Available online at www.sciencedirect.com
ScienceDirect
Current Opinion in Insect Science

Bee nutrition and floral resource restoration

Anthony D Vaudo, John F Tooker, Christina M Grozinger and Harland M Patch

Bee-population declines are linked to nutritional shortages caused by land-use intensification, which reduces diversity and abundance of host-plant species. Bees require nectar and pollen floral resources that provide necessary carbohydrates, proteins, lipids, and micronutrients for survival, reproduction, and resilience to stress. However, nectar and pollen nutritional quality varies widely among host-plant species, which in turn influences how bees forage to obtain their nutritionally appropriate diets. Unfortunately, we know little about the nutritional requirements of different bee species. Research must be conducted on bee species nutritional needs and host-plant species resource quality to develop diverse and nutritionally balanced plant communities. Restoring appropriate suites of plant species to landscapes can support diverse bee species populations and their associated pollination ecosystem services.

Address
Department of Entomology, Center for Pollinator Research, The Pennsylvania State University, 501 ASI Building, University Park, PA 16802, USA

Corresponding author: Vaudo, Anthony D (adv124@psu.edu)

Current Opinion in Insect Science 2015, **10**:133–141

This review comes from a themed issue on **Social insects**

Edited by **Christina M Grozinger** and **Jay D Evans**

For a complete overview see the Issue and the Editorial

Available online 22nd May 2015

http://dx.doi.org/10.1016/j.cois.2015.05.008

Introduction

A key factor driving pollinator declines is anthropogenic land-use intensification, which, among interacting factors such as pesticide use and introduced pests and pathogens, dramatically reduces the diversity and abundance of flowering plant species [1–5,6••,7••]. Bees (Hymenoptera: Apoidea: Anthophila), as a monophyletic group of ~20 000 species [8], depend entirely on nutrition derived from floral resources (especially nectar and pollen) obtained from diverse plant species [9]. Bees therefore experience nutritional stress when limited in their choices of host-plant species or when only suboptimal floral resources are available, both of which could result in reduced population sizes and pollination efficiency [1–5,6••,7••]. We propose a rational approach for restoring and conserving pollinator habitat that focuses on bee nutrition by firstly, determining the specific nutritional requirements of different bee species and how nutrition influences foraging behavior and host-plant species choice, and secondly, determining the nutritional quality of pollen and nectar of host-plant species. Utilizing this information, we can then thirdly, generate targeted plant communities that are nutritionally optimized for pollinator resource restoration and conservation. Here, we review recent literature and knowledge gaps on how floral resource nutrition and diversity influences bee health and foraging behavior. We discuss how basic research can be applied to develop rationally designed conservation protocols that support bee populations.

Bee nutrition

Adults and larvae of nearly all bee species depend on nutrients obtained from floral resources for development, reproduction, and health [9,10••]. Adult foragers are challenged with seeking out appropriate nutrients from the environment for developing larvae and/or nurse bees and queens confined to a nest [9]. At the simplest level, bee nutrition is partitioned between nectar and pollen: nectar provides bees' main source of carbohydrates, whereas pollen provides proteins, lipids, and other micronutrients [11–13]. To obtain optimal nutrition, insects can balance their nutrient intake from complementary food sources, which is considered one of the most important factors shaping foraging behavior and insect fitness [14••].

Bee species likely have different quantitative and qualitative nutritional requirements, which are suggested by their differences in life history, brood size, social structure, and different distributions among plant species. Whereas most bees are solitary and oligolectic (a single reproductive female lays eggs and provisions brood; specializes on one plant family or genus), the majority of literature studying the nutritional needs of bees have focused on two species of long-tongued bees: honey bees and bumble bees, both of which are generalists (foraging on a wide range of plant species in different families) and social (living in colonies with cooperative brood care and overlap of generations) [8,10••,11,15]. The nutritional requirements of honey bees (colony, adults, and larvae) has been comprehensively reviewed [10••], and even though this level of detail does not exist for other bee species, we can assume that other species have similar macronutrient demands; the proportions of macronutrients required may be species-specific (as exemplified in other closely related insect species that share the same host-plants [14••,16]).

