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POPULATION ECOLOGY – ORIGINAL RESEARCH

Demographic benefits of early season resources for bumble bee (*B. vosnesenskii*) colonies

Rosemary L. Malfi[1] · **Elizabeth Crone**[2] · **Neal Williams**[1]

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Abstract
The temporal distribution of resources is an important aspect of habitat quality that can substantially impact population success. Although it is widely accepted that floral resources directly influence wild bee population sizes, we lack experimental data evaluating how resource availability affects colony growth via demographic mechanisms. To achieve this, we tracked marked individuals in bumble bee (*Bombus vosnesenskii*) colonies to evaluate whether worker survival and reproduction responded to experimentally elevated forage early in colony development. Specifically, we assessed the effect of early resource environment on worker and sexual offspring production, and the survival and body size of individual workers. We also assessed whether responses of colonies differed when exposed to higher or lower resource environments at a relatively smaller (~ 10 workers) or larger (~ 20 workers) size. Resource supplementation always resulted in greater total offspring and male production; however, the influence of supplementation on worker production and quality depended on colony size at the start of supplementation. Among colonies that were initially smaller, colonies that were supplemented produced fewer but larger bodied and longer lived workers compared to control counterparts. Among colonies that were initially larger, colonies that were supplemented produced more workers than corresponding controls, but without changes to worker quality. Collectively, these results provide clear experimental evidence that greater resource availability early in colony development increases overall productivity, and indicate that colonies may pursue different allocation strategies in response to the resource environment, investing in more or better workers.

Keywords Bumble bee · Demography · Floral resources · Life history · Population dynamics

Introduction

The timing of resource abundance and scarcity over an organism's life cycle can strongly affect individual fitness and population success. Across taxa, the resource environment during early life stages may be particularly important for long-term health and reproduction, because early growth trajectory influences later outcomes. Adverse conditions in early development can negatively influence growth and metabolism (Lindström 1999; Metcalfe and Monaghan 2001), longevity (Boggs and Freeman 2005; Vaiserman 2014), and fecundity (Haywood and Perrins 1992; Dimitriew and Rowe 2011). In social insects, fitness is governed by processes that operate at both individual and colony levels. Colony growth and reproductive output depend, in part, on both the quantity and quality (e.g., foraging lifespan and efficiency) of individual non-reproductive workers who tend and collect resources for offspring, which includes future workers and sexual progeny (i.e., males, new queens). As is the case in solitary organisms (cited above), the nutritional environment experienced early in the life of a colony may be critical for its overall development and ability to reproduce.

Bumble bees (*Bombus* spp.) are primitively eusocial insects with high economic and ecological value (Kremen et al. 2004; Memmott et al. 2004; Artz and Nault 2011)

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✉ Rosemary L. Malfi
rmalfi@ucdavis.edu; rmalfi@umass.edu

[1] Department of Entomology and Nematology, University of California Davis, Briggs Hall, Room 367, Davis, CA 95616, USA

[2] Department of Biology, Tufts University, Medford, MA 02155, USA

that are also a source of conservation concern, as a number of species have undergone population declines (Colla et al. 2012; Bommarco et al. 2011; Kerr et al. 2015; Wood et al. 2019). Floral food resources are a primary driver of the population dynamics of bumble bees and other wild (i.e., unmanaged) bee species, yet we lack experimental data demonstrating how temporal variability in food availability influences their population success (Roulston and Goodell 2011). To date, the majority of evidence demonstrating the connection between food resources and bee populations comes from correlative studies that generally find positive relationships between bee abundance and floral resource availability at both local and landscape scales (e.g., Bowers 1985; Potts et al. 2003; Westphal et al. 2003; Hines and Hendrix 2005; Hegland and Boeke 2006; McFrederick and LeBuhn 2006; Carvell et al. 2007). However, such correlations may reflect the attraction of bees to better resources rather than positive demographic impacts. For social bee species, correlative studies may be particularly misleading, because population sizes are often inferred from surveys of non-reproductive worker bees, rather than males and queens produced at the end of the colony cycle. Detailed assessments of vital rates (e.g., survival, reproduction) in relation to either or both the amount and seasonal distribution of resources are needed to mechanistically link variability in the resource environment to impacts on bee populations. Whereas surveys of the free-foraging population may confound foraging patterns and population response, measurements of demographic responses to differences in resource availability directly indicate the impact of habitat and landscape quality on population persistence, providing valuable insights that can be used to make management decisions to promote pollinator populations.

The temporal availability of resources, in particular, is an understudied but potentially highly influential aspect of habitat quality affecting bumble bees (Schellhorn et al. 2015). Limited previous work suggests that abundant early season resources are especially beneficial for their colony founding and growth (Carvell et al. 2017; Williams et al. 2012; Westphal et al. 2009). The majority of bumble bee species have annual colony cycles that typically grow for several weeks during the summer by producing sequential, overlapping cohorts of non-reproductive workers before switching to reproduction (i.e., the generation of males and new queens) and undergoing colony-level senescence. The ability of bumble bees to store food provisions is limited (Goulson 2010); at the same time, maximum colony size and growth strongly predict reproductive success in species, where these relationships have been examined (Müller and Schmid-Hempel 1992; Pelletier and McNeil 2003; Williams et al. 2012; Crone and Williams 2016; Spiesman et al. 2017). Thus, short-term fluctuations in resource availability, and the timing of resource abundance and scarcity relative to the progression of the colony cycle, have the potential to strongly influence both the growth and reproductive phases of colony development (Schmid-Hempel and Schmid-Hempel 1998). Although resource shortfalls at any point during the colony cycle may negatively affect productivity, food limitation may be particularly detrimental early in development when colonies are smaller and, therefore, more vulnerable to risks. Smaller colonies are less buffered against worker losses (Müller and Schmid-Hempel 1992), which are likely to increase during times when food resources are scarce owing to the increased foraging effort required (Westphal et al. 2006; Hemberger and Gratton 2018).

