Article

BUMBLE BEE COLONY HEALTH IS DIMINISHED IN A MESOTUNNEL ENCLOSURE PLANTED WITH A CUCURBIT MONOCULTURE CROP

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Journal of Pollination Ecology, 39(22), 2025, pp 289-305

DOI: 10.26786/1920-7603(2025)859

Received 23 April 2025, accepted 9 October 2025

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Abstract—The use of "mesotunnels" (mesh netting pest-exclusion structures) as a sustainable pest management strategy is increasing among organic vegetable growers. However, pollination management presents a challenge in this system, and little is known about how mesotunnels impact pollinator health. This study examines bee colony health in mesotunnels, using commercial *Bombus impatiens* colonies in cucurbit crop mesotunnels as a relevant model system in a two-year experiment. To assess colony-level health, we combined several variables into "colony health indices" that produce summary values of the somatic (related to pollination service delivery, including number of workers, worker and nest mass, and stored pollen and nectar), reproductive (related to sexual reproduction, including number of immatures, drones, and queen size), and overall colony health (including all variables in somatic and reproductive indices). We found that in 2023 *B. impatiens* colonies in a cucurbit mesotunnel foraging environment had worse reproductive health and overall health than free-foraging colonies, but performed similarly in their somatic health. In several measurements, colonies from mesotunnels performed similarly to colonies with no foraging access. Our results suggest that commercial colonies in mesotunnel environments are not compromised in their potential to provide crop pollination services, but are compromised in their ability to reproduce and persist year-over-year. Our colony health indices could be adapted to assess the status of reproduction and ecosystem service delivery for social bees.

Keywords—Pollinator health, protective cover agriculture, row covers, bee colony health, pollination management

INTRODUCTION

Sustainable pest and pollination management is necessary for a sustainable food supply, especially in the context of climate change (Settele et al. 2016) and the global biodiversity crisis (Raven & Wagner 2021). To address this challenge, protective covers and other forms of controlled environment agriculture are increasingly being used to protect crops from unfavourable climate conditions and insect pests (Dohlman et al. 2024). Protective covers, such as glasshouses, polytunnels, and insect netting, have potential sustainability advantages over conventional crop production, including the physical exclusion of insect pests reducing the need for pesticide use (Benke & Tomkins 2017; Cowan et al. 2022; Calvo-Baltanás et al. 2025).

In particular, the use of "mesotunnels" as a sustainable pest management strategy in horticultural crop production is popular among organic specialty crop producers (Cheng et al. 2023). Mesotunnels are a type of row cover that use fine-mesh netting to physically exclude pests from damaging crops (Sideman 2017). The fine mesh netting is woven from plastic threads, allowing air and water movement through the structure but preventing passage of insects larger than the pore size. The netting is draped over a support frame approximately 1 m in height, forming an enclosure around the crop field that is larger than a low tunnel, but smaller than a high tunnel/polytunnel or glasshouse (hence the name "meso-" tunnel) (Fig. 1A). Mesotunnels have modest microclimate effects (Nair & Ngouajio 2010; Acharya et al. 2019), allowing them to be used for pest exclusion for crops in climatic conditions where low tunnels, polytunnels, or glasshouses would trap too much heat and humidity for crop growth (Tillman et al. 2015; Díaz-Pérez et al. 2024). Recent studies have found the mesotunnel system to be highly effective at reducing pest pressure and improving yield for a number of crops, while reducing or eliminating the need for organic insecticide application (Skidmore et al. 2019; Nelson et al. 2023; Fiske et al. 2024). However, pollination management for insect-pollinated crops remains a challenge (Pethybridge et al. 2024; Mphande et al. 2024), since the netting also prevents most pollinators from reaching the crop.

Growers often use stocked bumble bee colonies (*Bombus* spp.) to provide pollination services to pollinator-dependent crops under protective covers. These colonies are typically sourced from commercial insectaries, such as BioBest Sustainable Crop Management, Inc. and Koppert Biological Systems, Inc. in North America and Europe, and are intended to provide on-demand crop pollination services during the 8-10 week lifespan of the colonies before dying off or being terminated by the user (Natupol Excel 2025). Commercial colonies may be used alone or to augment wild bee pollinators, but are not intended to establish permanent feral populations (Thorp 2003). Bumble bees are efficient pollinators of cucurbit crops (Artz & Nault 2011) and crops requiring "buzz" pollination, such as tomatoes (Toni et al. 2021), and are active in a range of environmental conditions (Guerra-Sanz 2008), making them ideal pollinators in protective cover systems. In particular, *Bombus impatiens* Cresson is commonly deployed in cucurbit crops (family Cucurbitaceae; melons, squashes, cucumbers) under protective covers, although cucurbit pollen has been observed to have detrimental effects on bumble bee fitness (Brochu et al. 2020, Treanore et al. 2019). Past research of cucurbit crops under mesotunnels has shown the tradeoffs and challenges of implementing pollination management in this system. Using stocked bumble bees in a sealed mesotunnel reduces pest pressure compared to management strategies that involve full or partial removal of the netting for wild pollinators to access the crop (Pethybridge et al. 2024; Mphande et al. 2024); despite these benefits, lower seed set and marketable crop yield has also been observed when using stocked bumble bees (Fiske 2024).

While a majority of studies find that stocked bumble bee colonies provide adequate crop pollination services in protective cover systems, there are insufficient studies examining pollinator health outcomes in these conditions (reviewed in Kendall et al., 2021). Of the studies reviewed that do consider pollinator health outcomes in protective cover systems, 50% found negative effects on *Bombus* spp., but each considers a different set of variables in assigning "pollinator health" (Kendall et al. 2021). Several elements of the conditions in protective cover systems could be contributing to these effects, including insufficient quantity and diversity of floral nutritional resources (Whittington & Winston 2003) and behavioral changes in response to the light, temperature, and humidity conditions (Birmingham & Winston 2004). Adequate pollination services from healthy bumble bee colonies are necessary for successful yields in protected cover agriculture, so it is important to develop a better understanding of pollinator health within protected cover systems.

