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Review Article

A primer of host-plant specialization in bees

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The bee-flower biological association is one of the most famous examples of insect-plant interactions, and it is axiomatic that these are of critical importance for sustaining thriving terrestrial ecosystems. Yet, the most familiar associations are often artificially managed agricultural ecosystems, reflecting an exceptionally narrow range of bee species (often only one) and a concomitantly restricted range of associated behaviors, morphologies, and mechanisms tied to pollination. Here we provide a brief account of the range of bee-floral associations encompassing floral specialization in terms of diet, behavior, and morphology. These natural associations not only promote healthy ecosystems, but also can be integrated in sustainable ways for more efficient pollination of crops by targeting bee species whose diets, behaviors, and pollen-gathering structures evolved precisely to visit such floral species rather than less efficient, and often non-native, generalists that are otherwise exploited for such purposes.

Introduction

Flowering plants and bees often share a mutualistic relationship, where flowers provide bees with food and other floral rewards such as oils, fragrances, and resins [1], while bees bring about pollen transfer during their floral visits, contributing to the sexual reproduction and ultimate survival of their hosts. In this process, known as pollination, pollen grains are transferred from the male anther of a flower to the female stigma of flowers from the same species [2,3]. This exceedingly important aspect of angiosperm life history has been heralded as one of the principle factors contributing to the radiation and global success of flowering plants [4]. Estimates indicate that the proportion of modern-day animal-pollinated flowering species ranges from a mean of 78% of the flowering plant species in temperate-zone communities to 94% in tropical communities [5].

Beyond the pivotal contribution of pollinators for the survival and diversification of wild flowering plants, this plant-animal relationship is also particularly important from an ecosystem-services perspective. Globally, more than 75% of our main crop species rely on or benefit from animal pollination for increased yield [6]. Despite the importance of agricultural productivity [7], crop yields rarely reach their full potential in part due to inadequate pollination [8]. Studies have shown that small-scale agricultural farms with proper pollination increase their yields by an average of 24% [8]. However, a single, managed pollinator species, e.g. the western honey bee (*Apis mellifera*), is usually insufficient for increasing yield alone [9]. It is the diversity in body size, ecological traits, evolutionary histories, and behavior of pollinators that secure efficient pollination, rather than the sheer abundance of a single managed species [10,11]. In addition, pollination also improves crop quality, size, and shelf life, which are important for an increased final market price [12–14].

Here we provide a primer to host-plant specialization in bees in order to: revive interest in these sometimes unusual forms of ecological specialization; identify current needs in terms of research; and highlight the importance of these traits and their diversity at the local scale for the study of pollination biology relevant to all flowers, wild and cultivated.

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Bee biology and foraging

Bee nests usually consist of individual brood cells, each containing food provisions and a developing immature bee. The cells can be located in a vast variety of substrates, including (but not limited to) burrows in the soil, wood or plant pith, and even in empty snail shells [15,16]. Whether the bees build their own nest or they are kleptoparasites that usurp the nests of other bees, the offspring almost exclusively and invariably develop upon stored volumes of pollen, an essential source of proteins and sterols, and carbohydrates in the form of nectar. Pollen also provides lipids and other important nutrients for the bees [17]. Adults mostly feed on nectar and to a varying extent pollen [15,18,19].

A number of bees either supplement or completely replace pollen protein in their diet. This includes the addition of floral lipids or oils [1,20], carrion [21], prey [22], vertebrate tears [23,24], and mold spores [25]. Lastly, recent research has shown that bees are omnivorous since they incidentally consume substantial quantities of microbes present in pollen. These microbial organisms are key to the overall fitness of the bees, and they underlie their health as adults as well as larval development [26–29].

Some bees, in particular eusocial species that maintain their colony year round, are generalist pollen foragers, or polylectic, with no apparently specialized plant associations. Other groups of bees have more specific pollen preferences, limited in range from one plant species only (strict monoleptic), to plant species belonging to a couple or more genera in the same family (oligolectic), or across a narrow range of plant families (mesolectic) [30].

A limitation for bee-plant associations is the availability and spatial distribution of their food plants. Bees can only fly a certain distance from their nest to a food source. The distance is determined by body size [31,32] and presumably their associated metabolic rate. Gathmann and Tscharrntke [31] experimentally recorded that select bees travel 150–600 m for food, although it may be that the majority of individuals do not forage over long distances, with only a few individuals capable of flying in excess of 1100 m [33]. An implication of increased foraging distance for solitary bees is a higher cost on the production of offspring. For example, it was found that the number of brood cells provisioned per unit time decreased by 23% or more, at a meager increase in flight distance of 150 m [34].

