The Role of Floral Density in Determining Bee Foraging Behavior: A Natural Experiment

•

Bethanne Bruninga-Socolar[1,2,4,5]

[1]Graduate Program in Ecology
and Evolution
Rutgers University
New Brunswick, New Jersey

Elizabeth E. Crone[3]
Rachael Winfree[2]

[2]Department of Ecology, Evolution,
and Natural Resources
Rutgers University
New Brunswick, New Jersey

[3]Department of Biology
Tufts University
Medford, Massachusetts

•

[4] Corresponding author: bethanne.ab@
gmail.com; 848-932-3538

[5] Current address: Rutgers University
14 College Farm Rd.
New Brunswick, NJ 08873

ABSTRACT: Animal-pollinated plants depend on sequential pollinator visits to conspecifics for successful reproduction. Therefore, in co-flowering plant communities, the proportion of visits to a focal plant species in individual pollinator foraging bouts determines reproductive outcomes for that species. We investigated the factors determining bee visits to the plant *Astragalus scaphoides* within foraging bouts in a natural multispecies community in the northern Rocky Mountains. We found that both conspecific and heterospecific floral density influenced the proportion of visits to *A. scaphoides* during foraging bouts, but these effects of floral density differed among two abundant bee groups. Our field observations reject the null expectation that bees visit plant species in direct proportion to their relative floral densities. *Bombus* consistently visited *A. scaphoides* more than expected, while solitary bees of the genera *Anthophora* and *Eucera* exhibited a nonlinear response to floral density.

Index terms: floral density, floral preference, pollinator, resource switching, solitary bees

INTRODUCTION

In natural plant communities, multiple plant species flower at the same time. Most of these plant species are visited by multiple pollinator species, and most pollinators visit multiple plant species (Michener 2000; Bosch et al. 2009). Animal-mediated plant reproduction is contingent on sequential (or nearly so) visits by a pollinator to multiple individuals of the same plant species, because pollen collected at one plant individual is generally deposited within a very small number of subsequent plant visits (Thomson 1986; Cresswell et al. 1995). In a natural plant community in which multiple plant species co-flower, the choices an individual bee makes within a foraging bout affect plant reproduction. Whether the bee visits multiple individuals of the same species within a foraging bout or switches among species affects the deposition of conspecific pollen and, thus, plant reproduction.

Bees use a variety of visual and other cues to make foraging decisions, but special attention has been paid to floral density as a key variable determining bee foraging behavior. The effects of floral density are complex and operate on multiple scales (Essenberg 2012). For a single plant species, there is a positive relationship between its floral density and pollinator visitation at small scales (e.g., patch sizes <400 m²) (Kunin 1993, 1997; Dauber et al. 2010). When multiple flowering plant species are considered, the effects of floral density on bee foraging behavior become more complicated. In a system with two co-flowering plant species, pollinator visits to the focal plant species increased with both conspecific and heterospecific floral density at very small scales (≤3 m) (Jakobsson et al. 2009). However, in a different two-plant system at a larger scale (plots of approximately 2600 m²), only conspecific density had an effect on pollinator visitation (Feldman 2008). In a system with four co-flowering plant species in approximately 13-m² plots (small scale), overall floral density had a positive effect on pollinator visitation to the focal plant species to a point, after which pollinator visitation decreased due to competition with one or more of the additional plant species (Ghazoul 2006). Such findings suggest that higher overall floral density causes more pollinators to visit a patch, but also may increase competition between individual plants since pollinators are shared by more plants in the patch, as predicted by theory (Rathcke 1983). In multispecies plant communities, increased competition at higher plant densities may be compounded by the presence of heterospecific plant species, as suggested by Ghazoul (2006) and Essenberg (2012). Additionally, four of these five studies were conducted in small patches of less than 400 m² (e.g., a patch size of 20 m x 20 m). However, even very small bees forage at distances of 100 meters or more (Greenleaf et al. 2007; Zurbuchen et al. 2010). Therefore, studies of the effects of floral density on bee behavior must consider larger spatial scales (Essenberg 2012). Measuring the relationships between pollinator visitation, competition versus facilitation among plant species, and floral density requires tracking the movements of individual bees among plant individuals across different relative densities of the plant species in the community (Kunin 1993), and at spatial scales large enough to encompass the true foraging mobility of the bees.

A final complicating factor of bee behavioral response to floral density is that we expect different bee groups to respond differently to floral density due to life history traits. For example, social bees and solitary bees differ in their foraging habits. The workers of social bee colonies often specialize individually on particular resources, for example, a single plant species, pollen, or nectar. Individual bees are, thus, less likely to change their foraging behaviors within foraging bouts (Heinrich 1976; Williams and Tepedino 2003). Individual females of solitary bee species must obtain all resources necessary for provisioning larvae, both pollen and nectar, by themselves. Polylectic solitary bees, those that feed on multiple plant species, may, therefore, be more likely to change their foraging behavior within foraging bouts based on resource availability (Tepedino and Parker 1982). In other words, solitary bees may need to visit multiple species within some foraging bouts in order to obtain both pollen and nectar, or a mixture of pollens with different nutritional properties (Eckhardt et al. 2014; Heinrich 1976; Bosch et al. 2009). Müller (1996) showed that polylectic solitary bees in the tribe Anthidiini (Hymenoptera, Megachilidae) visited 2.2 plant species on average in single foraging bouts. Oligolectic solitary bees, which specialize on single plant species or groups of related species (Michener 2000), are expected to exhibit much higher rates of floral constancy depending on their degree of specialization.

