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Abstract

Grasslands provide important resources for pollinators in agricultural landscapes. Managing grasslands with fire and grazing has the potential to benefit plant and pollinator communities, though there is uncertainty about the ideal approach. We examined the relationships among burning and grazing regimes, plant communities, and *Bombus* species and *Apis mellifera* L. abundance and nutritional indicators at the Grand River Grasslands in southern Iowa and northern Missouri. Treatment regimes included burn-only, grazed-and-burned, and patch-burn graze (pastures subdivided into three temporally distinct fire patches with free access by cattle). The premise of the experimental design was that patch-burn grazing would increase habitat heterogeneity, thereby providing more diverse and abundant floral resources for pollinators. We predicted that both bee abundance and individual bee nutritional indicators (bee size and lipid content) would be positively correlated with floral resource abundance. There were no significant differences among treatments with respect to bee abundance. However, some of the specific characteristics of the plant community showed significant relationships with bee response variables. Pastures with greater abundance of floral resources had greater bee abundance but lower bee nutritional indicators. Bee nutritional variables were positively correlated with vegetation height, but, in some cases, negatively correlated with stocking rate. These results suggest grassland site characteristics such as floral resource abundance and stocking rate are of potential importance to bee pollinators and suggest avenues for further research to untangle the complex interactions between grassland management, plant responses, and bee health.

Key words: grassland management, patch-burn grazing, honey bee, bumble bee, pollinator nutrition

Intensive agriculture across large geographic areas has greatly altered the landscape and forage plants available for both native and managed pollinators (Kremen et al. 2002, National Research Council 2006, Ricketts et al. 2008, Winfree et al. 2009). Remnants of native grasslands within an agricultural landscape have the potential to provide excellent food resources and nest sites for pollinators. However, grasslands may be managed in several different ways, leading to different plant communities, which can affect the abundance and health of local insect communities (Hines and Hendrix 2005; Moeller 2005; Davis et al. 2007, 2008; Slagle and Hendrix 2009; Hendrix et al. 2010). It is thus important to understand the ecological factors within grasslands that are most relevant to the abundance and health of bee pollinators.

Grassland vegetation characteristics such as nectar availability, pollen resources, and vegetation height have the potential to affect bees in a variety of ways. Vegetation height affects the distribution of nesting spots and refuges. Availability and diversity of floral resources can affect bee nutritional status. Foraging in landscapes with limited nectar and pollen sources has the potential to lead to nutritional deficits, which in turn may influence bees' susceptibility to fungal, bacterial, and viral diseases (Myack and Naug 2009, Di Pasquale et al. 2013). Bumble bee colonies closer to patches of rich floral resources produce more workers, healthier larvae, and larger individuals on average (Sutcliffe and Plowright 1990, Pereboom 2000, Pelletier and McNeil 2003, Westphal et al. 2009). Conversely, colonies next to abundant resources may also

experience higher rates of parasitism, negating some of the positive nutritive benefits (Carvell et al. 2008). Thus, a better understanding of the connections between grassland management, vegetation responses, and bee health is needed.

One opportunity for enhancing pollinator resources in the United States lies in the management of native (i.e., unplowed) Midwestern grasslands that are currently used for cattle grazing. Here we examine how fire and grazing management practices within grasslands affect the abundance and nutritional state of common bee species: native bumble bees (genus *Bombus*) and the nonnative honey bee, *Apis mellifera* L. We examined bees foraging in pastures managed using three different treatments: burn-only, graze-and-burn, and patch-burn graze (pastures subdivided into three temporally distinct fire units (patches) with free access by cattle). This work is part of an experiment to assess the effects of grassland management practices on vegetation and wildlife in the Grand River Grasslands, working agricultural grasslands of southern Iowa and northern Missouri (Debinski et al. 2011, Miller et al. 2012). This region is characterized by rolling hills that are low in corn suitability, and thus the predominant land use is cattle grazing. Most of the grazing is done at a high stocking rate, leaving very little in the way of vegetation structure in the pastures. However, there has been a concerted effort to protect and restore prairies in the region, so the landscape is a mosaic of grazed pastures, ungrazed grasslands, and rowcrops. Given the high potential for restoration, this region is an ideal location for testing how plant community characteristics and management techniques can affect the health and abundance of both wild and managed bees.

Returning two key and interconnected processes (fire and grazing) to native grasslands has the potential to enhance pollinator habitat, although there is still uncertainty and some controversy regarding the ideal approach to using grazing and burning for invertebrate conservation (Swengel 1998; Panzer and Schwartz 2000; Cook and Holt 2006; Vogel et al. 2007, 2010; Engle et al. 2008; Moranz 2010; Swengel et al. 2011). Burning stimulates flower production, which increases resources for pollinators (Platt et al. 1988, Rudolph et al. 2006, Brewer et al. 2009). Cattle grazing can increase plant species richness in grasslands, especially through preserving the diversity of forb species (Harrison et al. 2003, Hayes and Holl 2003). However, homogeneous application of grazing or burning can lead to less diverse wildlife (Holecheck et al. 2003, Kirchner et al. 2011) and insect communities (Reed 1997, Branson et al. 2006). Alternatively, a combination of fire and grazing has been proposed to maintain and restore essential habitat heterogeneity (Fuhlendorf and Engle 2001). The habitat heterogeneity provided by patch-burn grazing has the potential to provide more diverse and abundant floral resources for pollinators (Fuhlendorf and Engle 2001, Helzer and Steuter 2005). However, relatively few researchers have assessed the impacts of patch-burn-grazing on insect communities (Engle et al. 2008; Debinski et al. 2011; Doxon et al. 2011; Moranz et al. 2012, 2013, 2014), and none have considered the nutritional health of pollinators.

