

Winter Preference for Weed Seed and Waste Grain by Native Mice in Row-Crop Agriculture

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Consumption of weed seeds and waste grains by seed predators is an important ecosystem service that helps to regulate weed and volunteer crop populations in many agricultural systems. The prairie deer mouse is found in a variety of sparsely vegetated habitats throughout the central United States and is the dominant vertebrate seed predator in row-crop fields (corn and soybean) in this region. Evaluating the preferences of prairie deer mice for common agricultural weed seeds and waste grain is important to understand the potential ability of native mice to regulate volunteer crops and weed populations. We evaluated winter seed preference of deer mice using cafeteria-style feeding trials presented within row-crop fields in central Indiana and used compositional analysis to compare proportional consumption of seeds from five common agricultural weeds (common ragweed, common cocklebur, common lambsquarters, velvetleaf, and giant foxtail) and two grains (corn and soybean) during overnight feeding trials. Prairie deer mice significantly preferred corn to all other available seed types. Ragweed and soybean were also readily consumed and were preferred over seeds other than corn. Giant foxtail was intermediately preferred. Our results show that prairie deer mice have clear preferences for certain seeds commonly available in row-crop fields; mice likely contribute to reduction of waste grain and some weed seed populations.

Nomenclature: Common cocklebur, *Xanthium strumarium* L.; common ragweed, *Ambrosia artemisiifolia* L.; common lambsquarters, *Chenopodium album* L.; giant foxtail, *Setaria faberi* Herrm.; velvetleaf, *Abutilon theophrasti* Medik.; corn, *Zea mays* L.; soybean, *Glycine max* (L.) Merr.

Key words: Biological control, *Peromyscus maniculatus bairdii*, prairie deer mice, row crops, seed predation, seed preference, waste grain, weed seed.

Postdispersal consumption of weed seed and waste grain in crop fields is an important ecosystem service provided by vertebrate and ground-dwelling invertebrate seed predators in many agricultural systems (Power 2010; Tschardt et al. 2012). Multi-tactic weed control strategies that capitalize on natural seed predation may potentially reduce agrochemical use and improve farmland ecological integrity (Brust and House 1988; Tschardt et al. 2005). Studies of seed predation have shown natural consumers to be efficient in removing large proportions (e.g., >50%) of weed seeds presented during experimental trials (e.g., Westerman et al. 2003) to levels that effectively reduce weed germination in subsequent growing seasons (Blubaugh and Kaplan 2016; Davis et al. 2003). Therefore, it is important to understand factors that mediate the capacity of seed predators to regulate weed seed and waste grain populations in cultivated habitats.

The majority of seed predation studies have focused on factors that influence rate of seed removal, which can include cropping system, vegetation structure, and seasonality (e.g., Booman et al. 2009; Cardina et al. 1996; Fischer et al. 2011; Menalled et al. 2000; Navntoft et al. 2011). Additionally, although less frequently acknowledged as a key factor affecting removal rates of particular seed types, preference for different seeds by vertebrate and invertebrate seed predators likely influences the overall impact of seed predators on regulation of weed seed and waste grain populations (Brust and House 1988; van der Laet et al. 2015; White et al. 2007).

Selection of a seed type disproportionately more (or less) frequently than expected based on equal availability, i.e., preference (or avoidance), influences the capacity of seed predators to alter the amount and type of seeds entering the seedbank. Knowledge of seed preferences also establishes a baseline from which to understand better how physical and behavioral factors affect foraging decisions of seed predators in arable fields. Animal selection of seeds is influenced by seed characteristics such as size, shape, hardness, chemical defense, and nutrient content (Kelrick et al. 1986; Lundgren and Rosentrater 2007; Sundaram et al. 2015; Vander Wall 2010); animal

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characteristics such as body size, metabolic rate, and physiological state (Kaufman and Collier 1981; Lichti et al. 2015); and environmental context such as relative availability of seeds of different types (Sundaram et al. 2016; Sunyer et al. 2014; Theimer 2005) and spatiotemporal variation in foragers' fear of predation (Brown and Kotler 2004).