Early season resource environment may translate into later success through its impacts on individuals. For example, the amount of food bumble bee larvae consume affects adult body size (Plowright and Jay 1977; Sutclifffe and Plowright 1988; Couvillon and Dornhaus 2011), and larger workers appear to be better foragers [Goulson et al. 2002; Spaethe and Weidenmüller 2002 (*B. terrestris*); Kerr et al. 2019 (*B. vosnesenskii*)]. If workers produced during a period of elevated resources are larger and/or longer lived (higher quality) then resource return to the colony might be greater or more efficient even after resource levels diminish initially, because at least some of these workers live past the elevated resource period. Furthermore, the initially direct positive effect of resources on worker quality may continue to indirectly influence the quality of future worker generations as well as sexual progeny through a positive feedback between worker quality and resources returned to the colony for developing brood. Such "carry-over" effects, in which present conditions affect future performance, are well-documented in life-history literature for other organisms (Harrison et al. 2011). Experimental evidence is needed to demonstrate the demographic mechanisms through which early season resource abundance may improve bumble bee colony development and reproduction, and thus population success.

In this study, we assessed how differences in the food resource environment experienced by bumble bee (*B. vosnesesnkii*) colonies during the early growth phase of development influenced the quantity and quality of offspring production. We accomplished this through a season-long field experiment in which we manipulated the amount of forage available to free-foraging colonies and tracked the fates of all individuals belonging to them. Specifically, we evaluated the effects of a higher early resource environment (compared to ambient) on (1) the production of worker and sexual (i.e., male and queen) offspring and (2) offspring quality as measured by worker body size and worker survival. We expected that the higher resource environment would have a positive effect on both the number and quality of worker progeny produced, as well as the number of sexual offspring generated. We also assessed whether the response of colonies to food treatments was affected by their size at the time they experienced a higher or lower resource environment in the field. Specifically, colonies were subjected to food treatments (supplemented vs. unsupplemented) when either one or two cohorts of workers had eclosed, representing two slightly different but potentially consequential points in the early growth phase of the colony life cycle. Finally, we assessed whether supplementation improved worker quality during the period when colonies had access to supplemental forage and whether these effects persisted after access was removed.

Materials and methods

Overall field methods

Experimental setup and design

The yellow-faced bumble bee (*Bombus vosnesenskii*) is a common species along the west coast of North America, appearing from British Columbia to Baja, California (Williams et al. 2014). We caught 80 wild, post-diapause *B. vosnesenskii* queens at the University of California's McLaughlin Natural Reserve (Clear Lake, CA; N38 52 25.74, W122 25 56.25) between 27-March and 2-April in 2016. These queens were transported to the lab at UC Davis where they were hand-reared. After 6–8 weeks, the 14 strongest colonies (i.e., those with the healthiest-looking brood) were placed outdoors. The first six colonies were placed in the field (May 8th) when their first cohort of workers emerged (9.5 ± 1.9 workers, mean ± SD). The other eight colonies were kept in the laboratory for an additional 1–2 weeks until their second cohort of workers emerged (18.4 ± 2.6 workers, mean ± SD). In addition to differences in the available worker force, colonies that entered the experiment with one vs. two-worker cohorts also differed in the amount of developing brood they contained, with the two-cohort colonies having a greater number of pupae (see Table S1 in Supporting Information). All field colonies were placed in an agricultural field on UC Davis Experimental Farm property (N38 31 32.3, W121 46 56.54). The site was surrounded by cropland comprised largely of non-flowering cereals and corn and a single ribbon of riparian habitat, and reflects landscapes encountered by bumble bees in the northern Central Valley of CA.

In the fall and winter prior to colony placement, we established seven 6.1 × 9.1 m forb plantings at the study site to provide supplemental forage to select colonies. Plantings were sown with a mix of California native species (*Phacelia tanacetifolia*, *Phacelia ciliata*, *Collinsia heterophylla*, *Lupinus densiflorus*, and *Lupinus succulentus*) that bloom between late April and June. These plant species provide ample nectar and pollen resources and are known to host bumble bees locally (Williams et al. 2015). Once plots were well-established we covered each with a 6.1 × 9.1 × 1.8 m fine-mesh flight cage (Redwood Empire Awning, Santa Rosa, CA, USA).

Our experiment is a two-way factorial design, with two main effects: resource supplementation (supplemented vs. unsupplemented) crossed by the initial size (one vs. two eclosed worker cohorts) at which bumble bee colonies were placed in the field. On each date, colonies were deployed to the field ($n = 6$ on May 8th, $n = 4$ on May 14th, $n = 4$ on May 21st), half them were permitted exclusive access to supplemental forage cages for 3–4 weeks (hereafter "supplemented" colonies, $n = 7$), while the other half had access to ambient resources only ("control" colonies, $n = 7$). The last four colonies placed outside received 3 (vs. 4) weeks of access to supplemental forage owing to plant senescence within the cages. Bumble bee workers take about 3 weeks to develop into adults (Cnaani et al. 2002; Kerr et al. 2019); we supplemented colonies for up to 4 weeks to ensure that added forage would have the potential to fully and directly influence the development of at least one generation of workers. Supplemented colonies were constrained to forage in the cage for a full week to train them to use this space; after which they were permitted to forage either in the cage or in the natural environment through use of a bifurcated entrance tube (Fig. S1). The experiment continued until July 26, at which point colonies had senesced, indicated by the lack of tended, new brood, and in most, death of the foundress queen (Williams et al. 2012).