We measured plant community characteristics and sampled *A. mellifera* and several *Bombus* species from grazed, burned-and-grazed, and patch-burn-grazed grasslands. We then examined bee nutritional indicators to determine if bee nutrition was related to treatments, plant community characteristics, or both. Nutritional indicators included head width and wing length (both indicators of larval nutrition), lipid content (an indicator of adult nutrition), and abdomen mass (an indicator of both larval and adult nutrition; Winston 1987). We also estimated whether species abundance varied among pastures as a function of treatment or plant community

characteristics. Our hypotheses were as follows: 1) patch-burn-grazed treatments will lead to higher floral plant diversity and average floral resource abundance (FRA), 2) pastures providing greater floral resources will have more bees with higher nutritional indicators, and 3) pastures with heaviest grazing will support smaller numbers of bees with lower nutritional indicators.

Materials and Methods

Study Sites

We delineated 12 pastures in the Grand River Grasslands (see map in Supp. Fig. 1 [online only]) in 2006. All pastures are located in a ~160 square kilometer radius in Ringgold County of southern Iowa and Harrison County of northern Missouri. These pastures have served as study sites in previous studies, assessing the effectiveness of patch-burn grazing in improving habitat for grassland insects and birds (Moranz et al. 2010, Debinski et al. 2011, Pillsbury et al. 2011, Hovick et al. 2012). The pastures range in size from 15.6 to 37.4 ha and are a mix of public and private grasslands. For more information on the plant community of the study, see McGranahan et al. (2013). Pastures were allocated to one of the three treatments: 1) patch-burn-graze—annual burning of spatially distinct patches and free access by cattle, 2) graze-and-burn—burning entire tracts with free access by cattle, and 3) burn-only—burning of entire pastures with no grazing (typical management for protected lands in the region). The burning schedule was on a three-year cycle in all cases, and the number of cattle (stocking rate) was low. From 2007 through 2009, pastures in grazing treatments were stocked with cattle at a rate of ~3.4 animal unit months (AUM, the amount of forage consumed per animal unit per month, where an animal unit is defined as a 1,000-pound cow and her suckling calf) per ha between May 1 and October 1. The stocking rate was reduced to about 1.5 AUM per ha from 2010–2012 to maximize the treatment goal of creating heterogeneity among patches within the pastures. Each pasture was divided into three patches of approximately equal area. In patch-burn graze pastures, natural topographic features such as waterways, drainages, and ridgetops were used as patch boundaries to the extent possible. Each year, a different patch within each patch-burn graze pasture was burned in early spring. Burn-only and graze-and-burn pastures were burned in their entirety every three years. All pastures or patches were burned during mid-March of the burn years within approximately a two-week window of time.

During 2006–2009, all 12 pastures were used for the study (four pastures per treatment). During 2011–2012, only six pastures were used in the study (two pastures per treatment). See the Supp. Table 1 (online only) for a complete list of pastures and vegetation and bee sampling methods used each year. Most sites were separated by >1 mile; however, some sites were closer together (Supp. Fig. 1 [online only]) and, thus, may have partially shared bee communities. While honey bee and bumble bees may forage greater than 1 mile from their colonies (Beekman and Ratnieks 2001), many foraging flights occur closer to nests (Steffan-Dewenter and Kuhn 2003). Thus, we expect fairly distinct bee communities foraged on each of our sites.

Quantification of Vegetation Variables

We quantified three plant community features: 1) vegetation height using a Robel pole (quantified as in Debinski et al. 2011), 2) average FRA, and 3) number of flowering plants. Robel data were collected annually during the peak of the growing season in early July; vegetation height was measured to provide an indicator or the level of growth of a stand of grassland after burning or intensive grazing

(Moranz et al. 2012). We expected higher vegetation height to be associated with more floral resources, as there is little vegetation left beyond a “grazing lawn” 1 cm in height in intensively grazed pastures, providing no floral resources (Debinski, personal observation). In addition, FRA and diversity data were collected twice during summer (the first round between June 7–July 3, second round between July 5–August 5) starting in 2008. These dates were not necessarily the same dates on which bees were collected; instead, the two measurements were taken to capture overall trends in floral resources, not necessarily the floral resources available to bees at the time of capture. Two 100-m transects were established within each patch (three per pasture). Within each of the five 1- by 20-m segments within a transect, the number of flowering ramets were counted for each flowering plant species. We summed the total number of ramets by species within each transect and then averaged across transects for each pasture. We calculated floral plant diversity using Shannon’s Diversity Index (Magurran 2004). While these measurements of FRA and diversity do not provide specific information about the actual availability of nectar and pollen to bees, they do provide a proxy for the amount and diversity of potential forage available to pollinators. Note that data on several additional vegetation variables were collected as part of another related project (Debinski et al. 2011): cover of warm season grasses, cool season grasses, tall fescue (*Schedonorus arundinaceus* (Schreb.), nonleguminous forbs, leguminous forms, and woody species. We analyzed these data for relationships with bee abundance and nutrition but did not find meaningful correlations and, therefore, decided not to use them in further analyses.

Bee Collections for Nutritional Indicators

From 2006 to 2009, we collected *A. mellifera* and *Bombus*, representing several species (described in results), from 12 pastures solely to be used for analysis of nutritional indicators (described below). We collected twice each summer—once from June to early July and once from mid-July to early August—with an observer (the same observer across all sites within a year) using a nontargeted sweep netting (i.e., not specifically aiming to capture bees) along a 50-m transect. The number of net sweeps (40) rather than the number of minutes was standardized in this effort (see Debinski et al. 2011 for complete 2006–2009 methodology).

In 2011, we surveyed bees from a subset (6) of pastures, providing two replicates of each management treatment (see Supp. Table 1 [online only]). These bees were again only used for measurement of nutritional indicators, thus, times and sweeps were not standardized among the pastures. We collected once in June, July, and August for ~1.5-h periods. For these collections, a collector walked around the pastures, stopping at open floral blooms and netting in a targeted way in order to collect *A. mellifera* and *Bombus* species. *Bombus* were identified to species after collection (in the laboratory) using publicly available online keys (Ballew and Pickering 2002).

Bee Collections for Estimating Abundance

In 2012, we collected *Apis* and *Bombus* species in late June and early August of 2012 from the same six grassland pastures as the 2011 collections. Bee abundance in the August collection was abnormally low due to a prolonged drought and was therefore excluded from further analysis. A collector (G.W.S.) captured bees by walking three established 100-m transects in each pasture at a pace of 20 m/30 s. Bees spotted ~10 m ahead of or alongside the collector were captured via sweep netting. Each of the three surveys lasted for

10 min with the clock stopped for capture and handling of bees in order to identify them to species. Afterwards, bees were released.

