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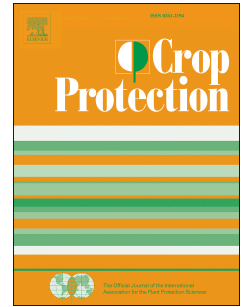
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Abby-Gayle Prieur: Methodology, Formal analysis, Investigation, Resources, Data curation, Writing, Visualization, Supervision, Project administration, Funding acquisition; **Robert Swihart:** Conceptualization, Methodology, Formal analysis, Resources, Writing, Visualization, Supervision, Project administration, Funding acquisition

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8 **Palatability of common cover crops to voles (*Microtus*)**

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15 Use of cover crops in intensive row-crop agriculture has dramatically increased over the
16 last decade. Cover crops provide vegetative cover and forage that may support more diverse and
17 abundant rodent communities than those found in conventional row-crop agroecosystems.
18 However, increasing vole populations can lead to depredation of the soybean (*Glycine max*)
19 commodity crop. We tested for selection of 13 commonly planted cover crops and 4-5 additional
20 benchmark species by meadow (*Microtus pennsylvanicus*) and prairie (*M. ochrogaster*) voles
21 using cafeteria-style feeding trials conducted in semi-natural outdoor enclosures. Red clover
22 (*Trifolium pratense*), alfalfa (*Medicago sativa*), and hairy vetch (*Vicia villosa*) were commonly
23 preferred among vole species, and canola (*Brassica napus*) was avoided. Meadow and prairie

24 voles consistently chose or avoided highly and minimally preferred species, respectively, but
25 were more variable in choosing moderately preferred species. Consumption scores were
26 negatively associated with the number of plants offered in a trial, and the relationship was
27 stronger for males than females. The interaction of protein and fiber content of plants, and vole
28 identity included as a random effect, were also important in predicting score probability for both
29 vole species. Identifying minimally preferred plants and factors that influence selection may
30 allow farmers to manage cover-cropped soybean fields to discourage immigration of small
31 mammals into fields, thus reducing negative consequences that might otherwise limit future
32 adoption of a valuable soil conservation practice.

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35 Key words: conservation agriculture; cover crop; damage management; foraging behavior;
36 individual variation; *Microtus*; vole

37 1. Introduction

38 Use of cover crops in conventional row-crop agriculture has increased greatly over the last
39 decade (White, 2014). In corn-soybean rotations of the Midwestern U.S., producers plant cover
40 crops after harvesting the commodity crop in fall and terminate in spring before the next
41 commodity crop germinates. Cover crops are used to improve soil health by retaining topsoil,
42 providing essential nutrients, and maintaining soil moisture (Fageria, 2007).

43 In addition to improving soil health, cover crops provide forage and vegetative structure in
44 fields that, under conventional tillage practices, contain only bare soil or crop stubble from late
45 fall to early spring. Improved overhead cover likely increases diversity of the small mammal
46 community in row-crop fields (Berl et al., 2018; Getz et al., 2007; Jug et al., 2008) and could
47 enable population growth of herbivorous small mammals that can incorporate the cover crops
48 into their diets. Although increased biodiversity can benefit farm management (Altieri, 1999),
49 some species, such as voles (*Microtus*), may deplete the commodity crop when their
50 populations grow too large (Wiman et al., 2009; Witmer et al., 2007). When appropriate cover
51 and food are available, voles reproduce year-round, and populations can quickly grow to large
52 numbers (Cole and Batzli, 1978; Getz et al., 2007; Goswami et al., 2011).

53 Vole depredation of crops in row-crop fields has been reported previously (Witmer et al.,
54 2007), and complaints of vole damage to soybeans (*Glycine max*) in cover-cropped fields are
55 numerous (Fisher et al. 2014; Prieur, 2019; Joe Rorick, [Conservation Cropping Systems
56 Initiative, West Lafayette, IN] personal communication, [August, 2017]). However, we are
57 unaware of research designed to evaluate which cover crops used in corn-soybean rotations may,
58 by virtue of their relative palatability, encourage vole use of fields and increase risk of damage to
59 soybeans. Our objective was to rate commonly used overwinter cover crops, including grasses,

60 clovers, brassicas, and others, for selection by meadow (*M. pennsylvanicus*) and prairie (*M.*
61 *ochrogaster*) voles. The geographic ranges of these two vole species encompass the bulk of the
62 Midwestern U.S., where row-crop agriculture dominated by soybean and corn (*Zea mays*) is
63 prevalent. Identifying cover crops that are avoided by voles provides producers with options for
64 planting cover crops of lower value to voles, which may discourage immigration and recruitment
65 in fields and thus reduce potential for feeding damage by voles to young soybean plants.
66 Alternatively, producers can anticipate damage in fields planted with highly preferred cover
67 crops and act preemptively to minimize damage in these fields by using farming strategies such
68 as spot tillage or manipulation of nearby grassland habitat (Prieur, 2019).

69 We expected clovers (*Trifolium*) and alfalfa (*Medicago sativa*) to be preferred, as they
70 ranked high in previous vole diet studies comparing plants from permanent vole habitats (DeJaco
71 and Batzli, 2013; Lindroth and Batzli, 1984). We anticipated that vetches, specifically hairy
72 vetch (*Vicia villosa*) and cicer milk vetch (*Astragalus cicer*), would be avoided, as *Vicia* was
73 suggested by Sullivan (2006) to be the most likely group of cover crops avoided by voles, and *A.*
74 *cicer* was reported to deter voles from entering fields (Lisa Holscher, [Conservation Cropping
75 Systems Initiative, West Lafayette, Indiana], personal communication, [August, 2017]).

76 In addition to establishing relative preference by voles, we evaluated factors hypothesized
77 to influence selection and avoidance of plant species. These objectives were operationally
78 motivated; plant species that consistently are avoided by voles are less likely to yield variable
79 results when used by producers compared to plant species for which avoidance varies with
80 factors such as vole sex or availability of alternative foods. Swihart (1990) found that
81 woodchucks (*Marmota monax*), a generalist herbivore, more consistently selected and avoided
82 highly and minimally preferred species of orchard ground cover, respectively. In contrast,

83 moderately preferred species were selected with more variation among feeding trials. Hence, we
84 predicted a similar unimodal relationship between relative preference and variation in selection
85 of cover crops for our vole species.