We used a natural co-flowering plant community to study the effects of multiple plant species' floral densities on bee foraging behavior. Our system focuses on a pollen-limited, biennially-flowering plant *Astragalus scaphoides* (Jones; bitterroot milkvetch), which provides a strong oscillation of floral density across years (Crone et al. 2009), while the densities of co-flowering plants remain roughly constant across years. We recorded bee foraging behavior by following individual flight paths (foraging bouts) within discrete communities of plants (patches in an otherwise arid habitat) ranging in size from 414 to 4327 m^2. We focused on two abundant bee groups that are known to visit *A. scaphoides* in our patches: the social genus *Bombus* and

the polylectic solitary genera *Anthophora* (Latreille) and *Eucera* (Scopoli), referred to as *Anthophora/Eucera* hereafter (Crone 2013). We asked two questions: (1) Do the densities of co-flowering plant species influence bee visitation to the focal plant, *A. scaphoides*? and (2) Does the relationship between *A. scaphoides* density (expressed as a proportion of total flowering plant density) and visits to *A. scaphoides* vary by bee group and across high and low densities of *A. scaphoides*?

METHODS

Study Area

We conducted all fieldwork in the Beaverhead Valley of southwestern Montana and adjacent Lemhi River Valley of Idaho. The valley floor elevations range from 1500 m to 2000 m and are predominantly vegetated by semiarid sagebrush steppe (Lesica and Cooper 1997). This shrubland ecosystem is dominated by wind-pollinated sagebrush (*Artemisia* spp. Linnaeus) with low densities of insect-pollinated flowering plants. Among these insect-pollinated plants is *Astragalus scaphoides* (Fabaceae), a regionally endemic perennial herb that grows in small, spatially discrete patches, generally less than one hectare in extent. Within patches, *A. scaphoides* is locally abundant, but patches are sparsely distributed over the immense sagebrush steppe. Three additional bee-attractive plants commonly co-occur with *A. scaphoides*, but typically in lower abundance: *Castilleja* spp. (Mutis; Orobanchaceae), *Lupinus* spp. (Linnaeus; Fabaceae), and *Penstemon albertinus* (Greene; Plantaginaceae).

Within each patch, *A. scaphoides* blooms synchronously approximately every other year in May and June. The mechanisms driving this biennial bloom pattern reflect resource costs of reproduction and do not affect the bloom frequency and magnitude of the co-flowering species (Crone et al. 2009). Thus, the biennial bloom pattern of *A. scaphoides* provides within-site variation in *A. scaphoides* floral resource density that is decoupled from variation in floral densities of co-occurring species, which are relatively constant within sites

and across years (E. Crone and B. Bruninga-Socolar, unpubl. data). Each patch, embedded in a vast arid matrix with few foraging opportunities for bees, provides a replicate natural experiment for examining the response of bee foraging bouts to variation in floral density. Due to the low herbaceous plant densities in this semiarid environment and the low plant species richness at individual patches, this simple study system allows easy observation of bee behavior in a natural, multispecies plant community. Further, local bee abundance as measured by bees seen per unit time is low (approximately five bees encountered per hour on average across sites (Appendix)); therefore, it is feasible to follow individual bees. Due to this low rate of encountering bees and the difficulty of identifying individual bees to species on the wing, we collected data on only the most common bees we observed, all of which fall into the social genus *Bombus* and the solitary group *Anthophora/Eucera*. Our voucher specimen collection of bees in *A. scaphoides* patches includes five species of *Bombus*: *B. appositus* (Cresson), *B. californicus* (Smith), *B. fervidus* (Fabricius), *B. huntii* (Greene), and *B. nevadensis* (Cresson). *B. huntii* is most abundant in our collection, represented by 68% of our specimens. We collected one species of *Anthophora*, *A. urbana* (Cresson), and two species of *Eucera*, *E. frater* (Cresson), and *E. fulvitarsis* (Cresson). All eight of these bee species are dietary generalists, using plants from four (*B. huntii*) to 33 plant families (*A. urbana*) (Koch et al. 2011; Ascher and Pickering 2015).

Data Collection

We selected nine patches for sampling using surveys conducted in the 1980s, when *A. scaphoides* was being evaluated as an endangered species (P. Lesica, unpubl. data; see Lesica et al. 2006). All patches constitute spatially distinct clusters of *A. scaphoides* with at least one of the following co-flowering, bee-attractive plants: *Castilleja* spp., *Lupinus* spp., and *P. albertinus*. We refer to these four species collectively as our focal species. We defined the patch boundaries to include the contiguous area with at least one individual of one focal plant species per square-meter.

Patches ranged in size from 414 to 4372 m². We collected data in all patches in May–June 2014, and we resampled three of these patches in May–June 2015. We collected data at each patch on three to seven dates within each year (Appendix).