"Pollinator health" can be described at scales ranging from the individual-level to the community-level, but lacks a unified definition and means of measurement (López-Uribe et al. 2020). Two major priorities of pollinator health are 1) pollination service delivery, a population's ability to provide sufficient pollination services to crops and wild plants; and 2) conservation, a wild bee population's ability to reproduce itself and persist in the environment over time (Jones & Rader 2022). For social, colony-forming species such as most bumble bees, the colony unit is the crucial level at which these processes occur (Goulson 2010). Foragers most meaningfully provide pollination services in the aggregate, since it typically takes multiple visits per flower to complete pollination and many individual bees are needed to cover any meaningfully large area (McGrady et al. 2021). Sexual reproduction also takes place at the colony-level due to the division of reproductive labour within social bee colonies

(Goulson 2010). Despite the importance of the colony-level unit for social bee species, we lack methods to assess the health status of a colony as a whole. This is complicated by the numerous variables that could be considered in assessing colony-level health, which may not respond uniformly and predictably to the environment. Selecting only one of these variables as an indicator may give a misleading impression of the overall colony status. There is a need for shared methods to synthesize the numerous elements of colony health into summary values that can be interpreted and compared across different contexts and species (López-Uribe et al. 2020).

The growing prevalence of stocked *Bombus* spp. use in protective cover agriculture presents the need for further investigation and standardization in evaluating the health outcomes of bumble bees under these conditions. In this study, we use commercial *B. impatiens* colonies in a cucurbit crop mesotunnel to determine the colony-level health outcomes of exposure to this foraging environment in a two-year field experiment. We selected *B. impatiens* because it is the only species of bumble bee reared commercially for pollination services in the eastern United States and is ubiquitous in wild bee populations across the eastern United States. We selected cucurbit crops (muskmelon and acorn squash) as examples of highly pollinator-dependent crops (Knapp & Osborne 2019) of economic importance to organic specialty crop producers, and which growers commonly produce with the mesotunnel pest exclusion technique (Cheng et al. 2023). This experimental system thus represents a realistic and relevant use case for commercial bumble bee colonies.

Our objectives are to 1) assess the colony health outcomes of *B. impatiens* in a cucurbit crop mesotunnel foraging environment, 2) synthesize the many variables that contribute to bee colony health with a colony health index, and 3) determine if any individual variables might serve as an indicator of the overall colony health status. We compare colonies in the mesotunnel foraging environment with colonies that foraged freely on an organic research farm (positive control) and colonies that did not forage (negative control). We dissected colonies to measure variables that contribute to colony-level health (e.g. nest mass, adult bees, and brood) and compare these across treatments and years. We hypothesize that bumble bee colonies in a mesotunnel foraging environment will have intermediate colony health measures compared to free-foraging and no-foraging colonies. We also present novel "colony health indices" to assess the performance of two major processes of pollinator health (pollination service delivery and reproduction) and compare these across foraging treatments and years. We hypothesize that the colony health index values will effectively summarize the numerous variables contributing to the colonies' overall conditions, and some individual variables may be identified to be closely correlated with the overall index value. In the context of commercial bumble bee colonies used on farms, pollination service delivery is essential whilst colony reproductive health is considered irrelevant, since the colonies' purpose is to pollinate crops during a limited time period. Commercial colonies are not intended to establish feral populations on farms, though they often do so inadvertently (Dafni et al. 2010). Our study thus approaches the reproductive outcomes of commercial colonies as potentially informative for wild bumble bee conservation, rather than a desirable outcome for commercial colonies themselves. Our experimental design does not allow us to identify which elements of the cucurbit crop monoculture-mesotunnel system are causative of the effects on bumble bee colony health, but does allow us to generate novel documentation of the health status of colonies in this environment.

MATERIALS AND METHODS

We conducted field experiments in the summers of 2022 and 2023 at the University of Kentucky Horticulture Research Farm (37°58′25.92″ N, 84°32′5.85″ W). This 40.5 ha farm is divided into conventional and USDA-certified organic zones in production with a range of horticultural and orchard crops; all experiments described took place on the organic section of the research farm using USDA-certified organic products and practices (National Organic Program 2025). The immediate surrounding landscape consists of suburban residential and mixed-use commercial development and open grassy fields.

EXPERIMENTAL DESIGN

To understand the impact of mesotunnels on bumble bee colony health, we compared colonies in the mesotunnel foraging environment with colonies that foraged freely on an organic research farm (positive control) and colonies that did not forage (negative control). To prepare the mesotunnel treatment, in 2022 we established "Athena" muskmelon (*Cucumis melo* L.) (Johnny's Selected Seeds, Waterville, ME, USA) seedlings in the greenhouse; in 2023, we established "Table Ace" acorn squash (*Cucurbita pepo* L.) (Seedway, LLC., Hall, NY, USA) seedlings in the greenhouse (Table 1). We prepared fields for plot establishment by forming plastic-covered raised beds (Berry Global, Evansville, IN, USA) with drip irrigation lines (20.32 cm Aqua-Traxx drip tape; The Toro Company, Bloomington, MN, USA) on 2.1 m centres with a Rain-Flo plastic layer implement (Rain-Flo Irrigation, East Earl, PA, USA) and Kubota m9540 tractor (Kubota, Osaka, Japan), and applied NatureSafe 10-2-8 coarse fertilizer (Darling Ingredients, Irving, TX, USA) at a rate of 18 kg/ha.

We transplanted the seedlings at a 0.91 m in-row spacing and installed mesotunnels over the plots on the same day of crop transplant. Mesotunnel establishment included placing bent electrical conduit hoops into the soil, draping the net (Protek-Net 60 gram, Dubois Agrinovation, Saint-Remi, Quebec, Canada) over the plot, and securing the net edges with rock bags (Fig. 1A) to seal the enclosure. On the transplant date, we also established a weed suppression practice in the furrows between the raised beds (brown soil space seen between white raised beds in Fig. 1A) to limit

Table 1. Field work activity dates for 2022 and 2023 experiments.

Task	2022	2023
Sow seeds in greenhouse	April 25	April 26
Bed formation	May 17	May 12
Transplant and install mesotunnel	May 25 and 31	May 25 and 26
Install bee boxes	June 07	June 13 and 20
Terminate bee boxes	July 07	July 12 and 18

Figure 1. A) Mesotunnel structure used by organic crop growers for pest exclusion. This structure is used in the "cucurbit mesotunnel" treatment in this experiment. B) Method of deploying bumble bee colonies in the field.

