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Habitat Preference and Phenology of Nest Seeking and Foraging Spring Bumble Bee Queens in Northeastern North America (Hymenoptera: Apidae: Bombus)

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ABSTRACT.—Bumble bees are among the most abundant and important wild pollinators in North America. Spring nest establishment is a brief and vulnerable stage in the colony life cycle that is poorly understood. Bumble bee nesting activity in temperate North America has received little recent attention, and this knowledge gap is a barrier to conservation efforts. The aim of this study was to investigate the habitat use, nesting phenology, and key food plants of spring bumble bee queens. Through 108 nonlethal surveys of bumble bee queens in spring 2018, researchers observed 451 nest seeking and 555 foraging queens of nine species in Ohio, U.S.A. Spring queen activity began in mid-April and peaked in mid-May, although nest seekers were observed into late June. Nest seeking queens favored woody transitional habitats over open habitats. In accordance queen abundance and diversity increased with the proportion of forest in the surrounding landscape. The proportion of row crops and urban areas negatively influenced queen diversity and the number of nest seekers, respectively. Through a literature review, the earliest emergence dates for each species were compared for 12 datasets to establish an order of species emergence in northeastern North America. Forty-seven species of flowering plants were used by foraging queens. Highly visited food plants included both native and nonnatives(*): *Lupinus perennis*, *Malus* spp., *Taraxacum officinale**, *Lonicera* spp.*, *Lamium purpureum**, *Glechoma hederacea**, *Trifolium pratense**, and *Mertensia virginica*. Systematic field surveys are needed by state to document the timing of spring queen emergence and nesting activities to inform conservation efforts.

INTRODUCTION

Bumble bees (*Bombus* spp. Latreille) are abundant and widely recognized as economically and ecologically important pollinators. Because they are larger bodied than most wild bees, they are better able to forage and transport pollen over long distances and to fly in cooler weather (Willmer, 1983; Cresswell *et al.*, 2000; Osborne *et al.*, 2008; Pope and Jha, 2018). The queens of nonparasitic *Bombus* species initiate their eusocial nests in the early spring. They are adapted to forage in conditions that are not ideal for most bees, making them key pollinators of native spring wild flowers (Fye and Medler, 1954; Macior, 1968, 1978; Thomson, 1986; Prusnek, 1999) and orchard crops (Javorek *et al.*, 2002; Drummond, 2012).

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Although bumble bees are among the most common wild bees in the Holarctic, their nests are notoriously difficult to find, because they are typically underground in abandoned rodent burrows and have their entrances concealed by dense vegetation, herbaceous debris, fallen logs, tree stumps, buttressing tree bases, brush piles, or manmade objects and structures (Franklin, 1912; Frison, 1923; Plath, 1934; Hobbs, 1965, 1966a, 1966b, 1967, 1968). Some species are also known to dig false entrances or to camouflage the nest entrance with moss or grass (*e.g. B. fervidus* Fabricius, *B. occidentalis* Greene) (Hobbs, 1966a, 1968; Richards, 1975). Historic studies often relied on placing large numbers of artificial domiciles to attract queens to obtain colonies for experiments (Sladen, 1912; Frison, 1923; Hobbs, 1964–1968). Contemporary studies have located nests using large groups of volunteers (Frison, 1923; Fussell and Corbet, 1992; Osborne *et al.*, 2008; Lye *et al.*, 2012; O'Connor *et al.*, 2012), trained detection dogs (Waters *et al.*, 2011; O'Connor *et al.*, 2012), and transect searches (Svensson *et al.*, 2000; Kells and Goulson, 2003; Lye *et al.*, 2009; O'Connor *et al.*, 2017). Advances in modern genetic tools have made it possible to estimate summer nest density from worker genetic diversity (Darvill *et al.*, 2004; Knight *et al.*, 2009; Lepais *et al.*, 2010; Dreier *et al.*, 2014; Carvell *et al.*, 2017). Direct surveys of spring foundress queens, however, provide essential ecological and phenological information on bumble bee natural history that can advance conservation efforts. In Europe studies have largely focused on how land management, particularly urbanization (Osborne *et al.*, 2008) and agriculture (Svensson *et al.*, 2000; Kells and Goulson, 2003; Lye *et al.*, 2009; Samuelson *et al.*, 2018), affect bumble bee nesting. The majority of work on the nesting ecology of North American species is limited to high latitudes and high-altitude montane habitat or was conducted before the period of documented bumble bee declines in the latter half of the 1900's (Plath, 1934; Hobbs, 1964, 1965, 1966a, 1966b, 1967, 1968; Macior, 1968; Macfarlane, 1974; Richards, 1975, 1978; Bowers, 1985; Macfarlane *et al.*, 1994). It is a barrier to bee conservation efforts that our understanding of their nesting biology and habitat use is incomplete for many species.

Recent and historic surveys and museum specimens have recorded 20 *Bombus* species in the state of Ohio, which is located at the convergence of the Midwestern and Northeastern regions of the United States. However, almost half of them have not been seen in Ohio for more than 20 y (Table A1) and several *Bombus* species have recently declined. Notably, the once common rusty-patched bumble bee (*B. affinis* Cresson) has declined dramatically in the last two decades and was listed as federally endangered in 2017 (Colla and Packer, 2008; Grixti *et al.*, 2009; Colla *et al.*, 2012; USFWS, 2017; Jacobson *et al.*, 2018). The cause of its sudden decline remains a mystery. Previous studies have investigated diet breadth, tongue length, body size, genetic diversity, pesticide exposure, and parasites and pathogens as possible agents of bumble bee decline worldwide (Williams *et al.*, 2007; Kleijn and Raemakers, 2008; Williams and Osborne, 2009; Williams *et al.*, 2009; Cameron *et al.*, 2011; Szabo *et al.*, 2012; Maebe *et al.*, 2015; Cameron *et al.*, 2016), although nesting ecology has received little attention.

The early stages in the bumble bee colony life cycle are a sensitive time (Macfarlane, 1974), yet the process of queen nest site selection and nest initiation are less understood than later colony growth and reproduction. Previous work on nesting biology suggest many species share similar nest site preferences, leading to strong intra- and inter-specific competition for nest sites (Plath, 1934; Hobbs, 1964–1968; Richards, 1975). For example the U.S. Federally Endangered *B. affinis* shares its nesting niche with other species (Plath, 1934) and so may experience high rates of usurpation and competition. Higginson (2017) concluded species with late-emerging queens, especially those with a relatively large body size, are at a disadvantage when competing for limited high-quality nest sites. On the other hand, queens that found nests early in the season may be more vulnerable to usurpation by other foundresses and invasion by social parasites in the *Bombus* subgenus *Psithyrus* (Hobbs, 1968; Richards, 1975). In addition to pressure from competitors and parasites, if climate change alters the onset and duration of spring weather, it could also change the dynamics of bumble bee nest founding. The timing of queen emergence and nesting, preferred nesting habitat, and other natural history traits will influence the evolution and long-term persistence of species. Therefore, contemporary baseline data are needed on the timing of queen emergence and nesting activities of both common and declining bumble bee species.

In this study the nesting and foraging ecology of bumble bees in Ohio, U.S.A. was investigated using standardized field surveys of spring foundress queens, augmented with observations of nest seeking queens submitted by trained volunteers. The objectives of this study were to: (1) identify the habitats where bumble bee queens search for nest sites and to evaluate the possible influence of the local landscape; (2) to delineate the phenology (timing and duration) of queen emergence and nest seeking; and (3) to compile a list of important food plants for foraging bumble bee queens.

METHODS

From 1 May–8 June 2018, researchers conducted nonlethal surveys of foraging and nest seeking bumble bee queens at 115 field sites in 28 counties in Ohio, U.S.A. (*see* Table A2 for GPS coordinates and other survey details). Survey sites included public parks, preserves, and private properties, with >0.5 ha of potential bee foraging and nesting habitat, and separated from one another by at least 3 km. Surveys were conducted on fair weather days when the air temperature was at least 15.5 C (mean temperature at time of survey 25.5 C ± 4.0) with little wind, between the hours of 0800 and 1900. Teams of one to five observers walked slowly and continuously through a site for a total of 60 min searching all available habitat types but paying particular attention to areas with dense vegetative or woody debris (*e.g.*, grass clumps, leaf litter, or fallen logs) or complex microtopography (*e.g.*, stream banks, buttressing tree bases, and road embankments). This approach allowed observers to cover a large area while maximizing survey yield. If bees were netted for identification, handling time was not included in the 60 min of searching time. Observers sought to minimize double-counting individual queens by moving to a new patch of flowers or potential nesting habitat after a queen was observed. At each site the start and end time of survey, the temperature, cloud conditions (sunny, partly sunny, or cloudy), average ground wind speed, and the amount of time spent searching each habitat type were recorded. Within a site habitats searched were classified into five categories based on their floral and nesting resources for bees: (1) wooded (evergreen and deciduous forest, riparian forest, and woodland); (2) edge (interface between wooded and open habitat); (3) field (grasslands and meadows); (4) wetland (seasonally inundated area); and (5) maintained area (flower beds, gardens, and lawns). The growing degree day (GDD) for each survey was obtained from the location and sample date using an online calculator available from the Ohio State University Extension (https://www.oardc.ohio-state.edu/gdd/). Queen surveys ceased after the first week of June when workers of most species had emerged (*see* also Macior, 1968).

Bumble bee queens, and later workers, were either identified to species in the field or netted and photographed in plastic vials for later identification using Williams *et al.* (2014) then rereleased on site. In rare cases, where species identity could not be verified in the field (such as the *B. sandersoni*), the specimen was vouchered.

During timed surveys researchers recorded a list of the flowering plant species in bloom at the site that were potential food sources for bumble bees, noting which species were flowering abundantly and likely to attract bumble bees. This method was chosen over the transect or quadrat methods typically used to survey plant communities because it captured bee-preferred flowers better given the wide foraging radii of queens and the patchy and three-dimensional distribution of tree, shrub, and herbaceous flower resources.

At the time of observation, each queen's behavior was categorized as either flying, foraging, or nest seeking. Flying queens made fast and mostly linear flights, usually >2 m above the ground. Foraging queens were those observed visiting flowers, and the species of plant was recorded. Nest seeking queens were recognized by their behavior; they mostly flew slowly and low to the ground, frequently changing direction and stopping to investigate crevices and cavities. For foraging and nest seeking queens, it was noted whether or not each queen was carrying pollen in her corbiculae, an indicator that she had already founded a nest.