Quantifying floral resources

We quantified the forage available to supplemented colonies within the flight cages on a weekly basis using quadrat sampling. We also surveyed ambient resources in the surrounding landscape every other week for the duration of the experiment. Using ArcGIS and satellite imagery (2014), we created a digital layer of land use within 1500 m of the bumble bee colonies, which captures a typical foraging range for *B. vosnesenskii* (Greenleaf et al. 2007) and estimated resources for each identified land use type (e.g., tomato field, semi-natural grassland; see Table S3) using quadrat sampling over the season. For each sampling round, we calculated an index of total resource abundance by multiplying the average floral density for each land use category on that date by its total area within the landscape. Following standard practice for quantifying floral food resources available to bees at the landscape scale (Williams et al. 2012; Lonsdorf et al. 2009), we then negatively weighted resources by the distance from the bumble bee colonies using a simple negative exponential function (see "Floral resource assessment" of Electronic Supplemental Material for additional methodological details). This is a simple method of accounting for the increased effort required to forage for resources further from the colony (Cresswell et al. 2000). Hereafter, we refer to this index of floral resource abundance as “ambient floral resources.”

We validated the supplemental forage treatment in two ways. First, we quantified resources added by the supplemental forage plantings relative to the calculated index of ambient resources (available to all colonies including the controls) throughout the supplementation period. Second, we estimated colonies’ use of the supplemental forage when given the choice between the caged supplement and the natural environment (Fig. S1) by recording the number of foragers returning to each colony from each entrance for 25 min each week. We analyzed forage return locations using Proc CATMOD, SAS 9.4; SAS Institute, Cary, NC, USA.

Capture–recapture monitoring of individual bees

We conducted a weekly mark–recapture study of workers in each colony. During weekly night-time surveys, we used a modified hand-held vacuum to extract all workers under red light. Radio frequency (RFID) chips (mic3-TAGv, 64-bit RO, iID2000 13.56 MHz system, 1.9 mm × 1.6 mm × 0.5, mm, Microsensys, Erfurt, Germany) were affixed to the thorax of each untagged bee in the field under brief CO_2 anaesthetization (< 15 s in accordance with the recommendation of Ebadi et al. 1980), a widely used method for subduing insects for manipulative experiments (e.g., Hagler and Jackson 2001; Martin et al. 2006; Malfi et al. 2018). At the time of tagging, we measured each bee’s intertegular span (ITS), an accepted proxy for bee body size (Cane 1987; Hagen and Dupont 2013), using digital calipers and a stereo dissecting microscope. Following a brief recovery period (10+ mins), newly tagged workers were returned to their colony. Previously tagged workers were recorded as present or absent (Cooch and White 2016); those present were immediately returned to their colony following identification. We tracked the fate of individual bees through time and developed weekly encounter histories for each of the 1601 tagged bees across the 14 colonies until colonies senesced. Males were permanently removed from colonies and stored in ethanol (99%).

On the day following a night-time survey/marking for a given colony, we tracked the foraging activity of that colony for a full day (6:30 AM to 8:00 PM) using a 2-reader RFID system (Fig. S1) and used these data to establish a separate presence/absence record for tagged bees over the course of the experiment. Because foraging bees sometimes stay out of the hive at night (Müller and Schmid-Hempel 1993), this can make recapture during night-time surveys more challenging. To improve recapture rates, we merged the encounter history generated from our RFID foraging records with the encounter history generated from night-time surveys to create a single, chronological encounter history with all observation dates for all bees. This single encounter history was subsequently used in our mark–recapture analyses (described below).

Effect of food treatment on offspring production

We measured three aspects of offspring production: (1) total brood cell (i.e., workers plus males) production, counted by dissecting colonies at the end of the experiment; (2) the total number of males observed in each colony over the season; and (3) total worker production, estimated from mark–recapture analysis.

At the end of the season, we dissected brood structures and counted all brood cells to obtain the cumulative number of offspring produced. Male and worker cells cannot be differentiated by their size (Williams et al. 2012). Although queen cells can be distinguished from worker/male cells because of their larger size, no queens were produced by any of our colonies during this season. We evaluated the effects of food treatment, colony size at the time of the food treatment, and their interaction on total brood cell production using a generalized linear model (Proc GLIMMIX, SAS 9.4; SAS Institute, Cary, NC, USA) with a negative binomial distribution to account for overdispersion in our count data (Bolker 2008).

We evaluated the numbers of males in colonies during each night-time survey (see mark–recapture methodology). During each monitoring event, all males were permanently removed from the colony. At the end of the season, we also tabulated uneclosed brood, and included any viable unenclosed males in our tabulation of male production. The total number of males detected in a colony was used as proxy for the total males produced. We assessed the effects of food treatment, initial size, and their interaction on total male production using a generalized linear model (Proc GLIMMIX, SAS 9.4; SAS Institute, Cary, NC, USA) with a negative binomial distribution. Insufficient male production by control colonies prevented us from testing the effect of supplementation on reproductive timing; however, within the supplemented treatment, we compared the effect of initial colony size on reproductive timing using a general linear model (Proc GLM, SAS 9.4; SAS Institute, Cary, NC, USA).

