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Research article

The contribution of human foods to honey bee diets in a mid-sized metropolis

Clint A. Penick,[1,2,*] Catherine A. Crofton,[3] R. Holden Appler,[3] Steven D. Frank,[3] Robert R. Dunn,[1,2,4] and David R. Tarpy[2,3]

[1]Department of Applied Ecology, North Carolina State University, Raleigh, NC, 27695-7617 USA, [2]Keck Center for Behavioral Biology, North Carolina State University, Raleigh, NC, USA, [3]Department of Entomology, North Carolina State University, Raleigh, NC, 27695-7613 USA and [4]Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, DK-2100 Copenhagen, Denmark

*Corresponding author. E-mail: capenick@ncsu.edu

Abstract

Concern for honey bee health has implicated both urbanization and nutritional stress as factors contributing to honey bee declines. The expansion of urban areas has resulted in reduced foraging habitat for bees, while at the same time introducing new food sources, such as foods unintentionally provided by humans as litter or in waste containers. While human foods play an important role in the diets of other urban animals, the extent to which honey bees feed on these resources has not been well characterized. Here, we compared the amount of human foods in honey bee diets across a rural-urban gradient in North Carolina, USA, using stable isotopes of carbon ($\delta^{13}C$). Human-produced sugars—primarily sugarcane and corn syrup—have a characteristic isotope signature that can be used to quantify the relative amount of human foods in animal diets. We predicted that urban bees would have an increase in $\delta^{13}C$ if they were feeding on human-produced sugars, but we found no change in $\delta^{13}C$ between urban and rural colonies. Instead, we found an increase in $\delta^{13}C$ in managed bees in both habitats, which is indicative of supplemental sugar feeding by beekeepers. Rather than switching to human food sources, urban bees seem to be feeding on urban flowers or insect-produced honeydew. This suggests an important role for urban flowers and green spaces in maintaining healthy pollinator populations in cities.

Key words: stable isotopes; honey bees; urban ecology; nutrition; pollinator health; *Apis mellifera*.

1. Introduction

In 2010, Brooklyn beekeeper Cerise Mayo was surprised when she opened her hives and found combs filled with bright red honey (Dominus 2010). At first, Mayo thought her bees were foraging on a strange plant, possibly sumac, but eventually she tracked her bees to a maraschino cherry factory where they were collecting sugar syrup tinted with Red Dye No. 40. Urban beekeeping, such as Mayo's operation in Brooklyn, is on the rise (Cockrall-King 2012; Moore and Kosut 2013), but there remain questions about what resources urban bees collect. While flowers are important resources for bees in natural and agricultural systems (Proctor, Yeo, and Lack 1996), urban bees are known to take advantage of human foods when available as litter or in waste containers (e.g., Chandrasekaran et al. 2011). Human foods make up a major portion of the diets of other urban animals (Newsome et al. 2010; Penick, Savage, and Dunn 2015), but the extent to which honey bees feed on human foods has not been examined thoroughly despite the potential consequences for honey bee health and honey quality.

Concern for honey bee health has risen in tandem with the discovery of widespread bee declines and heavy losses reported by beekeepers globally (Hayes, Underwood, and Pettis 2008; Evans et al. 2009; Potts et al. 2010). In addition to pesticides and novel parasites, habitat loss has been identified as a key factor contributing to bee declines (Goulson et al. 2015). Habitat loss has occurred with conversion of natural, flower-rich habitats to farmland and—increasingly—to urban areas. The expansion of urban areas has reduced foraging habitat for bees, which may lead to fewer colonies in a given area, force bees to take longer foraging trips, or both (Naug 2009). Furthermore, nutritional stress may compound the effects of other threats to honey bee health by, for example, decreasing tolerance to pesticides or by impairing disease resistance and immunity (Alaux et al. 2010; Brodschneider and Crailsheim 2010; Huang 2012).

On one hand, availability of human foods in cities could provide a boon to honey bee populations by supplementing bee diets where floral resources are scarce. The availability of human foods has a positive impact on urban populations of kit foxes and ants, for example, which reach higher population densities where human foods are present (Newsome et al. 2010; Penick, Savage, and Dunn 2015). However, sugars found in human foods may not be nutritionally equivalent to flower nectar (Frankel, Robinson, and Berenbaum 1998; Manson, Otterstatter, and Thomson 2010; Nepi, 2014), and human foods can contain compounds that are toxic to bees (LeBlanc et al. 2009). Switching to human food sources could therefore have negative health consequences for bees, especially in urban areas where bees may already face increased pathogen pressures (Youngsteadt et al. 2015). Whatever resources bees collect will also affect the composition of their stored honey. There has been concern over honey intentionally adulterated by adding human sugars (Downey et al. 2003; Guler et al. 2007; Chen et al. 2011), and urban bees may be incorporating these sugars into their honey directly along with other human-produced compounds.

