9.09	–	5.78[7]	15.20[7]	0.38
Raphanus sativus L.[a]	Forage radish	16.7	3.88	2.96	26.70	–	40.85[7]	30.60[7]	1.33
Secale cereale L.[a]	Cereal rye	33.6	7.35	2.83	46.23	5.12[2]	4.90[7]	17.10[7]	0.29
Sinapis alba L.[a]	White mustard	4.7	2.19	2.00	6.88	–	31.50[7]	31.70[7]	0.99
Trifolium incarnatum L.[a]	Crimson clover	5.0	2.58	1.92	7.47	–	4.30[7]	40.95[7]	0.11
Trifolium pratense L.[a]	Red clover	1.5	1.96	1.45	3.24	–	8.55[7]	37.15[7]	0.23
× *Triticosecale* Witt.[a]	Triticale	41.0	7.64	3.25	63.38	8.74[3]	2.40[8]	12.50[11]	0.19
Vicia villosa Roth.[a]	Hairy vetch	22.7	3.52	3.29	29.92	11.92[4]	0.70[7]	30.20[7]	0.02
Abutilon theophrasti Medik.[c]	Velvetleaf	9.8	3.32	2.97	23.00	8.37[5]	18.70[7]	12.90[7]	1.45
Ambrosia artemisiifolia L.[c]	Common ragweed	4.8	3.84	2.12	13.55	0.59[5]	18.31[9]	22.62[9]	0.83
Setaria faberi Herrm.[c]	Giant foxtail	1.2	2.36	1.34	3.33	8.74[5]	6.73[7]	16.43[7]	0.41

Seed length and width were determined by the average measurements of 50 seeds. Seed volume was estimated as the volume of a cylinder using: volume = $\pi \times$ length $\times (0.5 \times$ width$)^2$. Strength is the compressive yield strength (i.e., the amount of force per unit area required to break the seed), and was estimated from the literature (references below); strength for references 1–3 was reported in Newtons and converted to MPa based on our area measurements for each seed. Oil and protein are expressed as the % total seed weight. O:P is the oil-to-protein ratio of each seed species.

[1]Bargale and Irudayaraj (1995); [2]Dziki and Laskowski (2007); [3]Babić *et al*. (2011) (taken as the average for three wheat varieties); [4]Rybiński *et al*. (2009) (from the related *V. sativa*); [5]Lundgren and Rosentrater (2007); [6]Ryan *et al*. (2007); [7]Royal Botanic Gardens Kew (2017); [8]Price and Parsons (1975); [9]Roedel and Thornton (1942); [10]Stoger *et al*., (2005); [11]Linnemann and Dijkstra (2002).
[a]Cover crop species.
[b]A dash indicates no data are available.
[c]Weed species.

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 (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 of the same species were placed in a single container. Containers were placed in a large plastic tub with a lid to maintain darkness, and the tub was stored in a refrigerator at 5–7°C for 4 days. Cool and dark conditions prevent cannibalism during the starvation period (Honek *et al*., 2003). The duration of starvation used in this research (i.e., 4 days) was within the range reported in the literature (Honek *et al*., 2006; Lundgren and Rosentrater, 2007; White *et al*., 2007; Petit *et al*., 2014; Ward *et al*., 2014). After this starvation period, beetles and crickets were used in preference trials.

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

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[a]	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

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.
[a]Data are from www.wunderground.com.

Table 3. The number of choice and no choice replicate trials of each plant species for all ISPs.

	Number of replicate trials			
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

function (package lme4). However, models were overdispersed (package blmeco) and required optimizers to extend the maximum number of model iterations for convergence. Therefore, following the decision tree in Bolker *et al.* (2009), models were reanalyzed with glmmPQL (package MASS). This function uses penalized quasi-likelihood to estimate the parameters of a model to maximize the probability of the observed data (Bolker *et al.*, 2009). A mixed-model analysis of variance (ANOVA) (Wald χ^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:

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

where W_i is:

$$W_i = \frac{(r_i/p_i)}{\sum(r_i/p_i)} \quad (2)$$

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

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 × 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 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 ISP preference (using $E^\star$ as a proxy) was assessed with linear mixed-effect models. 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 $E^\star$ associated with each predictor trait. No choice trial intercepts and slopes are less intuitive to interpret because they are a component of the logit link of the glmm binomial model.