Using Program Mark (see Cooch and White 2016), we estimated overall worker production (N^*; i.e., the worker “population” size) for each of the colonies separately using the mark–recapture encounter histories we generated. Within the program, we used the POPAN parameterization of the Jolly–Seber model, an open population model that estimates recruitment and survival from mark–recapture data (Schwarz and Arnason, 1996; Schwarz 2001; see additional details in quality metrics below). Group means for worker production (N^*) were then calculated from the colony estimates of worker production for (i) each food treatment (control vs. supplemented), and also for (ii) each combination of food treatment and colony size (1 vs. 2 worker cohorts) upon placement in the field. Standard errors for each group mean were calculated using the delta method, a technique for calculating the standard error of a function of parameters (Williams et al. 2002). This method was executed using package “msm”, (Jackson 2011) in R (R Development Core Team 2008). Significant differences between group means were assessed using 95% confidence limits.

Effect of food treatment on worker quality

We analyzed differences in worker body size using general linear mixed models (Proc Mixed, SAS 9.4; SAS Institute, Cary, NC, USA). Models included the fixed effects of food treatment, initial colony size, and experimental period (supplementation vs. post-supplementation), as well as interaction terms for food treatment*initial size, period*food treatment, and period*food treatment*initial size. Colony identity was included as a random effect. Workers, and their associated body sizes (ITS), were assigned to a given period (supplementation vs. post-supplementation) based on the week that they were tagged (see mark–recapture methodology), which approximates when individuals eclosed. Body size (ITS) was power-transformed prior to analysis to normalize residual error.

We estimated daily worker survival in Program Mark using the POPAN parameterization of the Jolly–Seber model (Schwarz and Arnason 1996) which permits robust estimation of daily survival probability (ϕ), recapture probability (p), probability of entry into the population (*pent*; i.e., the proportion of bees that eclosed in each week), and population size (N^*). We ran separate POPAN models for each colony, because recapture intervals were not identical across colonies. For each colony, we estimated survival using two model structures. In the first, ϕ was calculated for two discrete periods: (i) in the lab, and (ii) in the field. In the second, ϕ was calculated for three discrete periods: (i) in the lab, (ii) in the field during supplementation, and (iii) in the field post-supplementation. The purpose of the first model structure was to assess whether survival, overall, differed between treatment groups. The second model structure generates specific information about whether the effect of food treatment on survival persisted beyond supplementation. Even though control colonies did not have access to supplemental forage, mark–recapture events were assigned according to when supplemented colonies had access to these resources, permitting comparison of ϕ between food treatment groups for the periods during and after supplementation. For each model structure, the lab period was included to separate out the varying amounts of time that colonies spent in the lab from time spent in the field. For the lab interval, $p=1$, because worker deaths could be easily tracked. Otherwise, p was allowed to vary for each interval. Group means for worker survival (ϕ) were calculated for (i) each food treatment (control vs. supplemented) and also for (ii) each combination of food treatment and initial size upon placement in the field (1 vs. 2 worker cohorts). Significant differences between group means were assessed using 95% confidence limits. Significant interactions between food treatment and initial size effects were assessed using 95% confidence intervals of the difference between the treatment groups within each size group. Standard errors for group means and differences were calculated using the delta method, a technique for calculating the standard error of a function of parameters (Williams et al. 2002, implemented using package “msm”, (Jackson 2011) in R (R Core Development Team 2008).

Results

Validating food treatment

Supplemental forage substantially increased resources available to bees. During the weeks in which supplemental forage was available to colonies, each planting added on average 9641 ± 7515 (mean ± std. dev.) additional blooms per week relative to the naturally occurring forage within 100 m of the colonies (~ 5–18% increase depending on the week; Fig. S2). Although bees’ use of the supplemental cage varied by week (week*foraging area: $\chi^2=32.7$, $p<0.0001$), in all but the final week for supplementation, workers returned to the colony entrance from the caged supplement much more frequently than from the entrance leading to ambient resources outside the cage ($\chi^2=25.6$, $p<0.0001$, Table S2).

Effect of food treatment on offspring production and quality

Overall, access to supplemental resources early in colony development improved both the quantity and quality of offspring production in the experimental bumble bee colonies. Colonies with access to supplemental forage produced significantly more brood cells over the season ($\bar{Y}=193$, $\mathrm{CI}_{95\%}=171, 217$) than did control colonies ($\bar{Y}=113$, $\mathrm{CI}_{95\%}=100, 129$) (Table 1). Worker production (N^*) was also higher for resource-supplemented colonies ($\bar{Y}=160$, $\mathrm{CI}_{95\%}=156, 164$; $N=7$) when compared to control colonies ($\bar{Y}=140$, $\mathrm{CI}_{95\%}=136, 144$; $N=7$) (Table 2), as was male production ($\bar{Y}_{\mathrm{supp}}=40$, $\mathrm{CI}_{95\%}=16, 99$; $\bar{Y}_{\mathrm{cntrl}}=5$, $\mathrm{CI}_{95\%}=2, 13$; Table 1). Indeed, of the seven control colonies, four did not produce any males. None of the colonies in the experiment produced gynes (new queens). Worker body size (ITS) was greater in supplemented

Table 1 Results of statistical tests for brood cells, male production, and body size