Granivorous ground-dwelling invertebrates (i.e., ground beetles [Carabidae] and field crickets [Gryllidae]) are common in agricultural fields throughout North America, and their ability to regulate weed seed populations has been well studied (e.g., Blubaugh and Kaplan 2016; Menalled et al. 2007). The role of small rodents as seed predators in cultivated habitats is less well known. The prairie deer mouse (*Peromyscus maniculatus bairdii*) inhabits a variety of sparsely vegetated habitats throughout the central United States and is the dominant vertebrate seed predator in row-crop fields (corn and soybean) in this region (Clark and Young 1986; Getz and Brighty 1986; Whitaker 1966). Prairie deer mice are year-round residents in corn and soybean fields and have adapted to capitalize on an abundance of grain and other seeds available in row-crop habitats (Doudna and Danielson 2015; Getz and Brighty 1986). Despite their potential impact as a dominant seed predator, particularly in overwinter removal of weed seed and consumption of waste grain (Williams et al. 2009), little is known about how prairie deer mice select among different food resources in row-crop habitats.

Deer mice are widely distributed and considered a "generalist" species, yet they are known to show distinct preferences for particular food resources and seeds in several habitat types (e.g., coniferous forests [Everett et al. 1978], deciduous forests [Cramer 2014], and grasslands [Drickhamer 1970]). Deer mice foraging in row-crop habitats select among multiple exploitable food resources, including various weed seeds and waste grains that vary in size, nutritional content, and seasonal availability. Understanding seed preferences of dominant agricultural seed predators is important, because it can help elucidate the role of seed predators in population regulation of particular weed species and waste grain in crop environments, yet few studies have explicitly tested seed preference of vertebrate seed predators in cultivated habitats (Gallandt et al. 2005; Marino et al. 1997; Mauchline et al. 2005). To address this knowledge gap, we evaluated winter preference for several common agricultural weed seeds and waste grains by prairie deer mice in row-crop habitats.

Materials and Methods

We conducted seed preference trials on eight privately owned row-crop fields (four corn and four soybean) in Tippecanoe County, IN. Fields ranged in size from 8.97 to 188.25 ha (mean = 60.08 ± 33.44 SE) and managed under reduced tillage regimes; fields were not tilled following fall crop harvest in 2015. The weed community within the study area consisted primarily of common lambsquarters, common cocklebur, common ragweed, giant foxtail, giant ragweed (*Ambrosia trifida* L.), green foxtail [*Setaria viridis* (L.) Beauv.], redroot pigweed (*Amaranthus retroflexus* L.), and velvetleaf.

Seed Preference Trials. We used cafeteria-style feeding trials to evaluate preference for weed seed and waste grain by prairie deer mice in row-crop fields. Feeding trials were conducted within arenas constructed from standard plastic rodent cages (38 by 30 by 25 cm) with individual seed trays (aluminum weighing boats) affixed to the bottom (Figure 1). We covered each arena with a clear glass sheet and drilled a 2.54-cm hole into the side of the cage to allow mice to freely enter and exit during trials. Within each feeding arena, we presented 2 g (weighed to nearest 0.001 g) each of five agricultural weed seeds (common ragweed, common cocklebur, common lambsquarters, velvetleaf, giant foxtail; Azlin Seed Services, Leland, MS) and two grains (corn and soybean). We provisioned 2 g of each seed type to ensure that the total amount of seed available exceeded the daily intake requirements of adult deer mice (Stebbins 1977). Arrangement of seed trays within arenas was randomized during each trial using a random number generator.

During trials we placed feeding arenas adjacent to (within 1 m) wooden mouse nesting boxes (15 by 15 by 15 cm) that were buried flush with the soil surface within the interior of study fields (>100 m from field edge) for use in a concurrent investigation of prairie deer mouse demographics in row-crop habitat. We installed a grid of 36 nesting boxes per field with 20-m spacing between boxes. We placed feeding arenas only next to nest boxes that were occupied by mice and conducted only one feeding trial per nest box to avoid sampling the same individual mice on multiple trials. Average interarena distance averaged 55.2 m (SE = 3.4) and ranged from 20 to 80 m. Feeding arenas were installed within fields at dusk (1900 to 2000 hours) and removed the following morning (0700 to 0800 hours); therefore, each trial consisted of a single night when seeds were exposed