For all years, surveys were limited to times when the temperature was between 21°C and 35°C, wind was <16 km/h, clouds did not obscure the sun, and between 0900 and 1800 hours. Although bee abundance and activity can vary greatly throughout the day, we were unable to finely control for the time of day of bee sampling due to logistical challenges of traveling to all of our sites.

Nutritional Indicators

We identified collected bees according to species, sex, and queen or worker caste. Only female workers were used for further analysis. To estimate overall bee size, we measured head width and wing length by photographing each specimen and measuring these features digitally using the Leica Application Suite (version 2.0.0). To estimate wet mass, we removed abdomens from each bee and weighed them on a microbalance. *Bombus* species have substantial variation in worker body size (up to 10-fold in body mass, Couvillon et al. 2010), whereas body size variation in *A. mellifera* workers is much lower. Nonetheless, *A. mellifera* worker body size can be significantly affected by nutritional stress during larval or pupal development (Brodschneider and Crailsheim 2010), thus, suggesting that such body size measurements had the potential to be informative for *A. mellifera* as well. We conducted lipid analysis via a colorimetric assay and estimated total lipid content of individual bee abdomens based on a standard curve of pure cholesterol (see Toth and Robinson 2005). Each species was analyzed separately. Wing length and head width data were available for all five years (2006–2009 and 2011), but lipid and abdomen mass data were only available for bees collected in 2011. Lipid stores are known to vary significantly across the lifetime of honey bee workers, with foragers having lower lipid stores than nonforagers (Toth and Robinson 2005). Nonetheless, these studies suggest there is some additional loss of lipid after the onset of foraging and variation in lipid stores between foragers (Toth and Robinson 2005); thus, examining lipid stores of foragers can still provide information about nutritional status of foragers.

Statistical Analyses

A complete list of vegetation and bee measures used each year is available in Supp. Table 1 (online only).

Vegetation Data

We tested for correlations among continuous vegetation and pasture variables with JMP 10’s multivariate feature using data for all years in which bees were collected (JMP Version 10.0.0). We then used ANOVA to test the relationship between treatment and all of the continuous vegetation and pasture variables. Note that we included data for all pastures where bee surveys were conducted, even if the bee abundance was zero.

Bee Data

We analyzed bee data with JMP software using three statistical approaches. First, we ran all variables—as model effects—against bee abundance and nutritional variables, using standard least squares models with an effect leverage emphasis and a restricted maximum likelihood (REML) method with pasture included as a random effect. For some of the nutrition relationships, the sample size was prohibitively small, preventing JMP from running the least squares model, and in these cases, we ran an ANOVA with no random effects (for treatment, the only discrete predicting variable) and

a bivariate regression analysis (for the four continuous predicting variables: AUM, vegetation height, FRA, and floral plant diversity) to test for relationships between vegetation variables and bee abundance or nutritional variables. We compared treatments using post hoc t-tests with a Bonferroni correction. We examined the responses of the total bee community, *A. mellifera*, all *Bombus* species combined (“total *Bombus*”), *B. griseocollis* and *B. impatiens* (the two most abundant *Bombus* species), and all other *Bombus* species (those that were not *B. griseocollis* or *B. impatiens*). Sample sizes were limiting, especially for analyses at the species level; however, we decided to analyze species separately due to concerns about lumping together bee species of different sizes and life histories and because we thought it would be informative to determine whether multiple species showed similar responses to treatment variables. Note that, because the study involved multiple years of data and site variables such as AUM and vegetation variables changed from year to year, we always used data from each pasture and for each year, and did not use any average values in our statistical analysis.

Results

Correlations Among Pasture Variables

To better understand the relationships between vegetation and stocking rate, we examined pairwise correlations across all continuous vegetation variables (floral plant diversity, vegetation height, FRA), in addition to examining correlations of each vegetation variable with AUM, across the six pastures. The correlations among the variables ranged widely (from $r = -0.90$ to 0.54), and were all highly significant (Supp. Fig. 2 [online only]). Higher FRA was correlated with lower floral plant diversity, lower vegetation height, and higher cattle stocking (AUM). Higher AUM was also correlated with lower vegetation height and lower floral plant diversity (Supp. Fig. 2 [online only]).

Relationships Between Treatment and Pasture Variables

We tested for differences among the three treatments for the four pasture variables (AUM, floral plant diversity, vegetation height, and FRA) for all years in which bees were surveyed. The three vegetation variables (Fig. 1) showed significant differences among the treatments ($P < 0.05$). Vegetation height (ANOVA $P < 0.0001$) and floral plant diversity (ANOVA $P = 0.0411$) both showed the same trend, having the highest means under burn-only conditions, the second highest under graze-and-burn, and the lowest under patch-burn graze. For FRA, the pattern was the opposite (ANOVA $P = 0.0208$, Fig. 1).

Bee Abundance

Bees were found on five of the six pastures sampled in 2012 (Supp. Table 1 [online only]). Abundance among the pastures was unevenly distributed, with collection counts ranging from 0 to 16 with an average of 4.5 bees collected per pasture. Of the 27 bees collected in 2012, 14 were *Apis* and 13 were *Bombus* species; *B. impatiens* and *B. griseocollis* were the two most abundant. The “other” *Bombus* included *B. pennsylvanicus*, *B. vagans*, *B. bimaculatus*, and two specimens that were unidentified *Bombus* sp.

Only one of the six bee abundance measures (abundance of “other” *Bombus*) showed a near significant difference among treatments (Table 1); however, the sample size was very small ($n = 6$, $P = 0.0741$). An average of 1.5 other *Bombus* species were found on

patch-burn graze pastures, 1.0 at burn-only pastures, and 0 at graze-and-burn pastures.

