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Bumble bee nest abundance, foraging distance, and host-plant reproduction: implications for management and conservation

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Abstract. Recent reports of global declines in pollinator species imply an urgent need to assess the abundance of native pollinators and density-dependent benefits for linked plants. In this study, we investigated (1) pollinator nest distributions and estimated colony abundances, (2) the relationship between abundances of foraging workers and the number of nests they represent, (3) pollinator foraging ranges, and (4) the relationship between pollinator abundance and plant reproduction. We examined these questions in an alpine ecosystem in the Colorado Rocky Mountains, focusing on four alpine bumble bee species (*Bombus balteatus*, *B. flavifrons*, *B. bifarius*, and *B. sylvicola*), and two host plants that differ in their degrees of pollinator specialization (*Trifolium dasyphyllum* and *T. parryi*).

Using microsatellites, we found that estimated colony abundances among *Bombus* species ranged from ~18 to 78 colonies/0.01 km². The long-tongued species *B. balteatus* was most common, especially high above treeline, but the subalpine species *B. bifarius* was unexpectedly abundant for this elevation range. Nests detected among sampled foragers of each species were correlated with the number of foragers caught. Foraging ranges were smaller than expected for all *Bombus* species, ranging from 25 to 110 m. Fruit set for the specialized plant, *Trifolium parryi*, was positively related to the abundance of its *Bombus* pollinator. In contrast, fruit set for the generalized plant, *T. dasyphyllum*, was related to abundance of all *Bombus* species. Because forager abundance was related to nest abundance of each *Bombus* species and was an equally effective predictor of plant fecundity, forager inventories are probably suitable for assessing the health of outcrossing plant populations. However, nest abundance, rather than forager abundance, better reflects demographic and genetic health in populations of eusocial pollinators such as bumble bees. Development of models incorporating the parameters we have measured here (nest abundance, forager abundance, and foraging distance) could increase the usefulness of foraging worker inventories in monitoring, managing, and conserving pollinator populations.

Key words: alpine ecosystem; Bombus spp., bumble bees; colony density; density dependence; foraging range; host-plant fecundity; Pennsylvania Mountain, Colorado, USA; pollination services; pollinator monitoring; spatial distribution; Trifolium dasyphyllum; Trifolium parryi.

INTRODUCTION

Recent declines of pollinating species in Europe (Goulson et al. 2008) and North America (Cameron et al. 2011) have prompted calls for greater monitoring of pollinator populations and greater understanding of relationships between pollinators and plants (NRC 2007). Organizations such as the Xerces Society and Great Pollinator Project have mobilized experts and citizen scientists across the United States to participate in species inventories. Inventory protocols typically involve counts of foraging individuals on transects or patches of blooming flowers (see, e.g., the Bee Inventory Plot, *available online*).[4] These protocols aim to identify

which species are doing well or are in decline, similar to breeding bird surveys conducted in the United States annually since the 1960s (USGS Patuxent Wildlife Research Center 2001). However, the usefulness of current inventories in assessing population health is unclear for important native eusocial pollinators, such bumble bees. For these species, where the bulk of floral visitors are rarely reproductive, measures such as colony abundance that are more closely related to the size of the breeding population (Crozier 1979) should be more meaningful to management and conservation efforts.

Until recently, robust estimates of natural colony abundance for *Bombus* species remained elusive due to difficulties in locating nests and lack of adaptable technologies (for a range of methods employed, see Cumber 1953, Harder 1986, Osborne et al. 2008*b*, Waters et al. 2011). Refinement of algorithms that reconstruct genetic relationships among sampled individuals (Goodnight and Queller 1999, Konovalov et al. 2004, Wang 2004, Konovalov et al. 2005, Kokuvo et al.

2007) has allowed estimation of nest abundance in different habitats. This method has been used frequently for *Bombus* species in Britain and Japan (Chapman et al. 2003, Darvill et al. 2004, Knight et al. 2005, 2009, Kokuvo et al. 2008). However, published studies of nest abundance for native *Bombus* pollinators in natural North American ecosystems are lacking (but see Rao and Strange [2012] for an arable landscape), despite their importance for numerous native plant taxa (NRC 2007).

Despite their usefulness, widespread assessments of *Bombus* nest abundance through molecular methods are likely to be impractical for North American pollinator monitoring networks that are just being established, as they would require financial and personnel resources that are not feasible for annual surveys. A better understanding of the relationship between nest abundance and that of individual *Bombus* foragers would increase the relevance of annual forager inventories, which can be conducted en masse by volunteers trained in species identification. Yet, to date, this relationship has not been explored.

Assessment of appropriate scales for bumble bee conservation and management efforts is dependent on more than an accurate understanding of nest abundance in different habitats. Data suggest that habitat- and landscape-level distributions of floral resources impact the abundance, diversity, and richness of floral visitors, and that these relationships exist at different spatial scales (habitat vs. regional landscape) depending on pollinator taxa (Westphal et al. 2006). Forging ranges determine the size of habitat utilized and the area over which the foraging shadow propagates for host plants (Knight et al. 2005). Molecular genetic methods of characterizing large-scale foraging patterns in heterogeneous landscapes are most promising, because mark–recapture methods underestimate the tendency to forage far from nests (Knight et al. 2005), whereas use of harmonic radar to track individual foragers is not practical in structurally heterogeneous vegetation and has a maximum detection range of 700 m (Osborne et al. 1999, Riley et al. 1999). Perhaps because of technological limitations, estimates of the scale for pollinator movement are primarily from agricultural habitats, where homogeneous vegetation ensures optimal detection.

