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The strength of seeds and their destruction by granivorous insects

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Abstract The influence of seed structure and strength on their destruction by granivores is central to understanding the dynamics of granivore-plant interactions. For up to nine seed species, the effects of seed size (cm^3), mass (mg), density (mg/cm^3) and coat strength (MPa) on the damage inflicted by three post-dispersal granivores (*Harpalus pensylvanicus*, *Anisodactylus sanctaecrucis*, and *Gryllus pennsylvanicus*) were evaluated. Seed destruction rates by *G. pennsylvanicus* were statistically unrelated to the size and toughness of the seeds. Seed densities significantly affected their destruction by *A. sanctaecrucis* and *H. pensylvanicus*, as did seed size, mass, and strength in *H. pensylvanicus* under choice conditions. The carabid beetles destroyed more of the small, denser seeds with stronger seed coats. The results show that different granivores are able to distinguish the structural strength and physical density of seeds as well as seed size. The relative ability of granivores to detect these seed characteristics offers a way in which diverse communities of post-dispersal insect granivores can persist within a single habitat. The authors redefine how the strength of biological structures should be evaluated in ecological studies, using guidelines commonplace in the field of engineering.

Keywords Biological control · Carabidae · Granivory · Gryllidae · Seed coat · Seed predation

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Introduction

Seeds are a nutritious and abundant food for epigeal organisms, and suffer high levels of mortality by post-dispersal granivore communities (Crawley 2000). Insects are frequently important components of these communities. This is particularly so in desert systems, where harvesting ants are abundant (Brown et al. 1979; MacMahon et al. 2000; Tevis 1958), and in temperate managed habitats such as agroecosystems, where granivorous carabids (Coleoptera: Carabidae, particularly Harpalini and Zabrini) and crickets (Orthoptera: Gryllidae: Nemobiinae and Gryllinae) frequently abound (Gallandt et al. 2005; Lundgren et al. 2006; Mauschline et al. 2005; Menalled et al. 2000). The carabids and crickets have earned an increasing appreciation from applied scientists as potential mortality sources for agronomic weed seeds. Within a habitat, insect granivore communities can be quite speciose (Berg 1975; Lundgren et al. 2006; MacMahon et al. 2000), and how these insects divide seed resources among each other remains an important question to ecologists and biological control scientists alike.

Granivorous insect communities distinctly prefer certain seed species, and a number of insect and seed characteristics influence their preferences. On one level, seed preferences by insects are influenced by the size of the seed predator; it is presumed that, all else being equal among foods, a seed predator will attack and consume the largest seed that it can manage (Schoener 1971). However, seeds are far from defenseless (Janzen 1971), and seed chemistry (Bell and Janzen 1971; Janzen et al. 1976), external appendages (Azcarate et al. 2005; Beattie and Culver 1981; Pulliam and Brand 1975), and nutritional quality (Crist and MacMahon 1992; Pizo and Oliveira 2001) are all known to influence the preferences of granivorous insects.

Seed characteristics such as structural strength of the coat and core also are known to serve defensive roles. A number of studies suggest that the strengths of the seed and seed coat dictate which seeds are preferred by granivorous birds (Smith 1990; van der Meij and Bout 2004), rodents (Janzen 1982; Smith 1970), and insects (Brust and House 1988; Honek et al. 2003; Morrison et al. 1997; O'Dowd and Hay 1980), but there are few reports where empirical data are used to support these observations. Those that have quantified seed strength evaluated the amount of force (in Newtons; N) used to crack the seed coat (Rodgerson 1998; Smith and Smith 1989; van der Meij and Bout 2000). However, strength is also related to the size of an object; all else being equal, the larger an object gets, the weaker it gets. Thus, measures of relative strength for objects that do not account for size of the object are confounded by it (Stroshine 2001). An evaluation of relative seed strength that accounts for differences in seed size (in Pascals; Pa, or N/mm^2) on granivore preferences remains to be conducted.

We examined the structural characteristics of some agronomically important seeds encompassing a range of sizes. Specifically, we examined seed mass, volume, density and compressive yield strength (CYS; accounting for seed size). These parameters were then related to the destruction rates of these seeds by three insect granivores that are frequently encountered in temperate managed habitats. The results provide a critical consideration in interpreting how granivore communities discriminate seed resources such that diverse species assemblages can share the seed resources within a single habitat.