86 Meadow and prairie voles are generalist herbivores (Reich, 1981; Stalling, 1990) that can
87 adjust diets to account for changes in plant availability (Haken and Batzli, 1996). Thus, we
88 hypothesized that voles would become increasingly willing to consume a plant as available plant
89 diversity and quality of forage declined (Haken and Batzli, 1996), resulting in greater relative
90 preference. To control for possible effects of plant diversity, we also tested whether voles
91 consumed less when presented with an equally diverse offering of plants rated as avoided versus
92 preferred based on prior trials. We expected voles to consume less of unpreferred forage, as
93 some minimally selected plants may be consistently avoided (Swihart 1990).

94 **2. Materials and Methods**

95 *2.1 Study site*

96 We captured voles and performed captive feeding trials at the Purdue University Wildlife
97 Area (PWA) located 11 km west of West Lafayette, Indiana. PWA encompasses 1.17 km² of
98 restored tallgrass prairie, savanna, and wetland habitat and is surrounded by row-crop
99 agriculture. We captured five female and five male meadow voles and two male prairie voles
100 within restored prairie at the site and at a nearby Purdue property. Low population levels during
101 the study prevented us from capturing sufficient prairie voles for our trials, so we acquired an
102 additional eight female and five male captive-bred prairie voles from Miami University, Ohio.

103 We placed outdoor enclosures used to house voles on a mown lawn at PWA. The
104 vegetation within enclosures consisted primarily of Kentucky bluegrass (*Poa pratensis*) and
105 fescue (*Festuca arundinace*), and we removed any broadleaf plants found within enclosures.

106 2.2 Feeding trials

107 To assess selection of common cover crops, we conducted a series of six feeding trials on
108 meadow and prairie voles from July to August 2018. We placed a single vole into one of 15 1.5
109 m x 1.5 m outdoor enclosures built to specifications outlined in DeJaco and Batzli (2013). To
110 protect study animals from exposure, we supplied dried hay and nest boxes within enclosures
111 and placed a sheet of metal above each enclosure to provide shade. Voles had access to unlimited
112 water and were provided rat chow (Laboratory Autoclavable Rodent Diet 5010, LabDiet) as
113 supplemental food when trials were not taking place.

114 We allowed voles at least 3 days to acclimate to enclosures before beginning trials. During
115 acclimation, we supplied one of each plant species to be tested to ensure equal exposure to plant
116 types that do not occur naturally in Indiana.

117 We tested 17 total plant species for meadow voles (Table 1) and 18 for prairie voles (Table
118 2). Yellow clover (*Melilotus officinalis*) was not included for meadow voles due to difficulty
119 growing sufficient plants to the appropriate growth stage. We included 12 winter cover crops and
120 a summer crop, sorghum-sudangrass (*Sorghum bicolor* x *S. bicolor* var. *sudanese*), that are most
121 commonly used in United States commodity agriculture (CTIC & SARE, 2016). Additionally,
122 we included three benchmark species that DeJaco and Batzli (2013) identified as highly,
123 moderately, and minimally palatable, respectively, in nonnative grasslands that serve as the
124 primary permanent habitat for these voles: alfalfa, orchardgrass (*Dactylis glomerata*), and giant
125 ironweed (*Vernonia gigantea*). We also included cicer milk vetch, which reportedly deters voles
126 (L. Holscher, Director, Conservation Cropping Systems Initiative, in litt.). Finally, we included
127 soybean to enable comparison with the commodity crop for which depredation was a concern.
128 We grew all plants from seed in a greenhouse and presented them to voles at approximately the

129 same growing stage within each species. Whenever possible, we offered plants in growth stages
130 1-2, during formation of leaves, side shoots, or tillers (Hess et al. 1997).

131 To initiate a trial, we removed supplemental food and placed one of each plant species to
132 be tested into each enclosure. Each vole tested in a trial received the same suite of species, and
133 all available voles were used in every trial. We placed potted plants flush with the soil surface in
134 the center of the enclosure to simulate a vole's natural encounter with forage. Each test period
135 began between 1900h and 2100h and lasted 12 hours, after which test plants were removed and
136 supplemental food was once again provided. Trials took place under ambient environmental
137 conditions.

138 Before we placed plants in the enclosures, we recorded number of leaves or stems, as
139 appropriate, for each plant and noted marks or tears that might mistakenly be attributed to voles.
140 After the test period, we removed plants from enclosures and again observed the number of
141 leaves or stems and damage to each plant. Following Dejacó and Batzli (2013), we then assigned
142 a score of 0-4, which represented five categories: plant not sampled (0), < 25% of the plant
143 missing (1), 25-49% missing (2), 50-74% missing (3), and $\geq 75\%$ missing (4).

144 After plant assessment, we averaged the number of voles that sampled a given species and
145 the total damage scores for that plant species together. We then used these averages to assign a
146 preliminary consumption score to plants and eliminate from the next trial's offerings for all voles
147 the plant species that on average were most preferred. Because we were most interested in the
148 least preferred species, we eliminated at least two species between each trial. The number of
149 species eliminated was determined by searching for natural breaks in scores for the most
150 preferred species and the remaining plants.

151 We conducted a series of six trials for each vole species, with 1-2 nights between each trial.
152 The first five trials consisted of sequential reductions of the most preferred species. For trial 6,
153 we offered voles a set of the most preferred plants, as determined in the first two trials. The
154 number of plant species we offered for trial 6 equaled the number offered in trial 4, thus
155 permitting comparison of feeding behavior for assemblages of equal diversity but differing
156 preference. We performed trials and selected plants for elimination separately for each vole
157 species. Methods were consistent with guidelines specified by the American Society of
158 Mammalogists (Sikes et al., 2016) and were approved by the Purdue University Animal Care and
159 Use Committee (protocol number 1710001635).

160 *2.3 Analysis*

161 Because meadow and prairie voles were presented with different sets of plant species
162 across their respective trials, separate analyses were run for each vole species. To assess relative
163 preference and variation in choice for each plant species, we calculated the mean and standard
164 deviation for each plant species in trials 1-5. We then compared observed means for each trial to
165 corresponding null distributions generated via 1,000 simulated trials in which mean scores were
166 assigned randomly to plant species offered in the trial. Observed means were then compared to
167 the null distribution to generate quasi-*P* values, i.e., the proportion of instances that the mean
168 observed consumption score was less (or more) than the mean score resulting from the simulated
169 trials. We used one-tailed tests for plants expected to be preferred or minimally preferred by
170 voles based on prior research (references in Introduction) and two-tailed tests for all other
171 species. Within each trial, we adjusted quasi-*P* values with Holm's procedure (Holm, 1979) and
172 used an alpha value of 0.1 to assess significance while balancing Type I and Type II errors.

