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Abby Baur
Utah State University

James P. Strange
Utah State University

Jonathan B. Koch
Department of Biology and Tropical Conservation Biology and Environmental Science

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Research

Behavior

Foraging Economics of the Hunt Bumble Bee, a Viable Pollinator for Commercial Agriculture

Abby Baur,[1] James P. Strange,[1] and Jonathan B. Koch[2,3],

[1]USDA – ARS Pollinating Insects Biology, Management and Systematics Research Unit, Utah State University, BNR 261, Logan, UT 84322-5310, [2]Department of Biology and Tropical Conservation Biology and Environmental Science, 200 W. Kawili Street, Hilo, HI 96792, and [3]Corresponding author, e-mail: kochj@hawaii.edu

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Abstract

Globally, there are only five bumble bee (Hymenoptera: Apidae, *Bombus*) species that have been successfully commercialized for agriculture. The Hunt bumble bee, *Bombus huntii* Green, 1860, has been recognized as a suitable pollinator of crops and has a broad distribution in western North America, making it a viable candidate for commercialization. In this study, our goal was to characterize the foraging dynamics of *B. huntii* female workers under open field conditions. To accomplish this goal, we monitored three *B. huntii* colonies over an 8-wk period in the summer of 2012 in northern Utah. Using marked bees, we studied the relationship between foraging duration/offloading and pollen/nonvisible pollen collection. In total, we observed 921 foraging events across all three colonies. Of our observations, 82% ($n = 756$) were foraging events that included both a departure and arrival time observation. Average duration of pollen and nonpollen (i.e., nectar) trips across foragers is 41.86 ± 5.65 min (±SE) and 32.18 ± 5.89 min, respectively. Workers spent a significantly longer time offloading pollen in the nest after a foraging trip relative to workers without pollen present on their corbicula. Pollen foraging rate increases over the course of the day, likely due to the time it takes to learn how to forage on a diverse array of flower morphologies. Our study provides data on how long it takes for *B. huntii* to forage in open field conditions and will be useful when comparing foraging rates in controlled crop systems.

Key words: bumble bee, foraging, pollination, pollen

Bumble bees (*Bombus* spp.) are important for crop pollination, including buzz pollination of crops such as tomato, bell pepper, and blueberry (Shipp et al. 1994, Javorek et al. 2002, Whittington and Winston 2004, Vergara and Fonseca-Buendía 2012, Strange 2015). In addition to pollinating crops with small flowers in Solanaceae and Ericaceae, bumble bees are also effective pollinators of crops that have large flowers, such as squash (Cucurbitaceae) (Artz and Nault 2011). Because of their ability to effectively pollinate a diversity of flowering plants, bumble bee colonies have been commercially produced to deliver pollination services to open field and greenhouse crops (Velthuis and Van Doorn 2006). As of the year 2004, it was estimated that at least one million bumble bee colonies had been distributed worldwide to meet the pollination demands of greenhouse crops (Velthuis and Van Doorn 2006, Thornberry and Jerardo 2012). Bumble bees are the primary pollinator of tomatoes grown in protected cultivation, a crop that is estimated to be valued at US$690 million dollars annually in Canada, Mexico, and the United States (Thornberry and Jerardo 2012).

Starting in 1992, two North American bumble bee species, *Bombus occidentalis* Greene, 1858 and *Bombus impatiens* Cresson, 1863 were evaluated for commercial production to deliver pollination services to agricultural crops in the United States (Flanders et al. 2003). However, shortly after 1997, the commercial production of *B. occidentalis* was abandoned by major producers due to an infestation of *Nosema bombi* in the commercial stock (Flanders et al. 2003). For two decades, *B. impatiens* has been the primary, mass produced bumble bee species to deliver pollination services in both open field and greenhouse crops in North America. Concerns about the impact of commercialized *B. impatiens* colonies on native bumble bee communities are warranted as studies have documented the threat and persistence of emerging infectious diseases associated with *B. impatiens* (Sachman-Ruiz et al. 2015), and observations of commercial *B. impatiens* interacting with native bumble bees outside of containment in the western United States (Hicks et al. 2018, Looney et al. 2019, Strange and Tripodi 2019).