Average FRA from 2008 to 2012 positively correlated with abundance of several different bee groups (data shown are from 2012 only). Pastures with greater average FRA had higher overall bee counts and more *Apis* and *B. griseocollis* ($P < 0.05$), and there were near significant positive trends for the total number of *Bombus* and “other” *Bombus* species with FRA ($P < 0.10$). Note that these results were strongly affected by one pasture, Ringgold South, which had a higher average FRA and more bees than the other pastures. With Ringgold South excluded, none of the relationships were significant. AUM, vegetation height, and floral plant diversity showed no significant or near significant relationships with any of the bee abundance measurements ($P > 0.10$).

Nutritional Indicators

Bees used in the analysis of nutritional indicators were collected from 2006–2009 and 2011. Note that *A. mellifera* yielded sufficient samples for analysis in all four years, but *B. impatiens* and *B. griseocollis* only yielded sufficient samples in 2011. *A. mellifera* collected before 2011 only have wing length and head width data, whereas all bees collected during 2011 also have lipid content and abdomen mass data. A total of 137 bees were found in eight different pastures; some sampled pastures yielded zero specimens. We sampled 83 *A. mellifera*, 32 *B. griseocollis*, and 22 *B. impatiens*.

B. griseocollis had lower abdomen mass in patch-burn grazed pastures ($P = 0.0242$, $F = 6.6307$, Table 2, Fig. 2). *A. mellifera* showed a similar trend, with lowest lipid stores in patch-burn grazed pastures, but this was significant only when using an ANOVA model ($P = 0.0017$, $F = 7.2351$, Supp. Table 2 [online only], Fig. 2). Bee taxa did not differ for any of the other nutritional indicators ($P > 0.10$) among treatments.

Cattle stocking rate (AUM) correlated negatively with *A. mellifera* wing length ($P = 0.0282$, $R^2 = 0.0652$) and head width ($P = 0.0206$, $R^2 = 0.1150$, Fig. 3). There were no significant correlations between AUM and nutritional variables for any other species, but many of the other relationships also showed negative (though nonsignificant) trends.

Vegetation height (Robel pole height) negatively correlated with *A. mellifera* abdomen mass (without pasture as a random variable) ($P = 0.0082$; pastures with greater vegetation heights had *Apis* individuals with smaller abdomen masses [Table 2]).

The average FRA in a pasture negatively correlated with several nutritional variables for *B. impatiens*: wing length ($P = 0.0467$), head width ($P = 0.0383$), and abdomen mass ($P = 0.0409$; Fig. 4). FRA was not correlated with nutritional indicators of other bee species or groups of species.

Floral plant diversity did not correlate with any of the nutritional measures for the three species ($P > 0.10$).

Discussion

This study provides new information about the potential impacts of grassland management on vegetation traits relevant to bee pollinators. Our data provide several new observations that suggest avenues for further study. First, we confirmed that management strategies involving burning, grazing, and patch-burn grazing can affect several, highly correlated vegetation variables (Debinski et al. 2011, Moran et al. 2012), some of which have the potential to be relevant to bee nutritional status. Second, our results verify (Morse 1980, Pleasants 1981) that FRA is important to the abundance of

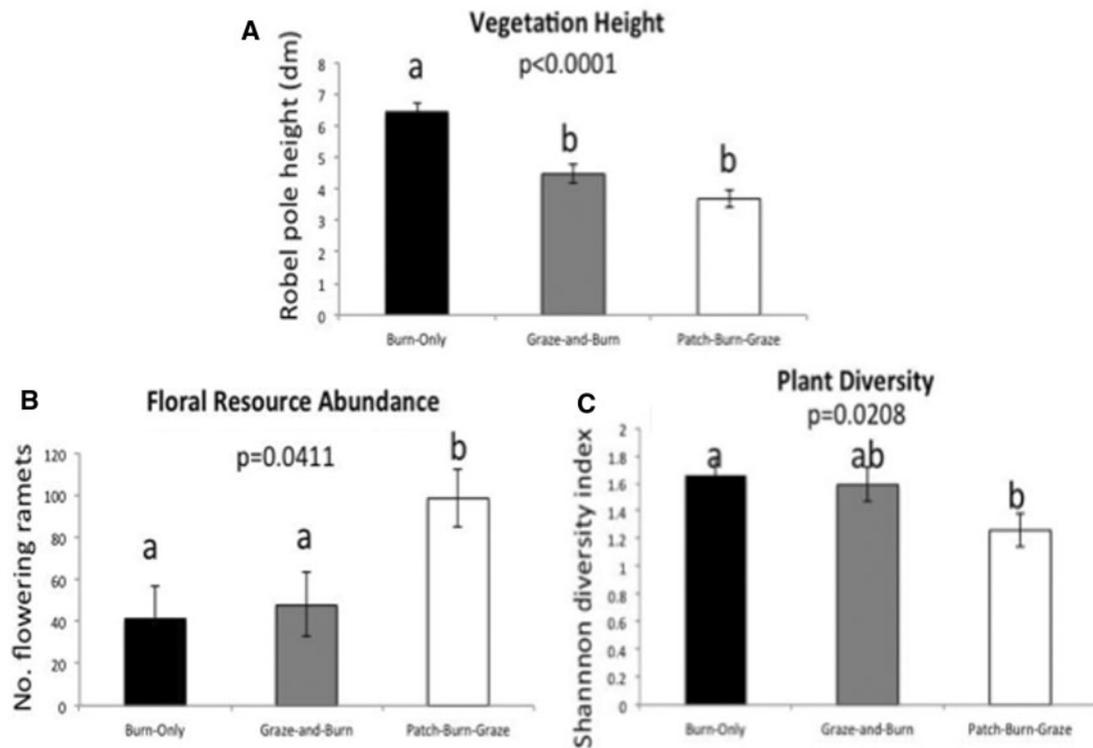


Fig. 1. Different land management treatments result in significant differences in (A) vegetation height, (B) FRA, and (C) floral plant diversity (Shannon's diversity index) of vegetation. *P*-values for the ANOVA for each variable are shown below the variable name, and different letters above the bars represent significant differences in post hoc tests. *n* = 4 sites per treatment.