Type of test	Brood cell production Generalized linear model			Male production Generalized linear model			Body Size (ITS) Mixed model		
Predictor variable	d.f. (num, den)	*F*	*p*	d.f. (num, den)	*F*	*p*	d.f. (num, den)	*F*	*p*
Main effects									
Food trt	1, 10	45.65	< 0.0001	1, 10	12.50	< 0.01	1, 1328	4.98	0.03
Initial colony size	1, 10	9.64	0.11	1, 10	0.26	0.62	1, 1328	0.07	0.79
Exp. period	–	–	–	–	–	–	1, 1328	3.58	0.06
Intx effects									
Food trt * initial size	1, 10	0.49	0.51	1, 10	1.30	0.28	1, 1328	0.98	0.32
Pd. * food trt.	–	–	–	–	–	–	1, 1328	2.83	0.09
Pd * food trt * initial size	–	–	–	–	–	–	3, 1328	1.40	0.38

Table 2 Means and confidence limits for all offspring production and quality metrics

	Food treatment		Initial size		Food treatment * initial size			
	Supp	Control	1-Cohort	2-Cohorts	Supp * 1-Cohort	Cntrl * 1-Cohort	Supp * 2-Cohorts	Cntrl * 2-Cohorts
Total brood cells								
$\bar{Y}$	193	113	131	167	166	103	224	125
L-CLM	171	100	114	149	138	84	192	105
U-CLM	217	129	150	187	199	126	261	147
Total males								
$\bar{Y}$	40	5	12	16	49	3	34	8
L-CLM	16	2	4	7	13	1	10	2
U-CLM	99	13	33	38	189	14	109	27
Total workers (N*)								
$\bar{Y}$	160	140	112	179	101	123	204	153
L-CLM	156	136	108	174	96	118	198	148
U-CLM	164	144	116	183	106	128	211	159
Body size (ITS, mm)								
$\bar{Y}$	3.33	3.14	3.25	3.22	3.38	3.10	3.27	3.17
L-CLM	3.21	3.01	3.11	3.11	3.20	2.91	3.12	3.00
U-CLM	3.44	3.26	3.37	3.33	3.55	3.29	3.42	3.23
Daily survival rate (ϕ)								
$\bar{Y}$	0.914	0.912	0.920	0.907	0.926	0.915	0.905	0.912
L-CLM	0.908	0.905	0.913	0.901	0.916	0.904	0.897	0.905
U-CLM	0.920	0.919	0.928	0.913	0.936	0.925	0.913	0.919

"Supp" and "Ctrl" denote supplemented and control colonies; "1-Cohort" and "2-Cohorts" denote colonies that initially had one or two worker cohorts

colonies ($\bar{Y} = 3.33$ mm, $CI_{95\%} = 3.21, 3.44$) compared to controls ($\bar{Y} = 3.14$, $CI_{95\%} = 3.01, 3.26$) (Table 1). Somewhat unexpectedly, the estimated daily rate of survival for workers was not significantly affected by food treatment ($\bar{Y}_{supp} = 0.9141$, $CI_{95\%} = 0.908, 0.920$; $N = 7$; $\bar{Y}_{cntrl} = 0.912$, $CI_{95\%} = 0.905, 0.919$; $N = 7$; Table 2).

Initial colony size influences food treatment effect

Although food treatment, overall, had a positive and statistically significant main effect on nearly all metrics of offspring quantity and quality, the particular effects of supplementation depended on the size of the colony when initially supplemented in the field. The effect of food treatment on total brood

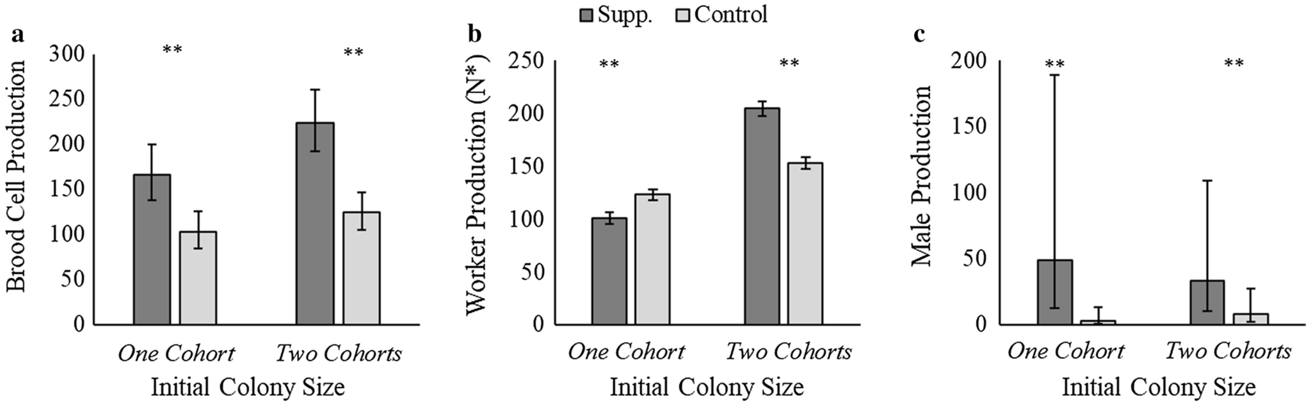

Fig. 1 Colony lifetime **a** offspring (worker + male) production, **b** worker production (N^*), and **c** male production by food treatment and initial colony size. Error bars represent 95% confidence limits. Stars indicate comparisons where 95% confidence limits do not overlap corresponding means within initial colony size categories