173 To examine the effect that preference had on the consistency with which voles chose a
174 plant species, we calculated the standard deviation of scores between trials (Swihart, 1990) for
175 each vole. Because we eliminated the most preferred set of plants after the first trial, we lacked
176 data from subsequent titration trials to calculate a mean and standard deviation for them. Instead,
177 we combined data from trial 6, in which only the most preferred species were offered, with data
178 from trial 1 to calculate a mean and standard deviation for the most preferred species. We tested
179 the relationship between average consumption score and standard deviation across trials for each
180 vole and plant species combination and tested for consistent differences among individuals by
181 incorporating vole identity as a random effect in R package lme4 (Bates et al., 2019). We used
182 AICc (Burnham and Anderson, 2002) to compare the evidence for intercept-only, linear, and
183 quadratic models. For assessing evidence of random effects, we used conditional AIC (Saefken
184 et al., 2014) and R^2 (Nakagawa and Schielzeth, 2013) as implemented in R packages cAIC4
185 (Saefken and Ruegamer, 2018) and MuMIn (Bartoń, 2019). Variation explained by random
186 effects was calculated using adjusted repeatability in package rptR (Stoffel et al., 2019). Fitted
187 values were then computed for AICc- or cAIC-best models.

188 We used a binomial test conducted on signed differences in consumption scores for
189 successive pairs of trials to test the hypothesis that scores would exhibit positive trends in
190 preference as food choices became more limited. To more formally account for the semi-
191 quantitative nature of our response variable, we also performed ordinal (proportional odds)
192 regression on results from all six trials to model the probability of consumption falling in score
193 class k ($k = 0-4$) as a function of plant diversity, vole characteristics, and the mean value of plant
194 nutritional factors as reported in the literature (see references in Appendices A & B).
195 Specifically, we fitted cumulative probability with logistic or probit links to the number of plants

196 offered in a trial, vole sex, crude protein, acid detergent fiber fitted as second-order polynomials
197 with the poly function in R package stats (R Core Team, 2018), and all two-way interactions. To
198 account for variation due to differences among individual voles, we incorporated vole identity as
199 a random effect. The interactive model and its proper subsets were compared using AICc and
200 likelihood ratio tests. Random-effects ordinal regression was implemented in R package ordinal
201 (Christensen, 2019). Following Bonnot et al. (2018), we replicated ordinal models by treating
202 consumption score as a continuous response in linear mixed effects models, which enabled us to
203 report adjusted repeatability estimates using R package rptR (Stoffel et al., 2019) and conditional
204 R^2 (Nakagawa and Schielzeth, 2013) for best models.

205 To separately test if relative preference affected the average score for voles when offered
206 plants of equal diversity but differing quality, we compared the means of differences in scores
207 for each individual vole in trial 4 ($n=5$ [meadow voles] or 6 [prairie voles] plants) and trial 6
208 ($n=5$ [meadow voles] or 6 [prairie voles] plants). Observed mean differences were compared to
209 distributions of null mean differences derived from scores in trials 4 and 6 in which pairs of
210 scores were assigned at random, and quasi- P values were computed by tabulating the fraction of
211 the null distribution greater than the observed mean difference. All analyses were conducted in R
212 (R Core Team, 2018).

213 **3. Results**

214 *3.1 Relative preference*

215 No plant species was wholly avoided, as both meadow and prairie voles sampled all plant
216 species at least once. However, canola (*Brassica napus*) ranked lower than most plant types for
217 both vole species and was chosen less than expected by meadow voles in trials 1, 2, and 4 (Table
218 1). Meadow voles also ate turnip (*B. rapa*) less than expected in trials 1 and 3.

219 Of the 17 plant species presented to both vole species, red clover (*T. pratense*), alfalfa, and
220 hairy vetch were consistently selected more than expected, though only selection by meadow
221 voles differed significantly from the null distribution in trial 1 (Table 1). Of the most-consumed
222 species, prairie voles ate only hairy vetch more than expected in trial 2 (Table 2). Both vole
223 species also highly preferred soybean, with meadow voles choosing it more than expected in trial
224 2 and prairie voles in trial 3. In general, meadow voles demonstrated greater levels of
225 discrimination among plant species than prairie voles. Meadow voles preferred red clover,
226 alfalfa, crimson clover (*T. incarnatum*), hairy vetch, soybean, winter wheat (*Triticum aestivum*),
227 cereal rye (*Secale cereale*), barley (*Hordeum vulgare*), and radish (*Raphanus sativa*) and avoided
228 canola, turnip, barley, and radish in at least one trial (Table 1). Interestingly, two species avoided
229 in early trials, barley and radish, were consumed more than expected in later trials from which
230 highly preferred species had been omitted (Table 1). In contrast, prairie voles demonstrated
231 strong preference only for hairy vetch and soybean (Table 2) and avoided none of the species,
232 with the possible exception of barley ($P = 0.11$).

Common name	Species name	Trial 1	<i>P</i>	Trial 2	<i>P</i>	Trial 3	<i>P</i>	Trial 4	<i>P</i>	Trial 5	<i>P</i>
Red clover	<i>Trifolium pratense</i>	3.0 ± 1.4	0.005 ^a								
Alfalfa	<i>Medicago sativa</i>	2.9 ± 1.7	0.008 ^a								
Hairy vetch	<i>Vicia villosa</i>	2.8 ± 1.6	0.016 ^a								
Crimson clover	<i>Trifolium incarnatum</i>	2.4 ± 1.5	0.241								
Soybean	<i>Glycine max</i>	2.5 ± 1.8	0.282	3.2 ± 1.6	0.025 ^a						
Winter wheat	<i>Triticum aestivum</i>	1.9 ± 1.9	1	3.2 ± 1.4	0.025 ^a						
Annual rye	<i>Lolium multiflorum</i>	1.8 ± 1.4	1	2.8 ± 1.6	0.511						
Oats	<i>Avena sativa</i>	2.4 ± 1.7	0.457	2.7 ± 1.7	0.623						
Barley	<i>Hordeum vulgare</i>	0.3 ± 0.9	0.018 ^b	2.0 ± 1.9	1	3.0 ± 1.7	0.072 ^a				
Cicer milk vetch	<i>Astragalus cicer</i>	1.6 ± 0.7	1	2.2 ± 1.6	0.953	2.8 ± 1.6	0.110				
Sorghum-sudangrass	<i>Sorghum bicolor</i> x <i>S. bicolor</i>	0.8 ± 1.3	0.516	2.2 ± 1.9	1	2.8 ± 1.6	0.227				
Orchardgrass	<i>Dactylis glomerata</i>	0.9 ± 1.0	0.709	1.7 ± 1.7	1	2.0 ± 1.4	1				
Cereal rye	<i>Secale cereale</i>	1.0 ± 0.8	0.878	1.1 ± 0.3	0.623	1.8 ± 1.5	1	3.3 ± 1.5	0.069 ^a		
Ironweed	<i>Vernonia gigantea</i>	1.3 ± 1.9	0.979	1.3 ± 1.8	0.623	1.8 ± 1.9	1	2.9 ± 2.0	0.248		
Radish	<i>Raphanus sativus</i>	0.3 ± 0.5	0.018 ^b	1.2 ± 1.6	0.630	1.1 ± 1.5	0.377	2.1 ± 2.0	1	2.6 ± 1.7	0.048 ^a
Canola	<i>Brassica napus</i>	0.4 ± 0.5	0.051 ^b	0.6 ± 1.3	0.020 ^b	1.0 ± 1.5	0.252	1.1 ± 1.5	0.042 ^b	1.6 ± 1.8	0.389
Turnip	<i>Brassica rapa</i>	0.2 ± 0.6	0.008 ^b	1.0 ± 1.3	0.436	0.6 ± 1.3	0.020 ^b	2.0 ± 1.3	1	1.5 ± 1.9	0.335

