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Floral resource continuity boosts bumble bee colony performance relative to variable floral resources

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Abstract

1. Centuries of landscape changes associated with agriculture have dramatically reduced the amount and increased the temporal variability of the floral resources that support key pollinating insects such as bumble bees. Adapting to these novel resource conditions is important to ensure the persistence of bumble bee species. While several species appear to be in decline in modern agricultural landscapes, others have thrived, suggesting adaptation to exploit highly variable floral resources. *Bombus impatiens*, the common eastern bumble bee, is a prime example of such a species.
2. We designed an experiment to compare how free-foraging colonies of *B. impatiens* performed adjacent to areas with either temporally continuous or variable (pulsed) patches of purple tansy (*Phacelia tanacetifolia*) plantings.
3. We found that colonies in *Phacelia* landscapes grew faster, had gained more mass, and produced more gynes than did colonies in reference landscapes with no *Phacelia*.
4. Comparing colony responses between pulsed and continuous flowering resources showed that total mass gain at the end of the experiment was greater with continuous flowering resources. In contrast, colony growth rate and total gyne production were comparable for colonies adjacent to *Phacelia* plantings that were continuous versus pulsed.
5. While low in statistical replication, given the scale of the experimental manipulation, our experiment shows that although *B. impatiens* colonies can exploit periods of resource discontinuity and gain mass, these continuously available floral resources appear important for colony growth and benefit gyne production.

KEYWORDS
agroecology, bumble bee, habitat management, pollination, resource continuity

INTRODUCTION

Recent evidence has shed light on alarming declines of important pollinating insects, particularly bumble bees (*Bombus* spp.) in Europe and North America (Cameron et al., 2011; Grixti et al., 2009; Hemberger et al., 2021; McArt et al., 2017; Wood et al., 2019). While several factors have been implicated in declines, the loss of floral resources within the landscape is among the most empirically supported causal factor across study regions (Carvell et al., 2006; Goulson et al., 2008; Goulson et al., 2015; Vaudo et al., 2018). Changes in global-scale agricultural practices, notably the loss of leguminous cover crops (Rasmont & Iserbyt, 2013), increased control of flowering weeds (Hicks et al., 2016), as well as transition to monocultural plantings of agricultural crops (Brown & Schulte, 2011), have each affected the total quantity and temporal availability of floral resources present in the landscape. These changes have had profound negative consequences for a range of pollinator taxa (Scheper et al., 2014), especially eusocial species like bumble bees (Apidae: genus *Bombus*; Biesmeijer et al., 2006; Bommarco et al., 2012).

Despite population decline and range contraction in many bumble bee species, several have established outside historical ranges (Palmier & Sheffield, 2019) and increased in occurrence regionally (Hemberger et al., 2021). One species, *Bombus impatiens* Cresson, has thrived, particularly in the agriculturally intensive Midwestern US despite unfavourable floral conditions and the decline of other bumble bee species (e.g., *B. affinis*, *B. terricola*). This suggests *B. impatiens* can adapt to variable resource environments, successfully establishing and growing colonies during periods of resource scarcity. Although an increase in floral resource abundance is known to have positive effects on bumble bees (i.e., shorter foraging durations, Westphal et al., 2006, Hemberger & Gratton, 2018, Malfi et al., 2019; increased growth and reproduction, Crone & Williams, 2016, Spiesman et al., 2017, Hemberger et al., 2020; enhanced reproductive recruitment, Carvell et al., 2017), how variability in floral resources over time affects bumble bees is less established.

Because bumble bee colonies are long-lived, the continuous availability of flowers during colony establishment and growth is thought to be critical to colony success (Hemberger et al., 2020; Kevan & Baker, 1983; Schellhorn et al., 2015). For example, worker production in colonies of *B. terrestris* Linnaeus and *B. vosnesenskii* Radoszkowski are positively linked to early-season resource availability, suggesting that shortfalls in these resources could negatively impact growing colonies, limiting their ability to produce reproductive individuals (gynes) later in the season (Crone & Williams, 2016; Malfi et al., 2021; Westphal et al., 2009; Williams et al., 2012). Additionally, late-season mass-flowering crops benefit queen production in *B. terrestris* by eliminating a late-season resource gap (Rundlöf et al., 2014).