Table 3 Differences in worker production (N^*) and survival (ϕ) means for supplemented and control treatments for colonies that started with either one- or two-worker cohorts and associated confidence limits produced using the delta method

Response var.	Life stage	$\bar{Y}_{\text{supp}} - \bar{Y}_{\text{cntrl}}$	U-CLM	L-CLM
Total workers (N^*)	1-Cohort	−22	−15	−30
	2-Cohorts	51	60	43
Daily survival rate ϕ	1-Cohort	0.0115	0.0264	−0.0034
	2-Cohorts	−0.0065	0.0055	−0.0185

When confidence limits do not overlap a corresponding difference, this indicates a significant interaction effect

cell production and male production did not depend on the size of the colony when supplementation began (interaction *NS*, Table 1; Fig. 1a, c). However, the effect of supplementation on worker production did depend on this initial colony size (Table 3). Colonies that began with two-worker cohorts and were supplemented produced significantly more workers ($\bar{Y}=204$, $\mathrm{CI}_{95\%}=198, 211$) than corresponding control colonies ($\bar{Y}=153$, $\mathrm{CI}_{95\%}=148, 159$), whereas colonies that began with one worker cohort and were supplemented unexpectedly produced fewer workers ($\bar{Y}=101$, $\mathrm{CI}_{95\%}=96, 106$) than corresponding controls ($\bar{Y}=123$, $\mathrm{CI}_{95\%}=118, 128$) (Fig. 1b). Colonies that were smaller when supplemented tended to initiate reproduction earlier, with males first eclosing 2 weeks earlier (11-June ± 8.6 days, Mean ± SE) than in colonies that were larger when supplemented (30-June ± 6.6 days) ($F_{1,7}=5.58$, $p=0.05$).

The initial size of the colony at the time of supplementation also influenced offspring quality. Resource supplementation improved worker survival in the colonies that started with one worker cohort ($\bar{Y}_{\text{supp}}=0.926$, $\mathrm{CI}_{95\%}=0.9158, 0.936$; $\bar{Y}_{\text{cntrl}}=0.915$, $\mathrm{CI}_{95\%}=0.904, 0.925$), but it had no effect on worker survival in the colonies that began with two-worker cohorts ($\bar{Y}_{\text{supp}}=0.905$, $\mathrm{CI}_{95\%}=0.897, 0.913$; $\bar{Y}_{\text{cntrl}}=0.912$, $\mathrm{CI}_{95\%}=0.905, 0.919$) (Table 3; Fig. 2a). The initial size of the colony, overall, did not significantly influence worker body size, nor was the effect of resource treatment significantly dependent on the initial size of the colony (Table 1).

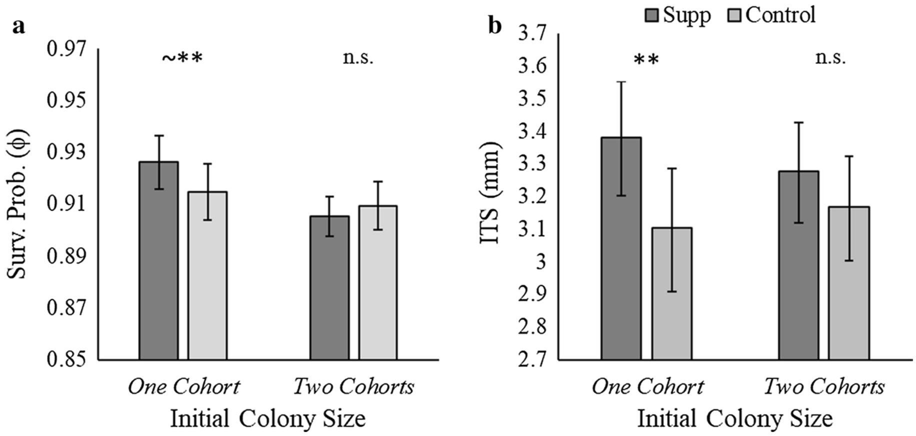

Fig. 2 **a** Daily survival probability and **b** worker body size by food treatment and initial colony size for the whole season. Error bars represent 95% confidence limits; ~double asterisks represent marginally significant differences for $\alpha=0.05$

However, the effect of supplemental resources on body size was stronger in the colonies that began with one worker cohort (Fig. 2b), with the difference in body size between control and supplemented colonies being ~ 3 times greater in colonies that were initially smaller ($\bar{Y}_{\text{supp}} - \bar{Y}_{\text{cntrl}} = 0.28$ mm) versus larger ($\bar{Y}_{\text{supp}} - \bar{Y}_{\text{cntrl}} = 0.11$ mm).

Supplementation vs. post-supplementation periods

When the effects of food supplementation were partitioned into during versus after the supplementation period, they largely paralleled the overall pattern of results (i.e., Fig. 2). Effects on worker quality were stronger for those colonies that started the supplementation experiment with one cohort of workers than for those that started with two cohorts. For these one-cohort colonies, access to supplemental forage increased mean worker survival during the supplement but not post-supplementation (Fig. 3a). The during supplementation effect was marginally non-significant based on the delta method, in part because partitioning mark–recapture observations between periods for estimates of survival reduced statistical power. Survival was not increased during either period for colonies that started with two-worker cohorts. The positive influence of supplementation on worker body size was evident both during and after the supplementation period (Table 1); in each period, the strength of the effect was more notable for colonies that started with one worker cohort compared to those that started with two-worker cohorts (Fig. 3b).