All bee observation data were collected on days that were sunny, partly cloudy, or bright overcast with wind less than 7 m s⁻¹ between the hours of 10:00 and 18:00 by the same observer (BBS) (Winfree et al. 2007). We used pin flags to delineate a 5x5 meter grid encompassing each *A. scaphoides* patch. On each sampling day, the observer began observations at a haphazardly chosen location within the patch and walked along the established grid lines to systematize the search for bees. When a bee was spotted, the observer followed the bee's movements through the patch, recording the species identity of each plant visited. Each bee was followed until it either left the patch or switched to a non-foraging behavior.

Within four days of each bee foraging observation, we counted the total number of plants of each species in bloom (i.e., with open flowers) at each patch. Previous work has shown that bloom turns over on timescales of longer than one week in this system (B. Bruninga-Socolar, unpubl. data).

Analyses

To assess the effect of co-flowering plant densities on bee visits to *A. scaphoides*, we modeled the proportion of visits to *A. scaphoides* within a given foraging bout using a generalized linear model (GLM) framework. Initial attempts at fitting GLMs with binomial error resulted in high residual deviance in all candidate models indicating overdispersion, so we fit the model using quasibinomial error and a logit link. We began with a complex model including the following predictor variables: *A. scaphoides* density, *Lupinus* spp. density, *Castilleja* spp. density, and fixed effects of pollinator identity and patch identity. We also fit separate models that treated patch identity as a random effect; these did not affect our conclusions and are not shown.

The density of *P. albertinus* was highly correlated with the density of *A. scaphoides* and was not included in our models. To obtain a parsimonious model, we used backward stepwise parameter selection in which the least significant parameter is dropped from the most complex model. The process is repeated for subsequent simpler models until a final model is obtained in which all parameters are significant and, therefore, retained (Zuur et al. 2007).

To assess the relationship between *A. scaphoides* density and visits to *A. scaphoides*, we asked whether the relationship between density and visits is a one-to-one relationship for each of our most abundant bee groups, *Bombus* and *Anthophora/Eucera*. If bees do not display floral preference, the null expectation is that bees will visit *A. scaphoides* in direct proportion to its density (a one-to-one relationship; Figure 1a, d). If bees show preference (or anti-preference) for *A. scaphoides*, then the proportion of visits should lie above (or below) the one-to-one line (Figure 1b, e). Lastly, if bees alter their preference depending on the density of *A. scaphoides*, then the proportion of visits should lie higher (or lower) above the one-to-one line at high *A. scaphoides* density than at low *A. scaphoides* density (Figure 1c, f).

To test these possibilities, we modeled the proportion of visits to *A. scaphoides* as a function of the proportion of *A. scaphoides* in the flowering plant community, fitting separate GLMs for *Bombus* and *Anthophora/Eucera* with quasibinomial error and a logit link. To visualize the results, we plotted the modeled expectation of the logit of the proportion of visits to *A. scaphoides* against the logit of the proportion of *A. scaphoides*. Thus, consistent floral preference will appear as a line with a significantly offset intercept from the one-to-one line (Figure 1b, e), while density-dependent floral preference will appear as a line with slope significantly different from one (Figure 1c, f).

All analyses were carried out in the program R version 3.1.3 (R Core Team 2014). All GLMs were fit using the R base package (R Core Team 2014) and parameter signif-

icances were estimated using the Anova function with an *F*-test (Crawley 2007) in package nnet (Venables and Ripley 2002). Inverse logits were calculated using the package boot (Canty and Ripley 2015), and confidence intervals were calculated using the package MASS (Venables and Ripley 2002).

RESULTS

In general, 2014 was a high floral density year for *A. scaphoides* and 2015 was a low floral density year, although this pattern was reversed at one patch. The density of flowering *A. scaphoides* plants ranged from 0.01 to 2.07 plants per m² in 2014 and 0.4 to 0.7 plants per m² in 2015 (Appendix). The proportion of blooming *A. scaphoides* plants out of the total flowering plant community ranged from 0.24 to 0.86 in 2014 and 0.09 to 0.25 in 2015 (Appendix).

In total we observed 158 individual bee foraging bouts, mostly of bees in the genus *Bombus* (69 bouts) and the combined genera *Anthophora/Eucera* (67 bouts). Pollinator identity, patch identity, *A. scaphoides* density, and *Castilleja* spp. density all had significant effects on bee visits to *A. scaphoides* in the best model (Table 1). Visitation to *A. scaphoides* was positively associated with *A. scaphoides* density and negatively associated with *Castilleja* spp. density (Table 1).