Table 1. Table of test statistics from standard least square models run with pasture as a random effect for 2012

| Bee group | Sample size | Treatment | Stocking rate (AUM) | Vegetation height | Floral resource abundance | Floral plant diversity |
|------------------------|-------------|--|--|--|--|--|
| Total Bees | 27 | <i>P</i> = 0.5390 <i>F</i> = 0.7649 df = 2 | <i>P</i> = 0.9626 <i>F</i> = 0.0025 df = 1 | <i>P</i> = 0.8524 <i>F</i> = 0.0394 df = 1 | <i>P</i> = 0.0251⁺ <i>F</i> = 12.1996 df = 1 | <i>P</i> = 0.3777 <i>F</i> = 0.9824 df = 1 |
| <i>A. mellifera</i> | 14 | <i>P</i> = 0.5514 <i>F</i> = 0.7308 df = 2 | <i>P</i> = 0.9564 <i>F</i> = 0.0034 df = 1 | <i>P</i> = 0.8372 <i>F</i> = 0.0480 df = 1 | <i>P</i> = 0.0095⁺ <i>F</i> = 21.7756 df = 1 | <i>P</i> = 0.2793 <i>F</i> = 1.5636 df = 1 |
| <i>Bombus</i> total | 13 | <i>P</i> = 0.5267 <i>F</i> = 0.8000 df = 2 | <i>P</i> = 0.8273 <i>F</i> = 0.0542 df = 1 | <i>P</i> = 0.8840 <i>F</i> = 0.0242 df = 1 | <i>P</i> = 0.0887^{!+} <i>F</i> = 5.0130 df = 1 | <i>P</i> = 0.5909 <i>F</i> = 0.3405 df = 1 |
| <i>B. impatiens</i> | 3 | <i>P</i> = 0.6037 <i>F</i> = 0.60 df = 2 | <i>P</i> = 0.3537 <i>F</i> = 1.0989 df = 1 | <i>P</i> = 0.5006 <i>F</i> = 0.5469 df = 1 | <i>P</i> = 0.6995 <i>F</i> = 0.1721 df = 1 | <i>P</i> = 0.6772 <i>F</i> = 0.2009 df = 1 |
| <i>B. griseocollis</i> | 4 | <i>P</i> = 0.5630 <i>F</i> = 0.70 df = 2 | <i>P</i> = 0.8958 <i>F</i> = 0.0195 df = 1 | <i>P</i> = 0.8565 <i>F</i> = 0.0372 df = 1 | <i>P</i> = 0.0147⁺ <i>F</i> = 16.9400 df = 1 | <i>P</i> = 0.3192 <i>F</i> = 1.2915 df = 1 |
| "Other" <i>Bombus</i> | 6 | <i>P</i> = 0.0741^{!#} <i>F</i> = 7.00 df = 2 | <i>P</i> = 0.6413 <i>F</i> = 0.2532 df = 1 | <i>P</i> = 0.4831 <i>F</i> = 0.5962 df = 1 | <i>P</i> = 0.0600^{!+} <i>F</i> = 6.7599 df = 1 | <i>P</i> = 0.1928 <i>F</i> = 2.4465 df = 1 |

Significant and near significant results are bolded and cells are shaded. + and - signs indicate if the relationship is negative or positive for significant results, # indicates nominal data (treatment), and ! indicates near significant *P*-values (greater than 0.05 but less than 0.10).

honey bees and some species of bumble bees observed foraging on flowers in those pastures, but surprisingly, high FRA in a pasture does not necessarily mean bees will have higher nutritional state. Third, our data suggest that bee nutritional state may depend on other habitat considerations beyond FRA; habitat traits such as stocking rate and vegetation height were associated with some

honey bee nutritional variables. Finally, our data show no clear relationship between diversity of flowering plants and bee abundance or nutritional state.

Returning to our first hypothesis that patch-burn-grazing treatments would lead to higher floral plant diversity and FRA, we found only partial support. Although patch-burn-grazed pastures had

Table 2. Table of test statistics from standard least square models run with pasture as a random effect and in ANOVA runs for applied to nutritional measures for 2006–2009 and 2011

