

LETTER

Bumble bee colony dynamics: quantifying the importance of land use and floral resources for colony growth and queen production

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Abstract

Bumble bee (*Bombus*) species are ecologically and economically important pollinators, and many species are in decline. In this article, we develop a mechanistic model to analyse growth trajectories of *Bombus vosnesenskii* colonies in relation to floral resources and land use. Queen production increased with floral resources and was higher in semi-natural areas than on conventional farms. However, the most important parameter for queen production was the colony growth rate per flower, as opposed to the average number of available flowers. This result indicates the importance of understanding mechanisms of colony growth, in order to predict queen production and enhance bumble bee population viability. Our work highlights the importance of interpreting bumble bee conservation efforts in the context of overall population dynamics and provides a framework for doing so.

Keywords

Bombus vosnesenskii, colony growth, floral resources, life history, population viability, reproduction, social insects.

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INTRODUCTION

Habitat loss and degradation are primary drivers of species endangerment and extinction (Thomas *et al.* 1994; Krauss *et al.* 2010). Bumble bees (*Bombus* spp.) are a prominent example of the impacts habitat alteration can have on population viability (Goulson *et al.* 2008; Winfree *et al.* 2011). Declines of many bumble bee species are well documented (Cameron *et al.* 2011; Kerr *et al.* 2015) and have been specifically associated with agricultural intensification and changes in floral resources (Carvell *et al.* 2006; Grixti *et al.* 2009). Bumble bees are also of particular conservation concern worldwide because they are dominant pollinators of many wild and crop plant species (e.g. Corbet *et al.* 1991; Winfree *et al.* 2007).

Population models, and population viability analyses based on them, are standard tools for understanding the causes of population declines and projecting the likely consequences of management actions (Caswell 2001; Morris & Doak 2002). The strength of population viability analysis depends on its ability to link field-measured parameters of populations with simple models that project their dynamics into the future. In spite of widespread interest in bumble bee conservation, these standard population approaches have never been applied to this taxon. Presumably, this gap exists at least in part because bumble bees are annual, social taxa. Therefore, they do not fit into the standard framework of demography based on survival and reproduction of individuals. Although population models have been developed to investigate the evolution of this life history strategy (Oster 1976; Beekman *et al.* 1998; Poitrineau *et al.* 2009), they are not based on field-measured parameters for specific populations and

have not yet been integrated with bumble bee conservation efforts.

In the absence of a population dynamic assessment, our understanding about the conservation status of bumble bees comes from three lines of inference. The first is a large set of studies that have documented differences in abundance of bumble bees in space and/or time (reviewed by Winfree *et al.* 2011). These studies overwhelmingly conclude that areas with higher abundance of floral resources are associated with higher bumble bee abundances. One problem with abundance surveys is that bumble bee workers forage widely for resources, and it is unclear whether the results of these studies reflect differences in true abundance (population size) vs. forager concentration at resource patches (behavioural response) (Carvell *et al.* 2015; but see Geib *et al.* 2015 for one example of a correlation between worker and colony abundance). A second set of studies has monitored abundance of reproductive bees and/or colony densities in space and time using direct census or molecular-based estimates (e.g. Lye *et al.* 2009; Goulson *et al.* 2010; Rundlöf *et al.* 2014; Carvell *et al.* 2015; Wood *et al.* 2015). These metrics more closely represent population size, although they could still reflect habitat selection, rather than habitat quality from a demographic perspective (cf. Van Horne 1983). This second set of studies also tends to conclude that floral resources increase bumble bee abundance, although the association is less consistent than in the first set of studies.

The third, and least common, set of studies monitor colony growth or size and reproductive output directly. To date, four experimental studies have placed bumble bee colonies in different landscape contexts and tested whether floral resource availability led to larger colonies and higher reproduction

(Goulson *et al.* 2002; *B. terrestris*; Elliott 2009; *B. appositus*; Westphal *et al.* 2009; *B. terrestris*; Williams *et al.* 2012; *B. vosnesenskii*). These studies found evidence for larger colony size in the presence of higher floral resources, but no significant increase in queen production, suggesting that floral resources increase the number of worker bees in bumble bee colonies, but not their reproductive output. This conclusion would directly contradict the general consensus that changes in floral resources are a primary cause of bumble bee declines and that restoring floral resources is a key step in conserving bumble bee populations. Although this conclusion would be surprising from a bee conservation perspective, it would not be unique in conservation biology. In other taxa, management efforts directed at a single life stage are not always sufficient to explain or reverse population declines (Crouse *et al.* 1987; Biek *et al.* 2002). Therefore, it is critical from a conservation perspective to understand the apparent discrepancy between demographic mechanisms of colony growth and larger-scale landscape patterns of abundance.