For nest seeking queens, additional information was collected. The habitat type in which each nest seeking queen was observed was categorized as wooded, edge, field, wetland, or maintained area as in timed surveys. The presence or absence of each of the following microhabitat features was noted in an approximately 2 m radius area around the location where a queen was searching for a nest site: leaf litter, herbaceous litter, grass clumps or tussocks, fallen logs or large woody debris, rock piles, mounds of bare soil, moss, stream or river, lake or pond, trees in full bloom, shrubs in full bloom, and herbaceous plants in full bloom.

Citizen science data were used to augment observations of *Bombus* queen nest seeking behavior collected by researchers in timed surveys. Fifty adult volunteers were recruited from the Ohio Certified Volunteer Naturalist program of the Ohio State University Extension program. Volunteers were trained in bumble bee species identification and nest seeking queen data collection through a combination of in-person (6 h workshop) and on-line tutorials (1.5 h interactive video lectures, http://u.osu.edu/beelab/bumble-bee-survey/). They were instructed to report queens encountered in any habitat, submit a photograph for species verification, and enter all locality, habitat, and microhabitat data on nest seeking using a dedicated Google Forms survey or by email on standardized data collection sheets. Assistance with data reporting and verification of species identifications was provided by email. Ultimately, 21 volunteers submitted data on 80 nest seeking queens between 1 April and 1 June, 2018, following the same format as the researchers for collecting data on individual nest seekers, but not participating in the timed researcher surveys.

This sampling approach yielded two data sets. The Timed Survey data set was used to investigate the influence of growing degree day, flower richness, and landscape factors on queen abundance and species richness, and to compose a list of key spring food plants for queens. The Augmented Nest Seekers data set, which included verified citizen science observations, was used to infer the habitat and microhabitat preferences of individual nest seeking queens.

For all sites where researchers conducted timed queen surveys, the surrounding land use was extracted in ArcGIS 10.6.1 software (ESRI, 2018) within a 1 km buffer area of the site center, a radius which encompassed all habitats types researchers searched and was relevant to bumble bee foraging distances. Land cover was taken from the National Land Cover Dataset (NLCD, Homer *et al.*, 2015), which classifies land use with 30 m resolution into 15 categories for the conterminous U.S. For this study land cover categories in the original dataset were simplified into broader categories based on the quality of bumble bee nesting and food resources they offer, as follows: open water, developed lands, forest, shrubland, herbaceous land (including pasture), row crop agriculture, and wetland.

Data on the first sighting of each species during this study were compared to regional spring queen emergence data gleaned from the literature. The earliest emergence dates for each species in our study and in 11 other field surveys of bumble bee queens in Northeastern North America were compiled. Growing degree day for emergence dates in earlier studies could not be calculated because the survey locations were not reported in sufficient detail.

DATA ANALYSIS

All data analyses were conducted in R version 3.5.2 (R Development Core Team, 2018). To test the influence of time of day, weather, and habitat on total queen abundance, species richness, and nest seeking queens per minute of search time by habitat, nonparametric Kruskal-Wallis rank sum tests with Dunn's post hoc group-wise comparisons (function *dunn.test*; Dinno, 2017) were used. Spearman correlation analysis was used to determine the influence of growing degree day (GDD), flowering plant richness, temperature, and surrounding land use components on queen abundance and richness. The model residuals in parametric analyses (Pearson correlation and ANOVA) were tested for normality using Shapiro-Wilks tests (function *shapiro.test*) and found not to conform to a Gaussian distribution. Queens that were observed flying overhead (neither foraging nor nest seeking) that were not identifiable to species were included in tallies of queen abundance, but not in species-specific analyses or in analyses of nest-seeking or foraging queens.

To understand how land use, GDD, and flower richness influenced queen abundance and species richness in timed surveys, multivariate models were constructed. First, all predictor variables were standardized by subtracting the variable average from each observation and dividing by SD. Principal components analysis (PCA) with varimax rotation was then used to account for correlations among predictor variables (*prcomp* function, *varimax* function). The three factors that had eigenvalues greater than one were retained. Those principal components were used as predictors in generalized linear models (GLMs) of nest seeking and foraging queen abundance and queen species richness. The full models were constructed using Gaussian, Poisson, and Negative Binomial family error distributions, and the model with the lowest AIC value was selected for each response variable.

In order to compare earliest queen observation dates between this and 11 other surveys across northeastern North America (1920–2018), latitude and year were regressed against earliest calendar observation day for each bumble bee species using Spearman correlation. If observation location was given only as a state or province, the latitude of the geographic center of that area was used. If observation dates were given as a range of years instead of a precise day, the most recent year was used.

RESULTS

In 108 timed field surveys, researchers observed a total of 1089 bumble bee queens of nine different species (Table 1). These species differed widely in abundance (ordered from most to least): *Bombus impatiens* Cresson (55.1 % of total queens), *B. griseocollis* De Geer (17.7 %), *B. bimaculatus* Cresson (5.1 %), *B. vagans* Smith (3.1 %), *B. fervidus* Fabricius (1.7 %), *B. auricomus* Robertson (0.6 %), *B. citrinus* Smith (0.4 %), *B. perplexus* Cresson (0.2 %), and *B. sandersoni* ($<$0.1 %). Of those 451 queens were searching for nest sites and 555 were foraging on 47 species of flowering plants. The remainder were observed flying overhead and exhibiting neither nest seeking nor foraging behavior. On average 10.08 ± 9.62 SD queens were observed per hour (range: 1–46, n = 108). Out of the 1006 nest seeking and foraging queens, 241 were observed carrying pollen, indicating they had already founded a nest. The raw data from timed bumble bee queen surveys, as well as additional information on individual nest seeking queens, is available through Dryad Digital Repository.

TABLE 1.—Summary of bumble bee observations in timed field surveys**.** *Bombus* species are listed in order of most to least abundant. Queen abundance (Total Queens) includes the total number of nest seeking, foraging, and flying queens of each species (sum of 108 one-hour surveys). The number of nest seeking queens and foraging queens of each species is also given, as well as the number of plant species used by foraging queens. GDD stands for cumulative growing degree day. The earliest queen observation, the earliest observation of queens with pollen loads, and the earliest worker observations are given for each species

Species	Total queens	Nest seekers	Foragers	Plant spp. visited	Date earliest queen	GDD earliest queen	Date earliest queen with pollen	GDD earliest queen with pollen	Date earliest worker	GDD earliest worker
B. impatiens	602	331	260	37	11-Apr.	69	5 May	208	24 May	426
B. griseocollis	193	24	168	23	1-May	148	9 May	279	24 May	429
B. bimaculatus	55	19	36	11	13-Apr.	97	18 May	329	24 May	426
B. vagans	34	3	29	14	1-May	143	5 May	208	29 May	752
B. fervidus	18	3	15	6	13-Apr.	98	18 May	330	7 June	763
B. auricomus	7	2	5	4	9-May	301	9 May	302	-	-
B. citrinus	4	4	0	0	24-May	607	-	-	-	-
B. perplexus	2	2	0	0	9-May	275	-	-	7 June	760
B. sandersoni	1	0	1	1	14-May	276	14 May	276	-	-
B. pensylvanicus	0	0	0	0	-	-	-	-	8 June	1046

HABITAT USE BY NEST SEEKING QUEENS AND INFLUENCE OF LANDSCAPE

In timed surveys significantly more nest seeking queens per minute were found along field-forest edges and in maintained areas (including flower beds, gardens, and mowed lawn) than in strictly wooded, field, or wetland habitats ($H = 14.91$, $df = 4$, $P < 0.01$; Fig. 1). This pattern was largely driven by the dominant species, *B. impatiens* ($H = 13.26$, $df = 4$, $P = 0.01$). No significant differences in habitat use by nest seeking queens of other species were detected, likely due to low sample sizes. However, queens of *B. auricomus* and *B. fervidus* were only found searching for nest sites in open areas (meadows, roadsides, and maintained flower beds/lawns). The parasitic species, *Bombus citrinus,* on the other hand was only observed seeking host nests in wooded areas. Several of the less common queen species in this dataset (*B. vagans*, *B. perplexus*, *B. citrinus*, and *B. auricomus*) were observed nest seeking in natural habitats but not in heavily maintained areas (lawns, gardens, and flower beds) (Table 2).

Queen abundance and species richness in timed surveys increased with the amount of forest in the surrounding 1 km landscape (abundance: Spearman $r_s = 0.31$, $n = 108$, $P < 0.01$, Fig. 2; diversity: $r_s = 0.33$, $n = 108$, $P < 0.01$). Queen species richness declined with the proportion of annual row crop agriculture ($r_s = -0.22$, $n = 108$, $P = 0.02$). The number of nest seekers was significantly lower in landscapes with greater proportions of urban developed areas ($r_s = -0.26$, $n = 108$, $P = 0.02$). Queen abundance, species richness, and activity (foraging versus nest seeking) were not influenced by the amount of herbaceous and pasture lands, shrubland, open water, or wetlands in a 1 km landscape.

A principal components analysis of predictor variables (standardized landscape components, GDD, and flowering species richness) generated three main components. After varimax rotation Principal Component One loaded heavily on herbaceous/hay habitat (loading = 0.52) and negatively on developed land (–0.74). Principal Component Two loaded heavily on forest cover (0.71) and negatively on crops (–0.67). Principal Component Three reflected GDD (0.74) and flowering species richness (0.58). Total queen abundance per timed survey increased significantly with Principal Components One (– developed, +

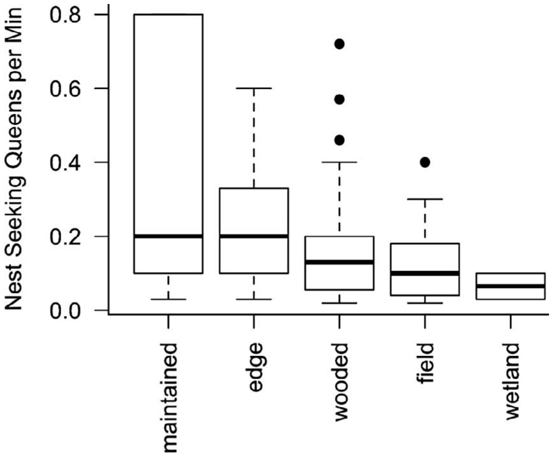

FIG. 1.—Habitat associations of nest seeking queens. Queen abundance is given as the number of nest seeking queens observed per minute by habitat type in timed surveys (n = 78 sites at which queens were observed nest seeking). The dark line represents the median queens per minute, with boxes as the upper and lower 25% quartiles

herb/hay) and Two (+ forest, – crop), and decreased with Principal Component Three (+GDD, +flowering species richness) in a generalized linear model with negative binomial family error (Table 3). Nest seeking and foraging queen abundance increased significantly with Principal Component One (– developed, + herb/hay). Meanwhile, queen species richness was positively related to Principal Components One (– developed, + herb/hay) and Two (+ forest, – crop). This analysis supports the importance of forest for overall queen abundance and diversity, and the negative effect of crop and developed land.