Methods

Insects and seeds

Three granivorous insect species were selected based on their regional prevalence as abundant post-dispersal granivores in cropland, including two carabids, *Anisodactylus sanctaecrucis* and *Harpalus pensylvanicus*, and a cricket, *Gryllus pennsylvanicus* (Brust and House 1988; Carmona et al. 1999; Lundgren 2005; Lundgren et al. 2006). Using dry pitfall traps in agricultural fields, adult carabids were collected in Champaign, IL, and adult *G. pennsylvanicus* were collected in Brookings, SD. Once collected, the adult insects were maintained on cat food (Iam's Original Formula, Iam's Company, Dayton, OH). Water was offered to the crickets in the form of a saturated cotton ball, and carabids received water in their dampened soil substrate. Insects were transferred to a Petri dish (100 mm diam.) and starved for 48 h prior to the assay; water was provided as a saturated cotton wick. Agronomically relevant seed species were selected to represent a range of sizes and strengths. Seeds (barring the crop species) were ordered from V & J Seeds (Woodstock, IL) and Valley Seed Service (Fresno, CA). All seeds were examined microscopically, and damaged ones were discarded.

Feeding assays

Feeding assays were conducted under choice and no-choice conditions, varying among seed predators largely because of restrictions in our ability to collect sufficient numbers of the different seed predators at key times of the experiment. Also, seed species offered to the granivores differed, based on the availability of the seeds at the time of the assays. All assays were conducted in growth chambers (environmental conditions were 27°C, 14:10 [L:D]) soon after collecting the seed predators in the field.

Anisodactylus sanctaecrucis of mixed sex ratio were offered seeds under no-choice conditions only. In each treatment, beetles (n = 15 for each seed species) were provided 0.25 g of a designated seed species and the number of seeds provided was recorded for each individual. Assays were conducted in 60 mm diam. Petri dishes, and water was provided as a saturated cotton wick. Seed species offered to *A. sanctaecrucis* were lambsquarters (*Chenopodium album* L.), alfalfa (*Medicago sativa* L.), crabgrass (*Digitaria sanguinalis* (L.) Scop.), ivyleaf morning glory (*Ipomoea hederacea* (L.) Jacq.), velvetleaf (*Abutilon theophrasti* Medic.), or broccoli (*Brassica oleraceae* L., var. Brigadier).

Gryllus pensylvanicus females were offered seeds under choice conditions only. In each treatment, crickets (n = 16) were provided with 0.15 g of each seed species that were gently affixed to the Petri dishes in discrete and equidistant patches using double-sided tape (Scotch® tape, 3 M, St. Paul, MN). This tape did not visibly reduce the ability of crickets to consume the seeds. In addition to the seed species offered to *A. sanctaecrucis*, seeds of giant foxtail (*Setaria faberi* Herrmann), and redroot pigweed (*Amaranthus retroflexus* L.) were provided.

The feeding behavior of *Harpalus pensylvanicus* was examined under choice and no-choice conditions. Beetles (n = 20 for choice; n = 15 per seed species for no-choice) of mixed sex ratio were provided with approximately 0.15 g of each seed species. The seeds offered to *H. pensylvanicus* were the same as those of *G. pennsylvanicus*, except that giant ragweed (*Ambrosia trifida* L.) seeds were also included. The difference between choice and no-choice assays is that all seeds were placed in a single Petri dish for the choice assays, and the seed species were offered individually in the no-choice experiment. All assays were conducted in 100 mm diam. Petri dishes, with a saturated cotton wick used as a water source.

After 48 h, the number of seeds destroyed by each beetle was recorded and divided by 2 to arrive at the seeds destroyed per day. After the feeding assays were terminated, the granivores were frozen at –20° C for at least 24 h, dried at 60° C for at least 24 h and weighed to the nearest 0.00001 g on an electronic balance. A seed was scored as destroyed if its coat was cracked. Thus, the measurement compared is not the actual mass of seeds consumed, as insects frequently only consumed portions of seeds, often leaving much of the external covering. The proportion of each seed species that was destroyed per granivore was calculated for each seed. Data from granivores that died during the assay were omitted from the analyses.