Even greater urgency for monitoring pollinator populations arises when considering the importance of pollination to plant species conservation and management. Pollinator forager densities correlate with those of linked plant species across continents (Biesmeijer et al. 2006) and with benefits to their host plants at the individual and population scales (Geib and Galen 2012). It is unclear clear whether plant reproductive success correlates with habitat-scale variation in pollinator abundance. Although yield of agroforestry resources (e.g., coffee; Klein et al. 2003a, b) often correlates with pollinator density and diversity in surrounding forest

ecosystems, it is unclear whether plants in natural communities show similar dependencies.

More extensive monitoring and in-depth study of relationships between plant and pollinator populations is needed for all native North American habitats, but greater priority should be given to habitats that currently or imminently may be experiencing threat from anthropogenic (e.g., habitat loss, urbanization) or climatic sources. Alpine vegetation and landscapes, for example, have experienced significant changes from mining and tourism, and have long been considered "canaries in a coal mine" for changes in climate (e.g., Diaz and Millar 2004). Signals of climate effects have recently manifested in long-term flowering phenologies of North American subalpine plant communities (Forrest et al. 2010, CaraDonna et al. 2014), and there is preliminary evidence for shifts in distributions of high-elevation *Bombus* species (Inouye 2009). Bumble bees are keystone pollinators in alpine habitats because cold temperatures can limit the distributions of smaller insects (Dillon et al. 2006); however, no estimates of alpine *Bombus* colony abundance exist at any scale. Foraging ranges for alpine *Bombus* species also have not been estimated, although a subalpine mark–recapture study (Elliott 2009) suggests that ranges may be small relative to those of *Bombus* in agricultural habitats. Whether and at what spatial scales fitness in alpine plants pollinated by bumble bees correlates with nest density of their pollinators should depend on the propensity for individual workers to forage near or far from their nest. Reproductive success of alpine plants visited by pollinators with large foraging ranges is less likely to vary among habitats, whereas for plants visited by pollinators with relatively short foraging ranges, fecundity should correlate more closely with habitat-level colony abundance.

In our study we employed molecular techniques to ascertain nest abundances of *Bombus* species servicing flora of a North American alpine tundra ecosystem. Our specific aims were to (1) estimate the abundance and distributions of bumble bee colonies sending representatives to collect floral resources in each site ("effective colony abundance"), (2) examine the relationship between numbers of individual foragers and the number of colonies detected among samples at each site, (3) estimate foraging ranges of alpine bumble bee workers, and (4) test for correlations between *Bombus* species' abundances and reproductive rates in two host plants with contrasting pollination niche breadth.

MATERIALS AND METHODS

Study sites and system

Data for this study were collected on Pennsylvania Mountain (Park County, Colorado, USA) during the summer of 2008. Pennsylvania Mountain is divided by the headwaters of an east-flowing stream, Pennsylvania Creek. The southern portion of the mountain comprises a series of relatively gentle east-facing slopes, each topped by ridges or plateaus, extending from treeline

TABLE 1. Distribution of sister pairs (Sib 1 and Sib 2, respectively) for each *Bombus* species; values in the species columns are the total number of sister pairs found for the site(s) identified in column 1.

Site(s) where sisters were identified, respectively	Separation between sites (m)		Qualitative habitat features between sites	Total sister pairs found (within or between sites)			
	Elevation	Linear		B. balt.	B. flav.	B. bif.	B. sylv.
Site 1	0	0		1	9	3	0
Sites 1 and 2	39	784	willow canopy, interpeak valley	0	0	0	0
Sites 1 and 3	71	541	flat between slopes	1	0	4	0
Sites 1 and 4	76	681	snowbed, interpeak valley	0	0	0	1
Site 2	0	0		1	5	0	1
Sites 2 and 3	32	505	snowbed, flat between slopes	1	2	0	0
Sites 2 and 4	37	255	snowbed	10	4	0	0
Site 3	0	0		0	9	1	1
Sites 3 and 4	5	266	meadow and fellfield	1	0	0	1
Site 4	0	0		0	1	0	1

(3530 m) to the summit (4000 m). Within this area, we selected two low-alpine and two high-alpine sites (Appendix A: Fig. A1), all of which support a rich assemblage of bee-pollinated plant species (Byron 1980), and were in full bloom 1–15 August, typically the last weeks of the peak flowering season for this elevational range (e.g., see Pyke et al. 2011). Low-alpine sites (3659–3698 m) were bordered at their lower edge by the krummholz transition zone composed of meadow/shrub matrix. High-alpine sites (3730–3735 m) were surrounded by true alpine tundra (Appendix A: Fig. A1). Although the elevational differences between sites may not seem large (Table 1; Appendix A: Fig. A1), alpine habitats change sharply over a small spatial scale due to elevation gradients in biotic and abiotic environmental factors. Temperature, air density, and oxygen partial pressure, for example, decline with increasing altitude (Dillon et al. 2006), impacting bees' physiology and metabolic foraging costs, and potentially their brood-rearing success (Lundberg 1980, Bergman et al. 1996, Dillon et al. 2006). At the center of each site, we placed a marker and delineated a 50 m radius circle around it, resulting in site areas of 8000 m^2 (0.008 km^2, reported as 0.01 km^2 in similar studies). Linear distance between the center points of the sites varied from 255 m to 784 m (Table 1).

Our study surveyed native bumble bee pollinators (Hymenoptera: Apidae: *Bombus*) on Pennsylvania Mountain. Bumble bees are eusocial pollinators whose colonies are established annually by single foundress queens that produce broods of nonreproductive female workers (Heinrich 1979, Goulson 2003). In alpine habitats in the Central Rockies, mated *Bombus* queens typically emerge from overwinter diapause in mid-June to locate nest sites; their first worker broods appear in early July (Byron 1980, Pyke et al. 2011). Brood sizes for alpine and subalpine species that have colonized nest boxes range from 18 to 74 bees (J. C. Geib, *unpublished data*). Foraging worker abundances for Colorado alpine and subalpine *Bombus* species have been observed to peak concurrently during the last half of peak flowering

season (Pyke et al. 2011). Monoandrous broods are the norm in *Bombus*, although rare multiple paternities have been observed in subgenus *Pyrobombus*. For North American *Pyrobombus* species in which multiple paternities have been detected, effective paternities are less than 2 (1.19 ± 0.12 paternities, mean ± SE, $n = 23$; Payne et al. 2003). Behaviorally, *Bombus* are central-place foragers that return gathered resources (nectar and pollen) to their home nest (Heinrich 1979).