Individual nest seeking queens typically investigated several different microhabitats during our observations. They were most often found searching for nest sites near holes or crevices in leaf litter (70.8 % of queens were observed near this feature), beneath woody debris or at the base of a tree (46.7 %), in herbaceous plant debris (31.9 %), or near grass clumps (7.9 %). Some were also found investigating holes in mounds of bare soil, mulch

TABLE 2.—Habitat associations of nest seeking bumble bee queens during timed field surveys. Included in this table are the 438 nest seeking queens observed during timed researcher surveys. Total nest seeking queens are given separately by species: B. imp (*Bombus impatiens*), B. gri (*B. griseocollis*), B. bim (*B. bimaculatus*), B. aur (*B. auricomus*), B. cit (*B. citrinus*), B. fer (*B. fervidus*), B. per (*B. perplexus*), B. vag (*B. vagans*), and B. sp (*Bombus* sp. undetermined)

Habitat	Total time searched (min)	Total nest seeking queens	*B.imp*	*B.gri*	*B.bim*	*B.cit*	*B.fer*	*B.vag*	*B.per*	*B.aur*	*B.*sp
Wooded	1810	245	186	13	15	4	-	1	1	-	25
Field	955	90	56	7	-	-	2	-	1	1	23
Edge	460	77	60	3	4	-	-	2	-	-	8
Maintained	125	24	22	-	1	-	1	-	-	-	-
Wetland	40	2	2	-	-	-	-	-	-	-	-
Total	3390	438	326	23	20	4	3	3	2	1	56

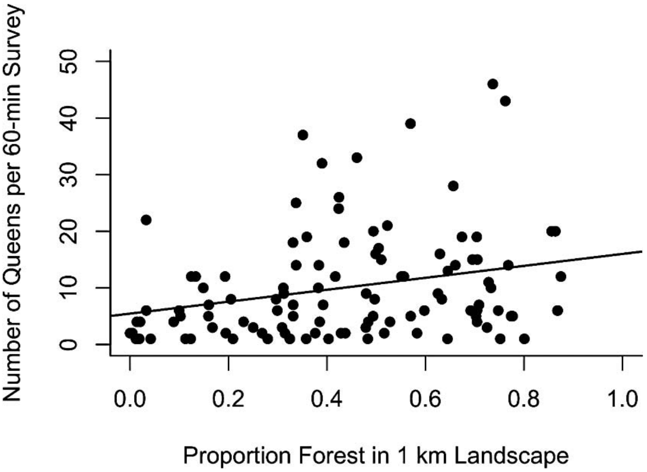

FIG. 2.—Influence of the proportion of forest in the landscape on queen abundance in timed field surveys. The proportion of forest was calculated in a 1km buffer area surrounding each site, for n = 108 queen survey sites. Queen abundance includes all queens observed during timed field surveys. The correlation between proportion of forest and queen abundance is shown as a black line ($r = 0.27$, $t = 2.84$, $df = 106$, $P = 0.01$)

piles, or in flower beds mulched with wood chips. The majority (64.4 %) of nest seeking queens were investigating potential nest sites with no flowers nearby. The associations between microhabitat features and nest seeking queens was similar among the three most abundant species in this survey – *B. impatiens*, *B. griseocollis*, and *B. bimaculatus* (Fig. 3).

PHENOLOGY: TIMING OF SEASONAL AND DIURNAL QUEEN ACTIVITY

In 2018 the earliest nest seeking queen was observed on 11 April (GDD = 69), and the latest was observed on 29 June (GDD = 1179). Queen activity peaked between GDD 221–466 (Fig. 4), a period corresponding to mid-May in Ohio. By growing degree day, the earliest bumble bee species to be active in Ohio in spring 2018 was *B. impatiens*, followed closely by *B. bimaculatus*, *B. griseocollis*, *B. fervidus*, and *B. vagans* (Table 1). However, because many more queens of *B. impatiens* were observed compared to other species, its status as the earliest emerging species may be overstated. In mid-May *B. perplexus*, *B. auricomus*, and *B. sandersoni*

TABLE 3.—Influence of Principal Components on bumble bee queen abundance and species richness in generalized linear models. Model estimates are shown for principal components (PC) 1–3, along with the predictor variables that loaded heavily on each principle component. Significant model coefficients are in bold text. * P < 0.01, **P < 0.001

Model parameter	PC heavily loaded on	Total queen abundance	Nest seeking queens	Foraging queens	Queen species richness
Intercept	-	**2.22****	**1.53****	**1.93****	**0.66****
PC 1	− developed, + herbhay	**0.23****	**0.29****	**0.23***	**0.09***
PC 2	+ forest, − crop	**0.19****	0.00	0.22	**0.13****
PC 3	+ GDD, + flower richness	**−0.23****	−0.12	−0.21	0.02

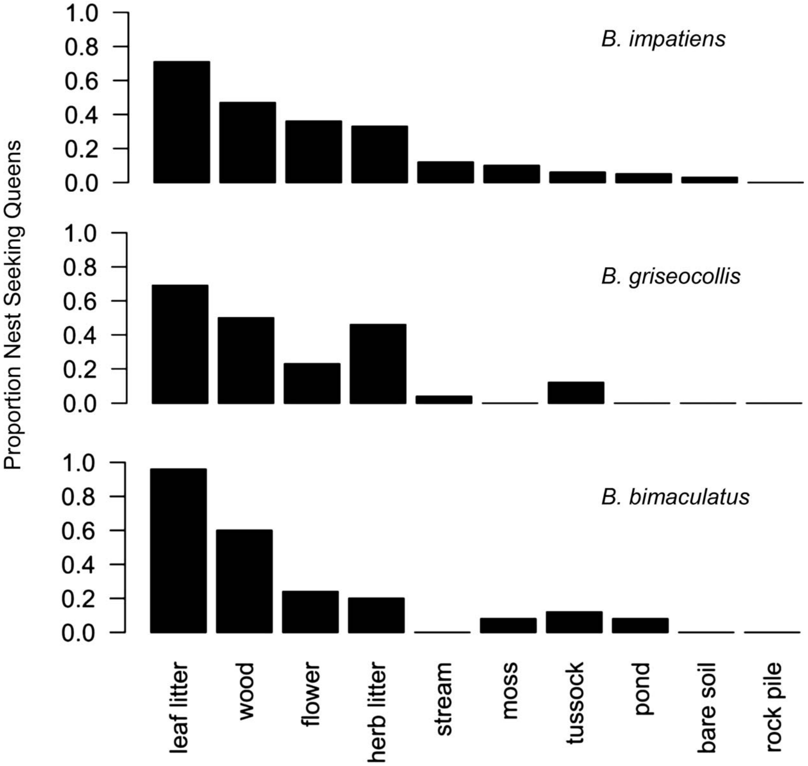

FIG. 3.—Microhabitat associations of nest seeking queens. The proportions of queens nest seeking near each microhabitat feature are shown for the three most abundant species: *B. impatiens* (n = 435 queens), *B. griseocollis* (n = 26), and *B. bimaculatus* (n = 25). Microhabitat features include leaf litter, herb litter (herbaceous plant litter), wood (fallen logs and branches, tree bases), grass clump / tussocks, bare soil mounds, moss (carpeting moss clumps), rock pile, pond (pond/lake), stream (stream/river), flower (flowering herbs, shrubs, or trees). Totals sum to >1 within each panel because each queen typically investigated more than one feature type

queens were observed. The last to emerge was the social nest parasite *B. citrinus* (24 May, about 1 mo after its primary host taxa – *B. impatiens, B. bimaculatus,* and *B. vagans*). *Bombus pensylvanicus* queens were not observed, although workers were found on the 8th of June.

Queen abundance in timed surveys showed a strong relationship with growing degree day (Fig. 4). The proportion of queens per timed survey that were observed nest seeking decreased with GDD (Spearman correlation $r_s = -0.24$, $n = 108$, $P = 0.01$), whereas the proportion of queens carrying pollen loads increased ($r_s = 0.35$, $n = 108$, $P < 0.01$). There was no significant difference in the number of nest searching or foraging queens based on time of day when the survey was conducted (nest seekers: Kruskal-Wallis $H = 5.95$, $df = 4$, $P = 0.20$; foragers: $H = 5.57$, $df = 4$, $P = 0.23$).

The first workers were observed on 24 May 2018. By the first week of June, 255 workers of seven species had been observed during timed surveys (Table 1), from earliest to latest: *B. impatiens* (24 May), *B. griseocollis* (24 May), *B. bimaculatus* (24 May), *B. vagans* (29 May), *B. fervidus* (7 June), *B. perplexus* (7 June), and *B. pensylvanicus* (8 June).

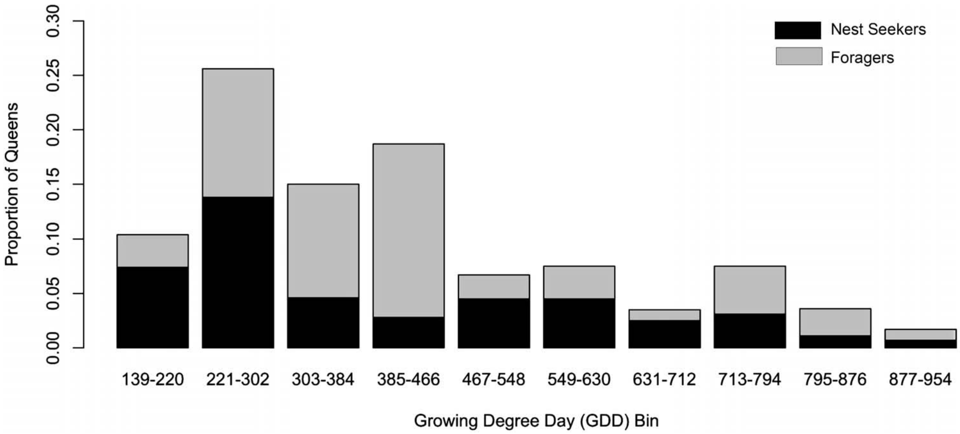

FIG. 4.—Phenology of nest searching and foraging queens during timed field surveys. Phenology is categorized by growing degree day (GDD) into 10 equal-interval bins. The black portion of each bar indicates the proportion of nest seekers and gray bars the proportion of foragers out of the total nest seeking and foraging queens found in all surveys. Growing degree day was calculated for each survey based on location and date

By comparing earliest emergence dates in this and 11 other surveys (Table 4), a continuum of bumble bee species queen phenologies has emerged (Table 5). In northeastern North America, the earliest species to emerge, in late March or early April, are *B. bimaculatus*, *B. affinis*, *B. terricola*, *B. impatiens*, and *B. ternarius*. They are followed in mid or late April by *B. griseocollis*, *B. fervidus*, *B. auricomus*, *B. vagans*, and *B. perplexus* (Table 5). The latest to emerge, beginning in May, are *B. pensylvanicus* and *B. sandersoni* and the more northerly-distributed *B. rufocinctus* and *B. borealis*. The social parasites, *Bombus ashtoni* (mid-April–mid-May) and *B. citrinus* (mid-May–June), appear about 1 mo after their hosts.