Here, we compared the relative contribution of human foods to honey bee diets across a rural–urban gradient using stable isotopes of carbon ($\delta^{13}C$). Human sugar sources, specifically sugarcane and corn syrup, have a characteristic isotope signature that can be used to quantify the relative amount of human foods in animal diets (Newsome et al. 2010; Hopkins et al. 2014; Penick, Savage, and Dunn 2015). We measured isotope content of bees from managed (beekeeper-owned) and feral (wild-living) colonies living in the Raleigh–Durham–Cary metropolitan area of North Carolina, USA (population ~2 million (US Census Bureau 2013)). We predicted that urban bees would have higher $\delta^{13}C$ than rural bees consistent with higher levels of $\delta^{13}C$ in human sugar sources (Jahren and Kraft 2008). Additionally, beekeepers often supplement their colonies with human-produced sugars, which has previously been associated with increases in $\delta^{13}C$ in managed bees (Anderson et al. 2014). Therefore, we predicted that managed bees would have higher $\delta^{13}C$ than feral bees in both rural and urban habitats. On the basis of our results, we evaluate the relative contribution of human foods to honey bee diets and discuss the importance of urban flowers as a nutrient source for bees and other pollinators.

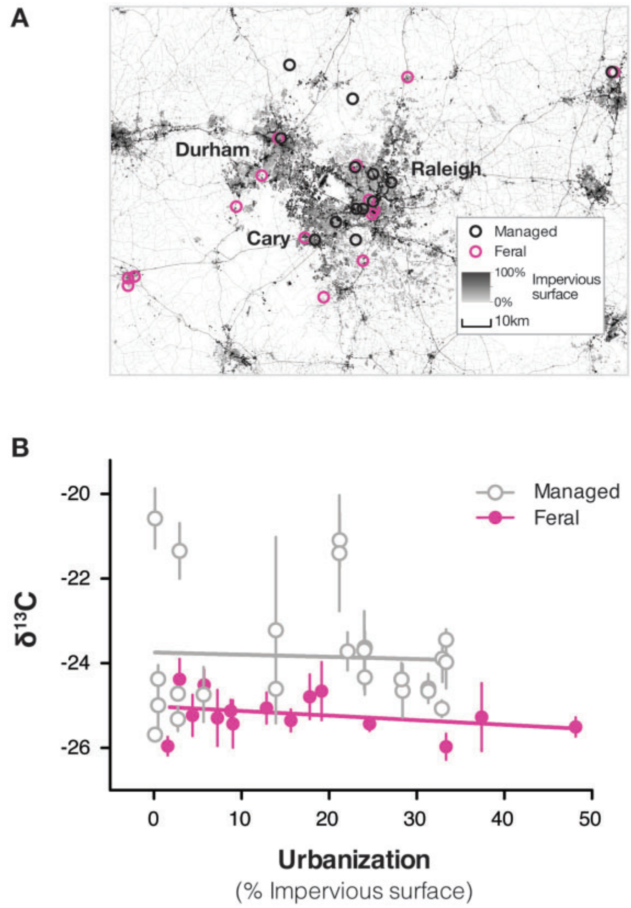

Figure 1. (A) Sample locations of managed and feral honey bee colonies across a rural–urban gradient in Raleigh–Cary–Durham, NC. Shading indicates percent impervious surface, and circles (1,500 m diameter) indicate sampling locations. (B) Relationship between $\delta^{13}C$ (a measure of human food consumption) and urbanization (quantified as percent impervious surface) for managed and feral bees. There was no significant effect of urbanization on $\delta^{13}C$ ($P = 0.58$), but managed bees had higher $\delta^{13}C$ compared to feral bees across all populations ($P = 0.0011$), which is indicative of supplemental sugar feeding by beekeepers.