Historic studies of the *Bombus* community on Pennsylvania Mountain identified only two species successfully nesting above treeline (a long-tongued species, *B. balteatus*, and a short-tongued species, *B. sylvicola*), which also comprised 99% of all observed foraging individuals in both low- and high-alpine habitats (Byron 1980). This is consistent with historical studies of similar alpine sites in Colorado (Macior 1974, Pyke et al. 2011).

Worker bee collection

We systematically sampled foraging workers bees within each of the four alpine sites on Pennsylvania Mountain. All workers were sampled during full bloom in our sites (1–15 August). This time period was selected for sampling because forager abundance of all *Bombus* species at these elevations typically peaks during the latter half of the flowering season (e.g., see Pyke et al. 2011) and to minimize negative effects of worker removal on brood rearing. Collections occurred at one or two sites per day, during conditions of no more than 50% cloud cover. Sites were rotated daily. Total collection effort was equal across sites (total ~6 h per site). During sampling periods, one individual collected bees by walking a spiral pattern from the site center and capturing all observed *Bombus* foragers. Upon capture, bees were cooled to torpor, placed in vials containing 95% ethanol, and stored in a −20°C freezer until analysis. We included the four most abundant species, *B. balteatus*, *B. flavifrons*, *B. sylvicola*, and *B. bifarius*, in subsequent analyses, as these species comprised 95.1% of all captures (see Appendix A: Fig. A2). Excluded species

(with percentage of total captures) included *B. frigidus* (4.3%), *B. mixtus* (0.4%), and *B. centralis* (0.2%).

Microsatellite genotyping of individual bees

We conducted *Bombus* DNA extraction, PCR amplification, and genotyping at the USDA-ARS Pollinating Insect Research Unit in Logan, Utah, USA, in February 2009 (detailed methods are in Appendix B). Samples that lacked data or were ambiguous at more than one locus were reprocessed from the original extracted DNA. Despite reprocessing, some individuals failed to yield genetic data. Genotyping success was generally high (85–92%), with the exception of samples from site 3. which had only a 50% success rate (Table 2). The underlying cause for low data resolution from site 3 is unclear, but tissue deterioration or problems with the extraction process may have contributed.

Estimates of Bombus colony abundance and distributions

We estimated the number of nests per species at each site from the number of full sister groups detected among genotyped worker bees within each sample. Sibship reconstructions were conducted with Colony 1.2 (Wang 2004, Lepais et al. 2010); software *available online.*[5] Eight to nine loci were included in the sibship analysis for each species, and only individuals with no missing data for all loci were used. The maximum likelihood algorithm (Wang 2004) assumes single queen matings, which is the norm for *Bombus*. Queens of one focal species, *B. bifarius*, occasionally mate with multiple males, but we assumed single mating here because polyandry is rare, and because *B. bifarius* parental genotype reconstruction probabilities here were very high (near 1.0 for each locus), indicating that the sister pair assignments were robust. To ensure convergence of results in the sibship reconstructions, each species' data set was analyzed three times. To account for variation in genotyping success, we divided the number of nest groups per site for each species as determined by Colony software ("raw" number of nests, N_{nr}) by the number of successfully genotyped individuals (N_g) in each sample and then multiplied by the actual number of caught individuals (N_i) to get a "standardized" nest number (N_{ns}) (Table 2).

Despite intensive searching for bees at each site, N_{ns} (nests detected, standardized for genotyping success) is certainly an underestimate of actual nests. Prior studies have attempted to estimate the number of unsampled nests by plotting the frequency distribution of nests represented by one, two, three, …, individuals within the sample and estimating the value of the "0" (unsampled) category through an iterative "trial and error" process until best-fit to a truncated Poisson distribution is identified (Chapman et al. 2003, Darvill et al. 2004, Knight et al. 2005). Nests detected by sibship

[5] http://www.zsl.org/science/software/colony

TABLE 2. Sample sizes and nest abundance estimates of four *Bombus* species at low- and high-alpine sites on Pennsylvania Mountain, Colorado, USA.

Species and sample	Low alpine		High alpine	
	Site 1	Site 2	Site 3	Site 4
B. balteatus				
N_i	18	29	46	51
N_g	16	24	25	47
N_{nr}	15	23	25	44
N_{ns}	16.9	27.8	46.0	47.7
N_c	25.3	41.7	69.0	71.6
B. flavifrons				
N_i	44	29	35	24
N_g	40	24	26	22
N_{nr}	33	10	20	21
N_{ns}	36.3	12.1	26.9	22.9
N_c	54.5	18.1	40.4	34.4
B. bifarius				
N_i	28	13	18	17
N_g	27	12	9	13
N_{nr}	25	12	8	13
N_{ns}	25.9	13.0	16.0	17.0
N_c	38.9	19.5	24.0	25.5
B. sylvicola				
N_i	9	11	23	15
N_g	9	9	10	12
N_{nr}	9	8	9	11
N_{ns}	9	9.8	20.7	13.8
N_c	13.5	14.7	31.1	20.6

Note: Abbreviations are N_i, number of *Bombus* spp. worker individuals sampled; N_g, number of successfully genotyped individuals; N_{nr}, number of detected colonies based on raw nest numbers; N_{ns}, number of detected colonies based on nest numbers standardized for genotyping success; and N_c, total estimated colonies (effective colony number), where $N_c = 1.5 \times$ standardized number of nests, N_{ns}.