233 ^a Indicates mean is greater than expected.

234 ^b Indicates mean is less than expected.

235

236 Table 1—Average scores ($\pm SD$) showing consumption of common Indiana cover crops offered to meadow voles (*Microtus*
237 *pennsylvanicus*) in cafeteria-style feeding trials, July to August 2018. Consumption scores range from 0-4, with higher scores
238 corresponding to higher relative preference. Observed means were compared to a null distribution to generate quasi-*P* values, that
239 were then adjusted using Holm's procedure. The most-preferred plants were removed from consideration in each subsequent trial.

Common name	Species name	Trial 1	<i>P</i>	Trial 2	<i>P</i>	Trial 3	<i>P</i>	Trial 4	<i>P</i>	Trial 5	<i>P</i>
Red clover	<i>Trifolium pratense</i>	1.3 ± 1.6	0.776								
Alfalfa	<i>Medicago sativa</i>	1.3 ± 1.4	0.776								
Cicer milk vetch	<i>Astragalus cicer</i>	1.2 ± 1.1	1								
Hairy vetch	<i>Vicia villosa</i>	1.0 ± 1.2	1	2.1 + 1.4	0.025 ^a						
Annual rye	<i>Lolium multiflorum</i>	1.6 ± 1.7	0.212	1.6 + 1.7	1						
Yellow clover	<i>Melilotus officinalis</i>	0.7 ± 1.2	1	1.4 + 1.2	1						
Radish	<i>Raphanus sativus</i>	1.2 ± 1.5	1	1.3 + 1.2	1						
Crimson clover	<i>Trifolium incarnatum</i>	1.1 ± 1.7	1	1.0 + 1.3	1						
Soybean	<i>Glycine max</i>	1.6 ± 1.9	0.212	1.4 + 1.9	1	2.5 + 2.0	0.001 ^a				
Oats	<i>Avena sativa</i>	0.4 ± 1.2	1	0.8 + 1.5	1	1.9 + 2.0	0.180				
Turnip	<i>Brassica rapa</i>	0.2 ± 0.4	0.852	0.3 + 0.9	0.902	1.5 + 1.4	1				
Winter wheat	<i>Triticum aestivum</i>	0.8 ± 1.2	1	1.2 + 1.7	1	1.0 + 1.6	1				
Ironweed	<i>Vernonia gigantea</i>	0.3 ± 0.9	0.852	0.7 + 1.6	1	0.5 + 0.9	0.416	1.2 + 1.8	0.303		
Orchardgrass	<i>Dactylis glomerata</i>	0.2 ± 0.4	0.852	0.6 + 0.9	1	0.6 + 1.2	1	0.9 + 1.7	1		
Cereal rye	<i>Secale cereale</i>	0.3 ± 0.9	1	0.7 + 1.4	1	1.0 + 1.5	1	0.8 + 1.5	1		
Sorghum-sudangrass	<i>Sorghum bicolor</i> x <i>S. bicolor</i>	0.4 ± 1.2	1	0.8 + 1.5	1	0.5 + 1.2	1	0.5 + 1.3	1	1.8 + 2.1	1
Barley	<i>Hordeum vulgare</i>	0.0 ± 0.0	0.314	0.4 + 1.2	1	0.3 + 0.6	0.416	0.0 + 0.0	0.108	1.3 + 1.5	1
Canola	<i>Brassica napus</i>	0.8 ± 1.5	1	0.7 + 0.9	1	0.6 + 1.4	1	0.9 + 1.5	1	1.2 + 1.9	1

240 ^a Indicates mean is greater than expected.

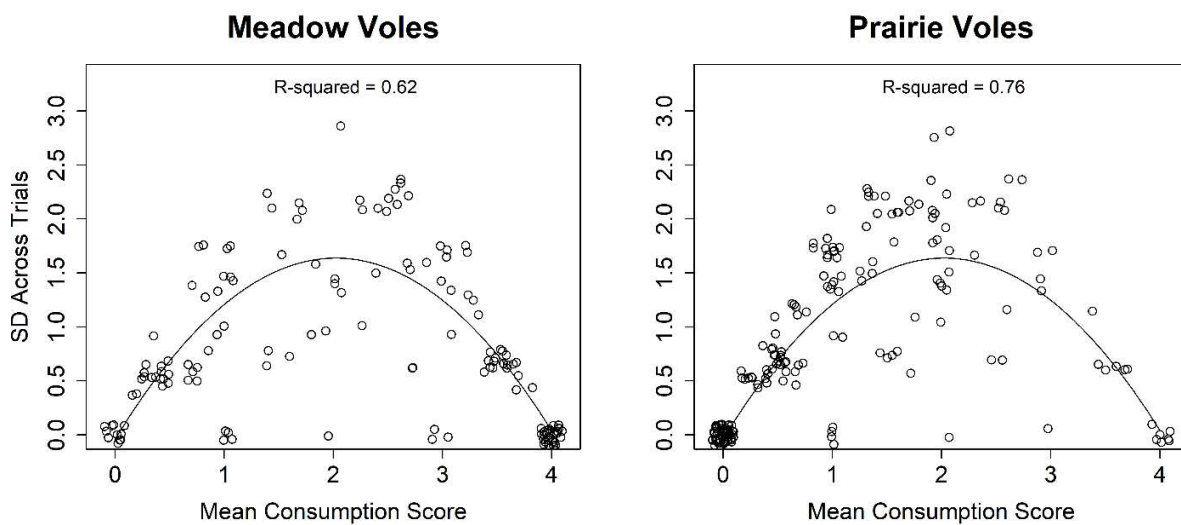
241 ^b Indicates mean is less than expected.