In a comparison of these 12 datasets (Table 4), there was a 1 to 3 wk range in the earliest observation date by species, depending more on the latitude of the study location than on the year. Several widespread and well-studied bumble bee species emerged significantly earlier at lower latitudes than higher ones (*B. bimaculatus* $r_s = 0.75$, $n = 9$, $P = 0.01$; *B. impatiens* $r_s = 0.63$, $n = 11$, $P = 0.04$; *B. perplexus* $r_s = 0.65$, $n = 9$, $P = 0.06$; Fig. 5). However, several of the less common species, that occur regularly in Ohio and elsewhere in northeastern North America, showed no relationship between spring queen emergence date and latitude (*B. auricomus*, *B. fervidus*, and *B. vagans*; Fig. 5). Although sample size was low ($n = 12$ datasets), there was no detectable general trend of earlier emergence by species over time between 1920 and 2018 (Fig. A1).

FLOWER USE BY FORAGING QUEENS

There was no significant effect of flowering plant species richness per site on foraging queen abundance ($r_s = 0.08$, $n = 108$, $P = 0.38$) or species richness ($r_s = 0.18$, $n = 108$, $P = 0.06$).

In timed surveys queen pollen and nectar sources included 47 different flowering plant species. The plant species that received at least five queen visits (out of 476 foraging queens identified to species in timed surveys) are listed in Table 6. The flowering species that were

TABLE 4. —Bumble bee spring queen emergence dates for present and historic field surveys. Datasets 1–12 and approximate GPS location were (1) present study, (2) iNaturalist 2018: 40.30437 / –82.69629, (3) Prusnek 1999: 41.2501 / –81.6236, (4) Macfarlane 1974a: 43.5329 / –80.2262, (5) Macfarlane 1974b: 43.5329 / –80.2262, (6) Macior 1968: 42.6781 / –88.2762, (7) Medler and Carney 1963: 44.437257 / –90.13216, (8) Medler 1962: 44.437257 / –90.13216, (9) Fye 1953: 44.437257 / –90.13216, (10) Plath 1934: 42.307223, –71.120776, (11) Frison 1923: 40.102, –88.2272, (12) Howard 1920 (in Fye 1953): 38.9072 / –77.0369. Note that in historic literature *B. griseocollis* was also known as *B. separatus*, *B. pensylvanicus* as *B. americanorum*, and *B. citrinus* as a variety of *B. laboriosus*. From the iNaturalist Ohio Bee Atlas citizen science dataset only verified observations from March – June were considered

Dataset location year(s)	1 OH, USA 2018	2 OH, USA 2012–2018	3 OH, USA 1998	4 ONT, CAN 1973	5 ONT, CAN 1972	6 WI, USA 1965	7 WI, USA n/a	8 WI, USA 1955–1961	9 WI, USA 1910–1953	10 MA, USA n/a	11 IL, USA 1915–1920	12 D.C., USA n/a
B. affinis	-	-	8-Apr	20-Apr	6-May	27-Apr	21-Apr	30-Apr	26-Apr	7-Apr	-	30-Apr
B. ashtoni	-	-	1-Apr	10-May	13-May	14-May	30-Apr	-	5-May	6-May	-	-
B. auricomus	9-May	9-May	-	-	-	11-May	30-Apr	4-May	30-Apr	-	13-Apr	6-Apr
B. bimaculatus	13-Apr	25-Mar	-	18-Apr	4-May	6-May	21-Apr	21-Apr	25-Apr	7-Apr	21-Mar	31-Mar
B. borealis	-	-	-	2-Jun	2-Jun	-	25-May	27-May	25-May	29-May	-	-
B. centralis	-	-	-	-	-	-	-	-	-	-	6-Jun	-
B. citrinus	24-May	29-May	-	29-May	5-Jun	-	6-Jun	-	-	28-May	6-Jul	17-May
B. fervidus	13-Apr	4-May	-	21-May	6-May	12-May	22-Apr	4-May	26-Apr	6-May	29-May	28-Apr
B. griseocollis	1-May	28-Mar	-	22-May	20-May	12-May	12-Apr	4-May	12-Apr	13-May	20-Apr	7-May
B. impatiens	11-Apr	3-Apr	-	21-Apr	10-May	6-May	18-Apr	22-Apr	18-Apr	15-Apr	13-Apr	16-Apr
B. pensylvanicus	-	3-May	-	31-May	11-May	14-May	14-May	19-May	2-May	27-May	23-Apr	22-Apr
B. perplexus	9-May	15-Apr	-	21-Apr	11-May	-	20-Apr	27-May	28-May	12-Apr	19-Apr	-
B. rufocinctus	-	-	-	2-Jun	2-Jun	14-May	28-May	28-May	10-Jun	-	-	-
B. sandersoni	14-May	14-May	-	-	-	-	-	-	-	-	-	-
B. ternarius	-	-	-	23-Apr	23-Apr	-	24-Apr	11-May	24-Apr	5-Apr	8-May	-
B. terricola	-	-	-	15-Apr	30-Apr	-	22-Apr	22-Apr	22-Apr	6-Apr	13-May	-
B. vagans	1-May	26-Apr	-	21-Apr	6-May	14-May	4-May	4-May	9-May	19-Apr	1-May	28-Apr
B. variabilis	-	-	-	-	-	-	-	-	-	-	22-Apr	-

TABLE 5.—Spring queen emergence period of bumble bee species for historical and current field surveys in northeastern North America. Cell values indicate the number of studies that recorded that species' earliest observation during a given time period. Cells are also color-coded on a gray scale (from 1 – light to 6 – dark) by the number of studies that list earliest emergence in that time period. Studies are listed in reverse chronological order: (1) our study, (2) Ohio Bee Atlas 2012–2018, (3) Prusnek 1999; (4) Macfarlane 1974 (1973 dataset), (5) Macfarlane 1974 (1972 dataset), (6) Macior 1968, (7) Medler & Carney 1963, (8) Medler 1962, (9) Fye 1953, (10) Plath 1934, (11) Frison 1923, and (12) Howard 1920 (in Fye 1953). See Literature Cited for full citations

Species	21-31 March	1-10 April	11-20 April	21-30 April	1-10 May	11-20 May	21-31 May	1-10 June	1-10 July	Studies
B. bimaculatus	2	1	2	3	2					1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 12
B. terricola		1	1	4		1				4, 5, 7, 8, 9, 10, 11
B. affinis		2		6	1					3, 4, 5, 6, 7, 8, 9, 10, 12
B. impatiens		1	6	2	2					1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 12
B. ternarius		1		4	1	1				4, 5, 7, 8, 9, 10, 11
B. fervidus			1	3	4	1	2			1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 12
B. ashtoni			1	1	3	2				3, 4, 5, 6, 7, 9, 10
B. auricomus		1	1	2	3	1				1, 2, 6, 7, 8, 9, 11, 12
B. griseocollis	1		3		3	3	1			1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 12
B. vagans			1	3	6	1				1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 12
B. perplexus			4	1	1	1	2			1, 2, 4, 5, 7, 8, 9, 10, 11
B. variabilis				1						11
B. pensylvanicus				2	2	4	2			2, 4, 5, 6, 7, 8, 9, 10, 11, 12
B. sandersoni						1				1
B. rufocinctus						1	2	3		4, 5, 6, 7, 8, 9
B. borealis							4	2		4, 5, 7, 8, 9, 10
B. citrinus						1	4	2	1	1, 2, 4, 5, 7, 10, 11, 12
B. centralis								1		11

highly visited by queens were primarily woody plants that occurred along field-forest margins (* denotes species considered invasive in the study region): *Malus* spp., *Lonicera* spp.*, *Ligustrum vulgare**, *Elaeagnus umbellata**, *Aesculus glabra*, *Robinia* spp, and *Rubus* spp. Temporarily-profitable habitats like patches of lupine (*Lupinus perennis*) in sand barrens, *Rhododendron* spp. in maintained areas, or purple deadnettle (*Lamium purpureum*) in untreated agricultural fields were also high yielding. Key native spring wildflowers used by queens included *Mertensia virginica* and *Hydrophyllum* spp. Nonnative weedy flowers that attracted large numbers of queens were: *Taraxacum officinale*, *Trifolium pratense*, *Glechoma hederacea*, *Trifolium pratense*, *Securigera varia**, and *Vinca minor*. Queens seemed to prefer abundantly flowering plants in the families Rosaceae, Fabaceae, and Lamiaceae, regardless of whether native or introduced.