Given the need for a western North American bumble bee to be commercially available to growers, *Bombus huntii* Green, 1860 has been identified as a candidate for domestication (Fig. 1; Strange 2015, Koch et al. 2018). It has a range similar to *B. occidentalis* (Williams et al. 2014), with the exception of its northern distribution limited to southern Canada, and its southern distribution reaching as far south as the Trans-Mexican Volcanic Belt (Koch et al. 2018). North of Mesoamerica, *B. huntii* populations are genetically diverse and appear to be panmictic from southern Canada to the Sierra Madre Occidental (Koch et al. 2018). Thus, there is likely no risk in introducing novel genotypes of *B. huntii* to wild populations should commercial populations be moved throughout the western United States and Canada (Koch et al. 2018). *Bombus huntii* is documented to be an effective pollinator for greenhouse grown tomatoes, performing similarly to *B. impatiens* and *B. vosnesenskii* (Strange 2015). The species produces relatively large nests and an abundance of queens (i.e., gynes; Hobbs 1967, Husband 1977), which ultimately provides future colonies that can be used to pollinate agricultural crops (Velthuis and Van Doorn 2006). Unlike its commercially defunct predecessor, *B. occidentalis*, wild *B. huntii* populations have been associated with low pathogen prevalence (Cordes et al. 2012, Blaker et al. 2014).

The broad geographic distribution of *B. huntii* in western North America, estimation of range-wide genetic diversity, favorable life history traits for domestication, propensity for low-infection of significant pathogens, and effectiveness as a greenhouse pollinator affirms the decision to commercially produce the species. Although research within the last decade has provided new knowledge regarding the