In this article, we develop a mechanistic model to analyse growth and reproduction of bumble bee colonies in the field. We use this model to re-examine a previously published dataset on colony growth and queen production in a mixed-use agricultural landscape (Williams *et al.* 2012). We focus on queen production because we assume females are the demographically limiting sex (cf. Caswell 2001, Goulson 2010). By using a mechanistic model, we document (for the first time) that floral resources do in fact increase queen production, as well as colony growth. Our results corroborate larger-scale field patterns and demonstrate the power of separating vital rates such as colony growth and reproduction, as a way of analysing and interpreting field data. They also provide a basis for evaluating the relative contributions of different factors to bumble bee population viability.

METHODS

Study system and field experiment

We hand-reared *B. vosnesenskii* colonies from queens collected in early spring while they searched for nest sites. We fed queens and developing colonies in the laboratory on pollen and sucrose syrup for 6.5–8 weeks until they had reached a standard size (28 ± 2.6 workers mean \pm SD) at which point we randomly assigned them to a study site (Williams *et al.* 2012). We placed two colonies in each of 39 sites within a mixed agricultural-natural region in Northern California, USA (Williams *et al.* 2012). We protected colonies from sun exposure, rain and predators. Sites were of three local land cover types, conventional farms, organic farms and semi-natural and all spanned a gradient of land use from those with higher proportions of semi-natural vegetation to those dominated by organic or intensive conventional agriculture (< 1–99% semi-natural; see Williams *et al.* 2012). The land use gradient created variation in resource availability to the colonies among sites, as well as possible differences in local environmental conditions, e.g., temperature, pesticide exposure. Fifty-nine colonies established and grew through time and were suitable for demographic analysis. We weighed each

colony weekly until its queen died and/or its worker population crashed. The moribund colonies were brought to the laboratory and dissected to assess the number of queens produced (Williams *et al.* 2012).

To estimate the floral resources within each landscape, we used a GIS (Williams *et al.* 2012) to categorise land use into 20 different types, and for each type, we repeated field surveys of floral resource densities every 3 weeks at replicate sites stratified across the landscape. This allowed us to robustly estimate floral resource availability in each landscape throughout most of the bumble bee flight season (Williams *et al.* 2012).

Analysis of colony growth

Bumble bees are annual social species. Newly established colonies grow by producing sequential cohorts of workers and then switch to making males and new queens (gynes). Once the colony switches, it ceases making new workers (Duchateau & Velthuis 1988; Goulson 2010). As newly emerging queens and males disperse to find mates, the workers and existing queen die and the colony declines. This annual social life history with a discrete shift from growth to reproduction and decline points to modelling the colony dynamics as a two-stage process that allows for exploring effects of forage resources on growth and reproduction.

We analysed colony growth using a mechanistic model of weight gain through time. Specifically, we hypothesised that colony weight (denoted as W_t) would increase exponentially until the colony ceases to grow and then decline exponentially as workers die and reproductive offspring disperse from the colony, a process represented by the following mathematical model:

$$\begin{aligned} W_t &= W_0 \lambda^t & t < \tau \\ W_t &= W_0 \lambda^\tau \delta^{t-\tau} & t \geq \tau \end{aligned} \quad (1)$$

where λ is the rate of increase in weight during the colony growth phase, τ is the week at which growth stops (an estimate of the switch time to reproduction) and δ is the rate of decay in weight as bees die/leave.

To relate colony growth to floral resources, we modelled colony weight gain in relation to cumulative floral resources, rather than cumulative time. This model is the result of assuming instantaneous colony growth rates, $[\ln(\lambda)]$, are directly proportional to floral resources. For example, assume colony growth over a given time period, d , $[\ln(\lambda_d)]$, is proportional to floral resources during the same period, (F_d), i.e., $\ln(\lambda_d) = F_d \ln(k) \rightarrow \lambda_d = k^{F_d}$, where k is a constant that converts between growth rate per time and growth rate per floral resources. (Note that the value of k is estimated as part of a statistical model, see γ_1 in eqn 4a and subsequent text.) Substituting this relationship into the first half of eqn 1, we have:

$$W_t = W_0 k^{\sum_{d=1}^t F_d} \quad t < \tau \quad (2)$$

where $\sum_{d=1}^t F_d$ is the cumulative floral resources available to the colony from week 1 to week t , which is equivalent to

$$W_t = W_0 k^{t\bar{F}_t} \quad t < \tau \quad (3)$$

where \bar{F}_t is the average weekly floral abundance from time 0 to time t , and all other parameters are defined as above. We assumed that once the colony switched from growth to reproduction, its (proportional) rate of mass loss did not depend on floral resources. Thus, we obtained the following set of equations:

$$\begin{aligned} W_t &= W_0 k^{t\bar{F}_t} \quad t < \tau \\ W_t &= W_0 k^{\tau\bar{F}_t} \delta^{t-\tau} \quad t \geq \tau \end{aligned} \quad (4)$$