analysis have then been summed with estimated unsampled nests to estimate "effective population size." However, small nest numbers precluded the fitting of a truncated Poisson distribution to our site-level data. In addition, bumble bee nests are most likely aggregated rather than randomly distributed (e.g., Harder 1986, Osborne et al. 2008b), making the assumption of a Poisson distribution untenable. Instead, we estimated detected plus undetected nests, "effective colony number" (N_c) as $N_c = 1.5\times$ standardized number of nests, N_{ns} (sensu Charman et al. 2010; Table 2). This calculation is based on the Crozier model for effective population size (N_e) of eusocial haplodiploid species characterized by monogyny and monoandry: $N_e = (4.5Nnm)/(1 + 2m)$, where N is the number of colonies, m is mating frequency, and n is the number of queens per colony (Crozier 1979). We termed our measure "effective colony number" rather than "effective population size," despite the use of the latter in similar studies, because we were interested in relative colony abundance among sites; N_e would be best applied to the whole of Pennsylvania Mountain as an assumed panmictic breeding population.

We could not statistically compare N_c among species within sites, due to lack of replication (sample size was one N_c estimate per species within each site). However, comparisons of N_c were conducted using ANOVA (here and elsewhere, SAS Version 9.2, Proc GLM) in three ways. First, to assess whether mean colony abundance of all *Bombus* differed among sites (species as unit of replication, $n = 16$ over four sites; $n = 4$ within each site) or whether mean colony abundance per site differed among *Bombus* species (site as unit of replication, $n = 16$ over four sites; $n = 4$ for each species), we included site and species as fixed effects in the analysis. Site was a fixed rather than random effect because sites were not randomly selected, and because, due to low sample size ($n = 4$ sites total, two within each elevation), no power would be gained in treating them as random effects; treating site as a fixed effect is the more conservative analysis (Bolker 2008). Second, we assessed whether relative species abundances differed among high- and low-alpine sites by analyzing N_c with species, elevation (high and low), and their interaction as fixed effects (N_c of species within site as unit of replication, $n = 16$ over four sites; $n = 8$ per elevation). Third, because tongue length is predicted to impact bee associations with specific flower species and/or types and thus floral resource partitioning, we assessed whether relative abundances of short-, medium-, and long-tongued *Bombus* differed among high- and low-alpine sites by analyzing N_c with tongue length group, elevation (high or low), and their interaction as fixed effects (N_c of species within site as unit of replication, $n = 4$ short-, 2 medium-, and 2 long-tongued species' N_c for each elevation). For the last two analyses, planned pairwise comparisons were conducted using least squares means; N_c was square-root-transformed for all analyses.

Relationship between forager abundance and nest abundance

We used ANCOVA to test whether the relationship between foragers captured (N_i) and the number of nests detected by sibship reconstruction software, standardized for genotyping success (N_{nr}), differed among species with N_i as the continuous covariate and species ($n = 4$) the categorical effect. Because of poor genotyping success, data from site 3 were excluded from the analysis.

Estimates of Bombus *foraging range*

We estimated foraging ranges for workers of each *Bombus* species from the distribution of nest mates among the four sites (Darvill et al. 2004, Knight et al. 2005). For siblings found in circular sites with radius r and centers separated by a distance x, we assumed that the nest was located at the midpoint of the line connecting the site centers (Appendix A: Fig. A1). The distance between the nest and edge of each site was calculated as $x/2 - r$. This is a conservative estimate of

foraging range, as it is unlikely that all siblings' nests were perfectly centered between sites (Knight et al. 2005). The upper foraging limit for each species was estimated from the greatest separation between members of sister pairs.

We analyzed differences in mean sister separation (mean distance between all separated pairs of sisters for each species) and foraging distances among species using ANOVA with *Bombus* species as a fixed factor in the model (unit of replication = pairs of sisters, $n = 58$). We conducted pairwise comparisons among species with least squares means.

Relationship between nest abundance and host-plant fecundity

To assess habitat-scale relationships between *Bombus* colony abundance and reproductive success of bumble bee-pollinated plants, we focused on two native alpine clovers, *Trifolium dasyphyllum* and *T. parryi*. Both species are abundant from the treeline upward in the central Rocky Mountains, are obligate outcrossers (Macior 1974, Bauer 1983), and depend to varying degrees on bumble bee pollinators. *T. parryi* is a *B. balteatus* specialist, whereas *T. dasyphyllum* has a more generalized pollination niche and receives visits from multiple bumble bee species (Macior 1974, Geib 2010, Geib and Galen 2012).

We randomly collected one infructescence per plant of *T. dasyphyllum* and *T. parryi* within large patches at each site in September 2008 ($n = 158$ inflorescences for *T. dasyphyllum* and 167 for *T. parryi*, 30–60 infructescences/0.01-km² site for each species). As each clover floret contains an ovary with multiple ovules, we assessed per-floret fruit and seed production for each individual and conducted ANCOVA (SAS Proc MIXED) on square-root-transformed fruit set and seed set to test for relationships to (1) site-level effective colony abundance (N_c) of *B. balteatus*, (2) site-level colony abundance of all *Bombus* species (ΣN_c), (3) site-level forager abundance of *B. balteatus* (N_i), and (4) summed forager abundance of all *Bombus* species (ΣN_i). To assess whether relationships differed between the clovers, we included "plant species" as a categorical variable in all models. In these analyses, we assume that our *Bombus* worker collections had negligible effects on the clovers' reproductive output. We believe that this is true because we caught only 1–2 representatives from 97% of detected nests, leaving the bulk of the colonies intact. In addition, as stated previously, this time period corresponds with peak forager abundance for all *Bombus* species.