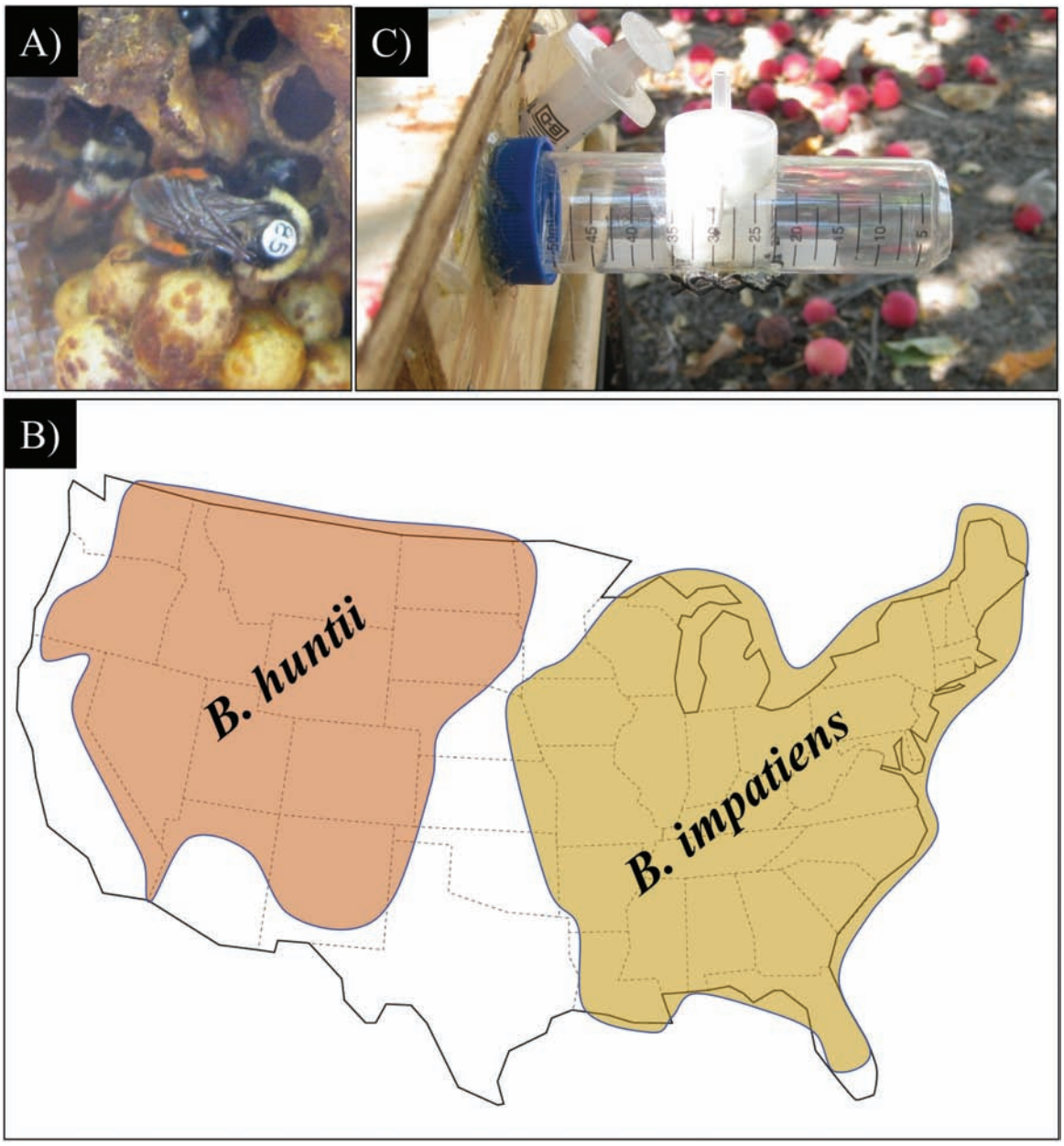

Fig. 1. (A) *Bombus huntii* forager with a marker on the dorsal mesosoma. (B) Approximate geographic distribution of *B. huntii* and *B. impatiens* in the conterminous United States [adapted from Williams et al. (2014)], and (C) modified entrance tube to slow down the departing/returning forager in order to record marker number and time of departure/return.

biology and natural history of *B. huntii*, no study has closely assessed colony foraging economics. Characterizing basic foraging behaviors at the colony level provides much needed insight into time of first flight in the day, duration of pollen and nonpollen foraging visits, and time spent in the nest (Brian 1952, 1954; Allen et al. 1978). Our goals in this study are to 1) test for duration differences in pollen and nonpollen foraging trips, and for duration differences in pollen and nonpollen offloading within the nest and 2) characterize the number of foraging trips performed throughout the day. The results of our study can guide growers in their management decisions as it presents data on the time of day *B. huntii* will be most active when foraging for floral resources. Identifying when *B. huntii* are most active in foraging for pollen can help growers determine when the best time to deploy their colonies for crop pollination.

Materials and Methods

Field Study

Three colonies of *B. huntii* were reared in the lab from wild-caught queens in northern Utah using the dual-queen nest initiation techniques described in Strange (2010). Colonies were held in the lab and fed sugar syrup and honey bee-collected pollen until at least 25 workers were present. After reaching a sample size of 25 workers, *B. huntii* individuals were marked with plastic honeybee queen markers from E.H. Thorne Ltd (Opalithplättchen) and Duro Super Glue (ethyl cyanoacrylate [$C_6H_7NO_2$] and glyceryl ester). Each female worker was placed into a 20-ml insect specimen vial on ice for 10–15 min until torpor was achieved. Workers were then removed from the ice, so as to quickly glue the markers onto the dorsal mesosoma, between the wings (Fig. 1A). Workers were then placed back on the ice for approximately 5 min to allow the glue to set. Following the treatment, workers were put directly back into their nests, as we observed a more expeditious return to nest duties by the workers, and better rates of marker retention when workers were not allowed to come back to thermal homeostasis in isolation. Markers were color-coded for quick identification to nest and numbered for identification to individual.

After workers from the three colonies were marked, the nests were placed into wooden boxes and deployed in Logan, UT (Latitude = 41.757450, Longitude = −111.812372). Nests were placed at approximately 10-m intervals in similar partial-shade microhabitats equidistant from the nearest floral resources. Observed nearby flowering plants included buckwheat (*Fagopyrum esculentum*), phacelia (*Phacelia* spp.), alfalfa (*Medicago sativa*), vetches (*Vicia* spp.), sunflowers (*Helianthus* spp.), nightshade (*Solanum dulcamara*), currant (*Ribes* spp.), dandelion (*Taraxacum* spp.), various mints (Lamiaceae), and clovers (*Trifolium* spp.). After deployment, nests were allowed to rest without interference by human observers for 2 d. Two of the nests (H44/45 and H4) were deployed on 8 July 2012, and the third nest (H27/28) was deployed on 15 July 2012. Based on a nearby weather station at the Ogden-Hinckley Airport, the observation period was predominantly warm (25.77°C ± 0.49 SE, maximum = 32.86°C, minimum = 19.14°C) and experienced little precipitation (0.13 mm ± 0.005 SE) (https://www.wunderground.com/history/monthly/us/ut/ogden/KOGD/date/2012–7).