| Bee measure | Treatment | Stocking rate (AUM) | Vegetation height | Floral resource abundance | Floral plant diversity |
|--------------------------------------|---|--------------------------------|---|--------------------------------|---------------------------|
| <i>A. mellifera</i> wing length | $P = 0.7870$ | $P = 0.0284$ | $P = 0.3030$ | $P = 0.6373$ | $P = 0.1602$ |
| | $F = 0.2521$ | $F = 6.2475$ | $F = 1.0941$ | $F = 0.2282$ | $F = 4.5195$ |
| | df = 2 | df = 1 | df = 1 | df = 1 | df = 1 |
| <i>A. mellifera</i> head width | $P = 0.5895$ | $P = 0.0206$ | $P = 0.1144$ | $P = 0.2428$ | $P = 0.3702$ |
| | $F = 0.5933$ | $F = 7.7616$ | $F = 2.6627$ | $F = 1.5386$ | $F = 1.3333$ |
| | df = 2 | df = 1 | df = 1 | df = 1 | df = 1 |
| <i>A. mellifera</i> abdomen mass | $P = 0.5454$ | $P = 0.2725$ | $P = 0.0082$ ⁺ | $P = 0.2147$ | $P = 0.1342$ |
| | $F = 0.7549$ | $F = 1.6825$ | $F = 7.5473$ | $F = 2.5371$ | $F = 4.7226$ |
| | df = 2 | df = 1 | df = 1 | df = 1 | df = 1 |
| <i>A. mellifera</i> lipid content | $P = 0.5626$ | $P = 0.7080$ | $P = 0.9702$ | $P = 0.8507$ | $P = 0.8883$ |
| | $F = 0.7374$ | $F = 0.1695$ | $F = 0.0016$ | $F = 0.0422$ | $F = 0.0233$ |
| | df = 2 | df = 1 | df = 1 | df = 1 | df = 1 |
| <i>B. griseocollis</i> wing length | $P = 0.1738$ [^] | $P = 0.7872$ | $P = 0.6325$ | $P = 0.1125$ | $P = 0.2080$ |
| | $F = 1.8642$ | $F = 0.0883$ | $F = 0.3740$ | $F = 2.6781$ | $F = 1.9668$ |
| | df = 2 | df = 1 | df = 1 | df = 1 | df = 1 |
| <i>B. griseocollis</i> head width | $P = 0.3679$ [^] | $P = 0.6811$ | $P = 0.4943$ | $P = 0.2424$ | $P = 0.4161$ |
| | $F = 1.0365$ | $F = 0.7351$ | $F = 0.4791$ | $F = 1.4238$ | $F = 1.4735$ |
| | df = 2 | df = 1 | df = 1 | df = 1 | df = 1 |
| <i>B. griseocollis</i> abdomen mass | $P = 0.0242$ [^] | $P = 0.7375$ | $P = 0.8912$ | $P = 0.1287$ | $P = 0.2658$ |
| | $F = 6.6307$ | $F = 0.1518$ | $F = 0.0228$ | $F = 5.9532$ | $F = 2.3508$ |
| | df = 2 | df = 1 | df = 1 | df = 1 | df = 1 |
| <i>B. griseocollis</i> lipid content | $P = 0.6991$ | $P = 0.3946$ | $P = 0.8389$ | $P = 0.6193$ | $P = 0.9052$ [^] |
| | $F = 0.7390$ | $F = 1.0179$ | $F = 0.0707$ | $F = 0.2847$ | $F = 0.0145$ |
| | df = | df = 1 | df = 1 | df = 1 | df = 1 |
| <i>B. impatiens</i> wing length | $P = 0.6050$ | $P = 0.5072$ | $P = 0.9670$ | $P = 0.0467$ | $P = 0.2654$ |
| | $F = 0.6172$ | $F = 0.5982$ | $F = 0.0021$ | $F = 7.4313$ | $F = 1.5604$ |
| | df = 2 | df = 1 | df = 1 | df = 1 | df = 1 |
| <i>B. impatiens</i> head width | $P = 0.5570$ | $P = 0.5040$ | $P = 0.9028$ | $P = 0.0383$ | $P = 0.2326$ |
| | $F = 0.7516$ | $F = 0.6038$ | $F = 0.0179$ | $F = 8.6756$ | $F = 1.7723$ |
| | df = 2 | df = 1 | df = 1 | df = 1 | df = 1 |
| <i>B. impatiens</i> lipid content | NA | $P = 0.1586$ | $P = 0.1586$ | $P = 0.1586$ | $P = 0.1586$ |
| | | $F = 15.4502$ | $F = 15.4502$ | $F = 15.4502$ | $F = 15.4502$ |
| | | df = 1 | df = 1 | df = 1 | df = 1 |

AUM—animal unit months, a measure of cattle stocking rate. Significant and near significant results are bolded and shaded in grey. + and - signs indicate if the relationship is negative or positive for significant, continuous results. ^notes relationships that could not be run with standard least squares models and are ANOVA results run without pasture as a random effect. ! indicates near significant P -values (greater than 0.05 but less than 0.10); NA denotes “not available” because of too few observations for analysis.

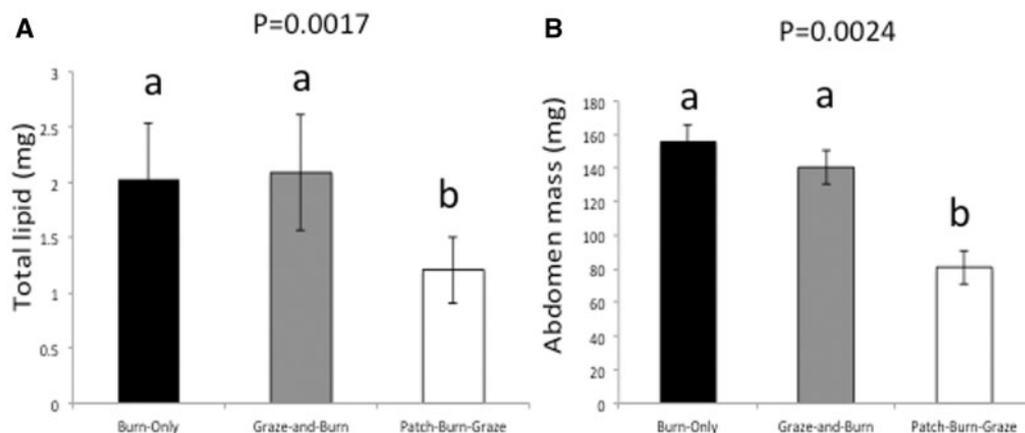


Fig. 2. (A) Lipid stores were significantly lower in *A. mellifera* ($n = 55$) collected in patch-burn-grazed pastures compared to other grassland management treatments. (B) Abdomen weight was lowest in patch-burn graze pastures for *B. griseocollis* ($n = 10$). Note that P -values shown reflect an ANOVA model for *A. mellifera* and a least squares model for *B. griseocollis*.