Seed traits

Seed mass (mg) and volume (cm^3) were measured for each seed species, and seed density (mg/cm^3) was then determined. The number of seeds per 0.15 g was calculated 13–15 times for each seed species. The effects of the actual dimensions of the seeds on granivory are difficult to quantify because of heterogeneity of the seed itself. Seeds varied substantially in their lengths, widths, and depths, but in all seed species there was at least one equivalent vertex that the granivores could use as a starting place for cracking the seed coat. For this reason, we used seed volume as a measure of overall seed size. Volume was calculated through fluid (water, or 70% ethanol when the seeds would not sink in the water) displacement. Seed density was calculated as the ratio of seed mass to volume.

Following the methods described by Stroshine (2001), the strength (compressive yield strength, CYS) of each seed was measured with an Instron compression tester (Model 5564, Instron Corporation, Canton, MA), using a 50 N loadcell. One seed at a time was placed on a fixed, flat lower plate, then a flat upper plate was lowered at a constant rate of 0.1 mm/min. The mean area (length × width) of the seed surfaces in contact with the plates were inputted into the analysis for each species. During testing, the force applied to the upper plate was measured, as was travel distance; thus stress and strain were determined via the compression tester's computer control software. Compression data were analyzed and seed coat fracture strengths were determined for each seed ($n = 20$; except for crabgrass, where $n = 15$). Throughout the course of experimentation, however, not all of the seeds produced useful information. Thus, the resulting data were screened, and actual sample sizes were accounted for in the subsequent statistical analysis.

Data analysis

The mean proportion of each seed species destroyed per beetle were compared for each predator using ANOVAs, and significantly different means ($P < 0.05$) were separated using least significant distance (LSD) comparisons (SYSTAT Software 2004). Least squares linear models using all the seed species examined were used to compare the correlations of inverse of seed volume, inverse of mass, density, and CYS (SYSTAT Software 2004). The mean destruction rates were compared with the inverse of mass and inverse of volume, density, and strength of seeds using least squares linear models.

Results

Feeding assays

All species displayed strong preferences for certain seeds, which generally varied among the granivores (Figs. 1–3). One consistent observation among the granivores is that the largest seeds, velvetleaf and morning glory, were only minimally damaged (<10% of these seeds) by the insects. Lambsquarters were the most acceptable seeds to *A. sanctaecrucis* (50 seeds damaged per beetle) (Fig. 1), which were damaged by at least 1.6 times the rate of the lesser damaged species. The seed destruction rates differed depending on whether seeds were offered to *H. pensylvanicus* under choice or no-choice conditions (Fig. 2). Lambsquarters seeds were the most acceptable and preferable species for *H. pensylvanicus* (100 seeds destroyed per beetle in the choice comparisons). Pigweed was also in the top three damaged species under both choice and no-choice conditions, but the remainder of the seeds varied in their

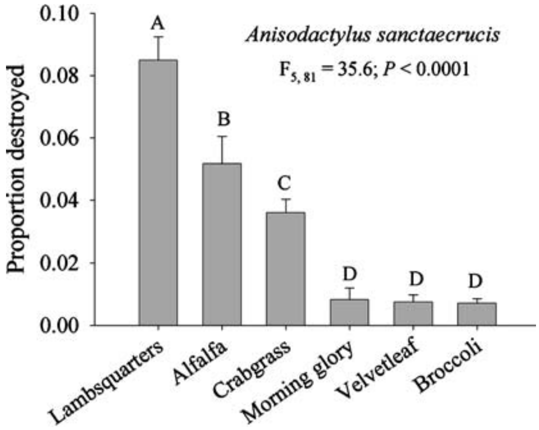

Fig. 1 The proportion of seeds destroyed by *Anisodactylus sanctaecrucis* under no-choice conditions