To clearly read the marker on the mesosoma, we slowed forager entry and exit by fitting all nests with clear entrance/exit tubes (Fig. 1C). These tubes had narrow openings on the distal end, which served both to limit the number of foragers passing at one time and to exclude larger, inquiline *Bombus* queens from entering the nests. Newly emerged workers were captured and tagged on their first observed exit and were returned to the entrance/exit tube to achieve thermal homeostasis. Nests were observed over 1-h intervals from 11 July to 17 August 2012 to note time of entry, exit, and presence or absence of pollen. Observation of H27/28 began on 15 July 2012. A total of 49 observation hours of *B. huntii* foraging events was completed, with 921 total observed events. Of the 921 observed events, 756 events were associated with both departure and arrival times and used in the final analysis. Duration measurements of both foraging and offloading behaviors were kept to the nearest minute. Offloading behaviors include any behaviors occurring in the nest when a returning forager is observed with pollen or no visible pollen enters into the nest. Thus, offloading behavior is not exclusive to removal of pollen from the corbicula or potential regurgitation of nectar from their crops, but can also encompass behaviors such as resting and defecation (Michener 1974). On some occasions, observations were made for a span of 2 h, in order to determine whether trips longer than 1 h were common. In total, we observed colonies for 92 h across 17 d (5.42 h ± 0.83 SE).

In addition to documenting the time of entrance and exit behaviors, we further determined whether pollen was observed on the forager's corbicula. Each foraging trip was designated as the forager having "pollen" or "no visible pollen" because there could be no reasonable assumption that a lack of pollen necessarily implied nectar collection. Furthermore, there were no data collected that would determine the presence or absence of nectar located within the forager's crop in any quantity. However, the survival of a bumble bee colony inherently dictates that there must have been an inflow of nectar, but foragers were neither weighed nor dissected to account for this process. To minimize observer impact on bee behavior, nests were only very rarely opened during the trials to inspect nest health. At the conclusion of the study, nests were destroyed by placing in a freezer at −20°C.

Statistical Analysis

We developed two global models to test for the effect of Julian day, the presence/absence of pollen on the forager's corbicula, and colony origin (H44/45, H4, H27/28) on the duration of 1) offloading (inside of nest) and 2) foraging (outside of nest). Models were developed and evaluated using *car* and *MuMIn* libraries in the R statistical programing language (R Core Development Team 2018). As the duration data followed a Poisson distribution (non-Gaussian), we elected to use a generalized linear model (GLM) with the Poisson link function.

Preliminary analysis found that the foraging model was overdispersed, which could ultimately affect β parameter estimates. To account for overdispersion we used the quasi-Poisson link function (Ver Hoef and Boveng 2007). Overdispersion was calculated by calculating $\hat{c}$ (residual deviance/degrees of freedom), where $\hat{c}$ values close to 1 imply that the model is not overdispersed. To determine whether any of the observations significantly influenced the model parameter estimates, we used the function *influenced.measures* that computes some of the regression diagnostics of GLMs discussed by Belsey et al. (1980) and Cook and Weisberg (1982). Observations that were identified as significant were removed from the model, with the model subsequently updated with the *compareCoefs* in the *car* library. β ± SE (model parameter estimates) of the updated and nonupdated model were compared to determine whether removal of an observation influenced parameter estimates. If SE of all β of the explanatory variables overlapped between the updated and nonupdated models, we elected to retain observation outliers as they did not influence the model parameter estimates.

Different link functions and filtering of significant observation outliers were observed in the foraging and offloading models. The global foraging model was highly overdispersed at $\hat{c}$ = 15.39. After iterative examination of β's following the removal of significant observation outliers, we elected to remove seven observations from the global foraging GLM. Removal of the outliers resulted in an overdispersion estimate of $\hat{c}$ = 12.45 (n = 270, 97% of data retained for analysis). The global offloading GLM was initially overdispersed at $\hat{c}$ = 4.33. However, after iterative examination of β's following the removal of significant observation outliers (n = 61), $\hat{c}$ was reduced to $\hat{c}$ = 0.97 (n = 408, 87% of the data retained for analysis).

We used the function *dredge* to examine all possible combinations of the models based on the parameters in the global model. We used Akaike's Information Criterion (AIC), corrected for small sample sizes (AICc) to determine which combination of model parameters best explained duration in the offloading and foraging models. Smaller values of AICc suggest better fit of the parameter combinations to the observed data, whereas larger values of AICc suggest poor fit of the parameter combinations to the observed data. The AICc guided approach to model selection is useful as it penalizes the model when new parameters are added, thus enforcing parsimony (Aho et al. 2014). We elected to use AICc, rather than the AIC because as sample size increases, the correction term in the AICc vanishes and AICc matches AIC. Models within 2 AICc are more or less equivalent and considered top competing models. To further determine the best model, we also calculated AICc weights (w_i), which is the probability of each model given the data and set of models. Thus, larger values of w_i suggest higher support of the model by the data, whereas smaller values of w_i suggest lower support of the model by the data. Finally, as the foraging duration model was constructed using the quasi-Poisson link function, we calculated the QAICc, which incorporates the variance inflation factor in its AICc calculation.