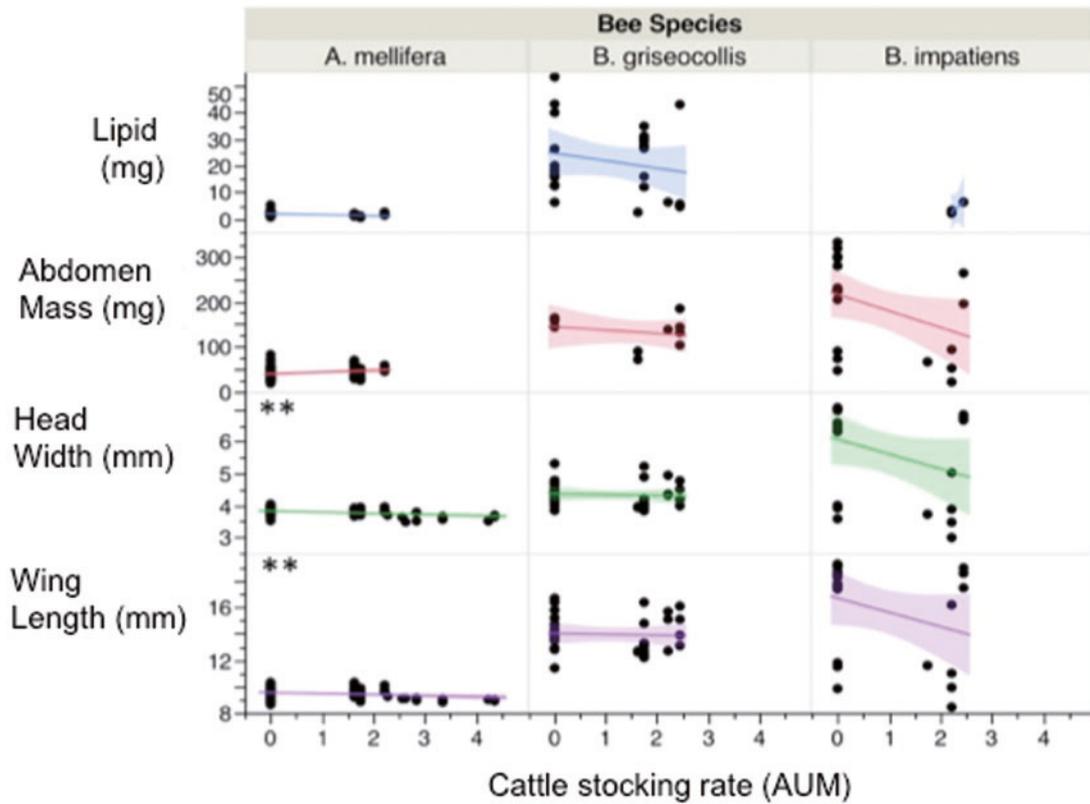


Fig. 3. Scatter plot for a measure of cattle stocking rate (animal unit months = AUM) plotted against bee nutritional variables. ** indicates significant correlation ($P < 0.05$). $n = 8$ pastures and 127 collected bees.

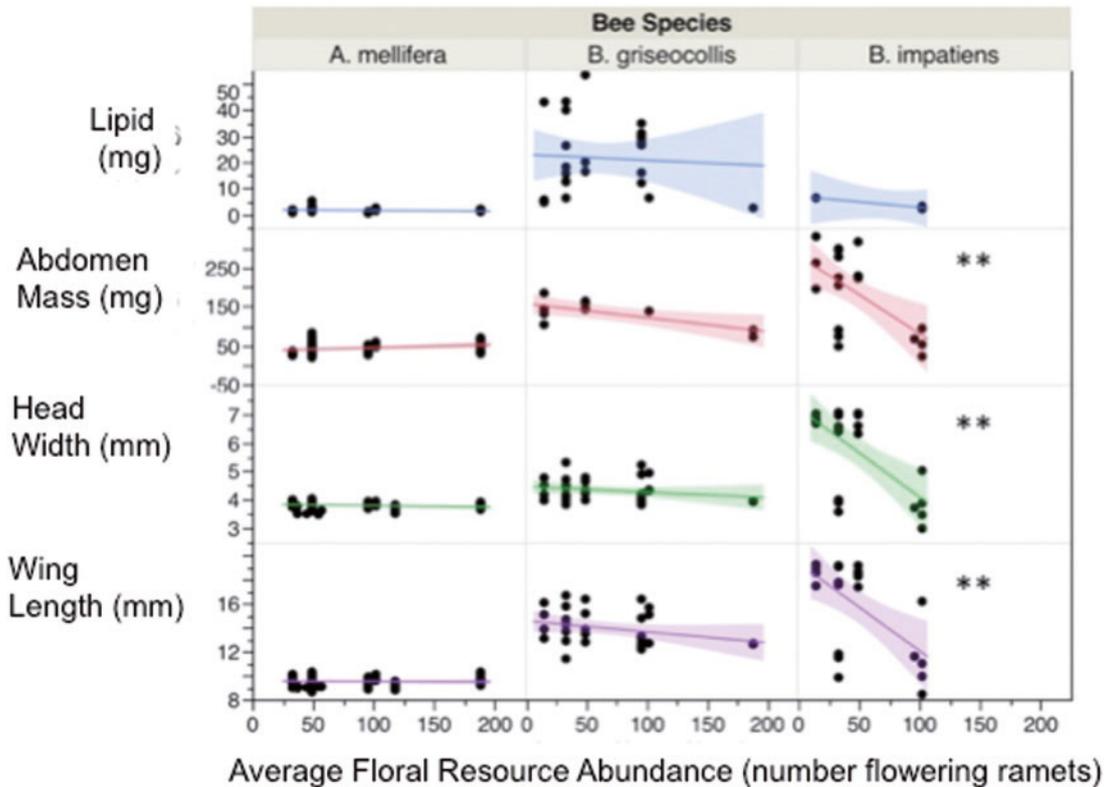


Fig. 4. Scatter plot for average FRA plotted against bee nutritional variables. ** indicates significant correlation ($P < 0.05$). $n = 8$ pastures and 127 collected bees.

higher FRA, they also had lower floral plant diversity. Patch-burn-graze pastures generally also had lower average vegetation height. Patch-burn grazing is intended to create heterogeneous vegetation height among patches within the pasture, so this result is not surprising (Fuhlendorf and Engle 2001, Helzer and Steuter 2005). Burning at least a portion of the pasture annually may stimulate more flowering on an annual basis than burning at a 3-yr interval. We found that the average FRA was higher on patch-burn grazed pastures, despite the fact that the flowering plant diversity was lower. Interestingly, two measures of bee nutrition (*A. mellifera* lipid content and *B. griseocollis* abdomen mass) were lowest on patch-burn grazed pastures. These responses hint at the potential for an inverse relationship between the nutritional value of the floral resources stimulated by patch-burn grazing and *A. mellifera* and *B. griseocollis* nutritional measures, but additional research is needed to better understand this pattern. It is possible that more flowers do not necessarily translate into a higher abundance of appropriate floral species or nutritionally rich floral resources for bees.