DISCUSSION

Researchers have advanced the study of bumble bee nesting biology using some innovative survey techniques to locate their cryptic nests, including trained dogs, intensive field surveys, and citizen science volunteers (Fussell and Corbet, 1992; Osborne *et al.*, 2008; Lye *et al.*, 2012; Waters *et al.*, 2011; O'Connor *et al.*, 2012). In our study observers took advantage of easily recognizable behavior in bumble bee queens – nest seeking – to survey queen abundance and distribution among habitats. Timed surveys also included foraging queens, which precede the

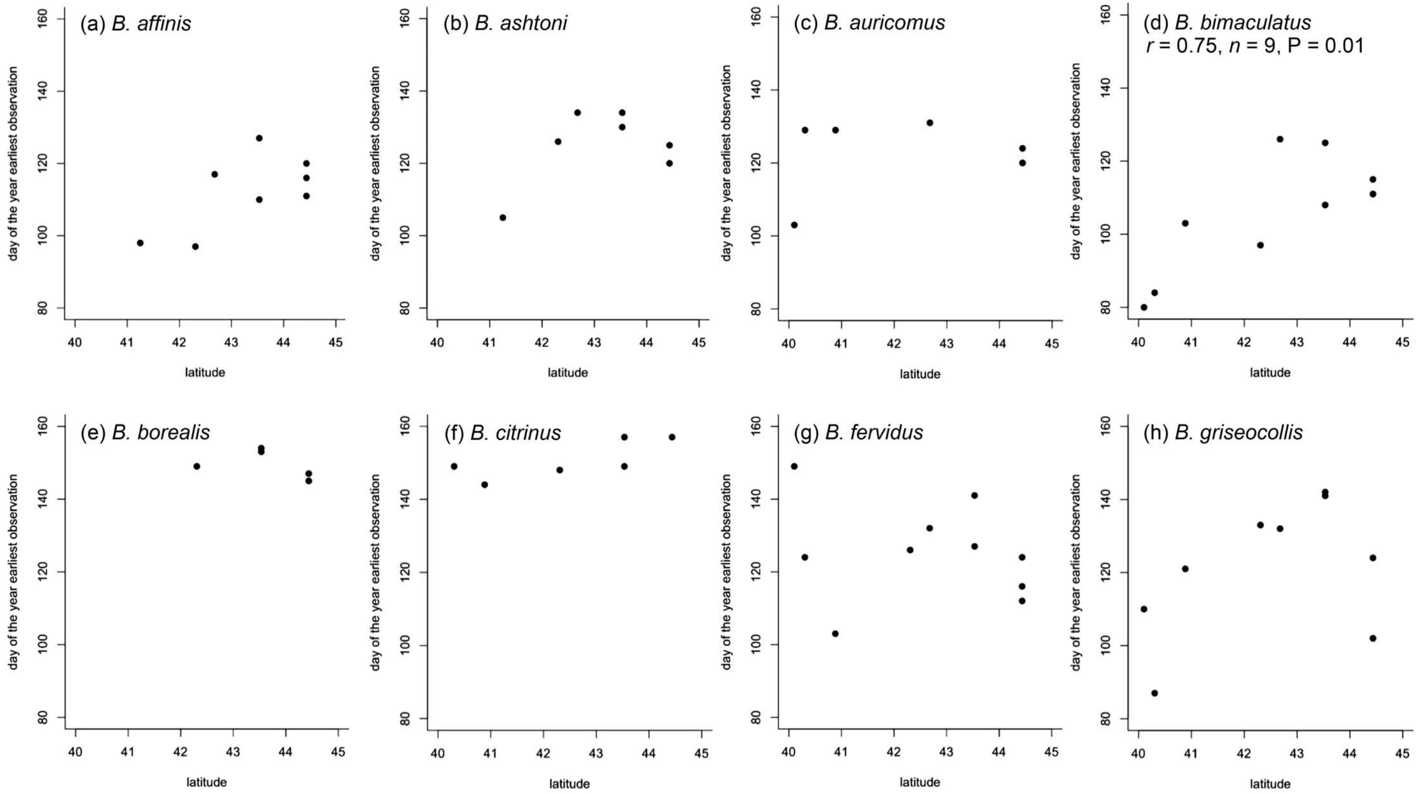

FIG. 5.—Earliest queen emergence date by latitude for each of 15 *Bombus* species in northeastern North America (1920 – 2018). Earliest collection date is given as day of the year. Species are in alphabetical order: (a) *B. affinis*, (b) *B. ashtoni*, (c) *B. auricomus*, (d) *B. bimaculatus*, (e) *B. borealis*, (f) *B. citrinus*, (g) *B. fervidus*, (h) *B. griseocollis*, (i) *B. impatiens*, (j) *B. pensylvanicus*, (k) *B. perplexus*, (l) *B. rufocinctus*, (m) *B. ternarius*, (n) *B. terricola*, (o) *B. vagans*. For species with a significant relationship between earliest observation day and latitude, the Spearman correlation values are given.

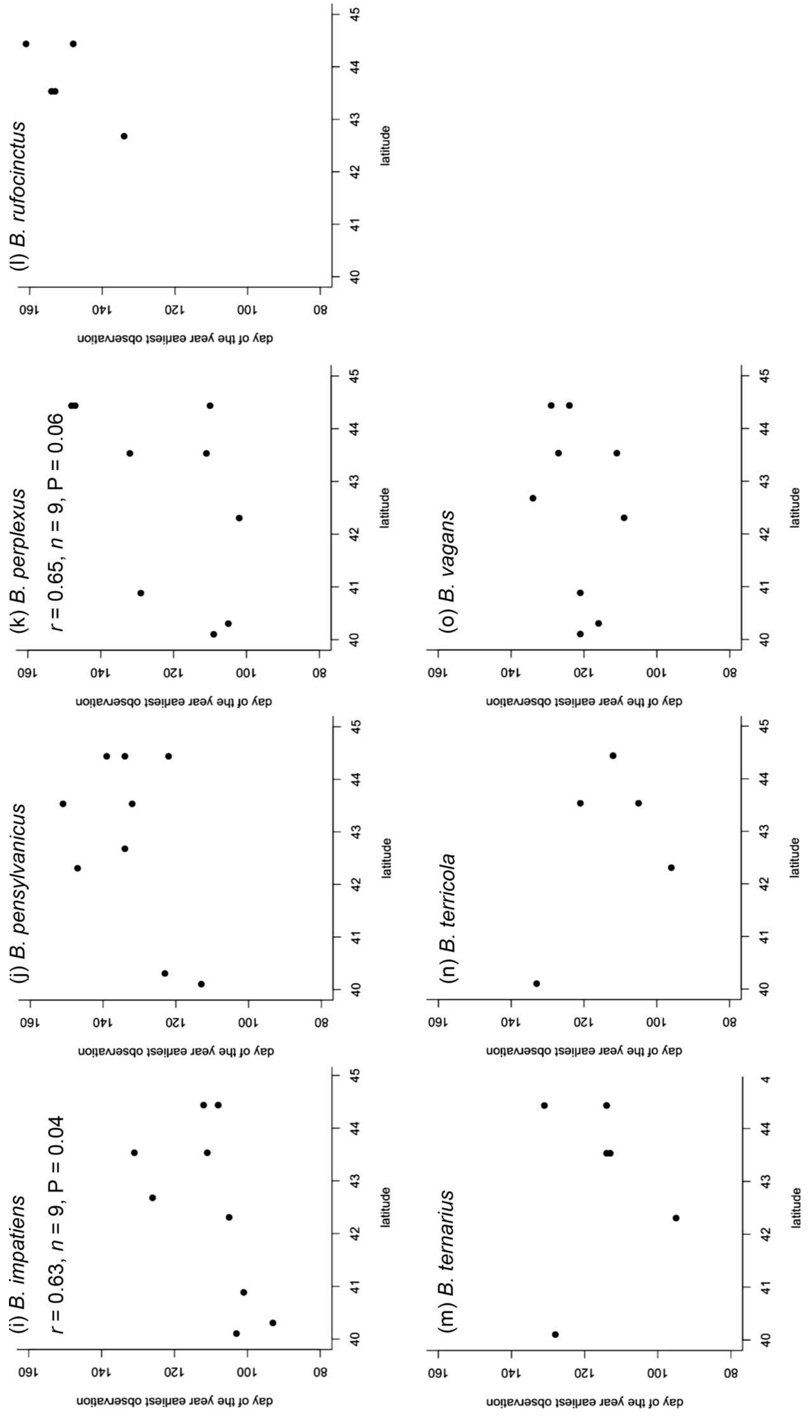

FIG. 5.—Continued

TABLE 6.—Host-plant associations of foraging bumble bee queens in timed field surveys. Plant species were excluded that received <5 visits. *Bombus* species are abbreviated: B.aur (*B. auricomus*), B.bim (*B.bimaculatus*), B.cit (*B. citrinus*), B.fer (*B. fervidus*), B.gri (*B. griseocollis*), B.imp (*B. impatiens*), B.per (*B. perplexus*), B.san (*B. sandersoni*), B.vag (*B. vagans*). Queens not identified to species were not included. Species origin is given as N (native) or I (introduced). Growth habit is denoted by H (herbaceous) or W (woody)

Species	Family	Origin	Growth habit	Total queen visits	B.aur	B.bim	B.cit	B.fer	B.gri	B.imp	B.per	B.san	B.vag
Lupinus perennis L.	Fabaceae	N	H	135	1	4	0	5	109	16	0	0	0
Malus sp. Mill.	Rosaceae	n/a	W	56	0	0	0	0	3	50	0	0	3
Taraxacum officinale F.H.Wigg	Asteraceae	I	H	44	0	1	0	0	0	41	0	1	1
Lonicera spp. L.	Caprifoliaceae	I	W	34	0	0	0	0	4	27	0	0	3
*Lamium purpureum*L.	Lamiaceae	I	H	39	0	8	0	2	3	20	0	0	6
*Glechoma hederacea*L.	Lamiaceae	I	H	27	0	5	0	0	3	17	0	0	2
Trifolium pratense L.	Fabaceae	I	H	26	1	2	0	4	13	4	0	0	2
Ligustrum vulgare L.	Oleaceae	I	W	24	0	0	0	0	1	20	0	0	3
Mertensia virginica (L.) Pers. Ex Link	Boraginaceae	N	H	18	0	5	0	0	2	9	0	0	2
Elaeagnus umbellata Thunb.	Elaeagnaceae	I	W	14	0	0	0	0	1	11	0	0	2
Vicia spp. L.	Fabaceae	n/a	H	13	0	0	0	2	7	3	0	0	1
Pedicularis canadensis L.	Scrophulariaceae	N	H	10	0	5	0	0	0	5	0	0	0
Hydrophyllum spp. L.	Hydrophyllaceae	N	H	9	0	3	0	0	1	5	0	0	0
Aesculus glabra Willd.	Hippocastanaceae	N	W	8	2	1	0	0	3	1	0	0	1
Robinia spp. L.	Fabaceae	N	W	6	0	1	0	0	2	3	0	0	0
Rhododendron spp. L.	Ericaceae	n/a	W	5	1	1	0	0	1	1	0	0	1

workers and males by several weeks in the spring and are readily distinguished by their large size. These surveys provided an opportunity to study queen nesting and foraging behavior and habitat use during a vulnerable and poorly understood stage in the colony life cycle. Through more than 100 h of searching, 1006 nest seeking and foraging queens of nine species were documented, one of which (*B. sandersoni*) is very rarely observed in Ohio and other nearby states. With the phenological data from this and other field surveys in the North American bumble bee literature, a timeline for spring emergence by species has been established. In the most common species, individual queens preferentially searched for nest sites along the forest-field interface (a partially wooded transitional habitat), and landscapes with more wooded cover were more likely to harbor high numbers of nest seekers. Spring queens relied on a mixture of flowering woody and herbaceous plants, both native and nonnative, that occurred primarily along the edges of forests but also in other seasonally flower-rich habitats like lupine sand barrens and untreated agricultural fields.