The relationship between the proportion of visits to *A. scaphoides* and the proportion of *A. scaphoides* differed significantly from one-to-one (slope of one and intercept of zero on the logit-logit scale) for both *Bombus* and *Anthophora/Eucera*. The intercept for *Bombus* was significantly greater than zero, indicating an overall preference for *A. scaphoides* (Table 2). However, the slope for *Bombus* did not differ from one, suggesting that their visitation was approximately proportional to density across the range of *A. scaphoides* densities. Furthermore, the 95% confidence interval for the expected proportion of *Bombus* visits to *A. scaphoides* lies entirely above the one-to-one line across essentially the entire range of observed *A. scaphoides* densities, from proportions of 0.12 to 0.88 (the inverse logits of -2 and 2, respectively; Figure 2a).
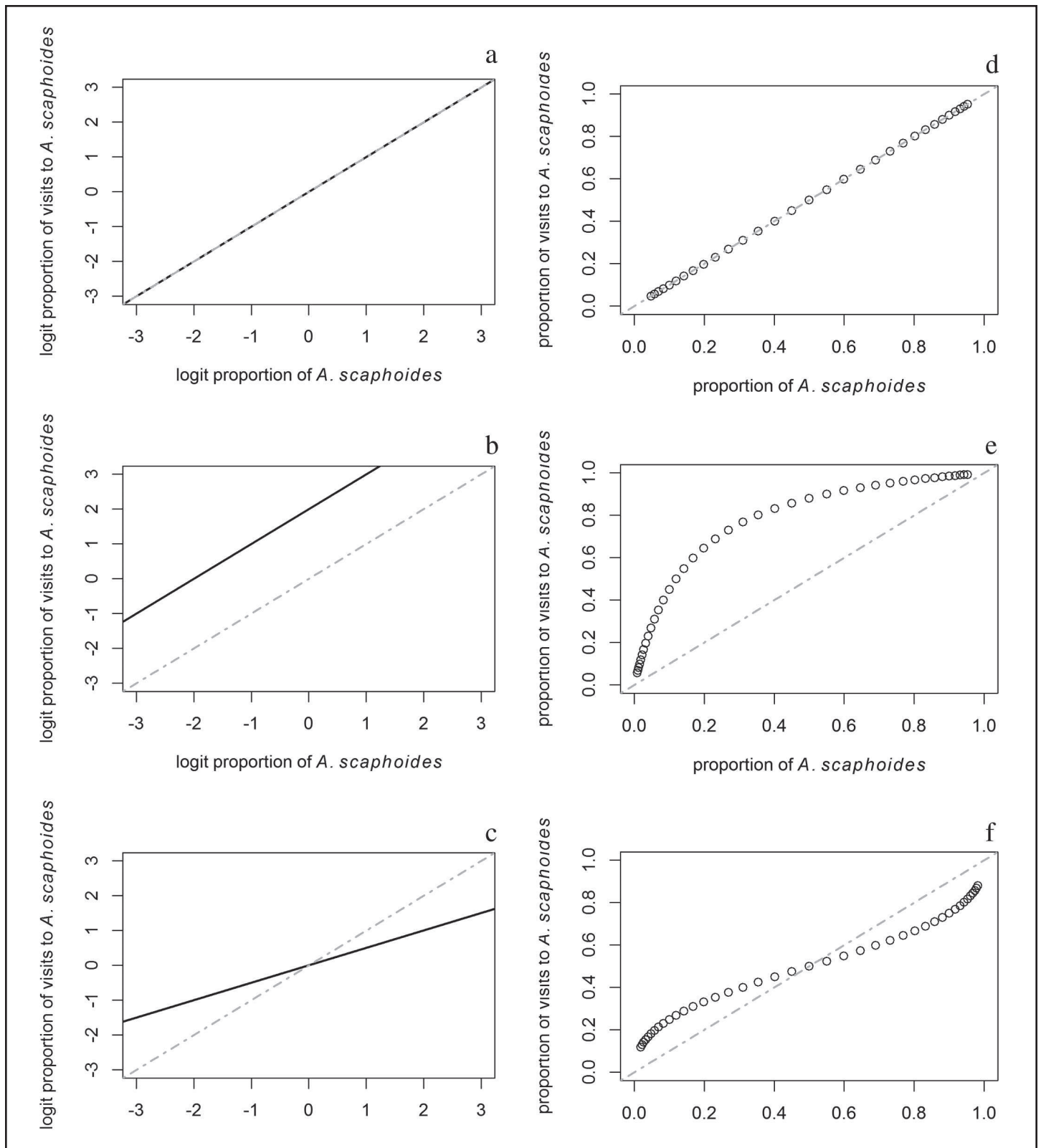
Figure 1. Hypothetical relationships between the proportion of visits per foraging bout to *A. scaphoides* and the proportion of *A. scaphoides* in the flowering plant community. (a-c) The dashed gray line represents the logit one-to-one relationship between these variables. The solid black line shows the expectation of the logit proportion of visits per foraging bout of *A. scaphoides*. (a) a one-to-one relationship and thus no bee response to floral density; (b) consistent positive floral preference; and (c) density-dependent preference. (d-f) The same relationships as (a-c) mapped back from the logit-logit scale to the identity scale.