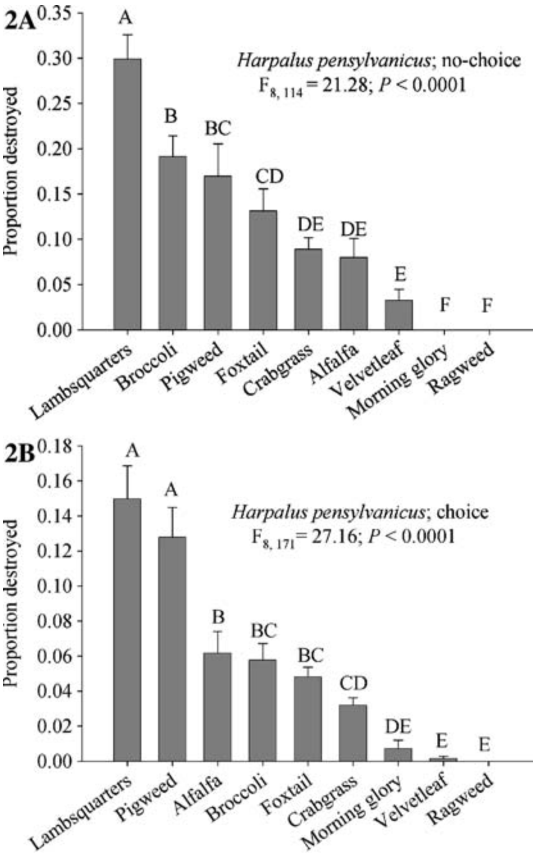

Fig. 2 The proportion of seeds destroyed by *Harpalus pensylvanicus* under no-choice (2A) and choice (2B) conditions

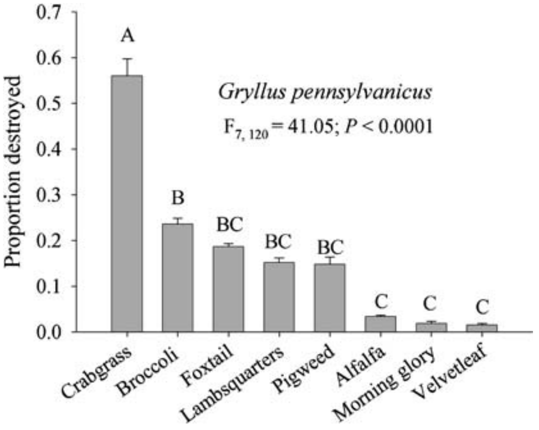

Fig. 3 The proportion of seeds destroyed by *Gryllus pennsylvanicus* under choice conditions

acceptability to and preference by *H. pensylvanicus*. *Gryllus pennsylvanicus* was particularly damaging to the grass species offered in this experiment, destroying more than twice the proportion of crabgrass seeds as any other seed species (90 seeds per cricket; Fig. 3). Mean ± SEM (n) dry weight for the three seed predators were: *A. sanctaecrucis*: 14.55 ± 0.47 mg (87), *H. pensylvanicus*: 56.95 ± 1.37 mg (123), *G. pennsylvanicus*: 173.58 ± 6.00 mg (20).

Seed traits

Lighter, smaller seeds were significantly stronger and denser than large, heavy seeds. Seed volumes were inversely related to seed strength ($F_{1,\,7} = 30.8$, $P < 0.001$, $r^2 = 0.82$) and density ($F_{1,\,7} = 8.32$, $P = 0.024$, $r^2 = 0.54$). Seed mass was also inversely correlated with strength ($F_{1,\,7} = 24.56$, $P = 0.002$, $r^2 = 0.78$) and density ($F_{1,\,7} = 7.35$, $P = 0.03$, $r^2 = 0.51$). Regression analysis also revealed that the density of seeds was positively correlated to seed strength ($F_{1,\,7} = 5.52$, $P = 0.05$, $r^2 = 0.44$). Table 1 presents the data for the different seed traits.