Resource shortages over shorter temporal scales can also influence developing bumble bee colonies, however, laboratory studies find mixed results. Schmid-Hempel and Schmid-Hempel (1998) found that when food availability was highly variable over time queen production and queen size, relative to a condition of continuous food availability, increased. This suggests that temporally variable floral resources positively impact the growing colonies of *B. terrestris*. However, Hemberger et al. (2020) instead showed that microcolony growth of *B. impatiens*, but not reproductive output, was enhanced under conditions of continuous resource availability. While laboratory studies can provide insights into the mechanisms driving colony responses to variable resource abundance, field experiments are needed to understand how colonies respond under more natural, free-foraging conditions where foraging energy expenditures factor into colony economics. To date, few studies address how variability in resources over time influences colony performance (but see Malfi et al., 2021).

We designed a field experiment to test if temporal resource variability affects the colony growth and reproductive output of free-foraging colonies of *B. impatiens*. Experimental queen-right colonies were reared in the field adjacent to replicated large (1.2 ha) fields of purple tansy, *Phacelia tanacetifolia* Benth, an attractive floral resource for many bumble bee species. The *Phacelia* wildflower plantings were sown either at staggered intervals to create a temporally continuous bloom ('continuous' resource treatment) or all at once to produce a single bloom of a large display but of short duration ('pulse' resource treatment). These two planting types were also designed to provide an equivalent amount of total floral resource supplementation relative to ambient floral resource abundance in the landscape and varied only in the temporal presentation of the floral supplement. We predicted that colonies with adjacent *Phacelia* plantings would grow larger and produce more queens (gynes) and forage more frequently than colonies placed in reference agricultural landscapes without nearby *Phacelia* plantings. Moreover, we expected that colonies exposed to continuously blooming *Phacelia* would grow larger and produce more queens than those exposed to the pulse flower plantings (Hemberger et al., 2020).

METHODS

Field and treatment design

In May and June of 2019, we planted *Phacelia tanacetifolia*, (Albert Lea Seed Company, Albert Lea, MN) into four fields (minimum of 900 m apart, Figure A1) of about 1.2 ha in size each at the UW Arlington Agricultural Research Station (Columbia County, Wisconsin, 43.303°N, 89.346°W). Two fields were assigned to the 'continuous' floral treatment. In this treatment, *Phacelia* was sown into 6 ~0.2-hectare blocks (~1.2 total hectares per field sown at 22.5 kg seeds per hectare) at weekly intervals such that blocks bloomed in succession for a total of 6 weeks. The remaining two fields were 'pulsed' flower treatments, whereby *Phacelia* was sown into 2 ~0.6-hectare blocks where blooms were available to foraging colonies for approximately 2 weeks each. In this design, each treatment had the same area of *Phacelia* available for bees (our proxy of flower availability) but varied the temporal window over which the blossoms were available during the experiment (continuous: 6 weeks, variable: 2 weeks). Continuous blocks were sown weekly in random order, and pulse treatment fields were sown in succession with the first and fourth blocks of the continuous treatment (Figure A1). Because the field shapes were variable, we adjusted the block dimensions (i.e., length and width) to maintain the quantity (i.e., block area) of *Phacelia* planted at each field.

Blocks were allowed to bloom for between 1 and 2 weeks depending on blossom density, which we tracked using percent area cover estimates, classifying each block weekly using a modified Daubenmire scale (<5%, 5%–10%, 10%–15%, 15%–25%, 25%–50%, 50%–75%, 75%–99%, 100%). After the bloom window, we mowed blocks to standardise the amount of *Phacelia* colonies had access to at