To account for model selection uncertainty, we performed model averaging with the function *model.avg*. We took the top competing models that produced ΔAIC ≤ 2, and averaged the predictions of the different models, weighted by probability of the models w_i. We examined the relative importance of each variable in the averaged model. Relative importance is calculated by summing w_i across all models in the top models where the variable occurs. Variables with strong support have a cumulative w_i near 1, whereas variables with weak support have a cumulative w_i near 0.

Finally, we were interested in testing for the effect of "time of day" on the number of foraging events associated with visible pollen collection. To examine this relationship, we performed logistic regression with GLM. To quantify the proportion of forager visits that resulted in a pollen load, we counted the number of total foraging events that occurred within a 10-min interval from 06:30 to 20:00 across all observations and colonies (75 10-min intervals and 278 pollen and nonpollen forager observations). We examined the proportion of pollen foraging events at 10-min intervals across all three colonies and accounted for all foraging events (pollen and nonpollen) in our analysis by weighting each observation. Preliminary analysis found no significant overdispersion in the model ($\hat{c}$ = 1.11), and thus no subsequent analysis to control for overdispersion was necessary. Data used for analyses are available on FigShare (https://doi.org/10.6084/m9.figshare.7698281.v1).

Results

Over the course of the study, approximately 125 marked foragers were recorded more than once, with 73 foragers seen in more than one day. We observed and marked a total of 56 foragers from H44/45, 39 for H27/28, and 30 for H4. Males and queens were observed but never marked; thus, we were unable to collect total colony size. The mean duration of a foraging trip resulting in pollen collection was 41.86 ± 5.65 min (±SE; Median = 38), and the mean duration of a foraging trip not resulting in pollen collection was 32.18 ± 5.89 min (Median = 30). On average, we observed 6.62 ± 2.81 foragers per colony per hour (Median = 6.17). The mean duration spent offloading between pollen trips was 6.02 ± 1.78 min (Median = 4), and the mean duration spent offloading with no visible pollen collection was 3.56 ± 1.44 min (Median = 2). The longest observed trip was 156 min and did not result in pollen collection. Because of our study design, it is impossible to determine whether trips of such duration were more common than observed. In fact, trips over 1 h accounted for less than 4% of all observed events (Fig. 2).

Various combinations of the variables explained the foraging and offloading global models. Based on $QAIC_c$ and w_i, the model that only included pollen presence/absence best explained the foraging data (Table 1). However, based on $\Delta QAIC_c$, the top three foraging models included different combinations of the variables (Table 1). Although none of the top three models performed significantly better than each other (all models within $\Delta QAIC_c$ = 2), all three top models performed better than the null foraging model ($\Delta QAIC_c$ = 12.23). Based on the model with the greatest w_i (Foraging Duration ~ Pollen), foraging duration increased when pollen was detected on the corbicula of a forager (Table 2). Specifically, if pollen was detected on the corbicula of a returning forager, there was a 69% (95% CL = 54%, 85%) increase in the duration of the foraging trip relative to a forager without pollen on the corbicula. Model averaging found that the relative importance of the pollen presence/absence was high (= 1), whereas the colony and Julian day had low relative importance to the averaged model (Table 2). Furthermore, the 95% CL of the colony and Julian day β's intersected 0 (Table 2), implying that these parameters are not important predictors of forager duration.

Based on AICc and w_i, the model that included pollen presence/absence, colony, and Julian day best explained the offloading data (Table 1). Only two of the top models were within the ΔAIC_c = 2 and had comparable w_i (Model 1: Offloading Duration ~ Pollen + Julian Day + Colony and Model 2: Offloading Duration ~ Pollen + Julian Day). When averaged, the two models could better explain offloading duration in comparison to the null model (ΔAIC = 87.55, Table 1). Specifically, if pollen was detected on the corbicula of a returning forager, there was a 39% (95% CL = 26%, 52%) increase in the duration of the offloading trip inside the nest relative to a forager returning without pollen on the corbicula. For each increase in Julian day, there was a 99% increase (95% CL = 98%, 99%) in the duration of the offloading trip inside the nest relative to a forager returning without a pollen on the corbicula. Finally, our results show that there are colony-level differences in duration of the offloading trips. Offloading by foragers in the H44/45 colony experienced an 84% (95% CL = 69%, 99%) increase in the amount of time it took to offload pollen relative to offloading foragers in the H27/28 colony. The 95% CL of the β accounting for the comparison of H4 and H27/28 colonies intersected 0 (Table 2), implicating that this parameter is not an important predictor of forager offloading.