The generalized linear models used for no choice trait analyses suppose that seed predation has a binomial distribution whose log-odds vary linearly with an independent predictor, in this case a seed trait. The simplified log-odds equation is expressed in Equation (3):

$$\log\left(\frac{P}{1-P}\right) = \beta_0 + \beta_1 X_1 \qquad (3)$$

where P is the probability of success (seed is consumed), $1-P$ is the probability of failure (seed is not consumed), β_0 is the intercept coefficient and β_1 is the coefficient (slope) of the predictor X_1. The log-odds equation can be expressed in terms of probability through the following rearrangement in Equation (4):

$$\frac{P}{1-P} = e^{\beta_0 + \beta_1 X_1} \;\; \rightarrow \;\; P = \frac{e^{\beta_0 + \beta_1 X_1}}{1 + e^{\beta_0 + \beta_1 X_1}} \qquad (4)$$

Unless a value for the X_1 is provided, the intercept and slope coefficients determined by the model can only be interpreted in terms of log-odds. For example, when the slope and intercept are determined, they can be interpreted as a one-unit increase in X_1 will result in the increase of β_1 on the log-odds of 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 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. pensylvanicus*. Lundgren and Rosentrater (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. pensylvanicus* 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 weed 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. pennsylvanicus* (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. pennsylvanicus*), 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 Rosentrater, 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. pennsylvanicus* 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
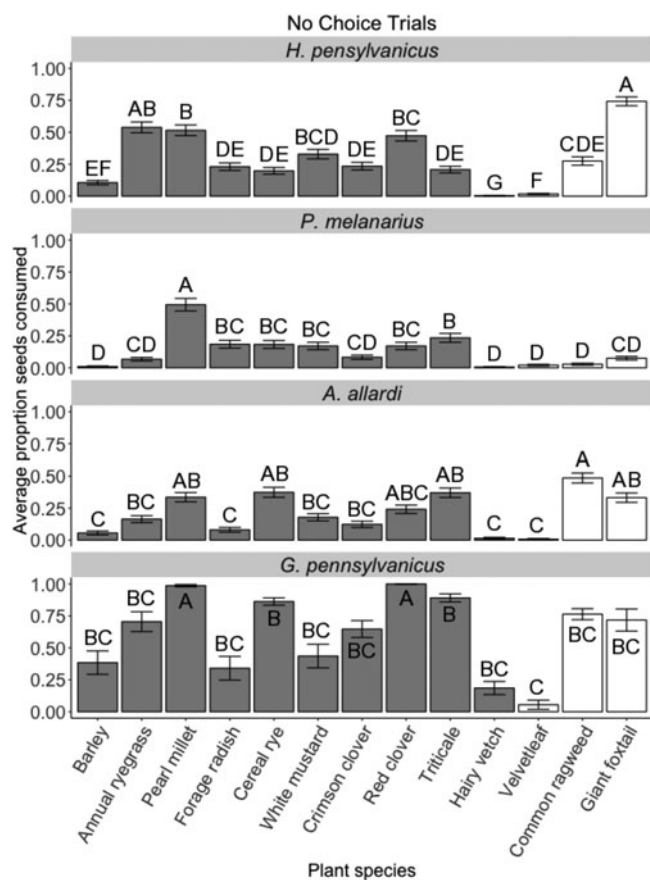
Fig. 1. Cover crop (grey) and weed (white) seed preference of invertebrate seed predators in no choice preference trials. Similar uppercase letters above bars within an invertebrate seed predator panel indicate no significant difference ($P > 0.05$) in preference between plant species.

Fig. 2. Cover crop (grey) and weed (white) seed preference of invertebrate seed predators in Choice preference trials. The electivity index (E^*) is used as a proxy for preference, where a positive value indicates preference and a negative value indicates avoidance. Similar uppercase letters above bars within an invertebrate seed predator panel indicate no significant difference ($P > 0.05$) in preference between plant species.