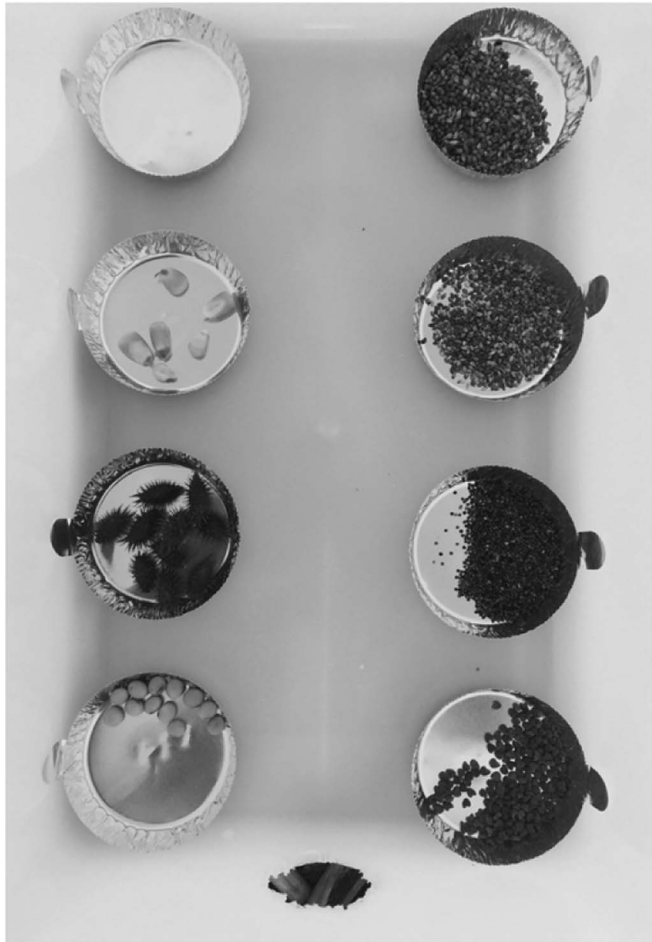


Figure 1. Overhead image of feeding arena (entrance hole at bottom) used in cafeteria-style feeding trials of seed preference by prairie deer mice in row-crop habitat in central Indiana.

and available for consumption by free-ranging mice. We weighed seed (to nearest 0.001 g) remaining in trays after individual trials and calculated the percentage (%) of each seed type removed. Because we did not track seed fate, we do not know whether seeds removed from trays were subsequently consumed or cached by mice. All seed preference trials were conducted during winter (February 1 to March 3, 2016); we chose this study period to control for potential removal of seed by invertebrates, because granivorous insects exhibit little or no activity during this period (Carmona and Landis 1999; Denlinger and Lee 1998). By conducting trials at night during winter in field interiors, we maximized the odds that prairie deer mice were the only active seed predator visiting trays, because invertebrates are dormant during this period and other potential vertebrate seed predators (i.e., ground-foraging birds) are diurnal. During our overwinter capture–mark–recapture efforts, prairie deer mice represented 98% of rodent captures (J Berl, unpublished data); the only other

rodents captured were prairie voles (*Microtus ochrogaster*), which are predominantly herbivorous and consume seeds infrequently (Zimmerman 1965).

Data Analysis. We used compositional analysis (Aebischer et al. 1993) and the multinomial distribution method of Neu et al. (1974) to determine whether removal of available seed types significantly differed from random (i.e., equal consumption). Both methods yielded qualitatively similar results; for clarity and brevity we report only the results from compositional analysis. Commonly used to evaluate habitat preference of radio-tracked animals (e.g., Owen et al. 2015), compositional analysis is well suited to evaluate seed preferences by comparing the proportional (%) removal of different seeds available during feeding trials. We conducted compositional analysis using the ‘adehabitat’ package (Calenge 2006) implemented within R (R Development Core Team 2016). We calculated log-ratio differences in seed consumption per trial and computed the compositional analysis test statistic λ from the matrix of log-ratio differences to test for overall nonrandom seed selection. Individual seed preferences were then ranked in order of selection preference, and Student’s *t*-test was used to test for pairwise differences in preference among available seed types (Aebischer et al. 1993). Compositional analysis calculates log-ratios, which cannot accommodate zero-values; therefore, if seed types were available but not selected during individual trials, zero-values were replaced with 0.007 to reduce the likelihood of type I error rates, as recommended by Bingham and Brennan (2004). We present means \pm SEs throughout.

Results and Discussion

We conducted 45 cafeteria-style feeding trials adjacent to actively used nest boxes over the course of the study, but only 27 trials were used in our analysis of seed preference; 15 trials were excluded because mice did not visit arenas and 3 were excluded due to disturbance by raccoons (*Procyon lotor*). On average, mice removed 2.97 g (± 0.36) of seed during preference trials, and the mean amount selected varied among seeds (Figure 2). Proportional selection was higher for waste grains than weed seeds, on average. Prairie deer mouse removal of seeds differed significantly from random ($\lambda = 0.086$, $P = 0.002$), with strong preference for corn over all other available seed types (Table 1). Soybean and common ragweed were also readily selected and were significantly preferred over seed types other than corn (Table 1).