Regressions of seed preferences with seed traits

The three granivore species responded differently to the seed parameters. Seed destruction by *G. pennsylvanicus* was entirely unrelated to the different seed traits (volume: $F_{1,\,6} = 0.57$, $P = 0.48$; density: $F_{1,\,6} = 0.06$, $P = 0.82$; mass: $F_{1,\,6} = 0.86$, $P = 0.39$; CYS: $F_{1,\,6} = 0.03$, $P = 0.87$). Destruction rates by *A. sanctaecrucis* were only correlated with the density of the seeds ($F_{1,\,4} = 9.94$, $P = 0.03$), but not the other seed characteristics (volume: $F_{1,\,4} = 2.68$, $P = 0.18$; mass: $F_{1,\,4} = 2.60$, $P = 0.18$; CYS: $F_{1,\,4} = 0.81$, $P = 0.41$). Under no choice conditions, the seed traits did not affect the acceptability of seeds to attack by *H. pensylvanicus* (volume: $F_{1,\,7} = 5.03$, $P = 0.06$; mass: $F_{1,\,7} = 5.03$, $P = 0.06$; density $F_{1,\,7} = 3.36$, $P = 0.11$; CYS: $F_{1,\,7} = 2.95$, $P = 0.12$). However, all of the seed traits strongly influenced destruction rates when *H. pensylvanicus* was offered a choice among the seeds (volume: $F_{1,\,7} = 14.46$, $P = 0.007$; mass: $F_{1,\,7} = 12.52$, $P = 0.009$; density: $F_{1,\,7} = 7.20$, $P = 0.03$; CYS $F_{1,\,7} = 11.07$, $P = 0.01$). *Harpalus pensylvanicus* preferred the stronger, denser seeds of smaller size than the larger, weaker seeds. The results of these analyses are summarized in Table 2.

Discussion

The structure of seeds clearly plays a role in their destruction by granivorous insects. In addition to the size of a seed, the internal strength and density are influential to which seeds a predator will decide to attack under some circumstances. Thus, these structural traits have important ecological and evolutionary consequences for both plant and post-dispersal granivore communities, as well as a functional importance in the biological control of weed seed banks.

Table 1 Summary of seed structural traits[a]

	Strength; MPa (n)	Mass; mg (n)	Volume; cm^3	Density; mg/cm^3
Pigweed	47.81 ± 2.12 (10)	0.33 ± 0.00097 (13)	0.0002110	1,563.98
Lambsquarters	24.38 ± 1.28 (14)	0.43 ± 0.0053 (13)	0.000275	1,563.64
Crabgrass	9.45 ± 1.12 (11)	0.51 ± 0.0028 (14)	0.0003713	1,373.55
Foxtail	8.74 ± 1.26 (18)	1.35 ± 0.015 (15)	0.001385	974.73
Velvetleaf	8.37 ± 0.37 (15)	9.00 ± 0.10 (14)	0.007246	1,242.06
Alfalfa	5.61 ± 0.485 (13)	2.42 ± 0.026 (14)	0.001629	1,485.57
Morning glory	3.95 ± 0.37 (18)	24.65 ± 0.39 (12)	0.02273	1,084.47
Broccoli	3.65 ± 0.24 (18)	4.09 ± 0.021 (15)	0.003623	1,128.90
Ragweed	0.59 ± 0.02 (6)	46.09 ± 2.97 (13)	0.0625	737.44

[a] Data is presented as mean ± SEM

Table 2 Summary of the interactions among seed traits and their destruction rates by three granivorous insects[a]

	Seed traits			
	Mass (mg)	Volume (cm^3)	Density (mg/cm^3)	CYS (MPa)
Anisodactylus sanctaecrucis (no-choice)	NS	NS	+	NS
Harpalus pensylvanicus (no-choice)	NS	NS	NS	NS
Harpalus pensylvanicus (choice)	–	–	+	+
Gryllus pensylvanicus (choice)	NS	NS	NS	NS

[a] Symbols in the table are 'NS' not significant, '–' negative association, '+' positive association. See text for additional information on the analyses

We hypothesize that the size of the granivore restricts the largest seed which it can consume, but within the acceptable size range of seeds for a given granivore, the relative sizes of seeds does not have great bearing on their destruction rates. For example, the largest seeds were undamaged by any of the granivores, suggesting an upper limit beyond which the tested granivores would not attack. Below this upper limit, the granivores reacted very differently to the various seeds. The smallest seed species were the most acceptable to *A. sanctaecrucis*, which left seeds larger than alfalfa undamaged. In contrast, *Gryllus pennsylvanicus* was able to damage seeds smaller than velvetleaf, although these seeds were damaged without regard to structural traits. Our data is consistent with the notion that size filters which seeds are acceptable to the granivore, after which mechanisms other than size begin to dictate destruction rates.

Seed strength or seed density influenced the destruction rates by two of the granivores to different degrees, but in a counterintuitive way. Essentially, the stronger and denser seeds were preferred by the granivores. Seed density was influential in decisions made by *H. pensylvanicus* and *A. sanctaecrucis*, and seed coat strength were correlated with the preferences of *H. pensylvanicus*. It is also noteworthy that although the traits were highly correlated statistically, seed density was evaluated independently of seed size by *A. sanctaecrucis*. The way in which these structural seed traits influence the destruction rates of seeds suggest that the different predators are using distinct mechanisms for assessing the relative quality of seeds.