Figure 2. Locations of cucurbit mesotunnel colonies (green) and free-foraging colonies (blue) in 2022 experiment (A) and 2023 experiment (B) on the University of Kentucky Horticulture Research Farm. Images adapted from Google Earth.

flowering weeds that could provide additional floral resources and compete with the crop. In 2022, we seeded teff grass (*Eragrostis tef* (Zucc.) Trotter) (Corvallis-nitro coat; Welter Seed, Onslow, IA, USA) in the furrows at a rate of 40.75 kg/ha; in 2023, we covered the furrows with black plastic woven landscape fabric (Martin's Produce Supplies LLC., Liberty, KY, USA). We irrigated the crop beds on an as-needed basis throughout the growing season using the drip irrigation system installed during field preparation. We visually surveyed plots for presence of insect pests and symptoms of plant disease (wilting, yellowing) weekly, but did not observe notable pest or disease pressure during the experimental period. No agrichemical products (insecticide, herbicide, or fungicide) were applied to the plots during the experimental period. In 2022, we applied green lacewing larvae (*Chrysoperla rufilabris* Burmeister) (Arbico Organics, Oro Valley, AZ, USA) at a rate of 2 larvae per 0.09 m^2 on June 2 to suppress aphid populations in the mesotunnels.

Each plot consisted of three raised beds covered by a 36.6 m by 6.4 m mesotunnel, resulting in a stocking rate of 1 colony per 234 m^2. The plot dimensions were determined by constraints in the field size and equipment size available, and were designed to be realistic to the field sizes of a central Kentucky diversified vegetable grower. We randomly assigned the plot locations in the fields. In each year the experimental plots were embedded within a separate experiment established with a randomized complete block design. In 2022, the muskmelon mesotunnel plots were a treatment within an experiment testing pollination management strategies for mesotunnels. In 2023, the acorn squash mesotunnel plots were a treatment within an experiment testing floral diversity within mesotunnels (Fig. 2). We counted the number of flowers available in the plots within 1 m^2 quadrats once per week and found an average of 26.1 flowers/m^2/week in 2022 and 21. 4 flowers/m^2/week in 2023.

We received Natupol-Excel *Bombus impatiens* colonies from Koppert Biological Systems, Inc. (Howell, MI, USA). Upon arrival, we opened access to the bladder of sucrose solution provided within each nest box and randomly assigned the colonies to one of three treatments (in 2022, $N = 4$; in 2023, $N = 5$). We initiated foraging treatments on the day of arrival. We deployed each colony in all treatments by placing each nest box on a cinderblock to elevate it from the ground, and placing an upside-down plastic laundry basket on top of the nest box to keep the box dry while still allowing foragers to enter and exit the nest (Fig. 1B). We allowed the colonies in all treatments continued access to the bladder of sucrose solution provided by Koppert through the duration of the study, but we did not monitor consumption, refill, or replace the sucrose solution. We placed colonies in the "mesotunnel" treatment in the center of the plot and allowed them to forage within the sealed mesotunnel. We placed colonies in the "free-foraging" treatment in dispersed locations on the research farm and allowed them to forage unrestricted (Fig. 2). In 2022, we terminated colonies in the "no-foraging" treatment by freezing on the day of arrival in order to characterize the health status of the colonies upon arrival (hereafter "no-foraging (DOA)"). In 2023, in order to allow colonies in the "no-foraging" treatment to reach the same age as colonies in the other treatment groups, we placed the colonies outdoors near the perimeter of the crop field area but did not open the nest box, keeping all bees contained within the nest box for the duration of the experiment (hereafter "no-foraging (starvation)"). These colonies had access to carbohydrate resources (sucrose solution) but no access to additional pollen resources for the study duration. Treatments continued until the end of the cucurbit crop flowering period, approximately 4 weeks (Table 1), after which point the cucurbit plants produce very few flowers. We terminated the colonies by closing the nest box entrance in the evening, when most bees are within the nest, and placing them into a -20°C chest freezer until dissection.

COLONY DISSECTION

We dissected each nest box to assess the colony health using a protocol adapted from Campbell et al. (2019). We weighed each nest within its plastic casing and removed all adult bees within the nest. We verified that all adult bees were *B. impatiens*, sorted adult bees into female workers, male drones, and female queens (including eclosed gynes), and counted and weighed the total members of each caste. We used forceps to open all brood cells and remove the immatures, and counted immatures as eggs, larvae, or pupae. We included immature gynes within the larvae and pupae counts. We did not determine the sex of the immature brood. Once we had removed all adult and immature bees, we broke apart the nest structure by hand or with lab spatulas to count the number of cells containing stored nectar or pollen. Our dissection protocol takes between 30-90 minutes per colony, depending on the size of the colony and skill of the technicians. Full documentation of our dissection methods is available in the supplementary material (Appendix I).

COLONY HEALTH INDICES

To better synthesize the numerous variables contributing to colony health, we created "colony health indices" (Fig. 3). The "reproductive health index" includes variables related to conservation and a colony's ability to grow its population and reproduce year-over-year, including the number of eggs, larvae, pupae, and drones, and the mass (g) of the queen(s). The "somatic health index" includes variables related to pollination service delivery and the colony's foraging and provisioning ability, including mass of the nest structure (kg), number of workers and stored nectar/pollen cells, and mean mass per worker (g). The "combined health index" includes all listed variables to provide an overall "snapshot" of a colony's health status. To account for the different units of measurement and ranges of values of each variable, we averaged the z-score centred value (using the scale() function) of each variable to produce the index value. To identify potential "indicator" variables correlated with overall colony health, we compared the correlations in the two-year data set between the colony health indices and individual variables using the package "corrplot" (version 0.95, Wei & Simko 2024).

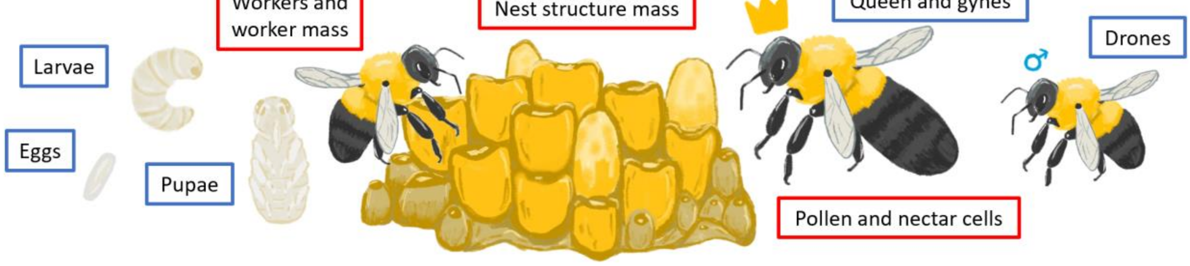

Figure 3. Variables from colony dissections included in the colony health indices. Variables outlined in a red box are included in the "Somatic health index." Variables outlined in a blue box are included in the "Reproductive health index." All variables presented are included in the "Combined health index."