Finally, there was a significant increase in the proportion of foragers associated with a pollen collection event for each 10-min increase in the time of day ($\beta = 3.8 \times 10^{-5} \pm 1.1 \times 10^{-5}$, 95% CL [$1.22 \times 10^{-5}$, 5.64×10^{-5}], z = 3.02, P = 0.003; Fig. 3). However, it is also clear that many foraging visits observed throughout the day also resulted in non-pollen visits (Supp Fig. S1 [online only]).

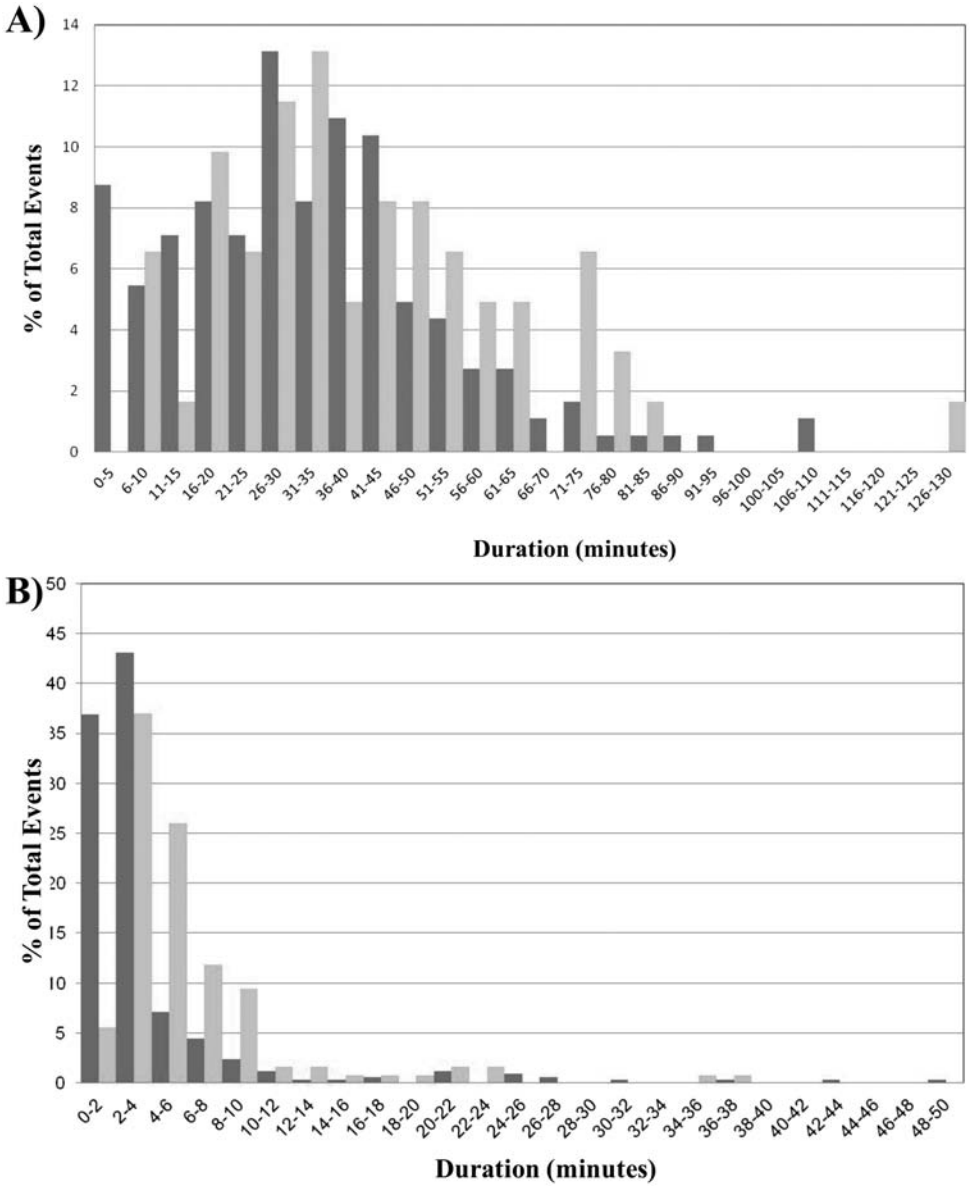

Fig. 2. (A) Percentage of total pollen (light gray bar) and nonpollen (dark gray bar) *Bombus huntii* foraging events across different duration intervals. (B) Percentage of total pollen (light gray bar) and nonpollen (dark gray bar) *B. huntii* offloading events by a forager across different duration intervals.