Bees are not limited to native host plants. They are also frequently visiting exotic plants and therefore can move to and thrive in adventive locations, eventually establishing themselves. Several species of bumble bees (*Bombus* spp.) introduced for crop pollination to New Zealand in 1885 performed better there than within their native range. For example, *Bombus ruderatus*, once critically endangered [35] and now extinct [36] in native Denmark, is apparently abundant in New Zealand [37]. Other bees are inadvertently exotic [38], in particular those species that nest in stems or wood and are polylectic [39–42]. Oligolectic exotic species are also known, but they usually remain specialized on pollen hosts closely related to those visited in their native range [39].

The effectiveness of a bee as a pollinator depends on many factors. It is important to establish if pollen is collected and placed on the bee, and if the bee continues to forage and visit the same floral species where pollen can be deposited [43]. Bees that carry pollen internally or have only limited external pollen-collecting hairs, such as species in the genus *Hylaeus* (Figure 1D), will carry less pollen available for cross-pollination, as will species that carefully pack and store pollen on certain body parts that are less likely to come into contact with floral stigmas before returning to the nest. Some bees end up not touching the pollen-loaded anthers or fail to deposit pollen on receptive stigmas, thus preventing effective cross-pollination. Examples include species of *Bombus* (Figure 1F) and *Xylocopa* that are commonly observed biting through the base of the corolla to access the nectar (nectar robbing), without entering through the corolla, thus never contacting the anthers and stigma [44].

Diet specialization

Host specialization is widespread among herbivorous insects, yet the selective advantage leading to the evolutionary origin of foraging specializations among bees is not fully understood. General characteristics of flowers, such as bilateral symmetry (zygomorphy), have possibly evolved as adaptations to pollination by bees [2,3], although a more refined understanding of the Cretaceous pollinating insect-angiosperm co-radiations and discerning between correlations *versus* causes and effects remain obscure [45]. For example, the evidence is lacking that a switch from ancestral wasp carnivory to pollen-feeding led to the diversification of bees [46]. Although pollen consumption was a necessary but seemingly insufficient condition for their diversification, other complementary innovations such as a broadening of host-plant diet, perhaps allowed for the radiation of major bee lineages. Notwithstanding the role of pollenivory in defining the *origin* of bees, the *radiation* of bees

Figure 1. Pollen and nectar foraging bees.

Photos by N. Vereecken except where noted. (A) *Chelostoma rapunculi* (Megachilidae) on *Campanula* sp., Campanulaceae (Belgium); (B) *Lipotriches clavatus* (Halictidae) collecting pollen moistened by morning dew on *Eleusine indica*, Poaceae (DR Congo); (C) *Panurgus* sp. (Andrenidae) on Asteraceae (Sardinia, Italy); (D) *Hylaeus signatus* (Colletidae) a specialist on *Reseda luteola*, Resedaceae (Belgium), this genus transports pollen internally and has limited pubescence for retaining pollen externally; (E) *Hoplitis cristatula* (Megachilidae) on *Malva sylvestris*, Malvaceae (France), notice the pollen-loaded scopa on the metasoma; (F) *Bombus terrestris* (Apidae) nectar robbing on *Aquilegia* sp., Ranunculaceae (Belgium); (G) *Geodiscelis longiceps* (Colletidae) specialized on Crinklemat plants (*Tiquilia*) (Chile) (photograph by Sam Droege).

should not be conceptualized as a single, Cretaceous-aged event tied to flowering plants. Instead, bee diversity is the result of numerous, individual radiations within the various lineages that undoubtedly took place at different times throughout bee evolution and as a result of unrelated biotic and abiotic factors. Future research should explore the extent to which host-plant shifts may have fueled the diversification of wild bees in groups

dominated by oligolectic species or species that are associated with particular floral morphologies, but avoid the pitfalls of over simplifying evolutionary processes by assuming accelerated change after ‘key innovations’ or arriving at an ‘adaptive zone’ e.g. [47]. Such work should be undertaken at a finer taxonomic scale, ideally at the level of species as it is at this level at which evolutionary processes unfold.

The protein content in pollen ranges from 2.5% to 61%, with most of the proteins being enzymes that function during pollen-tube growth and subsequent fertilization, but the specific protein content may be what drives floral host choice [48]. Because the attractive nutrients are encapsulated inside the highly resistant pollen grain and only available after a lengthy digestive process [17,49], pollen quality cannot be assessed *in situ* while foraging. Recognition of plants is typically based on visual and olfactory cues and signals, i.e. through peculiarities in the composition of floral volatiles [50]. By limiting foraging to a smaller number of closely related host plants, bees can ensure that the provisions are of a constant and known protein quality. Variable quality may provide inadequate energy for growth and even cause larval death [48,51], but research in this field targeting wild, solitary bees is still limited.