STATISTICAL ANALYSIS

To compare the impact of foraging treatments on the colony-level traits and colony health indices across each year of the experiment, we compared the response of each trait across treatments with linear models (LM) using R statistical software (version 4.2.2, R Core Team, 2022). We analysed LMs of each year of the two-year dataset with a fixed effect of foraging treatment. We assessed the normality of each model by comparing the residuals with a Shapiro-Wilk test. Some models were transformed with a logarithmic (+1) or a square root transformation to meet assumptions of normality. We assessed treatment effects using Type I Analysis of Variance tables using Satterthwaite's method. Tukey post-hoc analyses compared pair-wise treatment differences using the package "emmeans" (version 1.11.0-004, Lenth 2025). For models that still did not meet assumptions of normality using linear modelling, we performed a Kruskal-Wallis test and determined pairwise contrasts using a Dunn test.

RESULTS

SOMATIC HEALTH FACTORS

We found a significant effect of treatment on nest structure mass in each year (Table 2). In 2022, free-foraging colonies had a greater mass than no-foraging (DOA) and mesotunnel colonies (Fig. 4A, 5A). In 2023, mesotunnel colonies had a 1.3 times greater mass than no-foraging (starvation) colonies (Fig. 4B, 5B, Appendix II). In 2022, free-foraging colonies had significantly more workers than no-foraging (DOA) and mesotunnel colonies (Fig. 4A), but there was no significant effect of treatment on the average mass per worker. In 2023, we found a 1.6 times greater average mass per worker in the free-foraging treatment compared to the no-foraging (starvation) treatment, with the mesotunnel treatment being intermediate (Fig. 4B, Appendix II), but no significant effect of treatment

Table 2. Summary statistics of LM analysis. Bold text indicates there is a statistically significant (*P* < 0.05) effect of treatment. Asterisks indicate that a non-parametric Kruskal-Wallis test was performed instead of LM, and a chi-square test value is presented instead of an *F*-test value.

	2022			2023		
	DF	*F* (*χ^2)	*P*	*DF*	*F* (*χ^2)	*P*
Somatic health factors						
Nest structure mass	2	8.0*	**0.018**	2	8.1*	**0.017**
Workers (count)	2, 9	11.9	**0.003**	2, 12	0.4	0.675
Workers (mass per individual)	2, 9	0.3	0.767	2, 12	5.3	**0.023**
Stored honey & pollen cells	2, 9	5.6	**0.027**	2, 12	1.0	0.400
Reproductive health factors						
Eggs	2, 9	6.6	**0.018**	2, 12	6.5	**0.012**
Larvae	2, 9	2.5	0.135	2, 12	6.2	**0.014**
Pupae	2, 9	2.1	0.174	2	6.5*	**0.039**
Queen (mass)	2, 9	0.6	0.573	2, 12	0.2	0.792
Drones (count)	2, 9	0.6	0.586	2	0.9*	0.624
Colony health indices						
Somatic health index	2, 9	3.9	0.059	2, 12	8.7	**0.005**
Reproductive health index	2, 9	2.6	0.131	2, 12	8.8	**0.004**
Combined health index	2, 9	2.5	0.138	2, 12	11.3	**0.002**