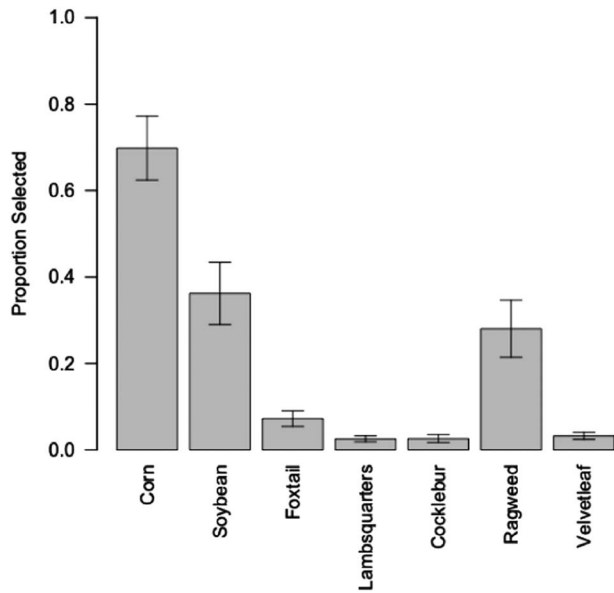


Figure 2. Mean (\pm SE) proportion of seed selected by prairie deer mice in experimental trials conducted on overwintering populations within corn and soybean fields in Indiana.

Giant foxtail was moderately preferred, whereas common lambsquarters, velvetleaf, and common cocklebur were rarely selected and significantly avoided relative to the other seeds (Table 1).

Our results suggest that the prairie deer mouse, a dominant vertebrate seed predator in row-crop agriculture in the central United States, shows strong preferences among seed types and select waste grains (corn and soybean) over several common agricultural weed seeds. As such, prairie deer mice likely contribute most to reduction of waste grain populations when seasonally available in row-crop fields. However, selection of particular seeds may depend on relative availability within a choice set (e.g., Sundaram et al. 2016; Swihart 1990). Our experiment presented equal availability of different seed types, but this scenario is unlikely to occur naturally within crop habitats. The extent to which deer mice

contribute to reduction of weed seed populations (e.g., giant foxtail and common ragweed) is probably mediated by relative availability of waste grain following crop harvest. Deer mice may contribute more to reductions of weed seed during periods when waste grain is generally unavailable, such as prior to crop harvest or after available waste grain has been exhausted or reached unprofitably low densities. Studies of dynamic preferences under varying levels of seed availability (e.g., with hierarchical multinomial logistic regression models; Blythe et al. 2015; Richardson et al. 2013) and studies of frequency-dependent seed selection (sensu Greenwood 1985; Sundaram et al. 2016) are needed to fully understand how seed selection by mice changes over time and as a function of background seed availability.

Optimal foraging theory and utility theory predict that foraging animals will balance trade-offs of energy gain and foraging costs and select the most profitable food item available (Brown and Kotler 2004; Pulliam 1974). Postharvest crop fields offer minimal protective cover besides residual crop material and substrate unevenness (Orrock et al. 2004), and foraging mice must select food resources that maximize energy gains while reducing costs associated with search time and foraging effort. Therefore, mice likely prefer grains because they are relatively large and easily detected and handled. Consumption of waste grain likely in part explains why prairie deer mouse populations have flourished in row-crop habitats of the central United States (Doudna and Danielson 2015; Whitaker 1966). In addition to direct consumption, deer mice actively cache waste grain in underground burrows following crop harvest (JL Berl, unpublished data), thus providing a high-quality overwinter food supply. In reduced-tillage systems where waste grain remains readily available on the soil surface, deer

Table 1. Preferences for weed seeds and waste grains (focal seed type in left column) by prairie deer mice during cafeteria-style feeding trials conducted on overwintering populations within corn and soybean fields in Indiana.^a

	Corn	Soybean	Foxtail	Lambsquarters	Cocklebur	Ragweed	Velvetleaf	Rank
Corn	0	+++	+++	+++	+++	+++	+++	6
Soybean	---	0	+++	+++	+++	+	+++	5
Foxtail	---	---	0	+++	+++	---	+++	3
Lambsquarters	---	---	---	0	+	---	-	1
Cocklebur	---	---	---	-	0	---	-	0
Ragweed	---	-	+++	+++	+++	0	+++	4
Velvetleaf	---	---	---	+	+	---	0	2

^a Within each row, cells indicate the focal seed type's positive (+) or negative (-) preference from compositional analysis log-ratios; triple symbols represent significant preference. The seed rank column indicates the order of preference (6 = most preferred; 0 = least preferred).

Table 2. Characteristics of seeds used in cafeteria-style feeding trials conducted on overwintering populations of prairie deer mice within corn and soybean fields in Indiana.