While specialization may seem like an evolutionary dead-end, diet breadth is in fact labile with frequent shifts in, e.g. *Andrena* (*Callandrena*), *Chelostoma*, and *Diadasia* from an oligolectic ancestor to descendants foraging across a broad range of pollen sources [52–54]. At the same time, rather highly conserved floral specializations within different clades of *Chelostoma* (Figure 1A), the exploitation of unrelated hosts with close floral similarity, as well as poor larval development on non-host pollen collectively suggest that floral host choice may still be constrained physiologically or neurologically within oligolectic bees [53,55]. Evidence from European species of *Colletes* indicates that an ‘invisible’ specialization might be driven by pollen chemistry — bees can be specialized on patterns of sterols and amino acids, and evolutionary shifts to morphologically contrasting host plants are facilitated by similarities in pollen chemistry rather than plant phylogenetic relatedness or morphological affinities [56].

How many bees are specialized on pollen sources? To a degree that they can only raise their larvae on pollen from a limited number of plant families or plant genera, Michener [15] refers to 69 of 443 genera in six bee families, corresponding to a global average of ~9% based on his numbers [1491/17187] of all bee species that are oligolectic. Specialization is not equally distributed across the globe, with the fewest specialists in tropical and high-latitude regions. Moldenke [57] reported the highest proportion of specialist pollen collectors as 60% among desert species and 50% in the Mediterranean-like climate areas of California. Westrich [58] recorded 30% of German bee species were specialists, while towards higher latitudes in boreal areas of Scandinavia <20% are oligolectic [59].

Although specialist bees are somewhat phylogenetically restricted, i.e. certain tribes or subfamilies encompass species that tend to have more restricted floral choices, specialists are still found in virtually every lineage of bees. Host plant specialization is particularly common among the following taxonomic groups: Euryglossinae and several groups of Paracolletinae (Colletidae); Panurginae (Figure 1C) and some Andreninae (Andrenidae); most Rophitinae (Halictidae); most Melittidae; many Fideiinae and some Lithurginae and Megachilinae (Figure 1E) (Megachilidae); some Eucerini and most Ancylini, Tarsaliini, and Emphorini (Apidae) [15,16,60]. Nonetheless, while useful in a descriptive sense, such broad ecological generalizations hold the potential to obscure finer-scale distinctions and lead to false positives or uninformative tests e.g. [47]. For example, it is important to note that many polylectic species at a local or short temporal scale have a functionally narrow diet range [61].

Plants in ~34 different plant families are more often the pollen source for specialized bees, among which Asteraceae, Myrtaceae, and Convolvulaceae each have more than 100 associated specialist bee species [15]. Other plant families have a lower total number of associated specialist bees, although they may all at the same time host a wide range of polylectic bee species. Plant families with just a single recorded oligolectic bee include *Niltonia virgilii* (Colletidae) visiting Bignoniaceae (*Jacaranda puberula*) [62], *Neffapis longilingua* (Andrenidae) visiting Malesherbiaceae (*Malesherbia*) [63], and *Anthemurgus passiflorae* (Andrenidae) visiting Passifloraceae (*Passiflora lutea*) [64]. The only oligolectic visitors to Hydrangeaceae (*Philadelphus*) are two disjunct species of *Chelostoma*, from North America and China, indicating a floral host choice that might have been conserved for several million years [53]. True monolecy is exceedingly rare and described as ‘oligolecty without a choice’ because it is often assumed that a bee specialized on a single plant species could also visit other closely related, morphologically similar, flowering plants whenever the latter would be available [30]. An apparent exception to this case is *Flavipanurgus venustus* (Andrenidae), a European species found in Mediterranean climates that consistently visits *Cistus crispus* (Cistaceae) across space (18 sites in SW Iberian

Peninsula) and time (three consecutive years) despite the presence of closely related congeneric plant species whose flowers are morphologically similar [65].

Behavioral specialization

Evolutionary adaptations to flower foraging are not only limited to structural modifications. As suggested by Mayr [66], the invasion of any new niche presents a range of new selective pressures that will lead to a change in behavior. Therefore, initial behavioral specializations may lead to subsequent structural changes, and thus act as a pacemaker for evolution. If this is the case, then it is critical to first look at behavioral specialization for pollen and nectar gathering by bees among other floral rewards. While structural specializations are more straightforward to identify, behavioral specialization is often subtle and requires in-depth field studies.