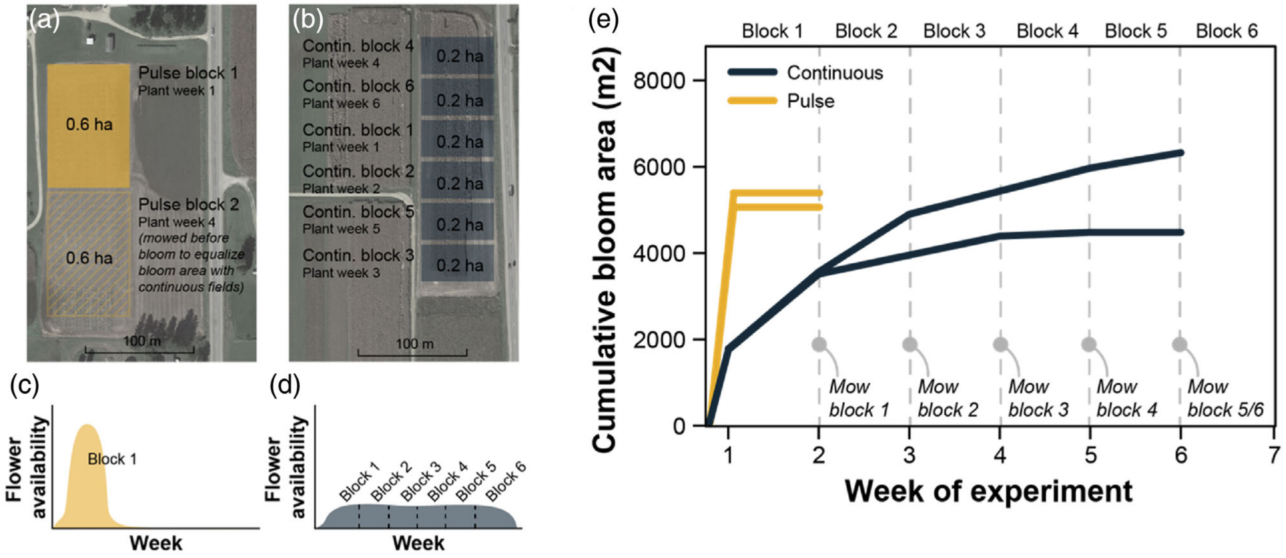

FIGURE 1 Planting scheme for pulsed (a) and continuous (b) field sites along with estimated availability of flowers across the temporal span of the study for pulsed (c) and continuous (d) fields. Because of weed pressure, pulse block 2 was mowed before bloom and continuous blocks 3–6 produced reduced numbers of flowers. We adjusted our mowing to maintain equivalent total flower availability between pulsed and continuous fields (i.e., the area under a curve in purple in (c) and (d) is equivalent). Block planting dates were randomised for both pulse and continuous fields. Planting dates are also indicative of approximate blooming dates. (e) Cumulative abundance (square meters) of *Phacelia tanacetifolia* flowers by flower planting treatment (orange = pulse, dark blue = continuous) for each field. Vertical dashed lines indicate when blocks were mowed. Differential weed pressure resulted in the difference in bloom area between the two continuous field sites. Because the two pulse fields contained the same estimated bloom area, the lines are vertically jittered for visibility.

a given field (Figure 1). The establishment of the first planting blocks (continuous block 1 and the pulse block) resulted in abundant *Phacelia* flowers with little weed pressure (Figure A2). Subsequent continuous blocks all contained increasing weed pressure (e.g., pigweed, grasses), reducing the total estimated area of *Phacelia* available to colonies at continuous treatment fields relative to each other and pulse fields. To correct this, we monitored the bloom area and adjusted the mowing schedule to equalise the bloom area between all fields. This necessitated that we mow the second planting in pulsed fields before it blooms to match the floral area within continuous fields. The total average area of *Phacelia* over the duration of the experiment in the pulsed fields was 5229 m^2, and the two continuous fields contained an average of 5403 ± 1305 (mean ± SD) square meters of *Phacelia* (Figure 1).

Treatment fields were compared against an unmanipulated reference landscape field containing no *Phacelia* plantings. The reference site served as a measure of ambient floral resource availability on our agricultural research station (i.e., how colonies would perform given no nearby *Phacelia*). The reference field was located approximately 3.5 km from the nearest treatment fields. We selected our treatment fields to maximise their distance apart within the confines of the research station, and the average distance between fields was 2550 m, and the closest distance was 900 m (Figure A1). Distances between our fields are encompassed by some of the largest bumble bee foraging range estimates of up to 11 km (Rao & Strange, 2012), however average foraging distance estimates are generally below 1000 m (Osborne et al., 2008; Redhead et al., 2016). Overall, the landscape composition was similar across all of the sites; agriculturally dominated landscapes with small sections of woodland. The crop fields surrounding our sites (<1 km distance) were dominated by corn, soy, and silage alfalfa which is cut before flowering. Our surveys of the area also showed no other *Phacelia* being grown at the research station or within 5 km of any colonies and the estimated floral resources landscape in the surrounding 1.5 km around each field were comparable across treatment and reference fields (Appendix A1).

Bumble bee colony deployment and measurements

We sourced 20 commercial bumble bee colonies (*Bombus impatiens* Cresson) from BioBest Biological (Romulus, MI) in late June of 2019. All colonies were at similar phenological stages, containing between 15 and 30 workers. For two days prior to field deployment, we kept colonies in constant laboratory rearing conditions (28°C and 60% relative humidity) with access *to* ad-libitum artificial nectar (ProSweet, MannLake LTD, Hackensack, MN). Prior to deployment, we measured the starting mass of each colony. We then placed colonies into insulated honey bee nucleus boxes (hereafter field boxes), randomly assigned to treatment by field combination and deployed them on a field edge within 100 m of *Phacelia* blocks on July 3, 2019. Four colonies were placed at each of the five sites (four treatment sites, and one reference).