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
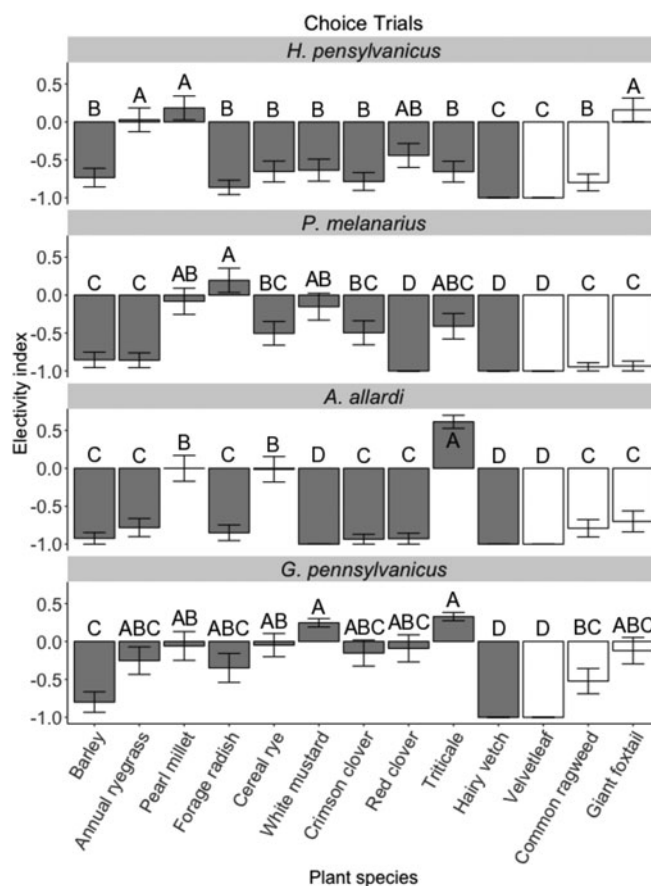
only species available, but preferred when other species are present (Fig. 2). In a similar preference experiment, Honek et al. (2003) found the preference of two carabid species for a reference seed was affected by what other seeds were offered. Previous research suggests that ISPs will change consumption 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).

Harpalus pensylvanicus consumed 30% of total seeds given in no choice trials and 20% of total seeds given in choice trials.
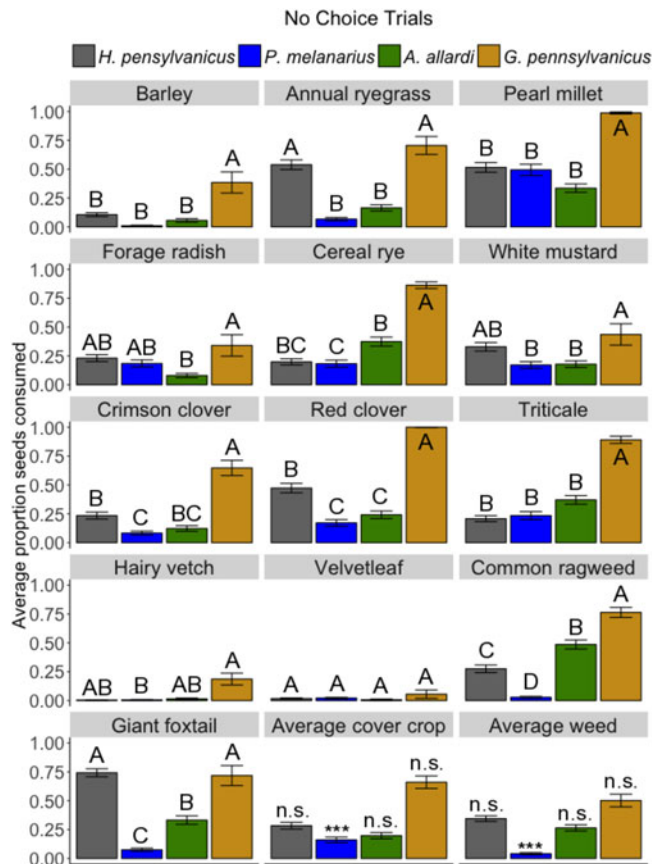
Fig. 3. Seed preference of invertebrate seed predators in no choice preference trials. Similar uppercase letters above bars within plant species panels indicate no significant difference ($P > 0.05$) between invertebrate seed predators for each plant species. Seed type (weed *vs* cover crop). Lower right panels show comparison of weed *vs* cover crop across each of the four invertebrate seed predators with an average seed preference pooled over all cover crop (left side) and weed (right side) species; n.s. indicates no significant difference between weeds and cover crops within an invertebrate seed predator; ***indicates a significant difference ($P < 0.001$).