RESULTS

Estimates of Bombus *colony abundance and distributions*

The estimated number of sampled plus unsampled nests per site (effective colony number, N_c) varied among and within species, ranging from 18.1 to 71.6 nests (Table 2). Mean *Bombus* N_c did not vary among sites ($n = 16$; Appendix C: Table C1A), but mean N_c per
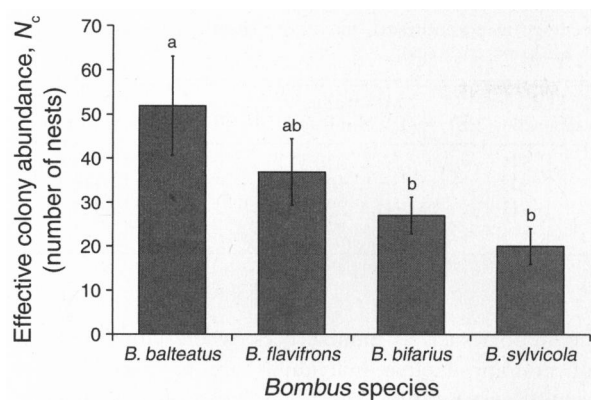
FIG. 1. Effective colony abundance per site, N_c, (mean ± SE) for four *Bombus* species on Pennsylvania Mountain, Colorado, USA. Effective colony abundance is defined as the number of detected plus estimated undetected nests ($N_c = 1.5 \times$ standardized number of nests, N_{ns}). Species sharing the same lowercase letters do not differ significantly at $P < 0.05$.

site varied among species ($F_{3,9} = 3.97$, $P = 0.0468$, $n = 16$; Table C1A). Abundance of *B. balteatus* colonies per site exceeded that of *B. bifarius* or *B. sylvicola* (LS means comparisons, $P < 0.05$; Fig. 1). *B. balteatus* nests were more frequently represented at high-alpine sites than were those of other species, and *B. balteatus* nests were more frequently represented at high- than at low-alpine
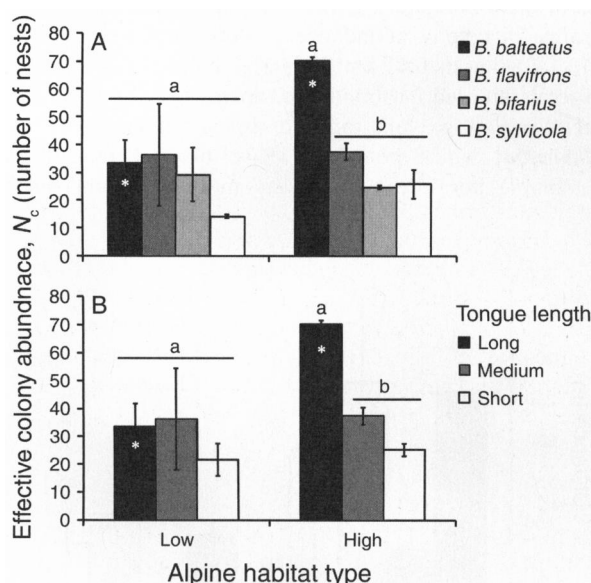

FIG. 2. (A) Comparison of effective colony abundance (N_c) between low-alpine (3659–3701 m) and high-alpine (3723–2735 m) habitats and among four *Bombus* species. (B) Comparisons of effective colony abundance (N_c) between low-alpine and high-alpine habitats and among *Bombus* spp. of different tongue length. All data are presented as mean ± SE. A single asterisk indicates that, within species, differences in N_c between low- and high-alpine sites are significant at $P < 0.05$. Within low and high sites, species sharing the same lowercase letters do not differ significantly in N_c at $P < 0.05$, as determined by pairwise least square means (LSM) comparisons.
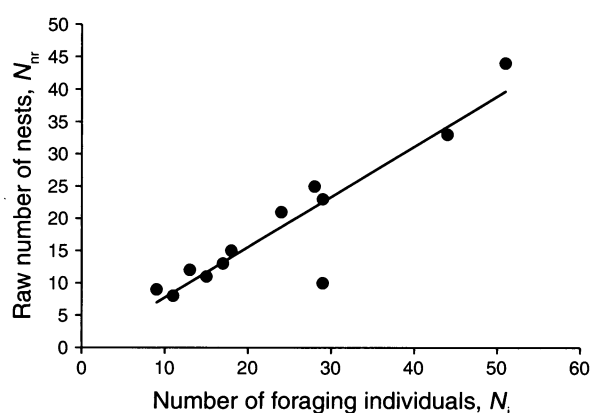

FIG. 3. The relationship between numbers of foraging workers caught per species at each site (N_i) and number of nests detected among samples by sibship reconstruction software (raw nest number, N_{nr}). Site 3 data were excluded from analysis due to low genotyping success. For the best-fit line, $y = 0.7793x - 0.037$ ($R^2 = 0.86$, $P = 0.002$).

sites (LS means comparisons, $P < 0.05$; Fig. 2A). Nests of long-tongued species were more abundant than those of medium- and short-tongued species, especially at the highest sites (LS means comparisons, $P < 0.05$; Fig. 2B). Both trends reflect the concentration of *B. balteatus* at high elevations, as it is the only long-tongued species. Interestingly, for three species, *B. balteatus*, *B. bifarius*, and *B. flavifrons*, the variation in N_c between the low-alpine habitats was very high, with sampled workers from site 2 representing 19.4 fewer *B. bifarius*, 36.4 fewer *B. flavifrons*, and 16.4 more *B. balteatus* nests than at site 1 (Table 2).

Relationship between forager abundance and nest abundance

Regardless of species or elevation, the number of nests detected at each site by the sibship reconstruction software (raw number of nests, standardized for genotyping success (N_{nr}), was closely correlated with the number of individual foragers caught (N_i) per site (site 3 was excluded due to genotyping issues; $F_{1,7} = 6.70$, $P = 0.002$, $R^2 = 0.86$; Fig. 3).