242 Table 2—Average scores (\pm *SD*) showing consumption of common Indiana cover crops offered to prairie voles (*Microtus*
243 *ochrogaster*) in cafeteria-style feeding trials, July to August 2018. Consumption scores range from 0-4, with higher scores
244 corresponding to higher relative preference. Observed means were compared to a null distribution to generate quasi-*P* values, that
245 were then adjusted using Holm's procedure. The most-preferred plants were removed from consideration in each subsequent trial.

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246 3.2 Variation in preference across trials

247 When testing the relationship of intertrial standard deviation and mean consumption score
 248 with vole identity included as a random effect, the quadratic model exhibited overwhelming
 249 support for meadow voles ($\Delta\text{AICc} = 132.6$ and 133.7 for linear and intercept-only models,
 250 respectively) and prairie voles ($\Delta\text{AICc} = 218.7$ and 260.0 ; Fig. 1). Fitted models demonstrated
 251 important quadratic effects for both meadow ($t = -15.0$, $P \ll 0.001$) and prairie voles ($t = -20.94$,
 252 $P \ll 0.001$). For meadow voles, the model containing a quadratic term without vole identity as a
 253 random effect was superior ($X^2 = 0.01$, $P = 0.920$) indicating no consistent differences among
 254 individual voles in their responses. However, for prairie voles the quadratic random-effects
 255 model was substantially superior ($X^2 = 11.71$, $P < 0.001$). Repeatability for prairie vole identity
 256 was slight, but significant ($r = 0.14$, $[0.02, 0.30]$, $P < 0.001$).

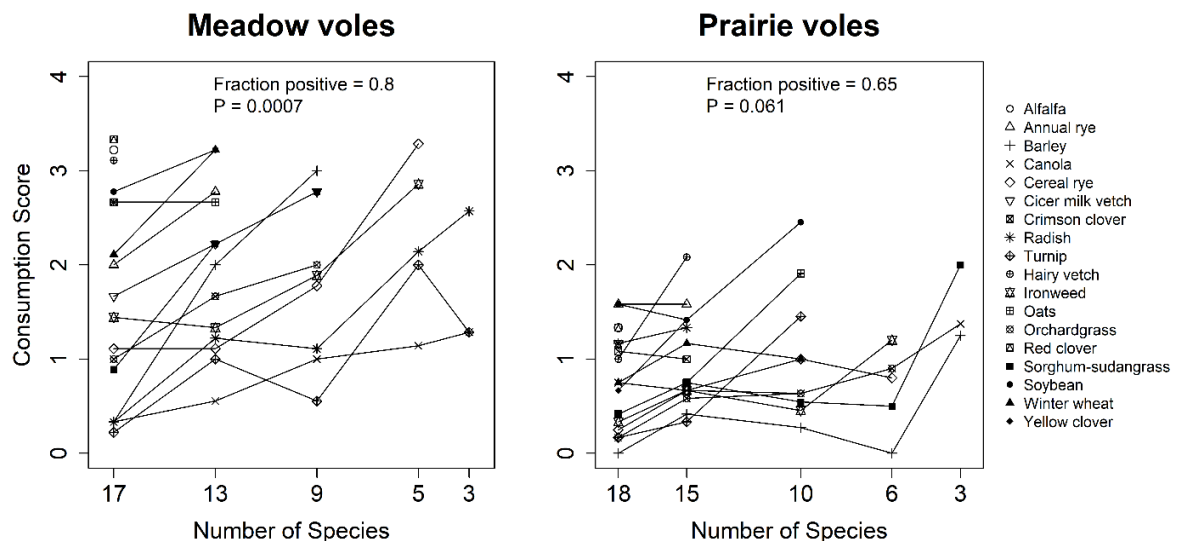


257
 258 Figure 1—Relationship of mean consumption to intertrial standard deviation for 17 and 18 plant
 259 species presented to meadow (*Microtus pennsylvanicus*) and prairie (*Microtus ochrogaster*)
 260 voles, respectively, in a series of six cafeteria-style feeding trials, July to August 2018. The most
 261 preferred plants were removed from consideration in each subsequent trial, except for trial 6

262 which consisted of only highly preferred plants. Consumption scores range from 0-4, with higher
 263 scores corresponding to higher amounts consumed.

264 3.3 Correlates of consumption level

265 Meadow voles yielded 30 sequences of trials for which differences in mean consumption
 266 scores could be computed. Of these, 24 (80%) resulted in increased consumption scores as the
 267 offered set of plants declined in overall diversity and quality, a greater fraction than expected by
 268 chance (binomial test $P = 0.0007$; Fig. 2). For prairie voles the fraction of sequential trials
 269 exhibiting an increase in mean consumption score was less dramatic, with 22 increases out of 34
 270 (65%) tests (binomial test $P = 0.061$; Fig. 2).



271
 272 Figure 2—Trends in mean scores for 15 common cover crops and 3 benchmark plant species as
 273 diversity and relative preference of plants offered were reduced. Plants were presented to
 274 meadow (*Microtus pennsylvanicus*) and prairie (*Microtus ochrogaster*) voles in a series of five
 275 cafeteria-style feeding trials, July to August 2018. The most-consumed plants were removed
 276 from consideration in each subsequent trial. Consumption scores range from 0-4, with higher
 277 scores corresponding to higher consumption. Each symbol represents a different plant species.

278 When plant diversity was constant, but quality differed in trials 4 (most avoided) versus 6
279 (most preferred), both meadow and prairie voles ate more of the preferred set of plants. Meadow
280 voles exhibited a 1.4-unit increase (quasi- $P = 0.008$) in consumption score in trial 6 ($\bar{x} = 3.69$
281 [3.21, 4.16]) compared to trial 4 ($\bar{x} = 2.29$ [1.10, 3.47]). The mean score for prairie voles
282 increased by 0.9 units (quasi- $P \leq 0.001$) in trial 6 ($\bar{x} = 1.75$ [0.97, 2.53]) compared to trial 4 ($\bar{x} =$
283 0.83 [0.01, 1.65]).