Table 1. Degrees of freedom and parameters included in the best model of visitation to *A. scaphoides* as a function of the densities of different plant species, with associated chi-square values and *p*-values. *F* and *p*-values were obtained from an ANOVA table using the *F*-test (see Methods).

	d.f.	Pollinator identity	Patch identity	*A. scaphoides* density
Best model	144	+	+	+
estimates				1.51 ± 0.7
F		9.94	5.15	6.39
p-value		<0.0001	<0.0001	0.01

The intercept for *Anthophora/Eucera*, by contrast, did not differ significantly from zero indicating no preference or lack of preference for *A. scaphoides* (Table 2). The slope was significantly lower than one indicating that the relationship between the proportion of visits to *A. scaphoides* per bee foraging bout and the proportion of *A. scaphoides* in the flowering plant community changes across different *A. scaphoides* densities for *Anthophora/Eucera* (Table 2, Figure 2b). The 95% confidence interval for the expected proportion of visits to *A. scaphoides* lies above the one-to-one line at low *A. scaphoides* densities, indicating that when *A. scaphoides* bloom is low (proportions of less than 0.18), *Anthophora/Eucera* preferentially seek out *A. scaphoides* (Figure 2b). However, the small slope indicates that this preference attenuates, and likely reverses when *A. scaphoides* bloom is high (Figure 2b). For both *Bombus* and *Anthophora/Eucera*, the effects reported here manifest themselves at biologically realistic values for *A. scaphoides* bloom: the sampled proportions of *A. scaphoides* range from 0.09 to 0.86.

DISCUSSION

We found that the co-flowering plant community influences bee visitation to a focal plant species, *A. scaphoides*. Although we did not measure reproductive outcomes (e.g., pollen deposition or seed set) in this study, our method of following individual bees and recording the proportion of visits in each foraging bout to different plant species allows us to make inferences about whether plant species facilitated or competed with each other since visits to multiple conspecific individuals in a foraging bout are required for plant reproduction. In our system, the proportion of visits to *A. scaphoides* per foraging bout is not affected by the plant group in the same family, *Lupinus* spp. (Fabaceae), but is negatively affected by the genus *Castilleja* (Orobanchaceae; Table 1) and positively affected by itself. Thus, greater densities of *A. scaphoides* result in intraspecific pollination facilitation, but *A. scaphoides* competes with *Castilleja* spp. for pollinators as *Castilleja* spp. density increases.

Flower morphology may play a role in determining whether the interspecific relationships between *A. scaphoides*, *Lupinus* spp., and *Castilleja* spp. are competitive or facilitative in this system. The flowers of both *A. scaphoides* and *Lupinus* spp. are complexly zygomorphic, with reproductive parts that remain recessed in the folded lower petal until pressure from a visiting pollinator (or researcher) exposes them (Lesica 2012). In contrast, the flowers of *Castilleja* spp. are simple tubes with protruding reproductive parts. Although beyond the scope of our study, the extra energy required to manipulate the flowers of the Fabaceae plants may instigate a switch to simpler flowers such as those of *Castilleja* spp. when they are available. Such a diet switch due to differences in handling time and energy cost at different flowers may be consistent with optimal foraging theory (Pyke 1978; Waddington and Holden 1979), although experimentation is required in this system to test this and elucidate the mechanism.

We found that the two most abundant bee groups, *Bombus* and *Anthophora/Eucera*, respond differently to the density of *A. scaphoides* as a proportion of the entire co-flowering plant community density. *Bombus* visited *A. scaphoides* more than expected based on the plant species' density across the entire range of *A. scaphoides* proportions in our study (Figure 2a). Our results indicate that as *A. scaphoides* density increases from zero, *Bombus* quickly increase their visits to *A. scaphoides* and use *A. scaphoides* nearly exclusively when it is common (Figures 1b, e and 2a). This rapid rise in use of *A. scaphoides* to saturation is consistent with an overall preference for *A. scaphoides* over the available co-flowering plant species. Pollen, nectar, and flower

Table 2. Parameter estimates with confidence intervals from the GLMs describing the relationship between the proportion of visits to *A. scaphoides* per bee foraging bout and the logit of the proportion of *A. scaphoides* out of the total flowering plant community for *Bombus* and *Anthophora/Eucera* considered separately. Estimates in bold lie outside of the confidence interval and are thus different from zero (for the intercept) or one (for the slope).