Estimates of *Bombus* foraging range

For all species, putative sisters were captured at different elevations (Table 1). No *Bombus* sisters in any species were identified among the samples collected from the two sites separated by 784 m (the maximum distance between any sites). For *B. balteatus* 87% of all sister pairs were site-separated, whereas for other species, site-separated sister pairs ranged from 20% (*B. flavifrons*) to 40% or 50% (*B. bifarius* and *B. sylvicola*, respectively; Table 3).

Mean sister separation and foraging distance (Fig. 4) differed among species (for sister separation, $F_{3,54} = 4.86$, $P = 0.0046$, $n = 58$; for foraging distance, $F_{3,54} = 4.20$, $P = 0.0096$, $n = 58$; Appendix C: Table C2), with *B.*

TABLE 3. Total sister pairs, total site-separated sister pairs (percentage in parentheses), maximum sister separation distance, foraging range upper limit, and mean foraging range (mean with SE in parentheses).

Species	Total no. sister pairs	Total site-separated sister pairs (%)	Max. sister separation (m)	Min. range upper limit (m)	Foraging range (m)
B. balteatus	15	13 (86.7%)	541	220.5	85.4 (15.0)
B. flavifrons	30	6 (20%)	505	202.5	23.8 (10.1)
B. bifarius	8	4 (50%)	541	220.5	110.25 (41.7)
B. sylvicola	5	2 (40%)	681	290.5	74.7 (56.3)

flavifrons having significantly shorter separation and foraging distances than two other species (LS means comparisons, $P < 0.05$). Estimates of the upper limits of foraging range also varied among species (Table 3). *B. flavifrons* again exhibited the narrowest foraging range (≤ 202.5 m), whereas *B. sylvicola* foraged over the broadest area (≤ 290.5 m).

Relationship between nest abundance and host-plant fecundity

Relationships between *B. balteatus* nest abundance ("effective colony number," N_c) and per-flower fruit set varied between *T. dasyphyllum* and *T. parryi* ($N_c \times$ plant species, $F_{1,321} = 7.51$, $P = 0.0065$, $n = 325$; Fig. 5A; see Appendix C: Table C3A). Fruit set per flower of *T. parryi* correlated positively with site-level variation in N_c of the long-tongued bee, *B. balteatus*, although the small R^2 suggests that other factors affect fruiting level in this species ($F_{1,165} = 15.76$, $P = 0.0001$, $R^2 = 0.088$, $n = 167$). Conversely, in *T. dasyphyllum* fruit production was independent of *B. balteatus* N_c ($F_{1,156} = 0.06$, $P > 0.80$, $n = 158$). Fruit set varied as strongly with the number of *B. balteatus* foragers sampled (N_i) as with colony abundance (N_c) (Fig. 5B; see Appendix C: Table C4A). *B. balteatus* abundance was not correlated with seed production of *T. parryi* (Appendix C: Tables C4B, C, and C5B, C). Fruit set of both clovers was also correlated with ΣN_c and ΣN_i for all *Bombus* species in each habitat (for ΣN_c, $F_{1,321} = 31.73$, $P < 0.0001$, $R^2 = 0.14$, $n = 325$; Fig. 5C; Appendix C: Table C3D; for ΣN_i, $F_{1,321} = 25.15$, $P < 0.0001$, $R^2 = 0.13$, $n = 325$; Appendix C: Table C4D), although the slopes of the relationship with ΣN_i differed between plant species ($F_{1,321} = 4.22$, $P = 0.041$, $n = 325$; Appendix C: Table C4D). Seed set per flower for both clovers was correlated with total forager abundance across all *Bombus* species, although the explanatory power of the model was low (for ΣN_i, $F_{1,321} = 4.61$, $P = 0.033$, $R^2 = 0.02$, $n = 325$; Table C4F).

DISCUSSION

Estimates of Bombus colony abundance and distributions

In light of dire reports on the status of pollinators worldwide (NRC 2007), monitoring efforts and resources devoted to pollinator population management and conservation have increased. However, many have recognized that forager counts are not the best representation of population health for important