284 For meadow voles, the ordinal regression model containing all additive effects and
285 interactions was AIC-best (second-best model $\Delta\text{AIC} = 28.2$). Models fit with probit and logistic
286 links received similar support ($\Delta\text{AICc} = 0.8$), so we present results from the logistic link model
287 (Table 3). The interaction of fiber and protein was important ($z = 5.83$, $P \ll 0.001$) and resulted
288 in a high probability of low consumption scores for plants with maximum fiber and minimum
289 protein and for plants with minimum fiber and maximum protein (see supplementary data SD1).
290 The interaction of sex and number of plants was also important ($z = -1.93$, $P = 0.053$). Male voles
291 produced higher consumption scores in any given trial and showed a stronger negative response
292 to reduction in plant diversity than females (see supplementary data SD2). Both sexes exhibited
293 an increased chance for lower scores as diversity increased. The random intercept for variation
294 captured by differences among individual voles improved model fit ($X^2 = 34.30$, $\Delta\text{AICc} = 32.2$,
295 $df = 1$, $P \ll 0.001$). Repeatability of the random effect was low ($r = 0.16$), but different from
296 zero (95% CI: [0.03, 0.33], $P \ll 0.001$). Improvement due to the random effect was best
297 demonstrated by comparing marginal (0.22) to conditional r-squared (0.35).

298 For prairie voles the best ordinal model (second-best model $\Delta\text{AICc} = 3.6$) was the model
299 including all additive effects and appropriate interactions (Table 3). The model fit with a probit
300 link was best, compared to a logistic link model ($\Delta\text{AICc} = 6.21$), so we present results from the

301 probit model. Both the interactions of protein and fiber ($z = 4.19$, $P \ll 0.001$) and sex and plant
302 diversity ($z = -2.26$, $P = 0.024$) were important to predicting the probability of a given
303 consumption score and had the same effect as for meadow voles. The random factor included to
304 account for prairie vole identity improved model fit ($X^2 = 74.72$, $\Delta\text{AIC} = 72.6$, $df = 1$, $P \ll$
305 0.001) and though the repeatability was small ($r = 0.18$), it differed from zero (95% CI: [0.05,
306 0.33], $P \ll 0.0001$). Marginal r-squared was lower than for meadow voles (marginal $R^2 = 0.04$)
307 but also was greatly improved by the inclusion of the random effect (conditional $R^2 = 0.21$)

308

Vole species	Effect	Coefficient	SE	z	P
Meadow	Plant Diversity	-0.14	0.20	-0.67	0.504
	Protein	0.08	0.13	0.61	0.539
	Fiber	10.58	2.99	3.53	<0.001
	Fiber ²	13.92	2.33	6.00	<<0.001
	Male	1.64	0.54	3.06	0.002
	Diversity*Male	-0.44	0.23	-1.93	0.053
	Protein*Fiber	1.07	0.18	5.83	<<0.001
Prairie	Plant Diversity	-0.05	0.06	-0.76	0.449
	Protein	0.03	0.07	0.48	0.631
	Fiber	2.78	1.77	1.57	0.115
	Fiber ²	2.65	1.36	1.94	0.052
	Male	-0.22	0.34	-0.66	0.507
	Diversity*Male	-0.23	0.10	-2.26	0.024
	Protein*Fiber	0.42	0.10	4.20	<<0.001

309 Table 3—Model summaries for AIC-best ordinal (proportional odds) regression models
310 predicting cumulative odds of consumption score, n , where higher scores indicated higher
311 consumption. Plant species were presented to meadow (*Microtus pennsylvanicus*) and prairie
312 (*Microtus ochrogaster*) voles in a series of six cafeteria-style feeding trials, July to August 2018.
313 The most-consumed plants were removed from consideration in each subsequent trial, except for
314 trial 6 which consisted of only highly preferred plants.

315 4. Discussion

316 We found pronounced differences in selection of commonly used cover crop species.
 317 Elimination of the most preferred plant species in successive trials allows us to present an
 318 estimated ranking of relative palatability for the species tested to aid producers in selection of
 319 cover crops to use in fields with historic vole issues (Fig. 3). However, we suggest consideration
 320 of all results presented before applying the rankings, as the order is subjective and based on the
 321 cumulative results of all trials.



322
 323 Figure 3—Approximate ranking of palatability of cover crop and benchmark plant species to
 324 meadow (*Microtus pennsylvanicus*) and prairie (*Microtus ochrogaster*) voles. Plants were
 325 presented to voles in a series of six cafeteria-style feeding trials, July to August 2018.

326
 327 As expected, alfalfa and clovers were preferred by both meadow and prairie voles.
 328 However, voles also preferred hairy and cicer milk vetch, in contrast to predictions. Though
 329 Sullivan (2006) suggested that *Vicia*, which includes hairy vetch, was likely to be avoided by

330 voles, his assessment was generalized across vole species and across species of *Vicia*. Vole
331 species are known to differ in preference for the same plant species (DeJaco and Batzli, 2013),
332 and plant species within the same genus may vary widely in nutritional and chemical
333 composition (Duke and Atchley, 1986); both factors presumably affected the consumption scores
334 we observed. Cicer milk vetch is planted by farmers to deter voles due to putative toxicity of its
335 roots (Lisa Holscher, [Conservation Cropping Systems Initiative, West Lafayette, Indiana],
336 personal communication, [August, 2017]). Our study did not assess selection of roots, but our
337 results indicate that above-ground biomass of cicer milk vetch is selected by voles.

338 Interestingly, we found that young soybean plants, the commodity crop of concern, were
339 also selected by voles. Soybean plants are available in conventional agriculture and no-till fields
340 but reports of vole damage typically are concentrated in cover-cropped fields (Berl et al., 2017;
341 Prieur, 2019). Our original hypothesis was that cover crops serve as a forage resource for voles.
342 Soybean depredation thus occurs once cover crops are terminated and soybeans are left as the
343 only source of vegetative forage in the field. In this scenario, farmers may successfully deter
344 voles by planting unpreferred cover crops. However, our finding that soybeans are selected by
345 voles, coupled with the limited damage to soybeans observed in conventional and no-till
346 systems, suggests two additional scenarios that may explain damage observed by farmers that
347 use cover crops.

348 First, cover crops may facilitate soybean damage primarily by providing overhead cover
349 necessary for voles to access soybeans. In this case, cover crops that are planted at low densities
350 or have growth forms that provide minimal overhead cover will best deter meadow voles. Prairie
351 voles, which can thrive in areas of comparatively sparse cover (Getz et al., 2001), may be more
352 difficult to manage in this fashion. Another possible scenario is that cover crops attract voles by

353 providing both forage and cover, in which case minimally preferred cover crop species that
354 provide poor cover would be best for limiting vole damage to soybeans. This solution is likely to
355 limit damage by meadow voles more effectively than prairie voles.