Every 3 days from 9 July to 22 August 2019, we visited each colony and measured the following: colony mass, reproductive status (presence of drones and/or gynes), foraging activity and pollen collection. Colony mass was determined by removing the colony box from field boxes and weighing them on a battery-powered, portable scale (0.1 g resolution). When weighing, we visually inspected the colony for reproductive evidence including egg clumps, pupae and the presence of gyne pupae or emerged reproductive individuals (gynes or males). If the brood mass was still visible, we estimated the number of gyne pupae present. At the conclusion of the experiment, colonies were collected, frozen, and dissected. From dissections, we determined the terminal brood mass, as well as the approximate reproductive output of gynes. Because colonies were in different states upon collection (e.g., still occupied, abandoned), the method of gyne enumeration was either done by summing the number of emerged gynes still in the colony plus un-emerged gyne pupae or if colonies were already abandoned upon collection, we counted the number of emerged gyne pupal casings.

We also evaluated bumble bee colony foraging activity to determine whether colonies were actively foraging on *Phacelia* plantings. We observed all colonies before recording mass measurements for 10 min each, enumerating entrances and exits by worker bumble bees. From observing these individuals, we also assessed pollen foraging, recording the pollen type that individuals carried as they returned to the colony and categorising corbicular loads into (1) *Phacelia* (purple pollen); (2) other (including all pollen colours except purple); or (3) no pollen. These observations allowed us to determine both whether treatment *Phacelia* plantings were being used, as well as if cross-field foraging was occurring. For example, if foragers in colonies adjacent to a field with no current *Phacelia* in bloom (e.g., reference sites, or pulse-treatment fields that had been mowed) returned to the colony with *Phacelia* pollen, we could infer those individuals had been visiting treatment fields that still had *Phacelia* in bloom.

Data analyses

We performed all data management and statistical analyses in R, version 4.0.3 (R Core Team, 2017). We fitted a generalised additive mixed model (GAMM) to determine whether treatments impacted the colony growth rate relative to each other and the reference colony growth rate using the mgcv package (Wood, 2017). GAMMs are useful for time series data given their increased flexibility to account for non-linear trends. Our model predicted colony mass difference from the first day in the field (i.e., mass gain relative to time $t = 0$) as a function of flower treatment, starting mass, and a day of experiment smooth by treatment group, fitting a separate smooth relationship for each treatment. We included the interaction of flower treatment and starting mass to determine whether colony growth rates depend on the initial size of the colony. This model was fitted using a gamma error distribution. We included colony identity as a random grouping factor to account for repeated measures and included a first-order autocorrelation structure (function: corAR1) with a time covariate of an experiment to account for residual temporal autocorrelation. To interpret and visualise predicted model results, we used the jtools and interactions packages (Long, 2020, 2019). All plots were constructed using the ggplot and affiliated tidyverse packages (Wickham et al., 2019).

To evaluate whether treatments affected total colony mass gained, we fitted a generalised linear mixed model (GLMM) with a fixed effect of treatment, starting mass, and their interaction using a gamma error distribution and a log link function, as our data distribution was non-negative and continuous. We included a random grouping factor of field. Upon examining results from this model, we fitted a model using the same structure omitting reference colonies to determine if there was a significant difference in total mass gain between continuous and pulse treatment colonies.

To determine if queen production varied by treatment, starting colony mass, or their interaction, we constructed a GLMM with a negative binomial error distribution and a log link function. We included a random grouping factor of field.

To determine whether colonies were using the *Phacelia* plantings, we assessed the proportions of collected pollen types across treatments using Pearson χ^2 tests. Confirmation of *Phacelia* use would provide further support that access to a mass-flowering resource was in fact impacting colony-level growth and reproduction metrics. We separated tests out based on the phenology of the pulse bloom, examining how the proportion of collected pollen types varied during pulse bloom, and after pulse bloom. In doing this we were able to evaluate whether there was any significant cross-field foraging occurring (i.e., whether individuals from pulse fields were collecting *Phacelia* pollen from continuous fields after the pulse had bloomed). We also tested whether pollen collection varied between reference and treatment field colonies across the entire experiment.

To assess whether bumble bee colony foraging activity varied across treatment fields, we fit a generalised linear mixed model with a negative binomial error distribution to the number of returning foragers per 10-min observation window as a function of the treatment. We included the field as a random grouping factor of colony identity nested within the field to account for repeated measures over time.