HABITAT USE AND INFLUENCE OF LANDSCAPE

Several criteria by which bumble bee queens select nest sites have been proposed – that the site should require little preparation by the queen, be situated in well-drained soil, and be sheltered from the elements (Frison, 1923; Alford, 1969). The greater abundance of nest seeking queens found in transitional zones between wooded and open habitats in our study, along with the large numbers of queens investigating areas with dense leaf litter, fallen logs and other features of woody habitats, supports these criteria. Queens' preference for these partially wooded habitats scaled up from the microhabitat- to the landscape level, as evidenced by increased queen abundance and species diversity in landscapes with higher proportions of forest.

In this study nest seeking *B. impatiens* queens demonstrated a strong association with wooded habitats, or boundaries between wooded and field habitats. Less abundant species, *B. bimaculatus*, *B. griseocollis*, and *B. citrinus*, appeared to share this habitat preference, although small sample sizes made it difficult to test rigorously. Frison (1923) noted similar habitat associations for *B. impatiens* and *B. bimaculatus*, saying that when attempting to lure them to use artificial nest boxes it was "folly to 'plant' the domiciles in the open fields or pastures." Nevertheless, individuals of the most abundant species in this survey opportunistically searched for nest sites in other habitats as well, such as mulched flower beds, fields, and rodent holes in mowed lawns, suggesting an adaptability to features of human-dominated habitats. Observations of the few *B. auricomus* and *B. fervidus* nest seeking in open grasslands and fields in this study corroborate other published accounts (Frison, 1923; Macfarlane, 1974).

This pattern, in which the majority of bumble bee species seek nest sites in at least partially wooded habitats, with fewer species nesting primarily in grasslands, seems to be consistent across the temperate Holarctic region (North America and Europe). Several European studies have also documented bumble bee queens' preference for the forest-field interface or wooded habitats (Svensson and Lundberg, 1977; Svensson *et al.*, 2000; Lye *et al.*, 2009). Rather than comparing habitats based on vegetation alone, Osborne *et al.* (2008) suggested more nests occur in linear (fence lines, hedgerows) versus nonlinear habitats (large patches of either woodland or grassland). Boundary zones and wooded habitats typically have more complex microtopography and vegetation structure than do large tracts of grasslands, as well as higher abundance and wider variety of potential nest sites (tree and shrub bases, stumps, brush piles, holes beneath fallen logs, partially eroded stream banks with exposed roots, and dense leaf litter). Woods also harbor small rodents, whose abandoned burrows are prime nesting places for bumble bees (Frison, 1917; Plath, 1934). Grasslands, on the other hand, have the advantage of higher light exposure to warm the nest and potentially a closer proximity to summer forage, which can be limited in forests.

Bumble bee queens likely rely on multiple sensory inputs to locate potential nest sites. In this study potential visual cues were assessed within 2 m of each nest seeking queen. The most common species, *B. impatiens, B. bimaculatus,* and *B. griseocollis*, were most often found investigating apparent holes in leaf litter or bare soil in herbaceous plant debris, beneath fallen logs, and at the bases of trees. However, there were not sufficient numbers of queens observed for most species to determine species-specific preferences. In addition to visual cues, queens may also detect olfactory or chemical cues that help them to locate one of their preferred nest sites - abandoned rodent burrows. Frison (1917, 1923), guided by Sladen (1912), reported high colonization of artificial domiciles that he had baited with grasses from field mouse nests. Future research on bumble bee queen nest site selection is needed to quantify the relative importance of visual and olfactory cues on nest seeking behavior.

In northeastern North America, bumble bee queens appear to select nest sites without regard to cues indicating where food will be most available later in the season, as approximately 60% of nest seeking queens in our study were observed searching in places with few or no flowers. Research elsewhere also suggests a queen's choice of nesting habitat is independent of her choice of foraging habitat (Suzuki *et al.*, 2009; O'Connor *et al.*, 2017). Nevertheless, there is likely value for queens that choose nest sites that are in sheltered locations but also within flight range of multiple habitat types to ensure the availability of summer forage. Landscapes in the eastern U.S. are often mosaics of forest patches interspersed with open field habitats. Based on our findings, to maximize conservation potential for bumble bees land managers should seek to maintain patches of high-quality wildflower foraging habitat in close proximity to at least partially wooded sheltered nesting habitat.

PHENOLOGY: TIMING OF SEASONAL QUEEN ACTIVITY

Based on this study and 11 other datasets of earliest queen observation date, the order of bumble bee species' seasonal appearance in northeastern North America has been fairly consistent (Howard, 1920, in Fye, 1953; Frison, 1923; Plath, 1934; Fye, 1953; Medler, 1962; Medler and Carney, 1963; Macior, 1968; Macfarlane, 1974; Prusnek, 1999; iNaturalist 2018; Table 4). Notably, several of the rare or endangered species in Ohio have emergence times on the tail ends of the emergence season for queens, either tending to appear earlier (*B. affinis, B. terricola*) or later (*B. pensylvanicus*) than the majority of species. To the best of our knowledge, no other North American surveys have reported spring queen emergence dates for the rare *B. sandersoni*, which we collected on 14 May in Lake County, OH.

First observation dates for queens in this study were somewhat earlier for many species (*B. bimaculatus, B. citrinus, B. fervidus, B. griseocollis,* and *B. impatiens*) than those of older published studies from eastern North America (Plath, 1934; Medler, 1962; Medler and Carney, 1963; Macior, 1968; Macfarlane, 1974). Early emergence is a predicted consequence of climate change, which has caused warmer spring temperatures in Ohio and the U.S.A. (Calinger *et al.*, 2013). However, there was no relationship between study year and emergence date for most species. Earlier emergence dates were more likely an artefact of the lower latitudes where we surveyed, although long-term change in bumble bee phenology due to climate change cannot be ruled out. The fact our earliest observation dates did not differ dramatically from those in more northern locations, such as Wisconsin and Ontario, may suggest local adaptation to climate. Alternatively, shifts to more northerly distributions of some species over time may be masking local earlier emergence dates. Notably, the citizen science platform iNaturalist (which relies on crowd-sourced identification of uploaded photos by local and national bee experts) had the earliest verified spring observations of several common species in recent years (*e.g. B. bimaculatus* and *B. griseocollis* queens posted in late March). In the future studies that include verified citizen science observations may be better able to detect broad temporal and geographic changes in spring bee phenology than those that rely on the traditional museum specimens and published observations alone.

Queen nest seeking activity peaked in May for our study. However, queens of the most common species, *B. impatiens*, were observed searching for nest sites into late June in Ohio. Likewise, Frison (1923) observed queens of *B. fervidus*, *B. griseocollis*, *B. pensylvanicus*, *B. perplexus*, and *B. vagans* nest seeking in mid–late June in nearby Illinois. Plath (1934) observed *B. impatiens* and *B. fervidus* queens nest seeking as late as July in the more northern state of Massachusetts. There are several possible explanations for the long-tailed temporal distribution in nesting activity. First, the extended nesting phenology of *B. impatiens* may simply reflect its greater abundance, so even slender tails of the distribution are more readily observed. Second, widespread and abundant species like *B. impatiens* may have high natural variation in spring queen emergence time. While late-emerging bumble bees are at a disadvantage in competing for limited high-quality nest sites, they also lessen their risk of starving or freezing to death in bouts of inclement spring weather. Third, delayed nest founding may be a means of avoiding nest invasion by social parasites in the subgenus *Psithyrus* (like *B. citrinus*), if they establish their nests after their parasite's typical period of host seeking. Fourth, queens exhibiting later season nest seeking behavior may have been infected with the widespread nematode parasite *Sphaerularia bombi* Dufour, which prevents ovary development (Medler, 1962; Rutrecht and Brown, 2008) and causes queens to continuously seek, but never establish, a nest (Lundberg and Svensson, 1975). Other studies in northeastern North America have reported high queen infection rates by *S. bombi* (up to 38%) that differ among *Bombus* species (Fye, 1953; Medler, 1962; McCorquodale *et al.*, 1998). Lastly, highly successful species like *B. impatiens* or early-emerging species like *B. bimaculatus* may, under ideal conditions, have two generations per summer (Frison, 1923). Facultative bivoltinism is known in solitary bees (*e.g. Megachile rotundata*; Krunic, 1972), but nest initiation by nondiapausing mated queens has only been conclusively documented in captive bumble bee colonies in temperate regions (Röseler, 1985; Beekman *et al.*, 1999; but *see* also Potapov *et al.*, 2018, for anecdotal evidence of bivoltinism in bumble bees). In our study it is unlikely nest seeking queens of *B. impatiens* in late June were nondiapausing mated queens because males of that species were not observed until 5 July (although males of *B. bimaculatus*, *B. griseocollis*, and *B. citrinus* were sighted on 13 June).

FLOWER USE BY FORAGING QUEENS

The boundary between wooded and open habitats offered the most plentiful forage for spring bumble bee queens, because of the prevalence of early-flowering invasive shrubs (*Lonicera*, *Ligustrum vulgare*, and *Elaeagnus umbellata*) and other woody plants (especially those in the Rosaceae: *Crataegus*, *Malus*, *Prunus*, *Rosa*, and *Rubus*). Rich woods offered large patches of spring ephemeral wildflowers including *Mertensia virginica* and *Hydrophyllum*. Gardens and other planted areas had concentrated pockets of highly-rewarding resources like *Rhododendron* and *Vaccinium*. In agricultural fields and roadsides, *Taraxacum officinale*, *Lamium purpureum*, *Trifolium pratense*, and *Vicia* spp. attracted large numbers of queens. Lastly, pockets of lupine (*Lupinus*) in oak savanna and sand barrens, which are a rare habitat type in Ohio, were especially high-yielding for queen bumble bees and attracted large numbers of *B. griseocollis* in particular. In surveys of flower use by spring bumble bee queens in the northern state of Wisconsin, Fye (1953) and Macior (1968) found many of the same plants to be staples of queen diets, including *Malus*, *Prunus*, *Rubus*, *Rosa*, *Lonicera*, *Taraxacum*, *Trifolium*, and *Vicia*.

Bumble bees, including queens, are generalist foragers that use a wide variety of plants, native and nonnative, of many families and floral morphologies. Therefore, the abundance and proximity of flowers to potential nesting habitat is likely more important than the particular species. From a management perspective, ensuring few gaps exist in seasonal flower availability is crucial. A continuous supply of floral resources is required to support the nest-founding stage of the bumble bee life cycle because each queen must forage for food as well as tend the nest, potentially limiting her mobility.