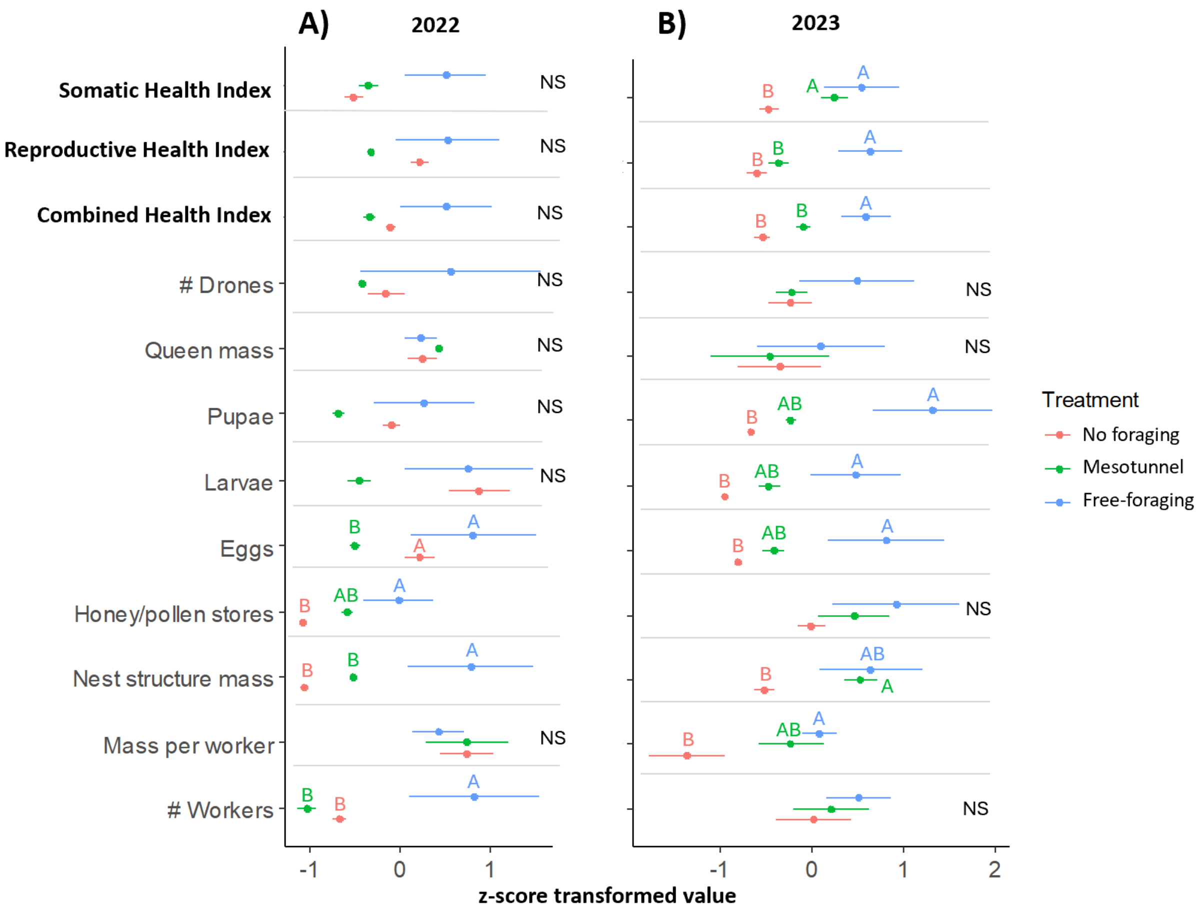

Figure 4. Mean (+/- standard error) of the scaled values of each variable and the colony health indices. Data presented is from 2022 (A) and 2023 (B) experiments. In 2022, "No foraging" treatment colonies were terminated upon arrival; in 2023, "No foraging" treatment colonies were starved for the trial duration. Letters indicate results of the Tukey (or Dunn) post-hoc test for treatment contrasts, "NS" indicates no significant effect of treatment.

on number of workers. In 2022, free-foraging colonies had almost 8.5 times more stored honey and pollen cells than no-foraging (DOA) colonies (Fig. 4A, Appendix II), with mesotunnel colonies not being significantly different from either treatment. This pattern was repeated in 2023, but was not statistically significant (Fig. 4B).

REPRODUCTIVE HEALTH FACTORS

We found a significant effect of treatment on the number of eggs in a colony each year (Table 2). In 2022, mesotunnel colonies had significantly fewer eggs than the free-foraging and no-foraging (DOA) colonies (Fig. 4A, 5A). In 2023, no-foraging (starvation) colonies contained an average of 0 eggs (Appendix II), and free-foraging colonies had significantly more eggs than no-foraging colonies, with mesotunnel colonies being not significantly different from either of the other treatments (Fig. 4B, 5B). In 2022, we found no significant difference in number of larvae or pupae between treatments. In 2023, free-foraging colonies contained on average 128 times more larvae and 10 times more pupae than no-foraging (starvation) colonies (Fig. 4B, Appendix II). We did not find a significant effect of treatment on the mass of queens or number of drones in the colonies in either year (Table 2).

COLONY HEALTH INDICES

Colony health index values were not significantly different across treatments in 2022. In 2023, free-foraging colonies had significantly higher combined health index and reproductive health index values than the other two treatments (Fig. 4B, 5B, Appendix II). In 2023, both free-foraging and mesotunnel colonies had a significantly greater somatic health index value than no-foraging (starvation) colonies (Fig. 4B, 5B, Appendix II).

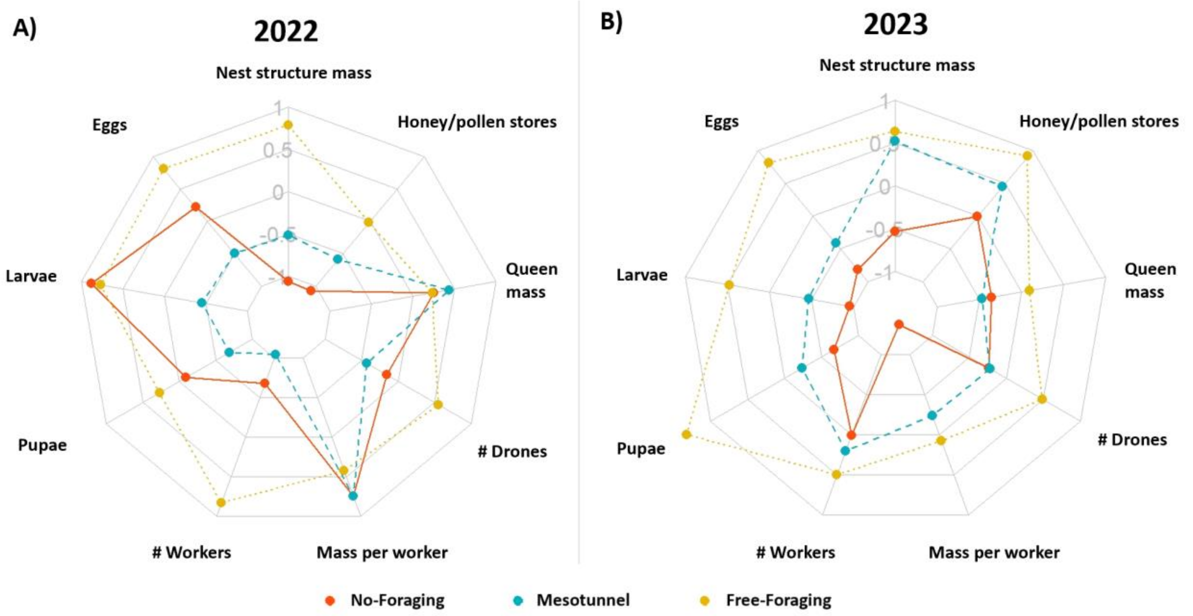

Figure 5. Radar chart displaying the mean of the z-score centered values of each variable by foraging treatment. Data presented is from 2022 (A) and 2023 (B) experiments. In 2022, "No foraging" treatment colonies were terminated upon arrival; in 2023, "No foraging" treatment colonies were starved for the trial duration.

INDICATORS OF COLONY HEALTH

To understand if there are specific individual colony factors that could act as indicators of the overall colony health metrics, we assessed correlations between all factors using the two-year dataset. The somatic (R = 0.84, P < 0.005) and reproductive (R = 0.91, P < 0.005) health indices were each highly correlated with the combined health index, but less correlated with each other (R = 0.53, P = 0.005) (Fig. 6). Nest structure mass was especially well-correlated with the somatic health index value (R = 0.95, P < 0.005). All factors of the reproductive health index were highly correlated with the index value except queen mass. Eggs (R = 0.88, P < 0.005), pupae (R = 0.83, P < 0.005), and nest structure mass (R = 0.80, P < 0.005) were each well-correlated with the combined health index value (Fig. 6).