We fit both models (eqns 1 and 4) to observed patterns of weight dynamics for each of our 59 colonies, using standard maximum likelihood methods (Bolker 2008). Specifically, we linearised the colony growth model by log-transformation, created a dummy variable to account for the time period (before or after τ), and fit a model to the weight trajectory of each colony by searching over all possible values of τ in weekly increments (weeks 0–14 of the 14-week experiment). Linearisation is a convenient way to log-transform the response variable (which is bounded at 0) while maintaining the correct relationships among variables in the mechanistic model. The linearised versions of these models are as follows:

$$\ln(W_t) = \beta_0 + \beta_1 \times [\text{weeks}] \times [\text{before } \tau] + \beta_2 [\text{weeks after } \tau] \quad (5a)$$

$$\begin{aligned} \ln(W_t) &= \gamma_0 + \gamma_1 \times [\text{sum_flowers}] \times [\text{before } \tau] \\ &+ \gamma_2 [\text{weeks after } \tau] \end{aligned} \quad (5b)$$

where β_0 and γ_0 are estimates of $\ln(W_0)$ in each of the two models, β_2 and γ_2 are estimates of $\ln(\delta)$, the rate of mass decline after τ , and β_1 and γ_1 are estimates of $\ln(\lambda)$ and $\ln(k)$, respectively. These models were fit using Gaussian family, log-link generalised linear models, implemented in the open-source software program, R (R Core Team 2013).

A separate model was fit to each colony's weight trajectory because the switch dates, τ , clearly varied among colonies. To evaluate whether a discrete switch from growth to decline in mass was better than other statistical forms that are not based on biology, we compared a set of five models using AICc (see, e.g. Bolker 2008). This set included the two mechanistic models of colony growth (with and without floral resources) and three other models in which weight changed quadratically, changed linearly, or was constant over time. Although a separate set of parameters was estimated for each colony, model competition was based on the likelihood of all 59 colony trajectories, for each given model (Table 1A). As an additional check on fitted models, we calculated R^2 of observed vs. fitted growth rates through time and correlated the estimated maximum weight gain with final brood cell counts (reported by Williams *et al.* 2012).

We explored relationships between colony growth parameters and local land cover type using generalised linear mixed models (GLMMs) with random effects of site, to account for non-independence of colonies placed at the same site. We used normal distributions to model starting colony mass, average growth rate per flower and flower density in the surrounding landscape. We used a Poisson distribution to model switch time, since it was a discrete count variable (number of weeks).

Table 1 AIC model competition statistics for (A) models of colony growth, as measured through weight gain, and (B) error structures for models of queen production vs. colony growth parameters

Model	d.f.	dAIC	dAICc
A. Colony growth through time*			
<i>Mechanistic models:</i>			
Basic exponential growth	295	68.7	68.7
Growth as function of floral resources	295	0.0	0.0
<i>Phenomenological models:</i>			
Quadratic	236	219.8	37.5
Linear	177	6.7	10.2
Constant	118	1339.4	1341.7
B. Queen production†			
Poisson GLMM	9	46.3	46.3
ZIP, covariates affect count only	8	1107.5	1106.7
ZINB, covariates affect count only	9	0.0	0.0
ZIP, covariates affect both 0 and count	14	1118.3	1124.2
ZINB, covariates affect both 0 and count	15	8.1	15.6

*For colony growth parameters, the total number of observations is 716 colony mass estimates, and the number of estimated parameters (d.f.) is 59 colonies \times parameters per colony-specific model.

†For queen production models, the total number of observations is 59 colonies.

All models used log-link functions to improve normality. GLMMs were implemented using the lme4 package in R (Bates *et al.* 2014).