FUTURE RESEARCH

This study provides much-needed contemporary baseline data on the natural history and nesting behavior of North American bumble bee queens during this critical spring nest founding stage. However, much more work is needed to evaluate other aspects of their nesting biology, such as the prevalence of parasite infection in late season nest seeking queens, the relative importance of visual and olfactory cues in nest site selection, or the possibility of bivoltinism in temperate species. Long-term monitoring of spring *Bombus* queens that includes both traditional and citizen science approaches may reveal broad-scale responses to changes in climate or land use, or provide additional data on less common species to help refine interspecific differences in nest site preference.

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TABLE A1.—Bumble bee species known to occur in Ohio. Species are listed alphabetically. The most recent observation of each species (not including the present survey) and the source of that record is given. Note that some species lists for Ohio include *Bombus ternarius*, but there are no verifiable specimens or sightings of that species from the state

Species	Recorded in the present survey?	Most recent record from Ohio	Source of most recent record if not observed in the present survey
B. affinis Cresson 1863	no	2013	Toledo Zoo specimen, coll. Mitch Magditch
B. ashtoni Cresson 1864	no	1998	Prusnek 1999
B. auricomus Robertson 1903	yes	2018	-
B. bimaculatus Cresson 1863	yes	2018	-
B. borealis Kirby 1837	no	2018	Cleveland Museum of Natural History specimen, coll. Jessie Lanterman
B. citrinus Smith 1854	yes	2018	-
B. fervidus Fabricius 1798	yes	2018	-
B. flavidus (incl. *fernaldae*) Eversmann 1852	no	1936	in Williams *et al.* 2014
B. fraternus Smith 1854	no	1967	Ohio State University Triplehorn Insect Collection, OSUC 100833
B. griseocollis De Geer 1773	yes	2018	-
B. impatiens Cresson 1863	yes	2018	-
B. insularis Smith 1861	no	1933	Cleveland Museum of Natural History specimen
B. nevadensis auricomus Cresson 1874 †	no	1988	Ohio State University Triplehorn Insect Collection, OSUC 100757
B. pensylvanicus De Geer 1773	yes	2018	-
B. perplexus Cresson 1863	yes	2018	-
B. rufocinctus Cresson 1863	no	1919	in Williams *et al.* 2014
B. sandersoni Franklin 1913	yes	2018	Cleveland Museum of Natural History specimen, coll. Jessie Lanterman
B. terricola Kirby 1837	no	1981	Ohio State University Triplehorn Insect Collection, OSUC 100532; USDA-ARS Bee Biology & Systematics Lab, BOMBUS27762
B. vagans Smith 1854	yes	2018	-
B. variabilis Cresson 1872	no	1962	Ohio State University Triplehorn Insect Collection, OSUC 124128

† not included in species count due to likely synonymy with *B. auricomus*

TABLE A2.—Bumble bee queen field survey sites, spring 2018. This list includes timed 60 min researcher surveys only, without additional citizen science observations of nest seeking queens. Sites are listed in chronological order of sampling date

Site	Latitude (N)	Longitude (W)	Date	GDD	Flowering species richness	Total bombus queens	Queen species richness
Walter Best Wildlife Preserve	41.55459400	81.20030800	1-May	139	10	1	1
Frohring Meadows	41.41235556	81.36186944	1-May	142	10	4	2
Old Field South Chagrin	41.44574167	81.40938056	1-May	143	7	5	2
Foxfield	40.68200700	81.63214100	1-May	162	0	10	1
Big Creek Park	41.60851389	81.20902778	2-May	157	2	5	1
Skok Meadows	41.65725833	81.19035000	2-May	153	14	6	1
Highbanks MetroPark	40.15072300	83.03264000	2-May	271	12	6	2
Burton Wetlands	41.44282778	81.18068889	5-May	214	11	16	2
Hiram College Field Station	41.29954200	81.11062600	5-May	208	19	25	3
Eagle Creek State Nature Preserve	41.28956900	81.05710800	5-May	208	19	33	4
Hellbender Bluff	40.69371944	80.64580833	6-May	238	18	12	2
Sheepskin Hollow State Nature Preserve	40.74944400	80.52551700	6-May	238	7	20	4
Hinckley Buzzard Roost	41.21546400	81.70842500	8-May	241	15	11	1
Brecksville Nature Center	41.31861200	81.61697300	8-May	242	20	12	2
Hinckley Redwing Cabin	41.21982000	81.72292000	8-May	241	16	13	2
University of Akron Field Station	41.18438300	81.65144200	9-May	258	13	5	1
Mogadore Reservoir Congress Lake Rd	41.06020900	81.32205900	9-May	256	16	7	1
Swine Creek	41.44208889	81.02785278	9-May	260	14	14	2
Wilson Cemetery	40.12079100	82.42827200	9-May	302	12	14	4
Wolfrun Regional Park	40.39845210	82.43246010	9-May	279	17	18	2
Brown Family Environmental Center	40.37439000	82.40645000	9-May	281	18	18	3
Thomas Swift MetroPark	41.23933600	80.91774400	9-May	258	19	21	2
Grand River Wildlife Area	41.38919444	80.91515556	9-May	259	8	24	1
Furnace Run at Brush Creek Rd	41.25014100	81.62355800	9-May	258	15	28	4
Hogback Ridge	41.74396944	81.03079444	14-May	276	12	19	2
Observatory Park	41.58586389	81.08312500	14-May	293	14	43	4

TABLE A2.—Continued

Site	Latitude (N)	Longitude (W)	Date	GDD	Flowering species richness	Total bombus queens	Queen species richness
Springfield Bog MetroPark	41.01042500	81.39771700	15-May	320	15	5	1
Kokosing State Wildlife Area	40.51347300	82.58913500	16-May	365	24	9	3
Orchard Hills Park	41.56203056	81.36681667	16-May	323	12	37	3
Killbuck	40.80235000	81.76260500	17-May	384	4	6	1
Oak Hill Entrance	40.83617800	81.96042400	17-May	379	4	7	2
Friends of Conneaut Creek	41.89799100	80.55799100	18-May	302	9	14	2
Dorset Wildlife Area	41.69124500	80.64290600	18-May	330	7	19	2
Penn Line Fen CMNH	41.70033300	80.52156800	18-May	329	16	39	4
Lake Erie Bluffs Metroparks	41.78842222	81.17471389	21-May	358	20	10	2
Pleasant Valley	41.58903056	81.40321944	21-May	385	23	17	4
Rogers Rd Field	41.56947222	81.41544167	21-May	388	22	19	3
University of Akron Field Station	41.18438300	81.65144200	22-May	436	20	7	1
Shawnee Superior Fibers	39.61007000	82.21098000	23-May	632	17	1	1
Driscoll Farm	41.11538056	82.29348611	23-May	440	0	8	1
Maumee Bay State Park	41.67550833	83.37435000	24-May	415	2	1	1
Toledo Solar Panel	41.62741000	83.57286800	24-May	423	2	2	1
Pearson Park	41.64305278	83.44251667	24-May	420	4	3	2
Highbanks MetroPark	40.15072300	83.03264000	24-May	607	19	4	2
Scioto Audubon MetroPark	39.94535278	83.00676389	24-May	618	21	4	1
Rock Run reclaimed mine	39.58486389	82.22050000	24-May	658	18	6	3
Spencer Hollow reclaimed mine	39.52135000	82.17408000	24-May	679	19	6	3
Sharon Woods MetroPark	40.11708889	82.96375833	24-May	611	13	8	3
Innis Woods MetroPark	40.10154700	82.89956600	24-May	612	26	8	2
Lou Campbell	41.59167984	83.77754200	24-May	429	10	12	4
Norma Johnson Center	40.51199167	81.53874722	24-May	506	16	12	2
Kitty Todd- South Piel	41.61830382	83.78563300	24-May	424	11	15	3
Irwin Prairie	41.65643600	83.78191400	24-May	449	13	16	2
Oak Openings Monclova	39.80399300	84.06096400	24-May	621	5	22	2
Dawes Arboretum	39.98004000	82.40808000	24-May	617	18	26	4

TABLE A2.—Continued

Site	Latitude (N)	Longitude (W)	Date	GDD	Flowering species richness	Total bombus queens	Queen species richness
Meilke Road - Blowout	41.63804700	83.76545300	24-May	421	12	32	2
Kitty Todd - Sweet Fern Savanna	41.61163936	83.80451100	24-May	426	9	46	4
SR-64	41.52668889	83.87331667	25-May	460	0	1	1
Brandywine Falls	41.27627500	81.53948889	25-May	471	17	1	1
Prairie Oaks MetroPark	39.98928889	83.25982778	25-May	639	16	1	1
Eber Road Prairie	41.56719167	83.78464167	25-May	454	0	3	1
Scioto Grove MetroPark	39.85537200	83.02304600	25-May	641	11	3	1
Battelle Darby MetroPark	39.89121111	83.20126667	25-May	640	16	4	2
Walnut Woods	39.83528000	82.86269000	25-May	641	21	5	2
Blossom/Porthouse	41.18399300	81.55225200	25-May	473	25	6	1
Oak Openings Evergreen	41.55723600	83.85397600	25-May	456	1	20	3
North Road Preserve	41.22584400	80.75860000	26-May	497	0	12	2
Cascade MetroPark	41.34590000	84.00239000	27-May	522	22	1	1
Denison Bio Reserve	40.08371000	82.51744000	27-May	688	13	10	2
Smuckers Cafe Pollinator Plot	41.00595500	81.97617000	29-May	588	26	1	1
Rupp Prairie	40.89422500	82.31842300	29-May	604	23	1	1
Infirmary Mound	40.02506200	82.51275100	29-May	745	12	1	1
Tallmadge Meadows	41.13057200	81.43557600	29-May	587	7	2	1
Johnson Woods SNP	40.88925300	81.74658700	29-May	605	14	2	1
Huston-Brumbaugh Nature Center	40.82230000	81.09396900	29-May	617	2	2	1
Three Creeks MetroPark	39.89391700	82.90946400	29-May	748	18	2	1
Clear Creek MetroPark	39.59676389	82.55215833	29-May	781	18	3	1
Quail Hollow	40.97898400	81.31004700	29-May	590	3	5	1
Scenic Vista Park	40.73636667	80.81840556	29-May	622	2	5	2
Highlandtown Wildlife Area	40.65263000	80.77216000	29-May	621	5	6	3
Slate Run MetroPark	39.76173600	82.85087700	29-May	752	12	7	4
Spangler Wooster Memorial Park	40.81212500	82.02295100	29-May	618	12	8	1
Malek Park	41.94321667	80.59560278	29-May	498	35	9	3
Hellhollow Wilderness Area	41.68829722	81.11610556	29-May	537	8	14	1