2. Methods

2.1 Urban and rural sample populations

We sampled a total of 39 honey bee (*Apis mellifera*) colonies across an urban habitat gradient in Raleigh–Cary–Durham, NC, USA (Fig. 1A). Urbanization was quantified as percent impervious surface within a 1,500 m radius of each colony, which represents a typical foraging distance for *A. mellifera* (Steffan-Dewenter and Kuhn 2003; Couvillon et al. 2015). Areas with higher percent impervious surface have less green space and, therefore, less foraging habitat for bees. We used the NLCD 2011 percent developed imperviousness dataset in ArcMap 10.0 with a 30 m resolution (Xian et al. 2011). Foragers were sampled from 15 feral colonies and 24 colonies managed by 18 small-scale, non-migratory beekeepers between 13 June and 4 September 2013. Managed bees were collected from non-migratory beekeepers to ensure that colony diets were indicative of the local foraging area in addition to any foods fed by beekeepers directly. Feral colonies were collected from cavities where they had overwintered for at least one season (feral colonies were found using the website www.savethehives.com and with help from local beekeepers). We used a sweep net to collect foragers near the entrance of each colony, and bees were then frozen at –80°C until samples were prepared for stable isotope analysis.

2.2 Stable isotope analysis

We used stable isotope ratios of carbon to quantify the relative contribution of human sugars to honey bee diets. Human sugar sources (sugarcane and corn syrup) have a characteristic isotope signature associated with C4 photosynthesis in plants that has been previously associated with human food consumption by urban animals (Newsome et al. 2010; Penick, Savage, and Dunn 2015). Consumers that feed on C4 plants have an increased ratio of heavy to light carbon isotopes ($^{13}C/^{12}C$) compared with consumers that feed more heavily on C3 plants, which includes most flowering plants that honey bees rely on for nectar and pollen in natural habitats (Proctor, Yeo, and Lack 1996). Therefore, higher ratios of heavy to light carbon isotopes likely indicate a higher proportion of human-derived sugars in honey bee diets.

Stable isotope analyses followed standard protocols for insects (Tillberg et al. 2006; Feldhaar, Gebauer, and Blüthgen 2010; Penick, Savage, and Dunn 2015), including honey bees (Anderson et al. 2014). Each sample was composed of two honey bee legs (one front leg and one hind leg) that were cleaned of pollen and other debris using deionized water. Once cleaned, the legs were dried at 50°C for 48 h and weighed on an analytical balance (A&D Instruments, HR-202i, precise to 0.01 mg) to achieve an optimal mass between 0.5 and 1.5 mg of tissue. Each sample was then placed into a 5 by 9 mm tin capsule (Costech Analytical Technologies Inc., Valencia, CA), which was closed and crushed with sterilized forceps. Capsules were put individually into a 96-well plate and shipped to the Stable Isotope Facility at the University of California, Davis. There, a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) was used to examine the ratio of heavy to light isotopes of carbon (^{13}C-^{12}C). We tested carbon isotope ratios (given as $\delta^{13}C$ in permil units, ‰) in five bees per colony, which were averaged into a single value.

2.3 Statistical analyses

We used a linear mixed model to compare differences in the relative contribution of human foods to honey bee diets across colonies (measured as $\delta^{13}C$). In the model, $\delta^{13}C$ was the dependent variable, and urbanization (measured as percent impervious surface at 1,500 m), management regime (feral vs. managed), and their interaction were the independent variables. Because we collected some samples from independent colonies within the same apiary, we included apiary in our model as a random effect. All analyses were performed using JMP Pro 12.0.1 (SAS Institute Inc 2015).

3. Results

We found no relationship between urbanization (measured as percent impervious surface at 1,500 m) and $\delta^{13}C$ (Fig. 1B), which indicates human food sources did not make up a significant proportion of urban honey bee diets. In our mixed model, urbanization (df = 1, F ratio = 0.31, P = 0.58) and the interaction between urbanization and management regime (df = 1, F ratio = 0.046, P = 0.83) had no significant effect on $\delta^{13}C$. Instead, managed colonies showed higher $\delta^{13}C$ levels than feral colonies in all habitats (df = 1, F ratio = 12.96, P = 0.0011), which is consistent with findings that beekeeper kept colonies have increased $\delta^{13}C$ as a result of supplemental sugar feeding (Anderson et al. 2014). Managed bees had greater variation in $\delta^{13}C$ than feral colonies (Fig. 1B), which suggests some beekeepers provide more supplemental sugars to their bees than others. Overall, the increase in $\delta^{13}C$ for managed colonies was 1.25‰ compared with feral colonies (See Supplemental data), which was still relatively small compared with the increase in $\delta^{13}C$ found in ants (2.72‰) and kit foxes (2.40‰) that consume human foods in urban habitats (Newsome et al. 2010; Penick, Savage, and Dunn 2015).