Analysis of queen production

Queen production by each colony was analysed as a function of the three mechanistic model parameters fitted to the weight trajectory for that colony, initial mass [$\ln(W_0)$], colony growth rate per unit floral resources [$\ln(k)$] and the length of the growth period (τ), as well as the average floral resources during the growth period (\bar{F}_τ). All analyses were based on the growth model with floral resources (eqn 4) because this model was best for these data, based on AICc (see *Results: Colony growth*). Models were fit as generalised multiple regression models with linear combinations of predictor variables.

Counts of queens produced per colony were clearly overdispersed, relative to a simple Poisson model. Therefore, we compared five models for queen production, based on standard probability distributions (cf. Martin *et al.* 2005): (1) a GLMM with observation-level random effects (to account for overdispersion; Elston *et al.* 2001) and random effects of site (note that this is nearly identical to a negative binomial model, except that the variance in expected counts is explicitly partitioned between site differences and residual variance); (2) a 0-inflated Poisson model in which the covariates only affected the count of queens given reproduction; (3) a 0-inflated negative binomial model in which the covariates affected only the count of queens given reproduction; (4) a 0-inflated Poisson model in which the covariates affected the zero term (probability of not producing queens) as well as the count term; and (5) a 0-inflated negative binomial model in which the covariates affected the zero term and count term. These error structures were compared using AICc, with the full set of covariates included in each model. Count models

used log links and zero terms in 0-inflated models used logit links (Martin *et al.* 2005). The GLMM was fit using the lme4 package (Bates *et al.* 2014), and 0-inflated models were fit using the pscl package (Zeileis *et al.* 2007) in R.

Once we had selected a model structure, we evaluated the statistical significance of each predictor variable using likelihood ratio tests of the full model, relative to models with each term excluded, in turn (type II marginal hypothesis tests, implemented with the car package in R; Fox & Weisberg 2010).

Perturbation analysis

We used the fitted colony model to explore how changes in colony growth and queen production parameters would affect population dynamics, i.e. perturbation analysis *sensu* Caswell (2001). We first performed a general elasticity analysis of colony population dynamics to evaluate the relative importance of proportional changes in vital rates (Caswell 2001; Morris & Doak 2002). The elasticity analysis used a statistical model fitted to queen production, i.e., a log-linear model of queen production as a function of $\ln(W_0)$, $\ln(k)$, τ , and \bar{F}_τ . To convert colony growth to population growth rate, we included a parameter for the probability of overwinter queen survival and colony establishment. Note that, although we did not measure this parameter, the elasticity of the overwinter survival and queen establishment parameter does not depend on its value (see *Results: Model Exploration and Discussion*). These assumptions lead to the following model for population growth rate:

$$\frac{N_{t+1}}{N_t} = s_W p_Q \exp(\beta_0 + \beta_1 \ln W_0 + \beta_2 \ln k + \beta_3 \tau + \beta_4 \bar{F}_\tau) \quad (6a)$$

$$\ln\left(\frac{N_{t+1}}{N_t}\right) = \ln s_W + \ln p_Q + \beta_0 + \beta_1 \ln W_0 + \beta_2 \ln k + \beta_3 \tau + \beta_4 \bar{F}_\tau \quad (6b)$$

where N_t is the number of nests in year t , s_W is overwinter queen survival and colony establishment, p_Q is the probability a colony produces queens (the binomial term in the 0-inflated queen production model, which did not depend on colony growth parameters in our study; see *Results*), β_i is the regression coefficients from the count term of the queen production model, and colony growth parameters, W_0 , k , τ and \bar{F}_τ are as defined above (see also Supplement material). The intercept, β_0 , differs among farm types. Elasticities were calculated analytically from eqn 6b as $\frac{\partial \ln \frac{N_{t+1}}{N_t}}{\partial \ln x}$ and evaluated at the values of β_i from the statistical queen production model.

Elasticity analysis is a prospective analysis (Caswell 2001), which quantifies the potential effects of future changes in demographic parameters. In addition to elasticity analysis, we performed a retrospective analysis (Caswell 2001) to quantify the contributions of observed variation in colony growth parameters to variation in growth rates. This analysis is similar to standard Life Table Response Experiments (LTRE; Caswell 2001), but was modified to account for structure of the colony growth model, and to include continuous variation

among colonies, as opposed to differences among fixed treatment groups. Specifically, we first calculated the value of the overwinter survival and colony establishment parameter, s_W , that would lead to constant population size under current conditions, given average values of other parameters. (Note that this retrospective analysis, unlike the elasticity analysis, requires an estimate of the s_W parameter.) Next, we varied each other colony growth parameter, in turn, to its lower 5% and upper 95% quantiles. We then calculated the growth rate that would result if that parameter were at its outer limits, with all other parameters at their mean values. We used the range of population growth rates that would result from the observed variation in each parameter as a retrospective metric of the realised importance of each parameter for population dynamics.