pollinators such as bumble bees, where large numbers of nonreproductive individuals are aggregated to a central nest location with a single reproductive female. Numerous studies have thus attempted to estimate nest abundances of *Bombus* species, although primarily in agricultural or urban/suburban habitats. Estimates for the mean colony abundance among species studied in the UK range from 20.4 to 150 nests/0.01 km^2 habitat (Darvill et al. 2004, Knight et al. 2005, 2009, Osborne et al. 2008b). The range in number of nests contributing floral visitors to mass flowering crops in a North American arable landscape was 0.76–22.16 nests/per km^2 (0.0076–0.2216 nests/0.01 km^2 adjusted for comparison) (Rao and Strange 2012). However, this might be an underestimate, because sampling areas described here were whole fields of patchy bloom, 6–25 ha in size. Results from our study in a North American alpine ecosystem were more in line with those in the UK, as the range in colony abundance of individual species was 18.1–71.6 nests/0.01 km^2 habitat. Co-occurring *Bombus* species differed in abundance. Specifically, nests of the relatively large long-tongued alpine bumble bee, *B. balteatus*, which potentially have broader ranges of available floral resources, were more abundant than
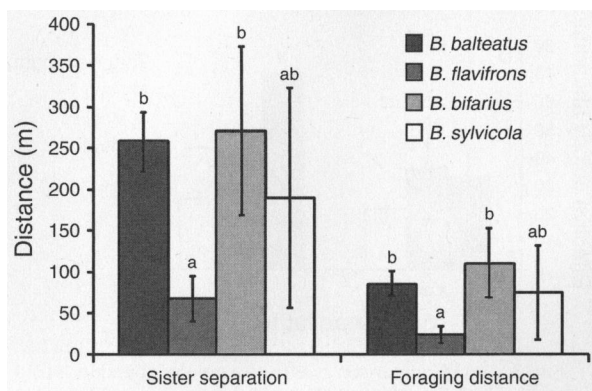
FIG. 4. Separation distance (mean ± SE) between worker nest mates (sisters) and foraging distance (mean ± SE) between workers for four *Bombus* species sampled in alpine habitats on Pennsylvania Mountain. Foraging distance of each individual in a sister pair was estimated by assuming that their nest was located at the midpoint of the line connecting sisters' site centers (a conservative estimate of foraging distance). Species sharing the same lowercase letters do not differ significantly at $P < 0.05$ for the designated distance metric.
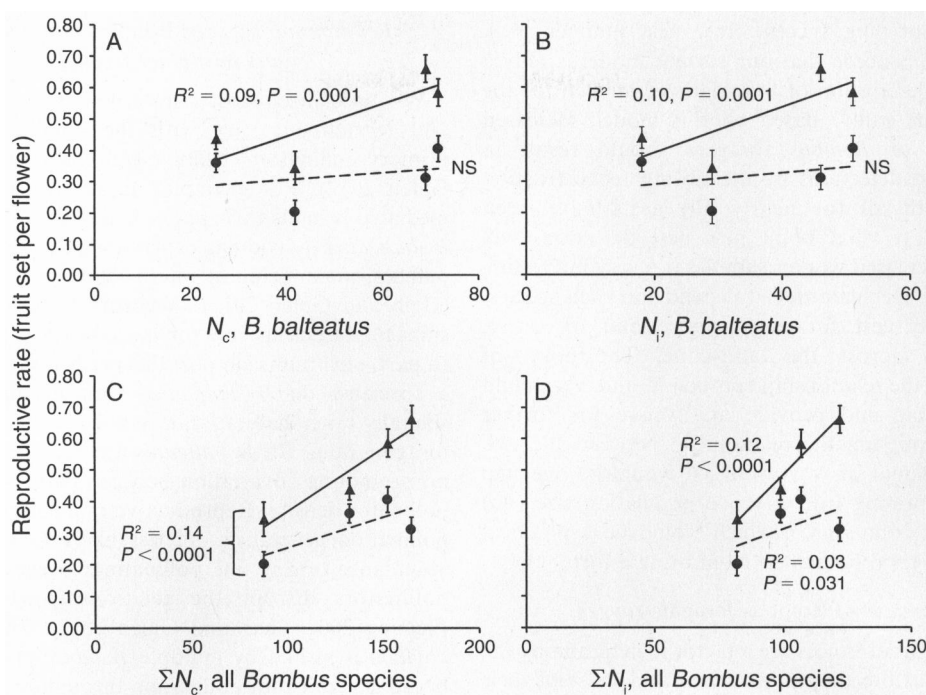
Fig. 5. The relationship between habitat-scale pollinator abundance and per-flower fruit production for *Trifolium dasyphyllum* and *T. parryi*. Pollinator abundance is represented by (A) *B. balteatus* nest abundance per site (N_c), (B) *B. balteatus* individuals caught per site (N_i), (C) summed N_c for all *Bombus* species per site (ΣN_c), and (D) summed *Bombus* individuals caught per site (ΣN_i). Triangles with solid lines indicate fruit set for *T. parryi*. Circles with dashed lines indicate fruit set for *T. dasyphyllum*. All data are presented as·mean ± SE.

nests of short-tongued species, *B. bifarius* and *B. sylvicola*, especially far above treeline.

That *B. bifarius*, a subalpine bumble bee, was equally represented among individuals and nests of short-tongued species at these sites (all >3600 m) was surprising. In extensive historical surveys of *Bombus* foragers in the Colorado Rockies, *B. bifarius* comprised only 1–10% of short-tongued individuals at elevation ranges of 3400–4000 m (Macior 1974, Byron 1980, Pyke 1982). We advise caution in interpreting these results, given that pollinator communities frequently exhibit temporal variation in composition, but these findings are in line with other recent preliminary evidence for upward range shifts of subalpine *Bombus* species in Colorado (Inouye 2009). If these results hold true in further inventories, they suggest that long-tongued bumble bees are not currently giving way, despite potential lowland invaders, and that floral niche breadth divisions among bees grouped by tongue lengths could remain stable. Other studies, however, have suggested that long-tongued bees are not faring as well relative to their short-tongued congeners (Goulson et al. 2005, Dupont et al. 2011, Colla et al. 2012).

These preliminary data on nest abundance set the stage for further explorations of this bumble bee community, and should provide a model for similar studies in other North American ecosystems. Here our

goal was to investigate colony abundance at the habitat scale, but future studies using the same methods and wider sampling could answer questions of even greater relevance to *Bombus* conservation and management, such as the actual size of the breeding population (effective population size, N_e). The parameter N_e has far more direct relevance to the health of *Bombus* populations than forager count data alone, or even habitat-level nest abundances, because it allows inferences about the rate of inbreeding and genetic drift (Caballero 1994). For species perceived to be in decline, assessing N_e is especially important. Low N_e in haplodiploid Hymenoptera can signal increased probably of rare matings where 50% of progeny are sterile diploid males due to a single-locus complementary sex determination, sl-CSD (Zayed and Packer 2005). We did not attempt to evaluate N_e in this study because we assumed that the *Bombus* breeding population extended beyond the scale of our small 0.01-km² habitats. This is an assumption that needs to be further tested.