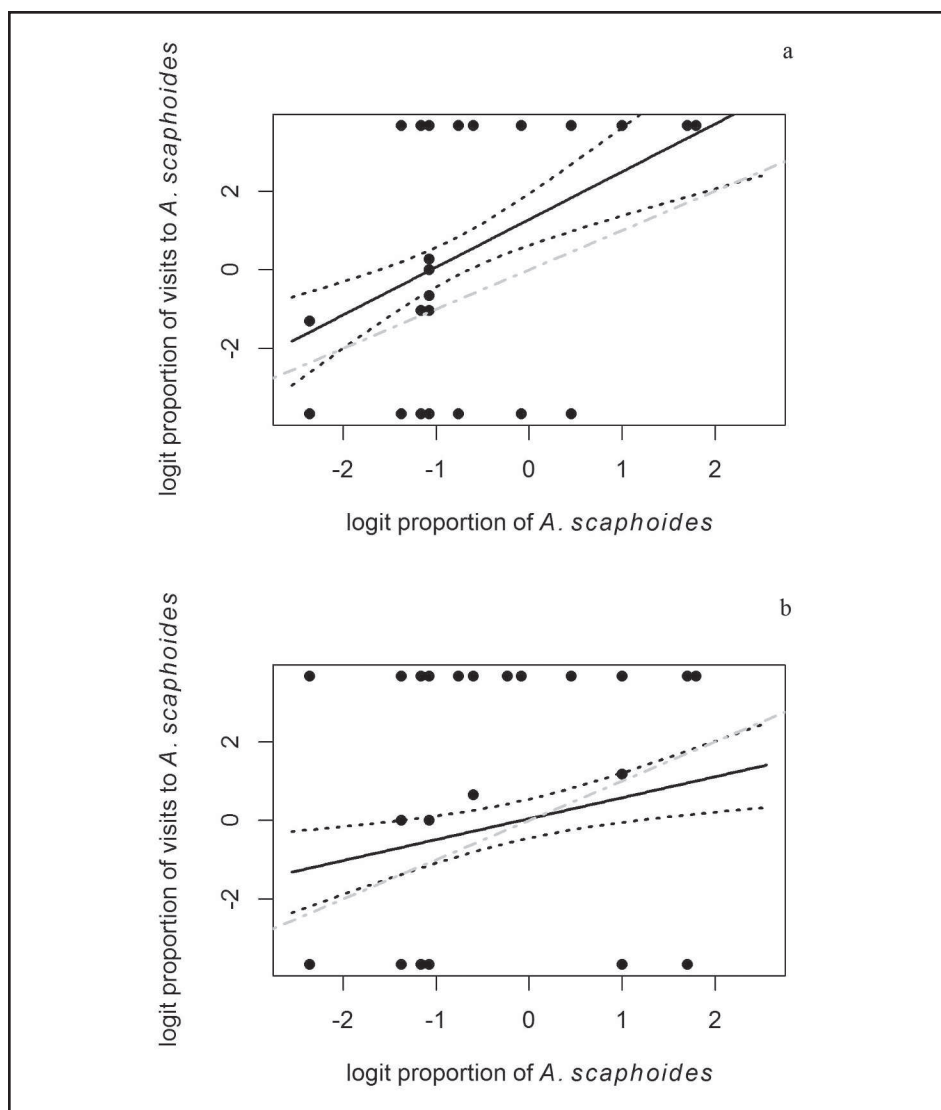|	Estimate	2.5%	97.5%
Bombus			
Intercept	**1.279**	0.683	2.022
Proportion of *A. scaphoides*	1.215	0.711	1.87
Anthophora/Eucera			
Intercept	0.045	-0.451	0.546
Proportion of *A. scaphoides*	**0.533**	0.181	0.917

Figure 2. Plot of the logit of the proportion of visits to *A. scaphoides* **per foraging bout as a function of the logit of the proportion of blooming** *A. scaphoides* **in the flowering plant community for (a) the bee genus** *Bombus***, and (b) the bee group** *Anthophora/Eucera***. The points show the raw logit proportions for each foraging bout (proportions of zero and one are plotted at logit(0.025) and logit(0.975), respectively). The solid black line shows the predicted logit proportion of visits to** *A. scaphoides* **from the GLM output with 95% confidence intervals (dotted black lines). The gray dashed line shows the one-to-one relationship between the proportion of** *A. scaphoides* **and the proportion of visits to** *A. scaphoides* **on the logit-logit scale.**

choice experiments could elucidate the proximate mechanisms that account for this preference.

Anthophora/Eucera visit *A. scaphoides* more than expected when it is rare, but in proportion to its relative density in the co-flowering plant community when it is common (Figure 2b). This result is consistent with pollen mixing behaviors such as the collection of pollen from different plant species to balance nutritional requirements (Williams and Tepedino 2003) or mitigate

exposure to harmful secondary compounds (Eckhardt et al. 2014). In the case of *Anthophora/Eucera*, if *A. scaphoides* pollen contains an essential nutrient missing from other components of their diet, we would expect to see these bees seeking out *A. scaphoides* when it is rare.

The pattern of *Anthophora/Eucera* response to *A. scaphoides* density is consistent with the general model prediction of Essenberg (2012), which stated that the effects of floral density of a focal plant

species on bee visitation would be positive at low densities and weaker or negative at higher densities. However, her model was based on the assumption that all flowers in a patch are identical (i.e., the same species) and should be rebuilt for a co-flowering plant community.

As expected, the social bee group, *Bombus*, responded differently to varying plant densities in a multispecies community than the solitary bee group, *Anthophora/Eucera*. *Bombus* visited *A. scaphoides* more than predicted by the null hypothesis (Figure 1a, d) across all proportions of *A. scaphoides* in the flowering plant community, consistent with an overall preference for this plant species (Figure 2a). However, despite the overall preference for *A. scaphoides*, 24.6% of *Bombus* foraging bouts contained no visits to *A. scaphoides* (data not shown), suggesting possible individual specialization. Larger sample sizes are required to test this. In contrast, the response of the solitary group *Anthophora/Eucera* to *A. scaphoides* density varied across proportions of *A. scaphoides* in the flowering plant community, suggesting changes in individual bee behavior in response to resource availability. Because individual female solitary bees need to collect all of the resources to provision each nest cell, individual *Anthophora/Eucera* may need a mix of *A. scaphoides* pollen with pollen and/or nectar from another species to provision each larva (Williams and Tepedino 2003). Testing the mechanism behind this observed pattern is outside the scope of this study, but could be done by the analysis of provision balls in *Anthophora/Eucera* nest cells and observation of pollen and nectar collecting behaviors in the field.