Table 1. Top competing models based on Akaike's information criterion adjusted for small sample sizes (AICc) and the null model are shown for models examining factors that influence the duration of (A) a foraging event across 270 foraging events of three *Bombus huntii* colonies and (B) an offloading event across 408 offloading events of three *B. huntii* colonies

Model	Model Description	df	ΔQAICc* or ΔAICc‡	w_i
(A) Foraging model	Pollen	2	0	0.42
	Pollen, Colony	4	0.35	0.36
	Pollen, Julian Day	3	1.31	0.22
	Null	1	12.23	0.001
(B) Offloading model	Pollen, Colony, Julian Day	5	0	0.57
	Pollen, Julian Day	3	0.57	0.43
	Null	1	87.55	0

The number of foraging and offloading events were reduced from a total of 1019 observed events (foraging + offloading) after accounting for observation outliers that affected parameter estimates (β). Fixed factors examined in the competing models included the following: presence/absence of pollen, colony origin, and Julian day. QAIC = quasi AIC, where AIC is calculated based on the model's variance inflation factor (see Methods for discussion), df = degrees of freedom. In addition, w_i (Akaike weights) for each model is shown. $\Delta QAIC_c$ is calculated for the foraging model (A), and ΔAIC_c is calculated for the offloading model (B).

*QAICc value of top foraging model = 414.4.

‡AICc value of top offloading model = 1486.4.

Table 2. Relative importance, model-averaged parameter estimates (β), and 95% CL of explanatory variables included in top models examining the duration of (A) foraging events and (B) offloading events

Model	Variable	Relative Importance	β	Lower 95% CL	Upper 95% CL
(A) Foraging model	Pollen	1	0.31	0.15	0.46
	Colony	0.36	–	–	–
	H4 vs. H27/28	–	−0.16	−0.34	0.03
	H44/45 vs. H27/28	–	0.02	−0.15	0.18
	Julian Day	0.22	0.003	−0.004	0.01
(B) Offloading model	Pollen	1	0.61	0.48	0.74
	Colony	0.57	–	–	–
	H4 vs. H27/28	–	0.08	−0.08	0.24
	H44/45 vs. H27/28	–	0.16	0.01	0.31
	Julian Day	1	0.01	0.004	0.02

See Table 1 for description of explanatory variables.

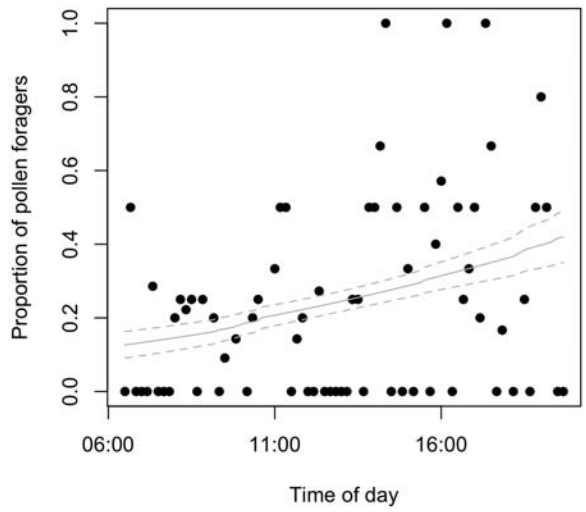

Fig. 3. Proportion of *Bombus huntii* foragers returning to the nest with pollen across time of day. Line represents fitted model using logistic regression with 95% CL.

Discussion

We found that foragers leaving the nest took significantly longer to return if they were bearing pollen upon re-entry. Foragers returning with pollen also remained in the nest longer before exiting the nest than those bees entering without pollen. In general, we found no difference in foraging duration between colonies. However, we did find colony-level differences in offloading pollen in two of the three colonies we observed. Furthermore, we found that the amount of time spent offloading pollen is positively correlated with Julian Day, suggesting that as the season advances, more time is spent in the nest during the pollen offloading phase. However, given the small effect size of Julian Day (β = 0.01) in our model, we suggest a cautious interpretation (Table 2). Why more time is spent in the nest may be due to the size of the pollen load obtained later in the season (Spaethe and Weidenmüller 2002), or potentially due to the fact that as a forager ages she might be unable to offload pollen loads as quickly (Cartar 1992, Foster and Cartar 2011; Fig. 2B).