TABLE A2.—Continued

Site	Latitude (N)	Longitude (W)	Date	GDD	Flowering species richness	Total bombus queens	Queen species richness
North Kingsville Sand Barrens	41.93105300	80.64820300	29-May	497	21	20	3
Mugrage Park	41.13828100	81.78343600	30-May	617	21	2	1
Granville GIS Land Lab	40.52173000	82.32428900	30-May	651	21	2	1
Spring Valley	40.05850000	82.53020000	30-May	771	17	4	2
Buck Creek	39.97000000	83.72920000	4-Jun	889	17	4	3
Waterman Farm	40.01083611	83.04063611	6-Jun	911	13	1	1
Blendon Woods MetroPark	40.06901944	82.87453611	6-Jun	909	17	2	2
Olentangy Park	40.11082000	83.03209500	6-Jun	905	21	6	2
Mill Creek Preserve	40.98850278	80.70032778	7-Jun	757	20	1	0
Woodbury WMA site 3	40.25680000	81.96020000	7-Jun	883	21	1	0
Woodbury WMA site 4	40.23370000	81.91560000	7-Jun	894	21	1	1
Mosquito Creek Parking Lot #15	41.44710833	80.78189167	7-Jun	750	17	3	2
Austintown Township Park	41.07384400	80.77872700	7-Jun	759	24	4	3
Fellows Riverside Gardens	41.09987900	80.67490700	7-Jun	760	27	4	2
OARDC Pomerene Forest	40.30880000	81.84020000	7-Jun	855	19	6	1
Mustill Store	41.09061300	81.51760700	7-Jun	763	4	12	2
Woodbury WMA site 2	40.27090000	82.00860000	7-Jun	876	24	12	3
I-77 Roadside Camden Ave	40.79222200	81.38944400	8-Jun	801	1	2	1
Egypt Valley	40.07053100	81.16986500	8-Jun	954	5	2	1
Holden Arboretum	41.59955000	81.30634722	8-Jun	742	43	5	2
Barkcamp State Park	40.03361400	81.01810500	8-Jun	863	7	9	1
Buffalo Hill Cemetery	40.38750000	80.88584400	8-Jun	836	11	10	2
Liberty Park	41.33350600	81.41073200	8-Jun	785	20	15	3
Spring Hill Park Aurora	41.30411700	81.30422200	8-Jun	789	12	15	3

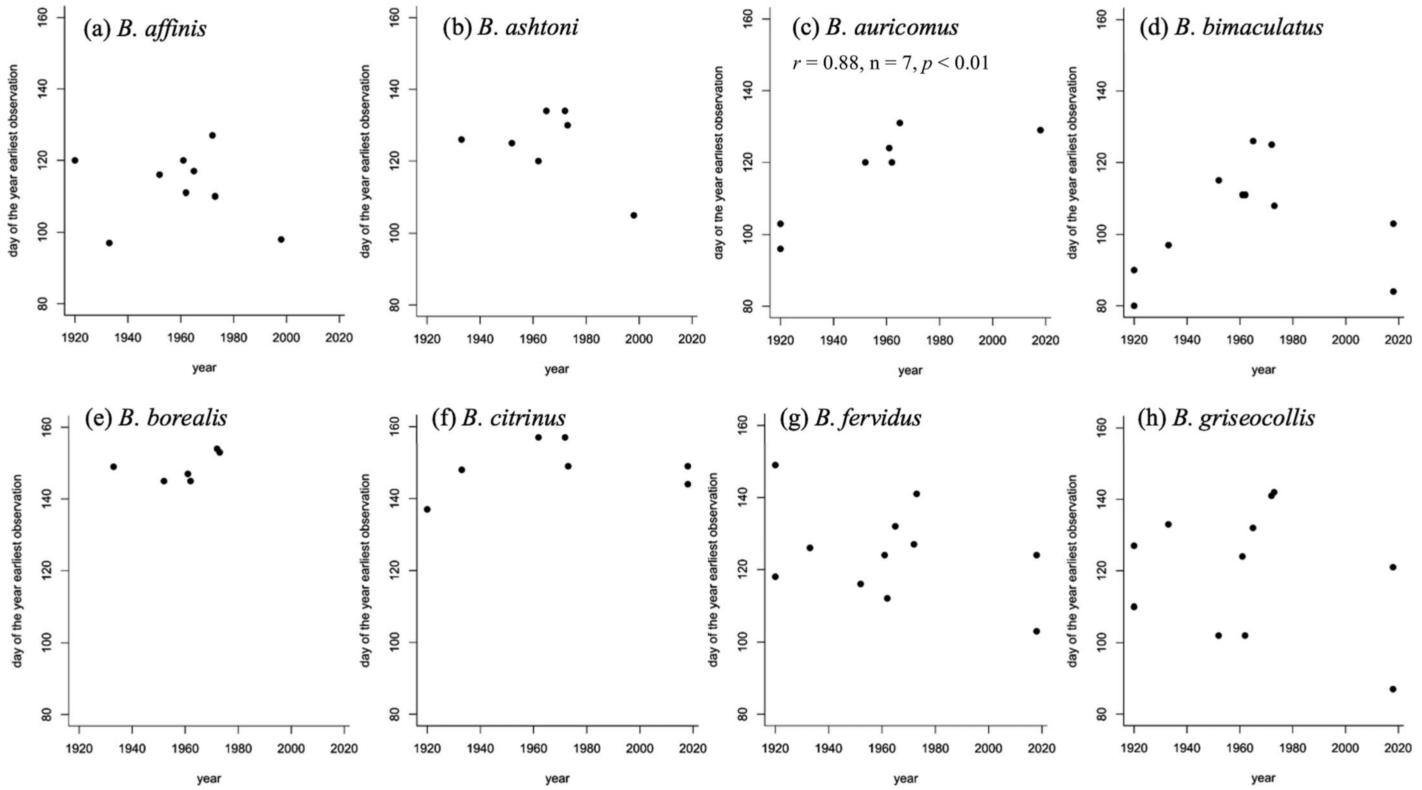

FIG. A1.—Temporal variation in earliest queen emergence date by year for each of 15 *Bombus* species in northeastern North America (1920 – 2018). Earliest collection date is given as day of the year. Species are in alphabetical order: (a) *B. affinis* (n = 9), (b) *B. ashtoni* (n = 7), (c) *B. auricomus* (n = 7), (d) *B. bimaculatus* (n = 11), (e) *B. borealis* (n = 6), (f) *B. citrinus* (n = 7), (g) *B. fervidus* (n = 11), (h) *B. griseocollis* (n = 11), (i) *B. impatiens* (n = 11), (j) *B. pensylvanicus* (n = 10), (k) *B. perplexus* (n = 9), (l) *B. rufocinctus* (n = 6), (m) *B. ternarius* (n = 7), (n) *B. terricola* (n = 7), (o) *B. vagans* (n = 11). For species with a significant relationship between earliest observation day and latitude, the Spearman correlation values are given.

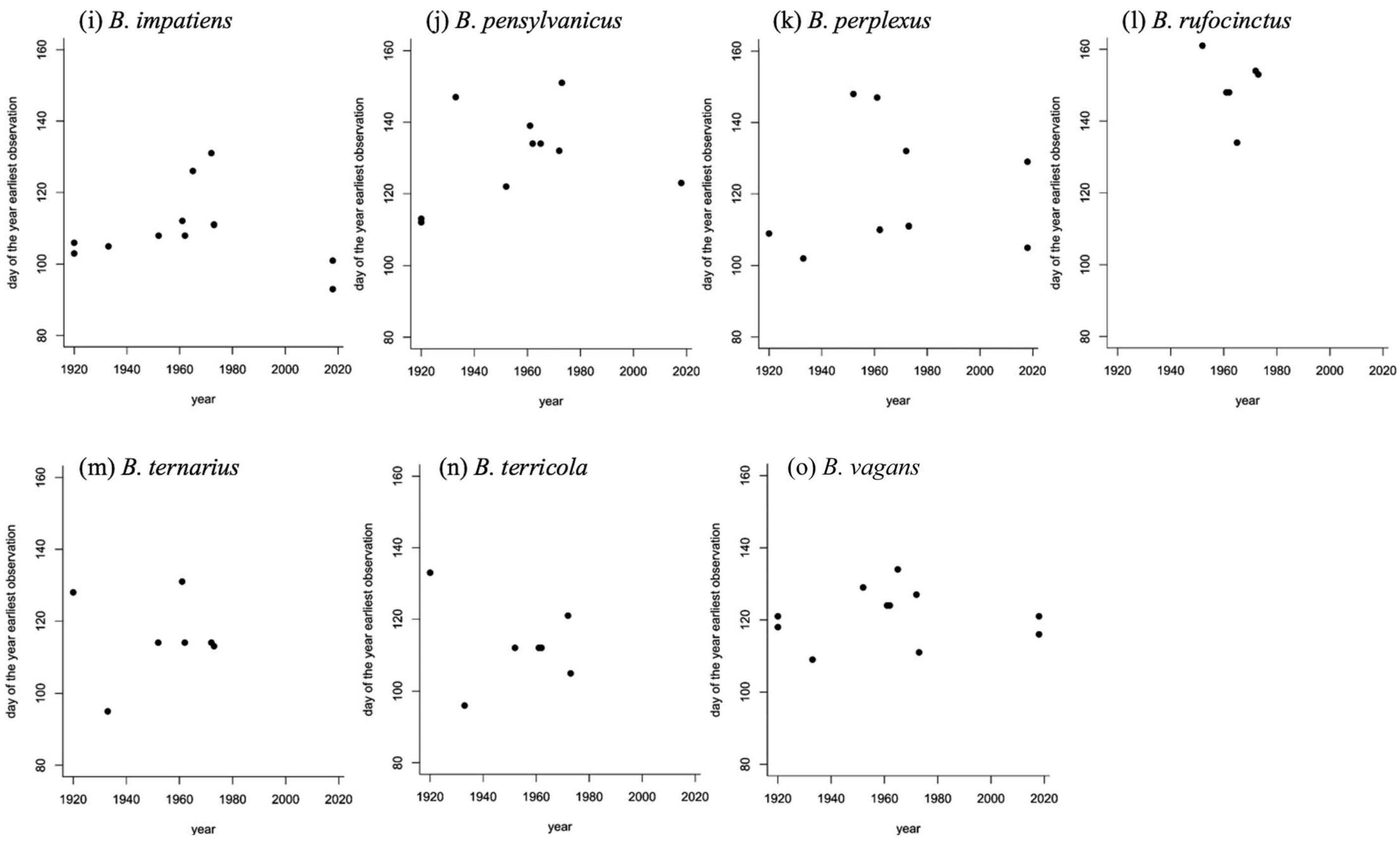

FIG. A1.—Continued