Previous work in this system has shown that *A. scaphoides* is pollen-limited at low floral densities (Crone et al. 2009). Our results show that, for this rare plant, heterospecific floral density affects bee visitation, with implications for pollen limitation and reproductive success. Alonso et al. (2010) conducted a meta-analysis across plant taxa and geographic regions showing that pollen limitation of endemic (range-restricted) species increases with regional species richness, but their study did not include a mechanism to explain

this pattern. Our results suggest such a mechanism in an endemic plant. We did not quantify pollination limitation of *A. scaphoides* in this paper, but two past experiments in this system have demonstrated pollen limitation at low floral densities (Crone and Lesica 2006; Crone et al. 2009). Our results here suggest that the mechanism for density-dependent pollen limitation is competition for pollinators with co-flowering, common plant species. Further research should measure reproductive success of *A. scaphoides* as a function of relative floral densities.

For other rare plant species, past studies have suggested that co-flowering plant species may compete for pollinators with a target species. Baskett et al. (2011) found that pollinator visitation to a federally threatened species, Pitcher's thistle (*Cirsium pitcheri*), increased in plots where two invasive species were removed, reaching the visitation levels of thistle plants in naturally uninvaded plots. If our goal were to enhance reproduction of *A. scaphoides* only, it might be useful to remove co-flowering plants from existing populations, or target sites with few other co-flowering plants for reintroductions. More generally, our results reinforce the general notion that ecological communities are highly connected, and that changes in community composition can have far-reaching effects on other species.

ACKNOWLEDGMENTS

Bethanne Bruninga-Socolar is a PhD Candidate in the Graduate Program in Ecology and Evolution at Rutgers University. She studies pollinator responses to floral density as well as the effects of prairie restoration on pollinator communities.

Elizabeth E. Crone is an Associate Professor in the Department of Biology at Tufts University. She studies plant and animal interactions at the intersection of theoretical ecology and natural history.

Rachael Winfree is an Associate Professor in the Department of Ecology, Evolution, and Natural Resources at Rutgers University. Her research interests include (1) how pollinators and the pollination services they provide are affected by global change, (2) the relationship between biodiversity and ecosystem services, (3) plant-pollinator networks, and (4) pollinator conservation and restoration.

LITERATURE CITED

Alonso, C., J.C. Vamosi, T.M. Knight, J.A. Steets, and T.-L. Ashman. 2010. Is reproduction of endemic plant species particularly pollen limited in biodiversity hotspots? Oikos 119:1192-1200.

Ascher, J.S., and J. Pickering. 2015. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Accessed 15 January, 2016 from <http://www.discoverlife.org/mp/20q?guide=Apoidea_species>.

Baskett, C.A., S.M. Emery, and J.A. Rudgers. 2011. Pollinators visits to threatened species are restored following invasive species removal. International Journal of Plant Science 172:411-422.

Bosch, J., A.M. Martin González, A. Rodrigo, and D. Navarro. 2009. Plant-pollinator networks: Adding the pollinator's perspective. Ecology Letters 12:409-419.

Canty, A., and B. Ripley. 2014. boot: Bootstrap R (S-Plus) Functions. R package version 1.3.11.

Crawley, M.J. 2007. The R Book. Wiley, Chichester, West Sussex, UK.

Cresswell, J.E., A.P. Bassom, S.A. Bell, S.J. Collins, and T.B. Kelly. 1995. Predicted pollen dispersal by honey-bees and three species of bumble-bees foraging on oilseed rape: A comparison of three models. Functional Ecology 9:829-841.

Crone, E.E., E. Miller, and A. Sala. 2009. How do plants know when other plants are flowering? Resource depletion, pollen limitation and mast-seeding in a perennial wildflower. Ecology Letters 12:1119-1126.

Crone, E.E., and P. Lesica. 2006. Pollen and water limitation in *Astragalus scaphoides*, a plant that flowers in alternate years. Oecologia 150:40-49.

Crone, E.E. 2013. Responses of social and solitary bees to pulsed floral resources. The American Naturalist 182:465-473.

Dauber, J., J.C. Biesmeijer, D. Gabriel, W.E. Kunin, E. Lamborn, B. Meyer, A. Nielsen, S.G. Potts, S.P.M. Roberts, V. Sõber, J. Settele, I. Steffan-Dewenter, J.C. Stout, T. Teder, T. Tscheulin, D. Vivarelli, and T. Petanidou. 2010. Effects of patch size and density on flower visitation and seed set of wild plants: A pan-European approach. Journal of Ecology 98:188-196.

Eckhardt, M., M. Haider, S. Dorn, and A. Müller. 2014. Pollen mixing in pollen generalist solitary bees: A possible strategy to complement or mitigate unfavourable pollen properties? Journal of Animal Ecology 83:588-597.

Essenberg, C.J. 2012. Explaining variation in the effect of floral density on pollinator visitation. The American Naturalist 180:153-166.