356 Some species, such as canola, were avoided by both meadow and prairie voles, but all plant
357 species except barley were sampled in each trial. Other studies have reported complete avoidance
358 of several plant species during feeding trials (DeJaco and Batzli, 2013; Marquis and Batzli,
359 1989), but they did not systematically restrict diversity or quality of available plants. Our results
360 indicated that limiting plant diversity increased the odds of voles consuming a species. Thus,
361 failure of voles to completely avoid some plant species throughout our study likely resulted
362 because more desirable food was unavailable during some trials.

363 Despite lack of complete avoidance, minimally preferred plants may still be used to
364 discourage vole use of agricultural fields if our original forage-driven hypothesis is correct. Vole
365 populations can quickly colonize and reproduce in fields containing preferred habitat, with lower
366 growth potential in areas where preferred habitat or food is lacking (Cole and Batzli, 1979, 1978;
367 Getz et al., 2001). If voles use cover crops solely because of their forage quality, plants such as
368 canola and barley, which are of limited attractiveness when other forage is available, may
369 encourage voles to use areas with more desirable and diverse forage. Alternatively, if cover
370 density is a mechanism that enables voles to depredate soybeans, the cover quality provided by
371 these plants must also be considered.

372 Prairie voles exhibited more muted trends of preference and avoidance compared to
373 meadow voles, presumably as a consequence of lower overall consumption of plants offered in
374 trials (Fig. 2). Thirteen of 15 prairie voles used in our study were bred in captivity. Other studies
375 (Batzli and Jung, 1980; Marquis and Batzli, 1989) reported similar selection of plants in

376 laboratory feeding experiments using captive-reared and wild-caught voles compared to results
377 of plants selected in the field but did not compare amounts of forage eaten. Captive-bred animals
378 not habituated to prolonged food stress may expect rat chow to be available at regular intervals
379 and thus wait for a familiar food source, rather than feed extensively on relatively novel plant
380 resources.

381 Consumption score was influenced by the interaction of plant protein and acid detergent
382 fiber. The increased chance of a low score for high fiber and low protein plants was expected
383 (Batzli, 1985; Bergeron and Jodoin, 1987; Marquis and Batzli, 1989), as plants with these
384 qualities are hard to digest and provide minimal nutrition. Other results of the interaction, such as
385 the high probability of a low score for high protein, low fiber plants are counterintuitive and may
386 be explained better by the presence of compounds such as phenolics and alkaloids that are
387 important in predicting plant consumption by voles (Dearing et al., 2005). However, we did not
388 conduct assays to test for the presence of chemicals important to deterring rodent herbivory in
389 the plants included in our trials.

390 Consumption score was predicted by plant characteristics and by the context in which a
391 plant was offered. Restricting the diversity of available forage increased the chance of plant
392 consumption, especially by male voles. Even if use of cover crop fields is based solely on forage
393 quality of cover crops, vole use of fields is likely to persist if there is insufficient preferred forage
394 elsewhere on the landscape. However, voles ate less of low-quality forage compared to equally
395 diverse offerings of preferred plants. Thus, voles are likely to eat less in fields planted to cover
396 crops they view as less preferred, with population densities limited by forage quality (Cole and
397 Batzli, 1979, 1978).

398 Highly and minimally preferred plants were chosen and avoided more consistently than
399 plants of intermediate preference (Fig. 1). Swihart (1990) observed a similar pattern for
400 woodchucks (*Marmota monax*) and cautioned against quantitative comparisons of food habits for
401 generalist herbivores from studies with differing vegetative composition. Our results suggest that
402 there are limits to the flexibility of voles at either extreme of forage quality. In contrast, plants of
403 intermediate quality appear to offer voles the option of tradeoffs among plants that are viewed as
404 roughly equivalent, or for which consistent individual differences in choice exist. Our data
405 supported the latter explanation only for prairie voles. Future discrete choice experiments could
406 improve our understanding of how voles perceive tradeoffs among traits for plants exhibiting
407 intermediate preference (Sundaram et al., 2018).

408 Consistent behavioral differences among individual voles may affect a local population's
409 ability to use cover crops as forage. Intraspecific variation in behavior too often is ignored
410 (Jenkins, 1997), despite its implications for ecosystem services and management (Brehm et al.,
411 2019; Feldman et al., 2019). Our results suggest that individual variation in vole behavior may
412 impact how vole populations interact with cover-cropped fields, as model fit was improved by
413 including vole identity as a random effect in all AIC-best ordinal models. Although repeatability
414 estimates were low, they were comparable to other studies that detected individual variation in
415 the context of foraging behavior (Dochtermann et al., 2015). The applied implications are clear:
416 some voles will consistently be more willing than conspecifics to consume any cover crop,
417 regardless of palatability. As such, it is unlikely that farmers will eliminate vole damage solely
418 by altering composition of cover crops planted in a soybean field.

419 From an ecological perspective, intraspecific behavioral variation may enable voles to
420 repopulate in areas of row crops that previously had not provided habitat. Row-crop fields

421 without cover crops tend to receive little use by voles (Berl et al., 2017). However, if some vole
422 phenotypes regularly incorporate cover crops into their diet, survive, and reproduce amidst
423 cover-cropping operations, vole populations may avail themselves of significantly more habitat
424 than in the previous decades of intensive row-crop agriculture with little use of cover crops.

425 Further study is needed within agricultural fields to determine if planting unpalatable cover
426 crops reduces damage to cover-cropped soybeans in natural conditions. In our study cover crops
427 were grown in a greenhouse and offered to captive voles during summer; it is possible that
428 selection of plant species may differ for field-grown plants in winter or spring. Researchers may
429 also monitor severity of soybean damage across years in fields using unpalatable species to
430 assess the role of in-situ flexibility of vole populations due to expression of behavioral diversity
431 in the population relative to biotic and abiotic factors that influence vole foraging and survival
432 (Sullivan and Sullivan 2018, Sullivan et al. 2018).

433 **5. Conclusion**

434 Common cover crop species range in attractiveness to meadow and prairie voles, and
435 palatability depends on availability of other forage. Red clover, alfalfa, and hairy vetch were
436 commonly preferred, and canola was avoided. Highly and minimally preferred species were
437 selected or avoided, respectively, more consistently than moderately preferred species. Farmers
438 can plant minimally preferred cover crops to deter voles, however, our findings suggest that the
439 effectiveness of this strategy may depend on availability of additional preferred forage on the
440 landscape and personality of voles that make use of cover-cropped fields. Alternatively, farmers
441 can anticipate greater risk of damage to soybeans in fields where highly preferred species are
442 planted, and act to manage vole populations in other ways.