RESULTS

Colony growth

Colony growth increased with floral resources. The floral resource model was better than a constant-growth model and also better than the simple quadratic, linear, and constant models ($\Delta\text{AICc} > 10$ for all model comparisons; Table 1A). The floral resource model reproduced the qualitative dynamics of colony growth and decline; $R^2 > 0.6$ for all of the 59 colonies, median $R^2 = 0.92$ (Fig. 1).

Growth parameters differed among colonies, but did not differ significantly among local land cover types (conventional farms, organic farms, or semi-natural areas) or correlate with average flower density (Table 2). In general, the estimated colony growth rate per flower was negatively correlated with other colony growth parameters (Table 2). Although this pattern might imply that factors other than growth rate and flower density limit colony size, it is also a statistical null expectation, because a lower growth rate and higher initial size estimate, or higher flower density, lead to the same maximum size. Observed average parameters were 2.06 for average initial colony size on a log scale ($\ln W_0$), 6.37 weeks for average switch time (τ), 14.4 for average flower density (\bar{F}_τ , in millions per km^2), and 0.50 for average growth rate per flower (k), leading to a discrete-time weekly growth rate of 2.05. After they were placed in the field, colonies grew for a median of 6 weeks before queen dispersal and decline.

The maximum colony weight, as estimated from derived parameters ($= W_0 k^\tau \bar{F}_\tau$), also did not differ significantly among local land cover types (Table 2). The estimated maximum colony weight correlated strongly with the number of workers and males produced by the colony (as reported by Williams *et al.* 2012; Pearson correlation: $r = 0.72$, $N = 59$ colonies, $P < 0.007$).

Queen production

Overall, queen production was best fit by a 0-inflated negative binomial model (model 3 in *Methods: Analysis of queen production*) in which covariates affected the count term only ($\Delta\text{AICc} > 15$ for all other model structures; Table 1B). Within this model structure, queen production differed significantly

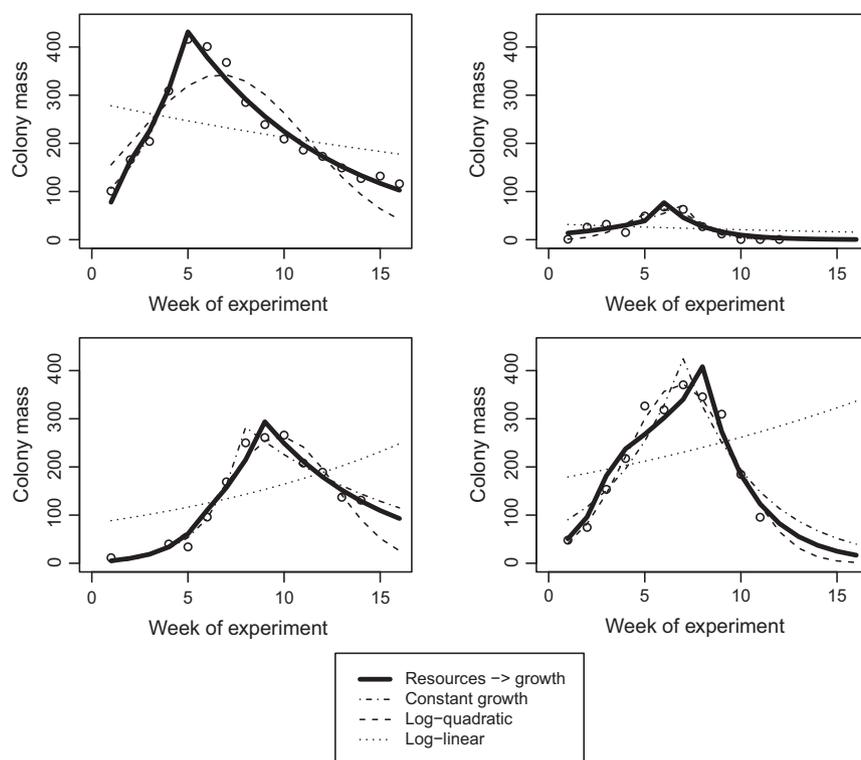


Figure 1 Weight gain trajectories of four representative colonies. Points (○) indicate observed mass (minus initial mass), and lines are the models fitted to the data.