The difference between compressive yield strength and seed density are critical to understanding the property that seed predators are detecting in the seeds. Seed strength is measuring the hardness of the seed coat, or the force that is required to crack the seed coat and access the internal nutrients. Seed density is a measurement of the relative hardness of the integrity of the entire seed. Thus, it is a measure of the hardness of the internal seed. In the case of *A. sanctaecrucis*, the beetles were able to distinguish the denser seeds and disproportionately destroyed them. Seed size, mass, and seed coat strength are closely related to seed density, but destruction rates by *A. sanctaecrucis* were unaffected by these correlated traits. This indicates that *A. sanctaecrucis* is evaluating a very specific quality of seeds in their decision to attack a seed. In contrast, *Gryllus pennsylvanicus* either could not evaluate the density of the seed without destroying the seed coat, or were unaffected by seed density. For *H. pensylvanicus* under no-choice conditions, the structural seed parameters did not affect their acceptability to the beetles; in a pinch, beetles could consume many of the seeds (exclusions being the largest seed species, as discussed above). But when allowed to choose amongst the seeds, the beetles favored the small, tough seeds with hard seed coats over larger, weaker seeds. A question that remains is why denser seeds with stronger seed coats are the most attractive to these granivorous beetles. Perhaps the stronger seeds have a greater nutritional payoff to the granivores, such that the energy expended in cracking into the seed coat is recouped by the caloric or nutritional contents of the seed. Therefore, if an insect is going to expend the energy to crack the seed coat, then potential nutritional pay-offs override other seed qualities as selective agents.

We found that the relative strengths of the seeds were negatively correlated with seed size, which is in contrast to previous findings that concluded that larger seeds required a greater force (N) to crush them (van der Meij and Bout 2000). One reason for the disparity between previous findings and our results is that we incorporated the area of the seed into our measurement of strength. An object loses strength as it grows, and so the results of previous research are confounded in that they were comparing the force required to break seeds of different sizes (Stroshine 2001). Research which measured the force (N) needed to crush a seed has consistently concluded that the hardness of the seed is a distinguishing factor in the preferences of granivores, and that harder seeds are less preferred (Rodgerson 1998; Smith 1990; van der Meij and Bout 2000). An alternative explanation for some of these findings that would not have been detectable in their analyses may be that the animals truly preferred larger seeds, a factor shown to operate in some granivores. Measuring strength (Pa) instead of force (N) allows us a true measure of the relative strength of seeds that is not confounded by seed size, and we advocate using this measurement in future studies.

Because seeds with the hardest seed coats were differentially preferred by at least one granivore, and other granivores were unhindered by seed coat hardness, this research calls into question the importance of the physical strength of the seed coat in defending relatively small seeds from predation by insects. This is not to say that the seed coat does not play a role in the defense of the seed, only that the protective benefits may rely on mechanisms other than strength. Laboratory feeding observations revealed that imbibing the unpreferred seeds (e.g., morning glory) in water for 24 h, or mechanically removing the seed coat rendered them susceptible to attack by *G. pennsylvanicus* (J. G. L., unpublished data). These observations are supported by literature on post-dispersal granivory by other insects as well (Cardina et al. 1996; Pausch and Pausch 1980; Ready and Vinson 1995), and lend credence to the idea that the seed coat is obstructing granivory. Perhaps phytochemical constituents of the seed coat are more important in restricting granivory of small seeds by insects than the physical strength of the covering itself. These other factors may explain the consumption patterns created by *G. pennsylvanicus* and *A. sanctaecrucis* observed in the current study.

Finally, the results presented here show that the structural integrity of a seed influenced the feeding behavior of three prominent granivores in agricultural fields, but that these insects used different qualifications for deciding whether a seed was worthy of attack. These fine differences in perceiving the structural characteristics of seeds may be one way in which insect granivore communities are able to divide a finite seed resource amongst numerous species within a single habitat. In biological control of weed seeds, determining which granivores are key consumers of target weeds, and what factors mitigate this relationship can facilitate the conservation of influential natural enemies within managed habitats.

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