Feldman, T.S. 2008. The plot thickens: Does low density affect visitation and reproductive success in a perennial herb, and are these effects altered in the presence of a co-flowering species? Oecologia 156:807-817.

Ghazoul, J. 2006. Floral diversity and the facilitation of pollination. Journal of Ecology 94:295-304.

Greenleaf, S.S., N.M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153:589-596.

Heinrich, B. 1976. The foraging specializations of individual bumblebees. Ecological Monographs 46:105-128.

Jakobsson, A., A. Lázaro, and Ø. Totland. 2009. Relationships between the floral neighborhood and individual pollen limitation in two self-incompatible herbs. Oecologia 160:707-719.

Koch, J., J. Strange, and P. Williams. 2011. Bumble Bees of the Western United States. USDA Forest Service and the Pollinator Partnership, Washington, DC and San Francisco, CA (respectively).

Kunin, W.E. 1993. Sex and the single mustard: Population density and pollinator behavior effects on seed-set. Ecology 74:2145-2160.

Kunin, W.E. 1997. Population size and density effects in pollination: Pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. Journal of Ecology 85:225-234.

Lesica, P., and S.V. Cooper. 1997. Presettlement vegetation of southern Beaverhead County, Montana. Unpublished report to the State Office, Bureau of Land Management and Beaverhead-Deerlodge National Forest. Montana Natural Heritage Program, Helena, MT.

Lesica, P., R. Yurkewycz, and E.E. Crone. 2006. Rare plants are common where you find them. American Journal of Botany 93:454-459.

Lesica, P. 2012. Manual of Montana Vascular Plants. Botanical Research Institute of Texas Press, Fort Worth, TX.

Michener, C.D. 2000. The Bees of the World. The Johns Hopkins University Press, Baltimore, MD.

Müller, A. 1996. Host-plant specialization in western palearctic Anthidiine bees (Hymenoptera: Apoidea: Megachilidae). Ecological Monographs 66:235-257.

Pyke, G.H. 1978. Optimal foraging: Movement patterns of bumblebees between inflorescences. Theoretical Population Biology 13:72-98.

R Core Team. 2014. R: A Language and Environment for Statistical Computing. Vienna, Austria. Accessed from <http://www.r-project.org/>.

Rathcke, B. 1983. Competition and facilitation among plants for pollination. Pp. 305–329 in L.A. Reak, ed., Pollination Biology. Academic Press, Orlando, FL.

Tepedino, V.J., and F.D. Parker. 1982. Interspecific differences in the relative importance of pollen and nectar to bee species foraging on sunflowers. Environmental Entomology 11:246-250.

Thomson, J.D. 1986. Pollen transport and deposition by bumble bees in Erythronium: Influences of floral nectar and bee grooming. Journal of Ecology 74:329-341.

Venables, W.N., and B.D. Ripley. 2002. Modern Applied Statistics with S. 4th ed. Package "MASS": R package version 7.3.33. Package "nnet": R package version 7.3.11. Springer, New York.

Waddington, K.D., and L.R. Holden. 1979. Optimal foraging: On flower selection by bees. The American Naturalist 114:179-196.

Williams, N.M., and V.J. Tepedino. 2003. Consistent mixing of near and distant resources in foraging bouts by the solitary mason bee Osmia lignaria. Behavioral Ecology 14:141-149.

Winfree, R., N.M. Williams, J. Dushoff, and C. Kremen. 2007. Native bees provide insurance against ongoing honey bee losses. Ecology Letters 10:1105-1113.

Zurbuchen, A., L. Landert, J. Klaiber, A. Müller, S. Hein, and S. Dorn. 2010. Maximum foraging ranges in solitary bees: Only few individuals have the capability to cover long foraging distances. Biological Conservation 143:669-676.

Zuur, A.F., E.N. Ieno, and G.M. Smith. 2007. Analysing Ecological Data. Springer Science + Business Media, LLC, New York.

Appendix
Summary data across all sites and years.

Site	Year	No. bees followed	No. sampling days	No. sampling hours	Bees/hour	A. scaphoides density	Lupinus spp. density	Castilleja spp. density	P. albertinus density	Proportion of A. scaphoides
AC	2015	25	5	6.5	3.8	0.07	0.18	0.02	n/a	0.25
HNC	2015	22	6	4.5	4.9	0.04	0.10	n/a	0.06	0.20
RC	2015	7	7	9	0.8	0.04	n/a	n/a	0.38	0.09
AC	2014	15	4	2	7.5	0.04	0.09	0.04	n/a	0.24
AC-1	2014	11	4	2	5.5	0.10	0.01	0.01	n/a	0.86
BC	2014	12	4	2	6	0.06	n/a	n/a	0.06	0.48
CSC	2014	16	4	2	8	0.09	0.01	0.01	0.01	0.73
HDC	2014	9	4	2	4.5	0.02	n/a	n/a	0.03	0.35
HNC	2014	19	4	2.5	7.6	0.12	0.02	n/a	n/a	0.85
MC	2014	7	4	2	3.5	0.03	0.02	n/a	n/a	0.61
RC	2014	12	3	1.5	8	2.07	n/a	n/a	4.41	0.32
SCG	2014	3	3	1.5	2	0.01	n/a	n/a	0.01	0.44