Table 2 Associations of colony growth parameters with local land cover types (GLMM with random effect of site) and each other (Pearson correlation)

Colony growth parameter	Difference among local land cover types*		Correlation matrix of colony-specific parameters			
	χ^2	P	W_0	k	\bar{F}_τ	τ
Initial mass, W_0	0.54	0.764	–	–0.483 [‡]	–0.209 [†]	–0.073
Growth rate per flower, k	2.66	0.265	–0.483 [‡]	–	–0.453 [‡]	–0.311 [‡]
Average flowers per week, \bar{F}_τ	3.45	0.178	–0.209 [†]	–0.459 [‡]	–	0.075
Switch time, τ	1.50	0.472	–0.073	–0.311 [‡]	0.075	–
Maximum colony size, $W_0 k^\tau \bar{F}_\tau$	1.30	0.501	–	–	–	–

*All tests have 2 d.f.

[†]0.15 > P > 0.05 for $N = 59$ colonies.

[‡] $P < 0.02$ for $N = 59$ colonies.

among local land cover types and was positively associated with average floral resources, as well as initial colony mass, growth rate per floral resources and the length of the growth period (Table 3). Queen production was highest in semi-natural areas, intermediate on organic farms, and lowest on conventional farms, although only the two extreme land cover types (semi-natural areas vs. conventional farms) differed significantly based on 95% confidence intervals (Fig. 2).

Table 3 Analysis of queen production in relation to colony growth and farm type. Coefficients are from the count term of a 0-inflated negative binomial model. P -values from likelihood ratio tests of the full model relative to reduced models with each factor removed, in turn ('marginal' hypothesis tests)

	Estimate	SE	χ^2	d.f.	P
Colony growth parameters					
Initial mass, $\ln(W_0)$	0.431	0.015	16.4	1	<0.001
Growth rate per flower, $\ln(\lambda)$	174.6	46.1	16.0	1	<0.001
Average flowers per week, \bar{F}_τ	0.014	0.004	12.1	1	<0.001
Switch time, τ	0.352	0.130	6.5	1	0.011
Local land cover type*					
Conventional	–1.083	0.337	9.1	2	0.011
Organic	–0.399	0.329			
Overdispersion, $\ln(\theta)$	0.353	0.236			

*Coefficients are differences of queen production in each land cover type relative to natural areas. Hypothesis test is for the overall effect of 'Land cover type', relative to a reduced model with all three groups combined.

Colony growth and land cover covariates affected the number of queens produced by colonies that produced queens (the count term), but not the probability that a colony produced queens (the zero term; Table 1B). We validated the conclusion that covariates did not affect the probability of queen production by adding each in turn to the 0 term of the model in which covariates also affected the count term. None of these additions improved the fit of the winning model ($P > 0.2$ for all comparisons).

Although they were not as good for our data as 0-inflated models, one advantage of the GLMMs is that they explicitly

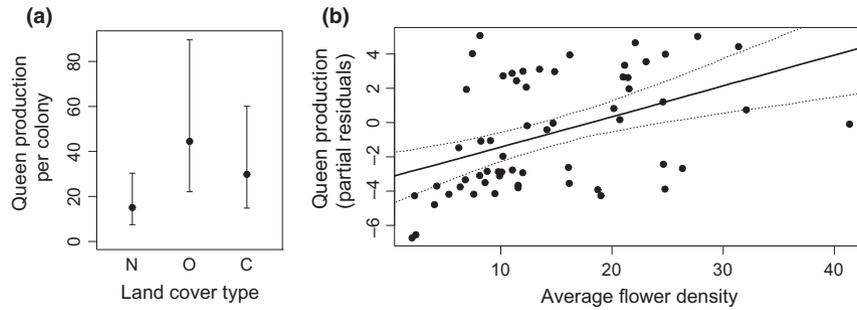


Figure 2 Queen production per colony vs. (a) local land cover type, and (b) average flower density (millions within 2 km per day, summed over a week). In (a) bars show ± 2 SE of the difference between values (added before back-transforming from log scale values), and N, O and C refer to semi-natural habitats, organic farms and conventional farms, respectively. In (b), dotted lines show 95% confidence limits of the slope of the partial residuals vs. flower density. For visual clarity, (b) is plotted on a log scale, i.e., the absolute value of residuals was log-transformed and multiplied by the sign (positive or negative) of its original value.

account for possible non-independence of the two colonies placed at each site. After accounting for local land cover type (as a fixed effect in GLMMs), variation among sites was much smaller than variation among colonies. In the GLMM with covariates of queen production, the random effect standard deviation for colony was 2.12, and the random effects standard deviation for site was 0.02.