We can infer the general dietary requirements of bees from existing research. It is clear that both adults and larvae will starve without a constant carbohydrate, mainly nectar, source [10••]. Relatively immobile larvae do not require the amounts of carbohydrate needed by foraging bees and their limited carbohydrate demands can be met by a blend of pollen, which contains digestible carbohydrates, and nectar [17–19]. Protein concentration of pollen is positively correlated with larval development and adult reproduction (ovarian development and egg laying) in honey bees, bumble bees, and the sweat bee *Lasioglossum zephyrum* [20–26,27••]. Lipids are crucial for a variety of physiological processes in bees (e.g. egg production, wax production, secondary energy source) and contribute to larval and adult health, ontogeny, and diapause/overwintering [10••,27••,28–30]. Linoleic acid (omega-6), an essential fatty acid for most insect species, in collected pollen has been associated with higher worker production in honey bee colonies [31]. A second essential fatty acid for insects, linolenic acid (omega-3), is also obtained from pollen, but its specific importance for bees is still not described [28]. Sterols obtained exclusively from pollen are the precursors for molting hormones, making pollen essential for larval development [10••,27••]. Recent research indicates that both honey bee and bumble bee foragers regulate their intake of carbohydrates and proteins to high ratios [32,33], and bumble bees can simultaneously regulate their intake of carbohydrates, proteins, *and* lipids (Vaudo *et al.*, unpublished). These studies reveal bees' specific nutritional requirements, and potentially highlight how adults prioritize their foraging efforts between nectar and pollen for their nutritional components.

Information is lacking for the specific nutritional requirements of the vast majority of solitary oligolectic bee species, though bee taxa appear to have different requirements in nectar sugar composition (see section 'Nectar' discussion below). Even less is known of bees' specific pollen nutritional requirements. For at least a few species of solitary bees, pollen quantity of brood provisions is linearly correlated to body size [34]. Additionally, some specialist bees do not survive well on non-host pollen [35], suggesting that either host-plant pollen is nutritionally optimal for specialists, or they cannot metabolize protective chemicals of non-host pollen. Because nectar and pollen quality varies considerably between host-plant species [11,12] and the bee community exhibits different host-plant visitation patterns over time [36–38], we can assume that different bee species have specific nutritional demands that may influence their host-plant foraging patterns [16].

Floral resource nutritional diversity and bee foraging behavior

Nectar

Nectar is the major carbohydrate source for most bee species [10••,39,40]. Bee larvae require carbohydrates for normal development often in the form of brood food (pollen and nectar mixtures), but the greatest quantity of carbohydrate-rich nectar is required for adult foraging [10••]. Nectar is an important floral reward and reinforcing stimulus for bee foragers, and profitable nectar sources can be learned and associated with floral characteristics such as scent and color [41–43]. Although nectar is a dynamic floral resource, varying by abiotic conditions and plant age [12,25,44–48], there are three relatively constant characteristics that influence bee host-plant choice for nectar: sugar composition, nectar volume, and nectar concentration [18,39]. Other characteristics of nectar composition undoubtedly play a significant role in nectar choice, such as amino acids, lipids, minerals, and secondary plant compounds [46,49–59]; however, research on these characteristics, perhaps with exception of amino acids (recently reviewed in Nepi [60]), has been limited and not systematic across bee species [59–63].

The three main sugars present in nectar are glucose and fructose (monosaccharide), and sucrose (disaccharide) [12,64,65]. Flowers of a given taxa vary in the relative amounts of these sugars and plant families show a characteristic pattern of sugar composition [12,48,64,65]. Early research found that long-tongued bees prefer high sucrose nectars and short-tongued bees prefer nectars with a higher percentage of monosaccharides [65]. Although the interpretation of these patterns has been questioned on many levels [12,66–68], it is likely that sugar composition of plant taxa is an important factor in determining pollinator host-plant choice [48,62,64,65,69–75].

Nectar concentration also determines patterns of pollinator host-plant visitation [12,76–79], limiting which pollinators can mechanically obtain the nectar, either by adhesion and capillary action or by suction. The rationale is that pollinators with long feeding apparatuses (long-tongue bees, moth/butterfly proboscis, long-tongue fly proboscis) will be limited to more dilute nectars. Although overall viscosity is affected by temperature (and sugar concentration) [80], patterns of preference are evident (reviewed by Willmer [81]) and therefore likely play a role in the evolution of plant-pollinator communities. For example, honey bees (a long-tongued bee species) prefer a concentration of 30–50% whereas short-tongued bees utilize higher concentration nectars of 45–60% [82].

It has been proposed that nectar volume, a third characteristic of floral nectar, is the result of an evolutionary tradeoff [83] between high volumes that are energetically costly (potentially influencing vegetative growth and