Fig. 4. Seed preference of invertebrate seed predators in choice preference trials. Similar uppercase letters above bars within plant species panels indicate no significant difference ($P > 0.05$) between invertebrate seed predators for each plant species. The electivity index (E^*) is used as a proxy for preference, where a positive value indicates preference and a negative value indicates avoidance. Lower right panels show comparison of weed *vs* cover crop across each of the four invertebrate seed predators with average E^* pooled over all cover crop (left side) and weed (right side) species; n.s. indicates no significant difference between weeds and cover crops within an invertebrate seed predator; **indicates a significant difference ($P = 0.01$).

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 ($P = 0.02$) trials (Table 4). A negative relationship was observed between seed strength and the probability of predation in no choice ($P < 0.001$) and choice ($P = 0.05$) trials (Table 4). A positive 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
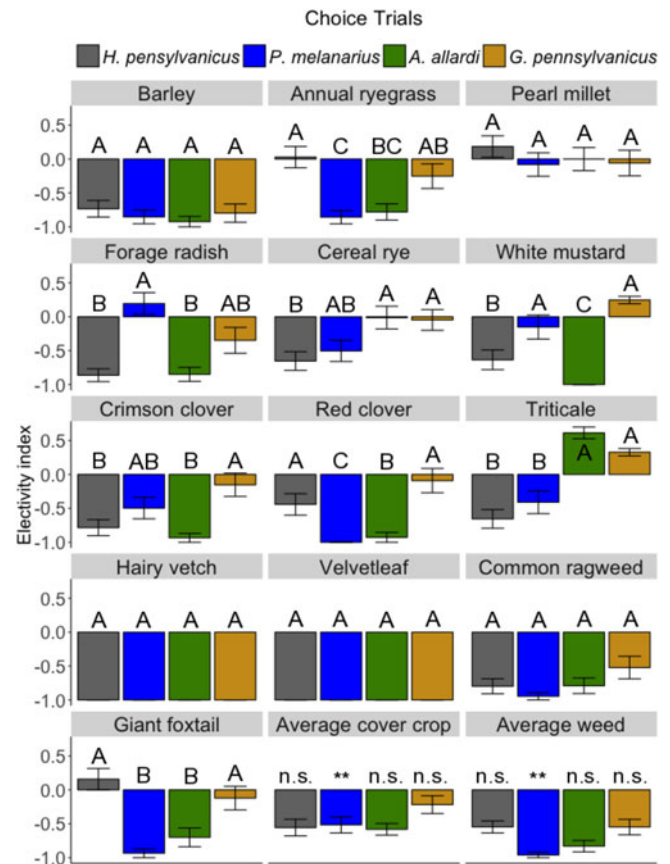
known as a slug predator (Symondson *et al.*, 1996), but will consume seeds (Fawki *et al.*, 2005) in the spring (Mauchline *et al.*, 2005). Kulkarni *et al.* (2015b) found *P. melanarius* will consume canola seeds (*Brassica napus* L.). Petit *et al.* (2014) found *P. melanarius* preferred seeds of shepherd's purse [*Capsella bursa-pastoris* (L.) Medic.] and Canada thistle (*Cirsium arvense* L.) more than common groundsel (*Senecio vulgaris* L.), 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	Equation	P
No choice								
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 (mm^3)	−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	0.002
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 (mm^3)	−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, triticale 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, triticale 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 triticale, 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.*, 2015*a*), while increasing seed-to-soil contact and improving crop establishment (Fisher *et al.*, 2011).

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