DISCUSSION

Our first objective was to assess the colony health outcomes of managed *B. impatiens* in a cucurbit monoculture-mesotunnel foraging environment. We found that the colony-level health of *B. impatiens* in a cucurbit mesotunnel environment was reduced compared to free-foraging colonies. For many variables, mesotunnel colonies were at similar levels to colonies that did not forage at all, suggesting that the cucurbit mesotunnel environment provides scant resources or applies great stress to bumble bee colonies (Cresswell 2017; Rotheray et al. 2017; Straub et al. 2023).

In 2023, we found that colonies from free-foraging and mesotunnel treatments had similar somatic health index values (Fig. 4b). This suggests that colonies within a mesotunnel have the capacity to provide pollination services at similar levels to freely foraging colonies during the time period of the experiment (~4 weeks). Cucurbit crops produce large volumes of nectar (Knapp et al. 2019), and stored nectar makes up the greatest proportion of nest structure mass (McMinn-Sauder et al. 2024). This factor could have helped boost the mesotunnel colonies' somatic health index score, since the nest structure mass is highly correlated with the somatic health index score (R = 0.95, P < 0.005) (Fig. 6). Colonies from the no-foraging (starvation) treatment had significantly lower somatic health index values in 2023, supporting that extremely resource-limited conditions compromise a colony's ability to provide pollination services.

The limited time period of this experiment may have limited our ability to interpret the somatic health performance of colonies within

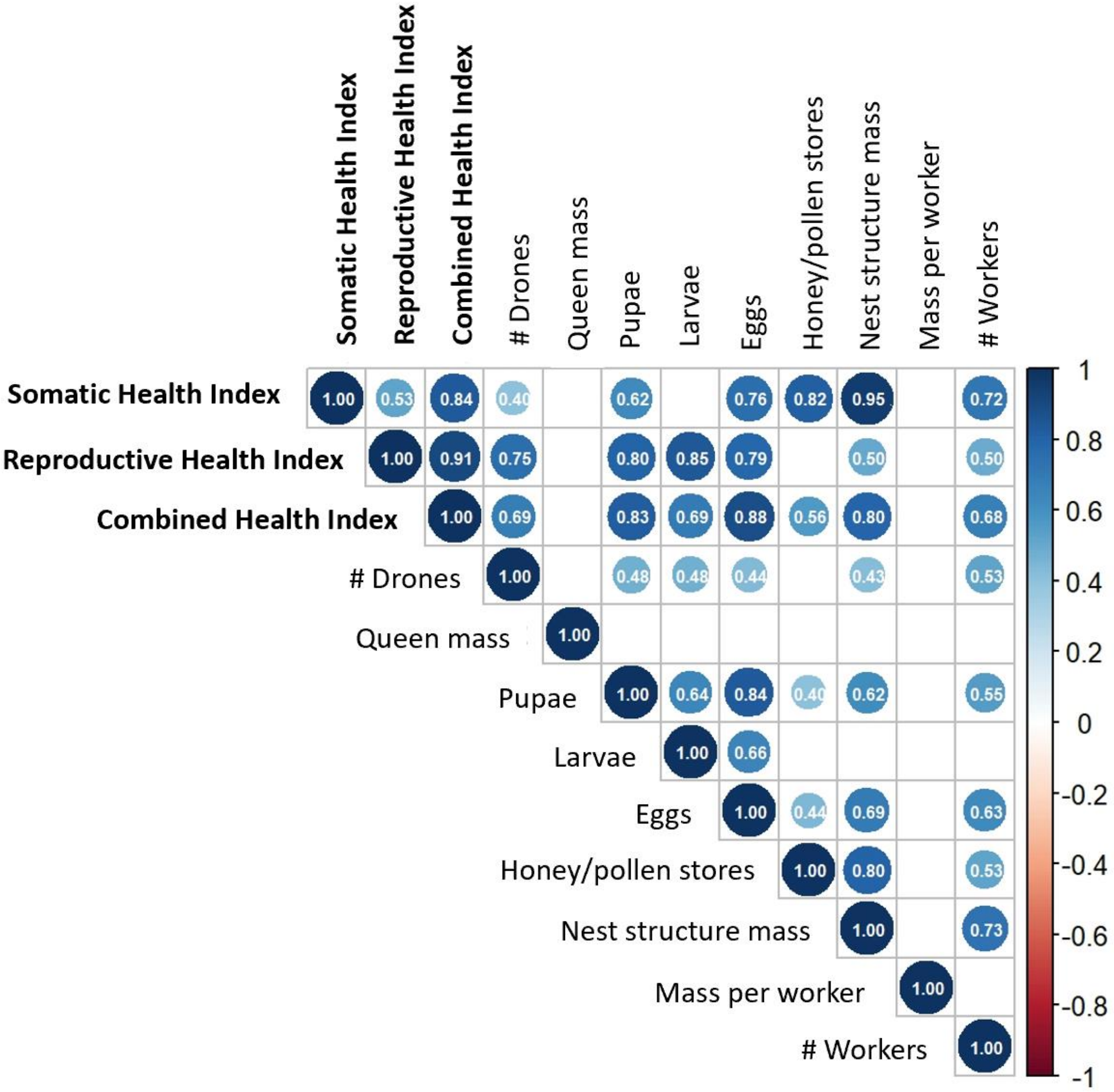

Figure 6. Pearson's coefficient of correlation between colony health indices and the variables that are factors within the indices using the two-year dataset. Blank tiles indicate that there was not a significant correlation (*P* > 0.05) between the variables.

mesotunnels. There could be a lagging effect of environmental stress on worker populations, which have a lifespan of 4-6 weeks (Goulson 2010), that was not observed during the experimental time period. We also did not monitor the colony members during the experimental period or account for colony members that may have died before the point of euthanasia. It is possible that if the experiment duration was extended, we would observe declining worker populations over time due to an inability to replace aging and dying workers. Growers using commercial colonies for pollination may therefore experience a decline in pollination service delivery over a longer time period, such as if reusing the same colony in a new crop field or using the colony in a crop with an extended bloom period. The manufacturer recommends using the Natupol Excel colonies for no longer than 10 weeks (Natupol Excel 2025). In order to provide further guidance to growers on the colonies' longevity, future work could use the somatic health index framework to examine commercial bumble bee colonies' pollination performance over longer time periods.