RESULTS

Colony growth

All twenty bumble bee colonies gained mass relative to their starting weight. Starting weight between colonies was largely similar, ranging from 212 to 240 grams. Two colonies, one from the reference field and one from a continuous field, were dropped from all analyses as the queen died during the experiment, potentially impacting subsequent colony performance. The growth rate of colonies was driven by a significant interaction of treatment and starting mass (Figure 2, Table A1, GAMM parametric term $F_{2,184} = 8.43$, $p < 0.001$). The growth rate of both continuous (reference condition, $t = 3.99$, $p < 0.001$) and pulse ($t = 3.91$, $p < 0.001$) colonies increased as starting mass increased relative to reference colonies ($t = -1.54$, $p = 0.12$). A subsequent GAMM omitting reference colonies revealed

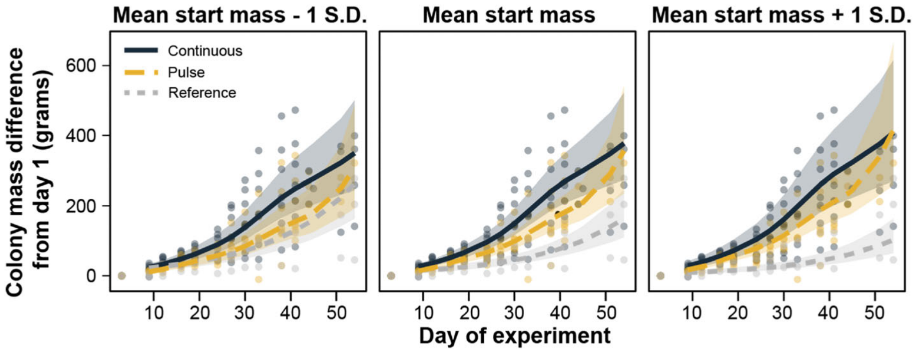

FIGURE 2 Generalised additive mixed model partial plots of the difference from starting mass for each treatment group with a random effect of colony identity (dark blue, solid = continuous, orange, long dash = pulse, grey, short dash = reference). To visualise the interaction between treatment and starting mass, panels are evaluated at three values of a colony starting mass for each treatment. Transparent points are raw data.

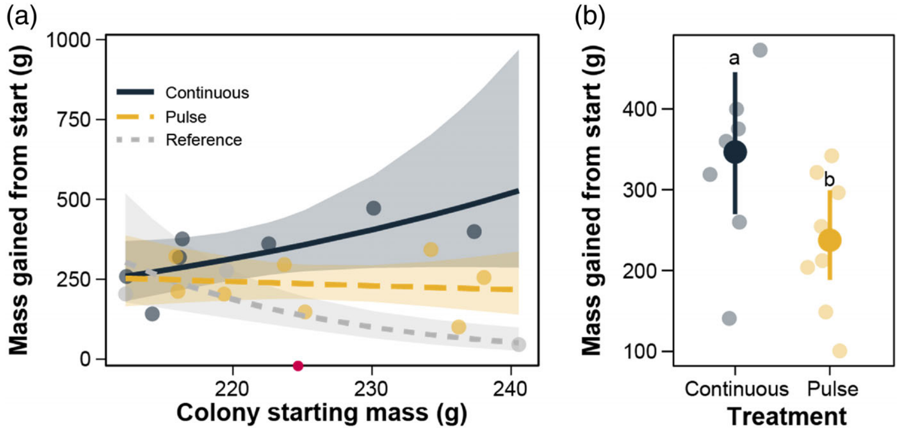

FIGURE 3 (a) Generalised linear mixed model interaction plot of the total mass gained for each treatment relative to the colony starting mass. The red dot on the x-axis represents the mean starting mass across all colonies. (b) Least-squared mean estimates of total mass gained for continuous and pulse treatments from a model omitting all reference colonies. Letters above indicate post-hoc, Tukey corrected significant differences. Transparent points are raw data.

no significant differences in growth rates between continuous and pulse colonies (GAMM parametric term $F_{2,184} = 0.29$, $p = 0.59$). Reference colonies also gained mass, but growth rates were markedly lower when starting mass was higher. Overall, the treatment colonies grew at elevated rates relative to reference colonies across most of the starting mass range (Figure 2: mean of starting mass and above).