Perturbation analysis

Based on elasticity analysis, population growth rate was most sensitive to the colony growth rate per flower ($\frac{\partial \ln \frac{N_{t+1}}{N_t}}{\partial \ln k} = \beta_2 = 174.6$). The second most important parameter for population growth was switch time ($\frac{\partial \ln \frac{N_{t+1}}{N_t}}{\partial \ln \tau} = \beta_4 \tau = 2.11$), followed by floral resource density ($\frac{\partial \ln \frac{N_{t+1}}{N_t}}{\partial \ln F_t} = \beta_4 \bar{F}_t = 1.17$), farm type ($\frac{\partial \ln \frac{N_{t+1}}{N_t}}{\partial \beta_0} = \left(\frac{\partial \ln \frac{N_{t+1}}{N_t}}{\text{difference in intercept terms}} \right) = 1.08$ for the largest difference, conventional vs. semi-natural) and overwinter survival and the probability of queen production ($\frac{\partial \ln \frac{N_{t+1}}{N_t}}{\partial \ln s_w} = \frac{\partial \ln \frac{N_{t+1}}{N_t}}{\partial \ln p_Q} = 1$). The least important parameter for colony growth was initial colony size ($\frac{\partial \ln \frac{N_{t+1}}{N_t}}{\partial \ln W_0} = \beta_1 = 0.431$).

Retrospective analysis of observed variation led to similar conclusions. The maximum likelihood estimate of the proportion of colonies that produced queens (p_Q) was 0.238, and the estimated growth rate intercept for the intermediate land use type (organic farms) was -2.19 . With these and the colony growth parameters (shown above), we calculated that the population size would be constant ($\frac{N_{t+1}}{N_t} = 1$ in eqn 5a) if the probability of overwinter survival and colony establishment (s_w) were 0.118. Relative to a baseline growth rate of 1, observed dynamics were most sensitive to observed variation in growth rate per flower (growth rate of 0.35 and 30.24 at 5 and 95% limits). Observed variation in initial mass, average flower density and switch time led to roughly similar differences in growth rates (range of 0.17–2.70 for initial mass, 0.36–3.38 for average flower density and range of 0.43–2.52 for switch

time). Estimated intercept terms for different land use types led to growth rates of 0.56 on conventional farms and 1.64 in semi-natural areas.

DISCUSSION

Our analyses demonstrated a positive impact of floral resources on bumble bee colony growth and queen production in real landscapes. The result provides a previously missing link from resources to reproductive success and subsequent population viability. In doing so, it partly resolves a mismatch between landscape- and colony-scale studies in the existing literature. By accounting for the dynamics of colony growth, we are able to reveal effects of resource environments on queen production.

Our ability to detect effects on queen production depended on the use of a mechanistic model to account for other sources of variation in the data. Therefore, it is important to ask whether our model adequately captures the experimental system. The trajectory of colony growth and decline we report for *B. vosnesenskii* is similar to patterns seen in other bumble bee species (Goulson *et al.* 2002; Whitehorn *et al.* 2012; bearing in mind that their figures average over individual trajectories for multiple colonies). In some bumble bee species (e.g. *Bombus terrestris*), there may be a transition to male production slightly before queen production (Duchateau & Velthuis 1988), such that the switch point in demography may slightly precede the mass decline. This timing has not been reported for species in North America (including not for *B. vosnesenskii*). Furthermore, even if the exact switch to reproduction occurs shortly before the start of mass loss, quantifying the switch from growth to decline allows us to use mass gain as a metric for colony growth rates and explore factors that contribute to spatial and temporal variation in growth rates.

An additional advantage of using a statistical model to quantify different processes is that we can evaluate the relative importance of different factors for colony dynamics. In our study, both the elasticity analysis and the retrospective perturbation analysis revealed that colony growth rate (per flower), rather than average flower abundance, was the most important parameter for population dynamics. Therefore, if we could understand and manage other factors that cause some colonies to grow quickly and others to grow slowly under the

same resource conditions, it would have a larger effect on colony dynamics than supplementing floral resources. We know that bumble bee colony growth depends on multiple drivers, such as parasites (Shykoff & Schmid-Hempel 1991), temperature (Holland & Bourke 2015) and pesticides (Whitehorn *et al.* 2012). Variation in these factors could cause differences in the observed colony growth rate per flower. Variation in plant communities could also lead to variable growth rates per flower. Pollen nutrient quality differs among plant species (Harmon-Threatt & Kremen 2015) and can affect bee performance (Roulston & Cane 2002; Tasei & Aupinel 2008). Although we know that all of these factors can affect colony growth rates, understanding their relative contributions to observed growth rates in the field remains a key gap in our knowledge.