In the 2023 experiment, no-foraging (starvation) and mesotunnel colonies did not have significantly different reproductive health index values, and the free-foraging colonies' scores were significantly higher (Fig. 4b). This suggests that the cucurbit mesotunnel environment significantly limits bumble bees' reproductive capacity to a similar level as total foraging deprivation. This could be attributed to pollen resource limitation preventing the workers from successfully provisioning for the brood, especially since no-foraging colonies had no access to pollen (the primary source of nutrition for developing brood, Goulson 2010) and mesotunnel colonies had access to only monofloral cucurbit pollen. Pollen diet diversity improves bumble bees' reproductive outcomes (Hulse et al. 2025) unless a monofloral pollen source is nutritionally optimized (Moerman et al. 2017). Cucurbit pollen is also thought to have physical and chemical defences (Brochu et al. 2020) and nutritional deficiencies (Treanore et al. 2019) that reduce bumble bees' fitness. The quantity of floral resources within the mesotunnel environment could also be a limiting factor. Our mesotunnel plots had an average of 26.1 flowers/m^2/week in 2022 and 21. 4 flowers/m^2/week in 2023, while the manufacturer recommends a range of 35-60 flowers/m^2/week for optimal pollination service delivery by the colonies used in this study (Natupol Excel 2025). However, the resource value provided by individual flowers of different species can vary widely (Treanore et al. 2019), and the floral resource quantities needed for optimal colony health versus for optimal pollination performance requires further investigation.

In response to resource limitation and stress, the queen may stop laying eggs (Peto et al. 2025) or the workers may terminate developing brood (Roger et al. 2017). Because we found no eggs but low numbers of pupae in the 2023 no-foraging colonies (starvation), we believe the former occurred, but both mechanisms may have contributed. Bumble bee colonies also tend to produce fewer or smaller drones and gynes under conditions of stress and resource limitation (Zhao et al. 2024). Our experimental design is unable to differentiate between whether the toxicity of cucurbit pollen, the monofloral resource environment, the quantity of floral resources, or a combination of these factors drove the reproductive health consequences we observed. Regardless of the mechanism, it is clear that the cucurbit mesotunnel environment prevented optimal reproductive health of the colonies used in this experiment.

Commercial colonies deployed on farms are not intended to proceed to sexual reproduction or establish feral populations in the surrounding area, though they have been documented to do so (Thorp 2003; Dafni et al. 2010) with a range of potential and realized consequences on the local wild bee populations (Chandler et al. 2019) including resource competition (Ings et al. 2006; Miller et al. 2023), genetic introgression, and pathogen and parasite transmission (Sachman-Ruiz et al. 2015; Martin et al. 2021). This study builds on prior work that has used commercial bumble bee colonies as an imperfect but useful model unit for understanding how social bees are affected by local- and landscape-level agroecosystem surroundings (Parmentier et al. 2014; Campbell et al. 2019; Gervais et al. 2020; Klatt et al. 2020). Commercial colonies can be more readily manipulated and replicated for field experiments, without the limitations of locating, manipulating, and evaluating wild bumble bee colonies. It is not yet known exactly how well observed effects on commercial colonies may represent effects on wild bumble bee colonies, and further investigation is required to evaluate the usefulness of this model system. If the reproductive health limitations observed in commercial bumble bee colonies in this study also exist in wild bumble bee colonies, this would have consequences for sustaining populations of wild colonies in landscapes with high mesotunnel prevalence.

In 2023, we found that colonies in the mesotunnel environment had significantly lower combined health index scores than the free-foraging colonies, and were not significantly different from no-foraging (starvation) colonies (Fig. 4b). This shows that when considering both pollinator health priorities (pollination service delivery and reproduction) together, the cucurbit mesotunnel environment is negative for commercial *B. impatiens* colonies.

While the patterns of response to treatment remained broadly similar between years (Figures 4-5), there are large differences in some of the values recorded from the no-foraging treatments between the two years of the experiment (Appendix II). We attribute this to the different approaches to the no-foraging treatment. In 2022, we dissected colonies immediately upon arrival to characterize the arrival state of the colonies (DOA). In 2023, we sealed colonies for the duration of the experiment, allowing them to access carbohydrates from the sucrose solution bladder but no additional pollen (starvation). The terminated-on-arrival colonies from 2022 had much more brood (eggs, larvae, pupae) and fewer workers compared to the starved colonies from 2023. These population traits boosted the colony health index scores of the no-foraging colonies, leading us to observe no significant effect of treatment on the colony health indices in 2022. In 2023, older brood present at arrival would have matured to adulthood, but not been replaced by the queen or new eggs reared to maturity under the resource-limited conditions (Roger et al. 2017), leading to higher numbers of workers but low numbers of brood upon termination. We recorded much higher numbers of stored honey and pollen cells in all treatments in 2023 compared to 2022, which we attribute to our improved skill in the dissection process. It is also possible that the different crop varieties in the two years provided different quantities of pollen and nectar resources (Edge et al. 2012; Fisher & Pomeroy 1989; Roldán-Serrano & Guerra-Sanz 2005), which would be reflected in the quantity stored.

Our second objective was to synthesize the many variables that contribute to bee colony health with a colony health index. We used colony health indices (Fig. 3) to assess the performance of key pollinator health processes (pollination service delivery and reproduction) and produce a summary value that represents the patterns present in the component parts. We found the colony health indices effectively met our goal of synthesizing colony health into succinct, digestible values across the two-year data set (Fig. 6). The methods presented are repeatable and could be applied in different contexts and with different colony-forming bee species. Future research could easily add variables of interest to the index calculation, such as individual health indicators like fat body size and genetic expression, or epidemiological health indicators like colony pathogen and parasite load, based on what factors are considered informative in that context. The reproductive health index ($R = 0.91$, $P < 0.005$) and somatic health index ($R = 0.84$, $P < 0.005$) were both very closely correlated with the combined health index (Fig. 6) but were not very closely correlated with each other ($R = 0.53$, $P = 0.005$). This suggests that these indices successfully represent contrasting characteristics within the colony. A growing body of literature indicates biodiversity conservation and pollination service outcomes do not always respond equally to pollinator conservation schemes (Jones & Rader 2022; Kleijn et al. 2015; Mallinger et al. 2019), and conservation efforts must be tailored to meet specific goals. Though further investigation would be necessary to determine if the indices developed for commercial bumble bee colonies in this study are also applicable to wild colonies, the reproductive and somatic colony health indices could be a useful tool for evaluating biodiversity conservation versus ecosystem service delivery performance of conservation schemes.