Total mass gained by the end of the experiment (45 days) was best explained by a significant interaction of treatment and starting mass (Figure 3a, Type III Wald $\chi^2 = 15.53$, $p < 0.001$). Treatment colonies whose starting mass was at or above the mean colony starting mass gained significantly more weight than reference colonies. A subsequent model omitting the reference colonies revealed that continuous treatment colonies had gained significantly more mass by the end of the experiment than pulse treatment colonies over the course of the experiment (Figure 3b, Type III Wald $\chi^2 = 4.72$, $p = 0.03$). Colonies exposed to a continuous bloom of *Phacelia* gained on average 110 g (347 ± 42.5 grams for continuous vs. 237 ± 27.2 grams for pulsed) more than the pulse treatment colonies.

Gyne production

Gyne production varied among colonies (range = 0–116). We found a significant effect of treatment (Figure 4, Likelihood ratio $\chi^2 = 7.96$, $p = 0.019$) on gyne production, with continuous (67.8 ± 26.8 SEM) and pulse (45.5 ± 16.8 SEM) fields producing on average over 10 times more gynes than the reference field (4.1 ± 3.2 SEM). However, the difference between continuous and pulse colonies was not statistically clear.

Pollen collection

The number of pollen loads on returning foragers containing *Phacelia* during the pulse bloom (when *Phacelia* was available to both continuous and pulse treatment colonies) was similar across treatment fields: continuous field, 57% (13/15) of pollen loads with *Phacelia*; pulse field, 32% (11/17) of pollen loads with *Phacelia* (Pearson $\chi^2 = 2.050$, $p = 0.23$). After *Phacelia* flowering at pulse fields concluded, foragers

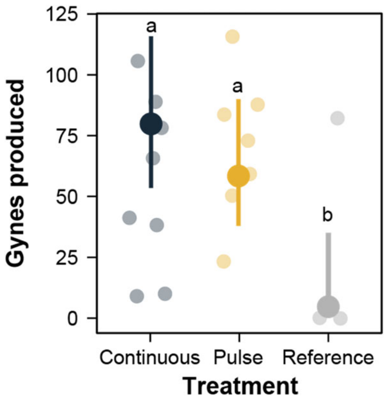

FIGURE 4 Least-square mean estimates of colony gyne production (large circles) with 95% confidence intervals. Transparent points are raw data. Letters above indicate post-hoc, Tukey corrected significant differences.

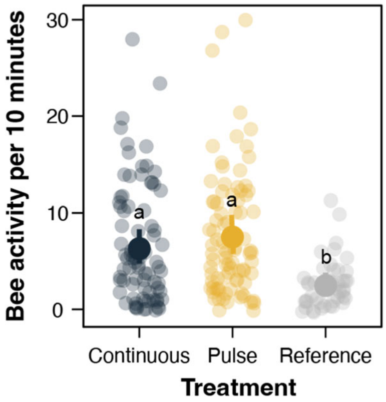

FIGURE 5 Least-square mean estimates of colony foraging activity (large circles) with 95% confidence intervals. Transparent points are raw data. Letters above indicate post-hoc, Tukey corrected significant differences.

returning to colonies in continuous treatment fields had ~10x more *Phacelia* pollen (14%, 36/204 pollen loads *Phacelia*) relative to colonies in pulse fields (1.3%, 4/228 pollen loads *Phacelia*; Pearson $\chi^2 = 32.367$, $p < 0.001$). Relative to reference colonies, over the course of the experiment there was a clear difference in the proportion of pollen types, with workers returning to treatment colonies having ~7x more *Phacelia* pollen loads (14%, 64/464 pollen loads *Phacelia*) than workers returning to reference field colonies (2%, 1/47 pollen loads *Phacelia*: Pearson $\chi^2 = 5.381$, $p = 0.02$).

Foraging activity

The observed foraging activity of colonies was highly dependent on the field treatment (Figure 5, Type III Wald $\chi^2 = 19.14$, $p < 0.001$). Bumble bees from colonies adjacent to continuous and pulse flowering treatments exhibited foraging rates on average ~ 3 x greater (6.30 bees per 10 min and 7.51 bees per 10 min, respectively) compared to reference colonies (2.47 bees per 10 min).