Relationship between forager abundance and nest abundance

Similar to Rao and Strange (2012), we found a strong linear relationship between the number of foragers sampled at each site (N_i) and the number of nests detected by sibship reconstruction software, standard-

ized for genotyping success (raw nest number N_{nr}). However, we concede that our current model is only a preliminary description of the relationship even for the species in our study. Based on this model, increased sample size of Bombus foragers should result in increased nest detections by the sibship reconstruction software until all (or nearly all) nests have been represented. At what point new nest detections will cease with increased worker samples is a very interesting question. We speculate that it depends on each species' brood size per nest, foraging distance, and, of course, nest density across the landscape. The point of saturation in the relationship between N_i and N_{nr} should be quantifiable and provide an avenue for further studies. Quantifying the relationship between the two parameters would be worthwhile; it would be one step toward interpreting true effective population size (N_e) from forager counts (N_i), which would be a practical tool for long-term pollinator monitoring efforts.

Estimates of Bombus foraging ranges

Bombus flight distances are a factor in determining the size of Bombus breeding populations and those of their host plants (but for plants, this depends on pollen carryover; see Waser and Price 1982). Flight distances vary among Apidae pollinators, with ranges extending up to many kilometers: e.g., up to 5, 10, and 24 km for Xylocopa spp., honeybees, and euglossine bees, respectively (Kapil and Daliwahl 1969, Janzen 1971, Visscher and Seeley 1982 in Cresswell et al. 2000). For bumble bees, energetics models suggest that individuals should rarely forage more than 1000 m from the nest, unless nearby resources are scarce or distant resources are so great that they outweigh metabolic costs (Cresswell et al. 2000). Species in agricultural habitats forage 275–800 m, on average (Osborne et al. 1999, Knight et al. 2005, Westphal et al. 2006, Osborne et al. 2008a). Foraging ranges reported in this study are probably underestimates because sisters caught in the same site were assigned a separation distance of 0 m but may have been separated by up to 100 m. In addition, small worker sample sizes reduced the likelihood of capturing sisters in separate habitats, and the maximum detectable foraging distance was limited by maximum distance between sites (784 m). Nonetheless, these findings, along with two subalpine studies (Bowers 1985, Elliott 2009), suggest that high-elevation bumble bees may have shorter foraging ranges than their lowland counterparts. Although nest mates of one species, B. balteatus, were often observed foraging at widely separated sites, average foraging distances were modest, 25–100 m. Elliott (2009) suggested that bumble bees may forage closer to their nests to maximize energy return under the shorter blooming season at high elevations (see also Hines and Cameron 2010). Reduced foraging ranges should increase the vulnerability of alpine plant populations to fluctuations in partner density at a more localized scale.

Relationship between Bombus nest abundance and host-plant fecundity

For specialized host plants, individual plant fitness and recruitment vary with the abundance of their primary pollinators (Pellmyr and Huth 1994, Geib and Galen 2012). For example, in past work, pollinator-mediated benefits to T. parryi varied with the number of B. balteatus individuals experimentally added to clover patches, maximizing at intermediate pollinator density (Geib and Galen 2012). Accordingly, similar relationships might be expected for specialists at a habitat scale. In part, our results support this prediction: for T. parryi, a specialist on B. balteatus, fruit production varied spatially with habitat-scale colony abundance. Mean foraging range for B. balteatus was relatively small, 85.4 m, promoting covariation between plant fecundity and pollinator density. Reproductive rates of plants that are pollination generalists are less likely to vary with the abundance of any one pollinating species, because co-pollinators disrupt the relationship (Holland and Fleming 2002, Geib and Galen 2012). Trifolium dasyphyllum is visited by multiple Bombus species and is a broad generalist for pollination throughout its blooming period (Geib 2010). As in past studies in which T. dasyphyllum fecundity, recruitment, and population growth rate were independent of the number of experimentally added B. balteatus individuals (Geib and Galen 2012), fruit set of T. dasyphyllum was independent of habitat-scale B. balteatus abundance, and instead correlated with total colony abundance of all Bombus species.

In contrast to fruit set, seed production did not correlate with Bombus nest abundance. Instead, seed set for plants of both species correlated with the total number of foraging Bombus individuals, suggesting that for clovers, year-to-year fluctuations in any one pollinating species may be balanced by influx of another. Nevertheless, the model explained little variation in seed set (only 2%), probably due to pronounced heterogeneity in resources in alpine habitats (Körner 1999). Prior studies in these populations suggest that seed set for both clovers is partially resource limited (Geib and Galen 2012). That forager abundance was as good as nest abundance in predicting benefits to plants from pollination services suggests that forager count inventories are relevant to predicting the health of plant populations even if they are limited in what they can imply about the pollinator populations themselves.

We have provided some of the first estimates of habitat-level nest abundance for important eusocial pollinators of native North American ecosystems. In connecting forager inventories to population-level data, we hope to provide a model for long-term monitoring efforts of bee populations in a variety of habitats. When evaluating the health of eusocial pollinating insects such as bumble bees is the target for assessment, investing in DNA extraction and molecular analyses to establish nest

abundance is warranted. For long-term population monitoring, which requires repeated assessments over time, establishing the relationship between forager and nest densities is recommended so that forager counts can serve as a nest estimation surrogate in future years with lower project costs. When services to plants from pollination are the target for assessment, forager abundance alone may be a good enough indicator. In the present study, longer term monitoring of these relationships (between foragers and nests and among foragers, nests, and plant fecundity) would be a useful extension, because it would provide us with data about the stability of the relationships over a broader range of year-to-year environmental variance. Given the ubiquitous importance of bumble bees and other pollinators to outcrossing plants in both natural and agricultural ecosystems, widespread documentation of *Bombus* species losses, and changes in the composition of some *Bombus* communities, long-term monitoring programs to build on these data in other habitats are strongly recommended.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: http://dx.doi.org/10.1890/14-0151.1.sm

Data Availability

Data associated with this paper have been deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.cr672