Predictors with similar effects to average floral resources include local land use and the duration of the growth period. Local land use effects match recent studies showing effects of pesticides on colony growth (Gill *et al.* 2012; Whitehorn *et al.* 2012). They could also relate to microsite characteristics such as temperature. In our Northern California study area, typical daily maximum temperatures in June exceed 30 °C, and temperatures above 38 °C are not uncommon. At these temperatures, many workers shift from foraging to fanning air through the colony to cool it (Vogt 1986; N.M.W., unpublished data), which could reduce resource intake. The other parameter, growth duration, is important for queen production because colonies that grow longer get larger, and all else being equal, larger colonies produce more queens (Westphal *et al.* 2009; Goulson *et al.* 2010; Williams *et al.* 2012). However, in our study, colonies that grew longer also tended to have lower growth rates per flower (Table 2). This trade-off could reflect demographic constraints such as egg or sperm limitation (Rosenheim 1996), ecological constraints such as heat stress (Vogt 1986) or evolutionary constraints (i.e. timing of reproduction in relation to colony size and mortality risk (Oster 1976; Beekman *et al.* 1998; Poitrineau *et al.* 2009).

Two vital rates in the colony growth model had elasticity values exactly equal to one, which is similar to, but slightly lower than, the elasticity of floral resources. These two rates are the probability that a colony produces queens and the probability that a queen survives the winter and successfully establishes a colony. For these two parameters, the elasticities are defined exactly as equal to one because the population growth rate is directly proportional to both parameters; in other words, these elasticity values are determined by the assumption of strict proportionality. In our analysis (Table 2), the probability that colonies produce queens did not depend on colony growth parameters or final colony size. Although other studies have shown that larger colonies produce more queens (Williams *et al.* 2012), few other studies have separated the probability of queen production from the number of queens produced. If we could understand the factors that cause some colonies to produce queens and some not to do so, this insight might lead to additional management options to enhance bee population viability. Similarly, other studies have shown that bee populations may be nest site limited, rather than queen limited (e.g. Byron 1974), which would lead to differences in s_w . For both of these parameters (probability

of queen production and nest site limitation), we did not measure variation among colonies and so could only conduct a prospective elasticity analysis, not a retrospective analysis that incorporates observed levels of variation in the field. If these factors differ among sites, which is likely (Kells & Goulson 2003), they might contribute substantially to realised population dynamics, in spite of low elasticities.

Initial colony mass had the lowest elasticity of any parameter in our model. The implication is that, on a proportional basis, this parameter is least important for population growth rates. However, in the retrospective analysis, initial colony mass was as important for realised variation in colony dynamics as flower density or switch time. Thus, despite establishing colonies in the laboratory, initial colony mass varied more than floral resources or switch time. The initial mass effect could reflect the size at which colonies were released into the field (which was partly controlled), or their very early growth rates after they were placed in the field. In her field study, Elliott (2009) reported that colony growth rates increased with supplemental resources but not with surrounding floral densities and speculated that colonies must reach a minimum size before they are limited by floral resources. It may be that establishing our colonies in the laboratory helped them become large enough to be resource limited and that their ability to grow immediately when placed in the field contributed in a synergistic way to their ability to use the surrounding floral resources.

There has been increasing concern among ecologists and conservation biologists over the long-term viability of bumble bee species (Goulson 2010; Cameron *et al.* 2011), and many conservation efforts have focused on providing them floral resources. Our analysis unambiguously demonstrates that floral resources increase bumble bee population viability. However, our results also show that other factors are likely to be equally important. The modelling framework presented here provides a basis for evaluating conservation efforts throughout the species life cycle, which has been called for, but not yet done (Winfrey *et al.* 2011; Williams *et al.* 2012; Carvell *et al.* 2015). Further applications of this model, and extensions to include standard demographic processes such as density dependence and stage structure within and among colonies, will provide a solid foundation for grounding bee conservation in ecological theory.

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AUTHOR CONTRIBUTIONS

NMW conducted the field experiment and participated actively in the discussion of model structure and interpretation and

the writing and editing of the article. EEC conceived the idea of analysing colony growth dynamics using weight gain data, developed the structure of mathematical and statistical models, ran all analyses and is the primary author of the text.

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