DISCUSSION

The continual supply of floral resources is generally thought to be important for developing social bee colonies (Kaluza et al., 2018; Roulston & Goodell, 2011; Vieli et al., 2016). Mounting evidence, however, suggests that some species may be better suited for periods of resource dearth (Austin & Dunlap, 2019; Hemberger et al., 2020; Schmid-Hempel & Schmid-Hempel, 1998). We found that free-foraging colonies of *B. impatiens* in agricultural landscapes with adjacent *Phacelia* plantings grew at a greater rate and gained more mass overall than colonies in reference landscapes that were not enhanced with *Phacelia* flowers. Contrary to our expectations we found that *B. impatiens* colonies grew at a similar rate regardless of large differences in the temporal availability (continuous vs. pulsed) of this locally abundant flowering resource. Despite similar growth rates, however, colonies adjacent to continuously blooming *Phacelia* gained more mass during the experiment. Colony production of female reproductives, gynes, was also enhanced when bumble bees were adjacent to *Phacelia* enhanced fields compared to colonies adjacent to a reference field. Moreover, colonies placed adjacent to *Phacelia* plantings produced on average 10 times more gynes than those in the reference landscape. Colony-level gyne production in bumble bees is known to be highly variable and such a difference in gyne production is likely due to increased resource intake associated with the adjacent *Phacelia* plantings, a feature evidenced also by greater colony growth rates, overall mass gain, and foraging rates when adjacent to *Phacelia*. Even though colonies in the pulse treatment fields also produced more gynes on average than those in reference fields, production was generally lower than in continuous field colonies, a trend consistent with other studies examining gyne production relative to resource availability (Williams et al., 2012).

The impact of *Phacelia* on gyne production in colonies adjacent to plantings was likely indirect. Much of the *Phacelia* bloom occurred early in the colony life cycle (July) before gyne production was first observed in mid-August. This early influx of *Phacelia* pollen likely led to an increased rate of worker production relative to colonies in the reference landscape. With more foragers able to collect more pollen and nectar (Pelletier & McNeil, 2003), colonies ultimately were able to provide these resources to developing gynes later in the season. This was evidenced by the observed increased foraging rates for field colonies near *Phacelia*. Such increases in early-season resources are known to elevate colony growth and worker production (Malfi et al., 2021), but the availability of late-season resources may have a more direct impact on drone and gyne production (Rundlöf et al., 2014). This carry-over effect of early-season resource exploitation exhibited by *B. impatiens*, also seen with *B. vosnesenskii* (Malfi et al., 2021), may help explain the ability of this species to exploit modern agricultural and human-dominated landscapes in which resources are temporally heterogeneous.

Despite total colony mass gain being significantly higher in continuous field colonies relative to pulse-field colonies, the difference in gyne production between them was not statistically evident. One reason for this may be that we did not have the necessary statistical power to resolve differences in among-treatment growth rates in this large-scale field study. The magnitude of the difference between these two treatments for model estimated mean total colony growth was 46%. However, bumble bee colony growth rates can be highly variable even under similar conditions (Hemberger et al., 2020; Rotheray et al., 2017). In this study, we attempted to create experimental floral enhancements at a large enough scale (0.6 ha) to influence colony-level responses and keep plantings far enough from each other (>900 m) to ensure spatial independence. Pollen collection information from returning foragers shows little evidence of foraging of bumble bees from areas with no *Phacelia* present (either from the reference sites or *Phacelia* pulse sites when not in bloom) to the continuously blooming *Phacelia* treatments. This provides support for the spatial independence of treatments at least at a scale of 900 m. In fact, the very low proportion (<2%) of *Phacelia* pollen found in foraging workers in reference landscapes shows that bees rarely found these flower patches 3.5 km away. However, having a few large flower plantings spaced far apart lead to a tradeoff of low treatment-level replication, which reduced our power to detect bumble bee response differences given the known heterogeneity in bumble bee reproduction (Hemberger et al., 2020; Rotheray et al., 2017; Williams et al., 2012). Although the reproductive differences in our experiment are not statistically significant between the continuous and pulse treatments, the trends observed in this study largely parallel the findings in laboratory microcolony manipulations using a similar experimental design (Hemberger et al., 2020). The combination of results from Hemberger et al. (2020) and this study suggests that continually available resources do indeed boost *B. impatiens* drone and gyne production, respectively; however additional, well-replicated field studies are needed to further resolve this effect. Colonies within landscapes containing highly variable floral resources may still perform well (i.e., grow large and produce gynes), but our results suggest this performance might not eclipse colonies with access to a continuous flowering resource. Future experiments with greater replication, and ideally using wild-caught and reared colonies, could more conclusively determine the relationship between colony growth rates and temporal resource variability and the differences between colony mass gains and gyne production.