With regard to the three treatments, there is an important caveat with respect to legacy effects. Due to constraints of pasture ownership and previous management, there were differential levels of grazing applied to pastures prior to our experiment (Debinski et al. 2011, Moranz et al. 2012). These land-use legacies may have influenced our ability to detect treatment effects. For that reason, the rest of our discussion emphasizes the results of bee responses to vegetation characteristics more than to treatment effects. It is also important to note that the vegetation measurements and bee collections were made on different dates; thus, the associations we report are not meant to reflect immediate associations between floral resources and bee measures. Rather, these measures are meant to serve as broad, annual indicators of overall patterns in bee and floral resource presence.

Returning to our second hypothesis, that grasslands providing greater floral resources would have more bees that exhibited positive nutritional indicators, we again find only partial support. There was a significant positive correlation between FRA and bee abundance for *A. mellifera* and *Bombus griseocollis*. However, one site (Ringgold South) had extremely high FRA compared to other sites, and this site strongly drove the positive relationship. Considering the impact of this single pasture, our data suggest that flowering ramet densities above 60 are most effective at attracting bees. For nutritional indicators, we found no relationship between FRA and nutritional state for most bee groups. Counterintuitively, *B. impatiens* in pastures with high FRA actually had lower nutritional parameters (weight, head width, and wing length).

It is possible that high overall FRA does not necessarily mean more or better nutrition for bees. Perhaps bees could have been attracted to pastures with many flowers, but the nectar and pollen resources they encountered may have proved unsuitable. Indeed, patch-burn grazed pastures had higher FRA but lower flowering plant diversity. Thus, these pastures could have been depauperate in bee-preferred flower species. For example, with *Bombus impatiens*, it is possible that the negative relationship between FRA and nutritional state relates to a lack of a particular floral species or set of species that are of importance for this bee species.

Second, perhaps there are complex interspecific interactions that may result when FRA is high. Davis et al. (2008) found an inverse relationship between bee and butterfly diversity in similar Midwestern grasslands. Competition both within pollinator taxa and among pollinator taxa is an area of research that warrants additional study.

Third, as previously noted, other studies have found that colonies in closer proximity to rich floral resources experience higher rates of parasitism (Carvell et al. 2008). Thus, bees found at pastures with higher quality nectar resources could also face a higher density of parasitism, affecting nutritional indicators.

Fourth, it is possible that nutritionally challenged bees had dispersed from neighboring patches, in search of floral resources. Foraging flight distances for both *Apis* and *Bombus* can occasionally be extensive (up to 10 km, Beekman and Ratnieks 2001). Given the size of our experimental pastures (15.6–37.4 ha), it is possible that in some cases, bees with nests outside of our pastures visited to forage. Locations with especially high FRA would be likely to draw more bees from poorer quality neighboring areas (Morse 1980). Bees have excellent spatial memories and can return to profitable foraging sites repeatedly over many days (Winston 1987), and honey bees can recruit their nestmate workers to high-quality food patches using the famous waggle dance (von Frisch 1965, Beekman and Lew 2007).

With respect to our third hypothesis, we did find evidence that less intense grazing was associated with higher bee nutritional state but not bee abundance. Grazing can affect both plant and insect communities in grasslands; previous studies have often found negative associations (Rambo and Faeth 1999; Kruess and Tschamtkke 2001, 2002) between grazing and the abundance of bees and other insects. Although we found no differences in bee abundance, ours is the first study to suggest a negative impact of grazing on bee nutritional state. Further work on the nutritional quality of available floral resources is necessary to understand whether this pattern may relate to quality or quantity of available forage.

We were somewhat surprised that the floral plant diversity did not show a relationship with bee abundance or nutritional measures. However, we used the Shannon diversity index, which may be too simplistic a measure. It may be more important to look in more detail at specific indicators of the true nectar and pollen resources available to bees. Moranz et al. (2012) found that although some Grand River Grasslands pastures had a large number of flowering species, plant abundance was dominated by a small number of species (*Trifolium repens*, *Lotus corniculatus*, *Erigeron strigosus*, *Pycnanthemum tenuifolium*, and *Trifolium pratense*). Three out of five of these are exotic species that may not be suitable for native *Bombus*, and many of the additional species that were observed in some pastures occurred at particularly low abundances compared to other Midwestern prairies. Thus, presence of additional species that may not provide good forage to bees could inflate the diversity index without providing substantial additional resources.

Another important finding from this study is the fact that we saw many similar patterns in bee responses for both *A. mellifera* and several *Bombus* species. Not only do these species occupy different ecological niches, *Apis* is nonnative and the *Bombus* species are native, but most strikingly, it is likely that the *Apis* sampled may have come from nearby, managed hives, whereas *Bombus* are wild and nonmanaged. There is great variation in how honey bee hives are managed by beekeepers with respect to supplemental feeding, antibiotic treatments, and parasitic *Varroa* mite treatments, among many other factors (VanEngelsdorp and Meisner 2010). We did not attempt to control for any of this variation in our study, and such colony or site-level variation may certainly have influenced our honey bee results. Despite this, we found correlated responses of both honey bees and bumble bees with regard to the following measures: 1) higher FRA was correlated with higher bee abundance, 2) higher nutritional indicators were associated with lower grazing intensity, and 3) there was not a strong relationship between bee abundance

and bee nutritional state. These data suggest that landscape and vegetation effects can affect both wild and managed bees in similar ways.

In summary, our data suggest that grassland management practices and some of their effects on vegetation and floral resources have the potential to impact the abundance and nutritional state of bees. In general, increasing floral resources will attract more bees, and patch-burn-grazing did have higher FRA, suggesting this treatment can be effective in attracting bees. However, our nutritional data were collected from bees foraging on these pastures that may have just been “visitors,” and thus the interpretation of the result must be considered with caution. In general, we found positive nutritional effects of lower grazing intensity, which is characteristic of burn-only treatments. Thus, there is no single best land management strategy to increase both bee abundance and nutritional state. High levels of grazing are likely to be detrimental to both bee abundance and nutrition. The results from this work provide useful insights for future studies and similar conservation efforts throughout the agricultural Midwest—a critical area for bee pollinators (Grixti et al. 2009).

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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