In addition to differences in foraging and offloading duration, we also discovered a significant shift towards increased pollen collection later in the day (Fig 3). The shift to increased pollen foraging in the afternoon, as opposed to the morning, is consistent with the results of previous studies on other bumble bee species (Allen et al. 1978). Nectar foraging requires less learning time than pollen foraging (Heinrich 1976) and may explain why it might be the most dominant foraging behavior earlier in the day (Fig. 2). The decision to pollen forage later in the day might not be limited to temperature (Heinrich 2004), but rather due to the time it takes to learn the complex motor skill of pollen removal from different flower morphologies (Raine and Chittka 2007). There is experimental evidence to support the hypothesis that *B. terrestris* pollen collection rate increases over the time of day because of the time it takes to learn the motor skills associated with effective pollen removal from a complex flower. Switching between complex and simple flower morphologies might pose a significant barrier to effective pollen foraging and may explain why some bee species are typically more specialized in their pollen foraging preferences.

Our study provides important groundwork of *B. huntii* foraging behavior, providing insight into their expected performance as a commercial pollinator. Our data suggest that *B. huntii* requires time to learn how to forage for flowers in the landscape (Raine and Chittka 2007), as evidenced by increased pollen foraging later in the day. However, we did not control for what types of flowering plants were available to *B. huntii* foragers. It is possible that limiting available pollen resources to a single crop might decrease the time it takes to learn how to forage for pollen and pollinate. In a greenhouse environment, *B. huntii* foraging rates might increase earlier in the day when compared with *B. huntii* foraging rates in the open field conditions as found in our study. However, limiting bumble bee colonies to single pollen source in a greenhouse might limit the nutrition they need to produce more offspring throughout the season, potentially limiting the number of workers that could be reproduced (Vaudo et al. 2016). Characterization of nutritional requirements of bumble bees and the pollination needs of greenhouse crops, especially in mixed crop systems may provide insight into how to maximize a colony for agricultural purposes.

The amount of time spent in and outside of the nest is linked to forager senescence, disease, and pesticide poisoning (Dukas and Visscher 1994, Feltham et al. 2014, Koch et al. 2017). Foraging duration may be a useful behavioral indicator for growers to track when working with bumble bees foraging in open field conditions (Feltham et al. 2014, Gill and Raine 2014). As pollen collection and removal is a complex behavior (Raine and Chittka 2007), the amount of time it takes to forage and offload pollen will likely be affected by biotic and chemical agents. Although our study shows that *B. huntii* forages more frequently in the afternoon, our data suggest that *B. huntii* is likely foraging for nectar (nonpollen foraging

events) in the early morning. Bumble bees are sensitive to the timing and concentration of pesticide application (Blacquière et al. 2012, Whitehorn et al. 2012, van der Sluijs et al. 2013). To reduce acute pesticide poisoning, some pesticides are applied to plants when they are not in bloom to ensure that beneficial insects, including bees, have limited direct exposure to residues (EPA Reg No. 86203-14). Failure to follow pesticide application regulations has resulted in a massive unintended killing of bees. Given that *B. huntii* likely forages for nectar in the morning, the timing of pesticide application on crops and phenology should be evaluated to ensure minimal impact to the health of commercial colonies foraging under open field conditions.

In summary, we capture detailed information on the duration of foraging and offloading behaviors of a promising insect for commercial pollination. Future studies of *B. huntii* foraging economics should consider the type and volume of resources being brought into the colony as it relates to colony growth and nutrition requirements (Allen et al. 1978, Goulson et al. 2002, Vaudo et al. 2016). Foraging duration for both pollen and nonpollen is affected by the available resources in the environment and the nutritional needs of the colony. In greenhouse settings, it is possible that *B. huntii* foraging rate per flower will increase, and therefore cascade towards peak foraging earlier in the day, as opposed to later in the day as documented in our study. Unlike a field setting, a greenhouse setting typically exposes foragers to a single crop and a single flower morphology. Exposure to a single floral morphology might require less learning time for a forager in comparison to a forager exposed to diverse floral morphologies and pollen rewards. The results presented here provide insight into *B. huntii* foraging dynamics in open field settings. Continued study of *B. huntii* foraging economics will aid in the evaluation of management techniques and feasibility of using the species to deliver pollination services to crops.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

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