Discussion

Our study demonstrates the importance of early food resources for bumble bee (*B. vosnesenskii*) colonies. Short-term access to higher resources early in colony growth generated a lasting benefit for colonies, increasing total offspring production, male production, and worker body size. Male production, in particular, was temporally removed from the direct influence of the supplemental forage we provided, with the bulk of males being produced several weeks after access to supplemental forage was removed (see Fig. S4). This pattern illustrates that the earlier resource environment had persistent, positive effects on colony development. In our predominantly agricultural study landscape, naturally occurring floral resources were characteristically low (Williams et al. 2012) when our colonies were introduced into the field in May. Thus, the supplemental forage provided colonies a resource pulse that was otherwise absent in the local environment. Although floral resources naturally increased in the wider environment as the season progressed (Fig. S3), this forage did not allow unsupplemented colonies to catch-up.

Previous work on select bumble bee species, including *B. vosnesenskii*, indicates that worker body size is an important aspect of individual-level quality: larger bodied workers tend to be more efficient foragers (Goulson et al. 2002; Spaethe and Weidenmüller 2002; Kerr et al. 2019). This individual effect can translate to overall colony performance. Mean worker body size is positively associated with increased colony mass and gyne production in *B. impatiens*, which is closely related to our study species (Herrmann et al. 2018). We found that access to flower plantings increased worker body size during the period of supplementation and that this positive effect persisted into the post-supplementation period. This result was especially pronounced for colonies that were less advanced in their development when supplemented (see Fig. S4). This outcome suggests that increased body size following the early resource pulse might have led to persistent increases in resource return throughout the colony cycle. Our finding echoes carry-over effects in other animal taxa (Harrison et al. 2011; Pechenik 2006), but is distinct in that it spans multiple cohorts of workers in a social colony, rather than resource storage within individual animals.

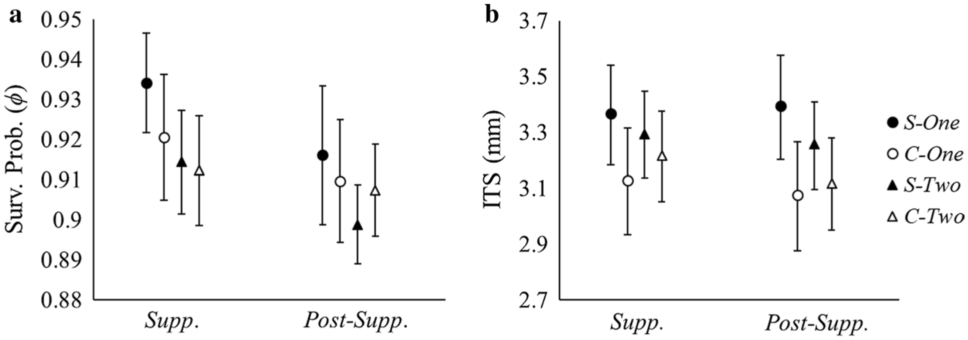

Fig. 3 **a** Daily survival probability and **b** worker body size during and after the supplementation period for supplemented (black markers) and control (white markers) colonies that started with one cohort of workers (circle) and two cohorts of workers (triangle). Error bars represent 95% confidence limits. *S-One* supplemented colonies starting with one worker cohort, *C-One* control colonies starting with one worker cohort, *S-Two* supplemented colonies starting with two-worker cohorts, *C-Two* control colonies starting with two-worker cohorts

Our experimental results complement recent correlational studies demonstrating positive effects of resource availability on bumble bee colony growth in select species (Crone and Williams 2016; Spiesman et al. 2017) and concur with field studies that have inferred a particular benefit of spring resources to bumble bee colony founding and development (Westphal et al. 2009; Williams et al. 2012; Carvell et al. 2017). Colonies in early development are likely to be more sensitive to the availability of food resources in the environment owing to their smaller size, which limits their capacity to gather food as compared to a larger, more mature colony. Indeed, Rotheray et al. (2017) found that very young *B. terrestris* colonies failed to grow unless provided unlimited nectar, suggesting that even modest resource limitation may have strong negative impacts during this vulnerable phase of development. Although early season resources provide important benefits for colony development, even an auspicious beginning may not shield a colony against later resource scarcity. For example, the reproductive output of bumble bee colonies may be compromised in agricultural systems where mass-flowering crops provide abundant resources for bees early, but not late, in the season (Westphal et al. 2009; Rundlöf et al. 2014). Additional, targeted study would help to reveal the demographic impact of differently timed resource pulses across the colony cycle, and how these impacts may vary across contexts in which the natural seasonal flowering resource dynamics differ.

Although we primarily discuss the benefit of our plantings in terms of the amount of forage they provided, it is likely that they generated simultaneous improvements in the diversity and nutritional quality of available forage for colonies with access to them. We deliberately selected plant species based on our knowledge of their attractiveness to bumble bees in the field (Williams et al. 2015) and the high-quality pollen and/or nectar rewards they offer (e.g., Williams and Christian 1991; Roulston et al. 2000). The diversity and nutritional value of flowering plants, in addition to their quantity, is important for bumble bee colony development and population health (Carvell et al. 2006; Vaudo et al. 2018). Understanding how to manage floral communities to be most beneficial to bees is an active area of research (Vaudo et al. 2015; McGonigle et al. 2017; Leach and Drummond 2018). Separating the precise mechanisms (e.g., quantity and quality) underlying the responses we observed, and evaluating nutritional needs of colonies during early development, could be interesting avenues for future investigation.