Seed type	Fat (%)	Protein (%)	Avg. weight ^c (g)	SE
Corn ^a	4.7	9.4	0.281	0.029
Soybean ^a	19.9	36.5	0.157	0.017
Common ragweed ^b	18.1	18.3	0.005	0.003
Giant foxtail ^b	5.4	14.3	0.002	0.002
Velvetleaf ^b	14.2	21.1	0.009	0.003
Common cocklebur ^b	13.1	24.5	0.158	0.053
Common lambsquarters ^b	5.8	19.6	0.001	0.004

^a Corn and soybean composition data from U.S. Department of Agriculture (2015).

^b Weed seed composition data averaged from Harrold and Nalewaja (1977), Schroeder et al. (1974), and Tkachuk and Mellish (1977).

^c Average seed weight obtained from 10 samples of 5–100 seeds sample⁻¹.

mice, which do not hibernate (Degen et al. 1998), likely rely on consumption and storage of grain to maintain their populations over the winter.

Previous investigations of weed seed predation have suggested that “field mice” (*Peromyscus* spp.) in cultivated habitats typically consume larger-sized seeds (Brust and House 1988; Harrison et al. 2003; van der Laet 2015). We observed a preference for large-seeded corn and soybean over most weed seeds, but seed size was not strongly associated with preference in our study, as the largest weed seeds presented in our choice set (common cocklebur and velvetleaf) were among the least preferred. Common ragweed was the most preferred weed seed among the choice set, and its high crude fat (18.1%, comparable to soybean) and protein content (18.3%; Table 2) may at least partially explain the high selection rates (equal to soybean) that we observed (Harrison et al. 2003). Our study was not designed to test the specific mechanisms that lead to preference or avoidance of different seed types, but it appears that neither seed size nor nutritional content alone can explain seed selection. Common cocklebur seeds had relatively high fat and protein content (Table 2) yet were the least preferred seed type, likely due to handling costs associated with extracting seeds from burs. Similarly, despite its relatively large size (volume and weight) and nutritional content, velvetleaf seed may have been avoided because its chemical composition and the hardness of its coat make it unpalatable to rodent seed predators.

The relative contribution of vertebrates (e.g., rodents) and invertebrates (e.g., ground beetles, crickets, and ants) to the regulation of weed seed populations has been the subject of extensive experimentation, with conflicting evidence for which group of seed predators has the greater impact on weed seed regulation (i.e., larger proportion of seeds removed;

Brust and House 1988; Menalled et al. 2007; Westerman et al. 2003). A number of factors influence the relative contribution of vertebrate and invertebrate seed predators to weed seed removal in crop fields, including cropping system, seasonality, vegetation structure, and local species pools (e.g., Booman et al. 2009; Fischer et al. 2011; Menalled et al. 2000). In addition, although rarely studied, preference by seed predators for different seed types likely contributes to the varied results of previous studies of weed seed predation. The majority of experiments on weed seed predation are conducted using seeds of a single (or select few) weed species; however, both vertebrate and invertebrate seed predators are known to preferentially select among different food resources (Cramer 2014; White et al. 2007). Previous authors have suggested that vertebrate seed predators generally prefer to consume larger seed types (e.g., velvetleaf) over smaller ones (e.g., lambsquarters) (e.g., Brust and House 1988); however, our results indicate that such generalizations cannot be reliably made and many factors other than size and shape can influence seed selection. Our study suggests that seed preference may partially explain the widely conflicting results demonstrated in previous investigations. For example, seed predation experiments that found minimal vertebrate consumption of velvetleaf (Cardina et al. 1996) or lambsquarters (Blubaugh and Kaplan 2016) could reflect avoidance of those seeds by rodent seed predators. Future experiments on seed predation should carefully consider the type of seed selected for use in experimental trials, in particular when trying to tease apart the relative contribution of vertebrates and invertebrates to rate of seed removal.

Preference for particular weed seeds or waste grains likely affects the capacity of specific seed predators to regulate the amount and type of seed that enters or

survives in seedbanks within crop fields. Although predation of weed seeds and waste grains by prairie deer mice can provide services that benefit farmers and potentially improve farmland ecological integrity through reductions in agrochemical applications, the role of these animals in agricultural habitats remains poorly understood. Deer mice show strong preference for waste grains over several common agricultural weed seeds and likely contribute to reductions in volunteer crops and certain weed populations. However, deer mice are omnivorous, and their diets shift seasonally (Whitaker 1966). Further investigations of prairie deer mouse diets and foraging behavior are needed to clarify the role of these seed predators in row-crop habitats.

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