Mass-flowering floral displays, including crops such as canola and sunflower, are known to be important foraging resources for eusocial pollinators, especially bumble bees (Hemberger & Gratton, 2018; Rundlöf et al., 2014; Westphal et al., 2009). We found that large *Phacelia* flower plantings were used by foraging bumble bees in this agricultural landscape. Moreover, the foraging activity rate of worker bumble bees between continuous and pulse colonies were nearly identical, suggesting that resource intake between colonies was similar and helping to explain the similar patterns of growth. A majority of returning foragers carried a large proportion of non-*Phacelia* pollen (60%–75%), consistent with what is known about bumble bees and their large foraging ranges (Rao & Strange, 2012; Redhead et al., 2016; Hemberger and Williams unpublished data). Perhaps surprising is that despite occupying a very small part of the total foraging area in the landscape, bumble bee foragers returned with between 25% and 40% *Phacelia* pollen. Important to note is that we were not able to control floral resources beyond the *Phacelia* plantings. While nearly all crop fields surrounding the experimental fields were of low foraging value (e.g., corn, soy), small pockets of high-value resources along field or road edges could have impacted bee foraging behaviour. Still, given the relatively large proportion of foraging on other flowers from the broader landscape, it is notable that *Phacelia* plantings resulted in significant differences in mass gain and gyne production relative to colonies placed far away from *Phacelia*, representing 'ambient' or reference conditions. This may be because *Phacelia* has a high concentration of sugar and protein relative to other pollen sources in the landscape (Page et al. personal communication) which even at lower proportions in the diet can still affect colony performance.

Conclusions

Temporal resource availability is thought to be a key driver of the population dynamics of many beneficial organisms (Iuliano & Gratton, 2020). Bottlenecks or gaps in resource abundance can reduce fitness (Persson & Smith, 2013, 2011) and may lead to local extinctions of organisms unable to adapt to the conditions of resource availability (Schellhorn et al., 2015). The decline of several bumble bee species has been linked to the loss of floral resources (Goulson et al., 2015), however, several species of bumble bee (e.g., *B. impatiens*, *B. bimaculatus*) seem able to exploit the same landscapes in which declining species have been lost (Wood et al., 2019). Such conflicting results suggest the adaptability of some bumble bee species, specifically an ability to survive dearth periods of resource abundance that are common in modern agricultural landscapes (Timberlake et al., 2019). Our study supports the observation that *B. impatiens* colonies can achieve high growth rates in landscapes with augmented floral resources regardless of the temporal availability of the floral resources. However, colonies exhibited consistently high gyne production when resources were continuously available. Each line of evidence we present points to a similar trend, suggesting that although *B. impatiens* appears too tolerant of variable floral resource abundance in terms of colony growth, they ultimately perform best that is, grow the largest colonies, and produce on average more gynes, under continuous resource conditions. Previous work has identified several mechanisms, including both interspecific (e.g., species diet breadth Wood et al., 2019) and intraspecific (e.g., body-size variation Timberlake et al., 2019) traits that may allow this species to persist under unfavourable resource conditions (Couvillon & Dornhaus, 2010).

Important to note is that, due to the scale of this experiment and the spatial constraints of the research station this experiment was conducted on, the reference field was unable to be replicated. This practice is not uncommon in a large, landscape, or whole-system manipulations (Carpenter et al., 1987; Likens, 1985), but requires data that provide evidence that '(1) changes in the manipulated system are much greater than those in the reference system, and (2) those changes are most plausibly explained by the manipulation' (Carpenter, 1989). We include the reference site in our analyses; however, comparisons to the reference must be made with this knowledge in mind. While there are innumerable ways in which the reference site could have differed from treatment sites that might explain the observed differences in mass gain and queen production, we argue that the addition of *Phacelia* to the treatment sites represents the most plausible explanation of the differences in bee performance when compared to reference sites given the similar landscape composition and no evidence of obvious confounding factors (e.g., colony disease, pesticide exposure, etc.). Despite the unreplicated nature of the reference conditions, the comparisons among treatment sites, while underpowered, are informative. Given this, we feel this work provides a starting point from which additional research can be launched to further our understanding of bumble bee responses to temporal resource heterogeneity.

Nevertheless, the patterns suggest that augmenting agricultural landscapes with flowers in ways that maintain or enhance resource continuity throughout the season can benefit bumble bees. Future work could explore how other bumble bee species respond to temporal resource heterogeneity, particularly those known to be in decline (Hemberger et al., 2021). In addition, this experiment may represent a best-case scenario with bumble bees placed directly adjacent to floral plantings. It would be useful to examine how colony performance is influenced when plantings are further apart or smaller in size. Such comparisons can shed light on drivers of bumble bee declines and may provide practical guidance for how we implement resource-based conservation initiatives in the landscape to increase the continuity of resources over the season.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Floral resource continuity increases bumble bee performance at https://doi.org/10.6084/m9.figshare.19372226, reference number 10.6084/m9.figshare.19372226.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Data S1. Supporting information.

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