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628

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629 **Appendix A**

Plant species	Crude protein (% DMB)	Reference
<i>Lolium multiflorum</i>	14.5	National Research Council, 1982
	18.5 ^a	Duke and Atchley, 1986
	23.2, 24.9	Han et al., 2018
<i>Secale cereale</i>	28.0	National Research Council, 1982
	21.4 ^a , 23.2 ^a	Duke and Atchley, 1986
	30.1, 23.6	Edmisten et al., 1998
	21.4, 24.8	Han et al., 2018
<i>Hordeum vulgare</i>	22.7 ^a	Duke and Atchley, 1986
	27.6, 20.4	Edmisten et al., 1998
<i>Triticum aestivum</i>	28.6	National Research Council, 1982
	18.1 ^a , 22.6 ^a	Duke and Atchley, 1986
	26.0, 22.2	Edmisten et al., 1998
<i>Sorghum bicolor x S. bicolor</i>	16.8	National Research Council, 1982
<i>Avena sativa</i>	18.0 ^a	Duke and Atchley, 1986
	18.2, 20.7	Edmisten et al., 1998
	15.9, 24.9	Han et al., 2018
<i>Vicia villosa</i>	30.5 ^a , 23.1 ^a	Duke and Atchley, 1986
	14.8, 27.4	Han et al., 2018
<i>Raphanus sativus</i>	21.1, 25.8	Han et al., 2018
<i>Trifolium pratense</i>	17.2	Dougall, 1962
	23.0	National Research Council, 1982

	20.7 ^a	Duke and Atchley, 1986
	18.9, 20.4	Brink and Fairbrother, 1988
	24.5	Hoffman et al., 1993
<i>Trifolium incarnatum</i>	18.8	Dougall, 1962
	17.0	National Research Council, 1982
	18.9 ^a , 16.7 ^a	Duke and Atchley, 1986
	10.2, 24.5	Han et al., 2018
<i>Melilotus officinalis</i>	21.0	MSU Extension, 2019
<i>Brassica rapa</i>	30.2, 29.4, 26.0, 17.4,	Duke and Atchley, 1986
	30.9 ^b	
<i>Brassica napus</i>	16.4	National Research Council, 1982
	16.0 ^a , 17.4 ^b	Duke and Atchley, 1986
<i>Astragalus cicer</i>	25, 21, 30, 17, 31, 20, 30,	Loeppky et al., 1990
	25, 35, 30, 38, 23, 27, 21,	
	30, 23, 35, 21, 38	
<i>Glycine max</i>	16.1 ^a , 16.6 ^a	Duke and Atchley, 1986
<i>Medicago sativa</i>	20.0	National Research Council, 1982
	25.3 ^a , 19.3 ^a	Duke and Atchley, 1986
	26.9	Hoffman et al., 1993
<i>Vernonia gigantea</i>	10.5, 12.5	Payne et al., 2010
	15.76	K. K. Payne, unpublished data
<i>Dactylis glomerata</i>	18.4	National Research Council, 1982
	12.6, 13.8	Duke and Atchley, 1986

630 ^a wet hay

631 ^b stage unknown

632

633 Table A.1—Protein values, represented as percent dry matter basis (DMB), for cover crops

634 tested for palatability to voles (Chapter 2) as found in the literature. Unless noted, values were

635 recorded only for fresh vegetative stage plants.

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636 **Appendix B**

Plant species	Acid detergent fiber (%DMB)	Reference
<i>Lolium multiflorum</i>	26.1, 25.6	Han et al., 2018
	40.9 ^b	Oliva et al., 2018
<i>Secale cereale</i>	17.8, 28.1, 20.1	Edmisten et al., 1998
	33.2 ^b	Lema et al., 2004
	25.4 ^b	Otal et al., 2008
	21.6, 21.0	Han et al., 2018
<i>Hordeum vulgare</i>	22.5, 20.6, 18.7	Edmisten et al., 1998
	24.4 ^b	Otal et al., 2008
<i>Triticum aestivum</i>	30.0	National Research Council, 1982
	20.1, 21.9, 29.1	Edmisten et al., 1998
	33.6 ^b	Lema et al., 2004
<i>Sorghum bicolor</i> x <i>S.</i>	29	National Research Council, 1982
<i>bicolor</i>	31.5 ^a , 41.1 ^a	Gerhardt et al., 1994
<i>Avena sativa</i>	19.0, 20.0	Edmisten et al., 1998
	20.5 ^b	Otal et al., 2008
	22.9, 23.5	Han et al., 2018
<i>Vicia villosa</i>	22.3, 23.5	Han et al., 2018
<i>Raphanus sativus</i>	25.5, 21.7	Han et al., 2018
<i>Trifolium pratense</i>	19.8	Hoffman et al., 1993
<i>Trifolium incarnatum</i>	23.3, 22.6	Han et al., 2018

<i>Melilotus officinalis</i>	33.4 ^b	Elgersma et al., 2013
<i>Brassica rapa</i>	23.5 ^b	Francisco et al., 2011
<i>Brassica napus</i>	27.8 ^a	Espinoza-Canales et al., 2017
<i>Astragalus cicer</i>	26.3 ^a , 24.5 ^a , 24.3 ^a , 33.9 ^a	Acharya et al., 2006
<i>Glycine max</i>	28.2 ^a	Hintz et al., 1992
	29.7 ^a , 38.8 ^a	Desborough and Ayers, 1988
	32.8	Peiretti et al., 2018
<i>Medicago sativa</i>	29.0	National Research Council, 1982
	20.4	Hoffman et al., 1993
<i>Vernonia gigantea</i>	30.8 ^b	K. K. Payne, unpublished data
<i>Dactylis glomerata</i>	31.0	National Research Council, 1982

637 ^a past vegetative stage

638 ^b stage unknown

639

640 Table B.1—Acid detergent fiber values, represented as percent dry matter basis (DBM), as found
 641 in the literature, for cover crops tested for palatability to voles (Chapter 2). Unless noted, values
 642 were recorded only for fresh, vegetative stage plants.

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Selection of common cover crops by voles (*Microtus*)

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Highlights

- Voles preferred clovers, hairy vetch, and alfalfa as forage, and avoided canola
- Voles consistently chose or avoided highly and minimally preferred species
- Voles were variable in choosing moderately preferred species
- Voles consumed more of unpreferred plant species when forage diversity was low
- Vole individuality contributed to probability of plants being selected as forage