4. Discussion

Humans throw out nearly 250 million tons of food waste in cities each year, which represents a massive potential resource for urban animals (Penick, Savage, and Dunn 2015). Honey bees living in North Carolina, however, are apparently not taking advantage of these resources. We predicted that urban bees would have an increase in $\delta^{13}C$ if they were feeding on human-associated sugars (i.e., sugarcane and corn syrup), but we found no change in $\delta^{13}C$ between urban and rural colonies. Instead, we found an increase in $\delta^{13}C$ in managed bees in both habitats, which is indicative of supplemental sugar feeding by beekeepers (Anderson et al. 2014). If urban bees are not feeding on human food sources, then they are likely feeding on flowers present in landscaped gardens and urban green spaces as well as honeydew produced by sap-feeding insects. The availability of flowers in urban areas, therefore, is likely important for maintaining healthy pollinator populations in cities.

The decreased presence of human foods in honey bee diets contrasts with findings from other urban species. Urban mammals (Newsome et al. 2010) and ants (Penick, Savage, and Dunn 2015) both show increases in $\delta^{13}C$ associated with human food consumption. A potential reason why urban bees differ from ants is that bees are capable of much longer foraging distances and can more easily cross environmental barriers, like roads, to find their preferred foods. In a city the size of Raleigh or Durham, bees may be able to find sufficient flowers within the vicinity of their nests and avoid having to forage for human sugars. It is unclear whether this would be true in larger cities, such as New York or Tokyo, where urban beekeeping has grown in popularity (Cockrall-King 2012). While the most urban site in our study had 48% impervious surface, the average site in New York has 91% impervious surface (Vermont 2012). In these larger cities, honey bees may be more likely to augment their diets with human sugars when available, and this would directly affect honey quality, such as the case with Cerise Mayo in Brooklyn (Dominus 2010). Future research in larger cities could help identify areas where honey bees collect human sugars more regularly.

Unlike feral colonies, managed bees did consume human sugars in rural and urban habitats, which is likely a result of sugar supplementation by beekeepers. The increase in $\delta^{13}C$ in managed bees has previously been associated with beekeepers supplementing their colonies with simple sugars after harvesting honey or in seasons when natural nectar sources are low (Anderson et al. 2014). Evidence that feeding simple sugars to honey bee colonies could have negative health consequences for bees is scarce (Brodschneider and Crailsheim 2010), but high fructose corn syrup can contain compounds that are toxic to bees, particularly hydroxymethylfurfural when exposed to temperatures above 40°C (LeBlanc et al. 2009). Additionally, a study using the same colonies we used here found that bees from managed hives had lower transcript levels of certain immune genes than feral bees (Youngsteadt et al. 2015) but no differences in other physiological measures of immunity (Appler, Frank, and Tarpy 2015). A low-quality diet that is high in simple sugars could contribute to this response, but a more direct study is needed to make a link between sugar supplementation and impaired immunity. Bees living in urban environments are faced with stronger pathogen pressures (Youngsteadt et al. 2015), and the interaction between diet and honey bee immune responses could play a major role in honey bee health.

Perhaps the most important implication of our study is that urban flowers, if not human food sources, likely support urban honey bee populations. The highly social nature of honey bees may allow them to locate and recruit to flower sources even if they are patchy and irregularly dispersed, but it remains to be seen whether native and solitary bees would be able to find adequate forage in highly urban areas. Low levels of urbanization can have positive effects on bee diversity and abundance due to greater floral richness associated with flowers planted around homes (Carper et al. 2014). In areas with much higher percent impervious surface, urban gardens and green roofs may help support bee communities by providing foraging habitat and nesting resources (Matteson, Ascher, and Langellotto 2008; Colla et al. 2009; Hernandez, Frankie, and Thorp 2009). The abundance of flowering plants is one of the strongest predictors of pollinator diversity in urban areas (Matteson and Langellotto 2010; Shwartz et al. 2013) and is also correlated with pollinator abundance (McFrederick and LeBuhn 2006). With growing interest in how urban green spaces promote biodiversity (Goddard, Dougill, and Benton 2010), our results provide additional evidence that urban flowers support pollinators and are important food sources for bees.

Data availability statement

Data are uploaded as supplementary information.

Supplementary data

Supplementary data are available at *JUECOL* online.

Conflict of interest: None declared.

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