Across taxa, organisms capitalize on trait plasticity in the face of variable resource conditions, sometimes employing different resource allocation strategies to achieve greater fitness. Although bumble bees are known to vary widely in their colony and body sizes both inter- and intraspecifically (Goulson et al. 2002; Couvillon and Dornhaus 2011; Cueva del Castillo et al. 2015), few studies have tested how the resource environment influences a bumble bee colony's resource allocation strategy (e.g., size and number of offspring) during development. We found that *B. vosnesenskii* colonies that were initially less advanced when placed in the field generated fewer, larger bodied, and longer lived workers in response to supplemental resources. Colonies that were slightly more advanced when placed in the field generated more workers in response to supplemental resources, but without the same increases in worker quality. A previous study on the solitary leafcutter bee *Megachile apicalis* determined that females in higher resource conditions made more, smaller progeny and females in lower resource conditions made fewer, larger bodied progeny (Kim and Thorp 2001). In effect, our more advanced (2-cohort) colonies experienced a higher resource environment earlier on because they received an additional week of ad libitum feeding in the lab. Male production was similarly improved in all supplemented colonies, irrespective of how colonies invested resources, indicating that having either more or better-quality workers at the time a colony switched to reproduction (see Fig. S4) benefitted this aspect of reproductive success. To further explore this pattern, we evaluated associations among average body size, colony size, and average survival across colonies, irrespective of treatment. In this post hoc analysis, only average body size was associated with male reproductive success across all treatments (Fig. S5), echoing the overall importance of body size for bumble bee colony success (cf. Herrmann et al. 2018; Kerr et al. 2019).

None of our colonies generated gynes, and so we were unable to assess the impact of the higher resources during early colony development on queen production. One possible reason for the lack of gyne production is the nutritionally challenging landscape in which colonies were placed, which offered few resources compared to the queen-producing landscapes from the previous work performed with *B. vosnesesnkii* in the region (Williams et al. 2012). As part of the experiment targeting individual-level data, we also frequently disturbed the colony to mark bees. Each marked bee was subjected to a single CO_2-anaesthetization event. Although the use of an anesthetic is generally necessary for mass marking, anesthetics including CO_2 and even cold can affect insect lifespan and/or foraging (Tustain and Faulke 1979; Poissonnier et al. 2015). It is possible that the stress of frequent colony invasions and handling of individual bees affected reproductive outcomes. Given the current methods available for bumble bee research, there may be a tradeoff in our ability to collect data on individual- vs. colony-level traits within a single study, due to colony-level effects of handling individual workers. It is reassuring that our results from experimental manipulations under stressful conditions (handling) broadly reflect patterns other studies have shown in less manipulative and, therefore, less controlled field studies (Williams et al. 2012; Spiesman et al. 2017). For example, the proportion of colonies that produced queens in our previous, less manipulative study was 0.24 (Crone and Williams 2016), which is just below the upper confidence limit (i.e., not significantly higher than) for 0 of 7 colonies producing queens in the high resource (i.e., supplemented) treatment in this study (based on simple likelihood profiling).

Concluding remarks

Our study emphasizes the importance of evaluating the temporal distribution of resources when considering habitat quality. Previous work linking resources to bumble bee colony development have generally relied on supplementing colonies in the nest (e.g., Schmid-Hempel and Schmid-Hempel 1998; Pelletier and McNeil 2003), which will remove important feedbacks in resource acquisition that are associated with foraging activity. Others have drawn relationships between colony performance and natural resource gradients (e.g., Williams et al. 2012; Spiesman et al. 2017), which can be confounded with other factors. In controlling the resource environment while permitting colonies to freely forage, we were able to avoid these liabilities. In doing so, we provide direct, experimental evidence that boosting the amount of local, high-quality forage available to bumble bee colonies early in development yields demographic benefits, bolstering previous studies that have determined the value of natural habitat and forage plantings in agricultural landscapes at a coarser scale (Persson and Smith 2011; Williams et al. 2012; Carvell et al. 2011; Rundlöf et al. 2014; Blauw and Isaacs 2014).

Our results also revealed different colony responses (quantity vs. quality of workers) to resource levels based on relatively subtle differences in colony development. This finding contributes to our understanding of the growth and life history of annual social insect colonies in general, highlighting the sensitivity of the early phases of colony growth to resource conditions that may affect how selection acts on alternative allocation strategies depending on local environment. Negative relationships between colony size (i.e., number of workers) and worker body size occur across species within bumble bees (Cueva del Castillo et al. 2015) and within ants (Shik 2008). Our results complement these cross-species patterns by showing that individual colonies displayed plasticity along this size-number continuum within species and that the alternative strategies they employed led to similar reproductive outcomes. Plasticity depending on internal state (colony size) and resources may allow for more finely tuned responses to variable environments throughout early development. This plasticity may be critical for colony success and population persistence in inherently variable environments (Austin and Dunlap 2019).

From a practical standpoint, our results reinforce the importance of developing a mechanistic understanding of how colonies grow and allocate resources for making management decisions for conservation and pollination services. Forage habitat to benefit pollinators may be particularly important in spring, as it will amplify bumble bee worker numbers and size. Consistent floral availability at those times may further ensure larger numbers and sizes of workers that particularly benefit pollination (Willmer and Finlayson 2014; Blauw and Isaacs 2014).

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Author contribution statement NW, EC, and RM collaborated on experimental design and methodology. RM and NW collected the data. RM and EC analyzed the data. RM led the writing of the manuscript with input from NW and EC. All authors contributed critically to the drafts and gave final approval for publication.

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