Our third objective was to determine if any individual variables could be identified as indicators of overall colony health. Our methods include a time-intensive destructive dissection process (described in Appendix I), making these methods less practical in contexts requiring very high replication or where depleting wild populations is of concern. Our dissection and analysis methods may not be feasible or appropriate for studies of wild bumble bee colonies. It would be highly informative if an "indicator" variable could be identified that is reliably predictive of the colony health index value but does not require destructive sampling. We found that nest structure mass is highly correlated with the somatic ($R = 0.95$, $P < 0.05$) and combined health indices ($R = 0.80$, $P < 0.05$) (Fig. 6), and is a factor that can be measured non-invasively for commercial colonies. Only pupae ($R = 0.83$, $P < 0.005$) and egg numbers ($R = 0.88$, $P < 0.005$) were more correlated with the combined health index, but would require destructive sampling. This is consistent with previous findings that nest structure mass is predictive of demographic growth in bumble bees (Lefebvre & Pierre 2006; Vaidya et al. 2018). Our results support the use of colony mass as an indicator of overall bumble bee colony health for studies that cannot undertake a full dissection protocol. Future work could continue to explore different combinations of variables included in the colony health indices in order to tailor protocols that meet unique study objectives, but require less time or sampling intensity.

In addition to possible nutritional resource limitation, microclimatic conditions under the mesotunnels could be a contributing factor to colony health decline which was not addressed in this study. Various forms of protective cover agriculture are known to cause changes in temperature, humidity, and light transmission that lead to negative behavioural or physiological effects on pollinators (Birmingham & Winston 2004; Kendall et al. 2021). For the Protek-Net 60 gram UV-treated knitted polypropelene mesh material used in this study, the manufacturer reports 92% light transmissibility and states that the netting threads "act as light scattering elements" but have a "very small shading effect" (Dubois Agrinovation 2023). A previous study using an identical mesotunnel design found no difference in temperature, humidity, and dewpoint between covered and uncovered acorn squash crops (Fiske 2024). While microclimatic effects of mesotunnels are modest compared to structures with impermeable coverings like greenhouses and high tunnels (Nair & Ngouajio 2010; Acharya et al. 2019), there is still more to be explored to understand how pollinators may be directly and indirectly affected. We are unable to draw conclusions about the contribution of microclimatic factors to the colony health decline observed within mesotunnels in this study.

A key limitation of this study is that our study design does not differentiate between the mesotunnel environment and the cucurbit crop monoculture in their effects on colony health, thus we cannot definitively attribute the colony health consequences observed to one factor or the other. Lack of diverse floral resources can result in decreased colony growth and reproduction (Leza et al. 2018; Hass et al. 2019; Requier et al. 2020), and when combined with other stress factors, can act synergistically to cause colony death and local extirpation (Dance et al. 2017; Roger et al. 2017) in bumble bees. Additionally, the negative effects of cucurbit pollen (Treanore et al. 2019; Brochu et al. 2020) may play a role in the colony health decline we observed in the mesotunnel colonies. Further documentation of microclimatic conditions within the mesotunnel system and the resulting behavioral and physiological effects on bumble bees is also necessary to understand how the mesotunnel system itself may impact bee health. Future work could test levels of floral diversity within the mesotunnel system to see if colony health is recovered with additional floral resources, indicating that the floral resource environment and not the mesotunnel itself is not the primary driver of colony health. If this is the case, the mesotunnel system could be used as an experimental unit for bumble bees or other bee species where floral diversity and other environmental factors can be manipulated in a field-realistic setting.

To face the challenges of sustainable pest and pollination management, we need more information about how pollinators are affected by protective cover agricultural systems. We also need unified methods to assess bee colony-level health for different pollinator conservation goals. Our study system of managed bumble bees in a cucurbit crop mesotunnel represents a growing crop production practice in the eastern United States. We found that commercial *B. impatiens* colonies in a mesotunnel environment had worse reproductive health and overall health than free-foraging colonies, but performed similarly in their somatic health in the 2023 experiment. Colonies in the mesotunnel environment were not compromised in traits related to their potential to provide crop pollination services, but were compromised in traits related to their ability to reproduce and persist year-over-year. Our colony health indices effectively summarized different aspects of colony-level health, and could be adapted to assess the status of conservation and ecosystem service delivery for social bees.

ACKNOWLEDGEMENTS

Thank you to Helder Avendado-Gomez, Chelsea Avery, Briana Bazile, Isaac D'Souza, Raine Esparza, Jessica Fischer, Karina Garcia, Allie Guy, Viktor Halmos, Sarah Jones, Ryan Kuesel, Delia Scott, and Kantima Thongjued for their help in manuscript review and/or field experiment operations. Thank you to Steve Diver, Aaron German, Jay Tucker, and Neil Wilson at the University of Kentucky Horticulture Research Farm for their assistance in field set-up and maintenance. Thank you to the journal editor and anonymous reviewers, whose suggestions were helpful in improving this manuscript. Funding for this experiment was provided by Organic Agriculture Research and Extension Initiative 'Resilient Systems for Sustainable Management of Cucurbit Crops' Grant #2019–51300-30248, Organic Agriculture Research and Extension Initiative 'Expanding resilient climate and pest protection systems for diversified organic specialty crop producers' Grant #2023-51300-40855, and United States Department of Agriculture Hatch grant (KY008079).

AUTHOR CONTRIBUTION

Conceptualization and methodology LG & DG; investigation LG, KFP, YC, MG, BM; visualization and formal analysis LG & DG; writing - original draft and preparation LG; writing - review and editing LG, KFP, YC, MG, BM, & DG; supervision LG, KFP, & DG; funding acquisition and project administration DG.

DISCLOSURE STATEMENT

The authors have no potential conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

The data used to write this article are available in Appendix III.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. Nest dissection protocol.

Appendix II. Untransformed treatment means of data.

Appendix III. Colony dissection data.

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