Linsley [67], while meticulously documenting how desert bees operate under harsh climatic conditions, noted that pollen collection primarily occurs from dawn and to the period before or just after sunrise, or at least late afternoon, when flowering plants in the genera *Mentzelia* (Loasaceae) and *Oenothera* (Onagraceae) release their pollen. This author also noted that of those bees active during the heat of the day, the majority were small-bodied and thus able to avoid sun exposure by entering flowers and remaining partly shaded. Bees' thermal tolerances may play a critical role in determining specific niche parameters including the timing of foraging bouts.

Although the timing of pollen collection is key to optimizing foraging, the ability of bees to moisten the pollen they collect may also play a critical role in the completion of their life cycle. For bees that either possess limited scopal hairs or bees that collect tiny pollen grains (e.g. from Boraginaceae or Poaceae), the foraging flight back to the nest can be made more efficient by packing up larger volumes of pollen through the active moistening of pollen grains with nectar, oil, saliva, or morning dew (Figure 1B). This behavioral adaptation allows for a larger and wider variety of pollen grains with different sizes and surface ornamentation to be transported by the same individual bee [68]. While wetting pollen may improve efficiency in pollen transport, it may also reduce the effectiveness of such pollen to be transferred to stigmas, thereby decreasing pollination efficiency.

While these specializations, timing and packing, can be found across different bee lineages, other behavioral adaptations are specific to certain lineages. Most gardeners know the sound produced by bees when pollinating plants in the family Solanaceae, and it is the sound of fruits to come. Pollen in most flowering plants are exposed and made available when the floral anthers split. However, in some plants the anthers do not split, but are instead poricidally dehiscent [69]. Buchmann [69] described the behavior, involving only the use of flight muscles for buzzing [also called sonication], as: 'Upon alighting, female bees curl around the 'anther cone,' if present or grasp clusters of stamens while rapidly shivering their large indirect flight muscles. This produces an audible buzzing sound and transmits strong vibrations to the floral androecium. In response to this vibration, the pollen is expelled striking and sticking to the venter of the bee where it is later groomed and packed into the scopa'. The night-shade family of Solanaceae is the best known of the families with poricidally dehiscent anthers, but such anthers are found in ~9% of all flowering plant species. The western honey bee (*A. mellifera*) is unable to vibrate its thoracic muscles and worker honey bees are usually regarded as poor pollinators of 'buzz' flowers. Their hives are therefore only placed in blueberry fields requiring buzzing because the high number of visits to the flowers compensates for the lack of specialization in behavior and low *per capita* pollination efficiency [70]. In contrast, bumble bees (*Bombus*) and certain members of the families Colletidae, Halictidae, and Apidae can 'buzz'. Members of *Megachile* and Andrenidae, except *Protandrena*, *Protoxaea*, *Alocandrena* and certain members of *Andrena*, are apparently unable to 'buzz' anthers [69,71–76].

An important behavioral aspect of adaptation relates to the phenological timing of the adult bee flight. In areas with a marked seasonality, adults are often only found in flight during specific dates, during either spring, summer or fall. As has been outlined in the phenological match-mismatch hypothesis, climate warming may cause different emergence patterns for plants and pollinators, with marked effects on phenology, demography, local abundance, and large-scale distribution of plants and pollinators [77]. Such mismatch may influence specific plant associations, although the large-scale implications are as of yet unknown [78–84]. Climatic warming may also result in the local exclusion and potential extirpation of bees with limited thermal tolerances.

Morphological specialization

Most foraging specialization has to do with pollen gathering, as it is the pollen sources that are restricted, while nectar preference is more general. Despite this, some bees also exhibit specialization towards nectar collecting. In one bee species from Brazil, the short-tongued colletid *Niltonia virgilii*, Laroca, Michener, and Hofmeister [62] discovered that the labial palpi were extremely modified, formed as an elongate tube, approaching the body length of the species, and augmented to imbibe nectar from *Jacaranda puberula* (Bignoniaceae) [62]. Other short-tongued colletids with modified mouthparts, achieved via an expanded head-length, include *Geodiscelis* from Chile and Peru (Figure 1G), that are specialized on nectar from Boraginaceae [85]. In fact, it may be that elongate-headed bees, which occur across various groups (e.g. *Thrinchostoma*, *Chlerogas*, *Chlerogella*, *Ischnomelissa*, *Chlerogelloides*), are specialized for particular floral morphologies and nectar rather than specific sources of pollen, although for most their biology remains to be discovered [86].

The external structures for the transport of pollen by the female bee from the flowers back to the nest can be classified under two broad and general categories: (1) scopae for areas of long, frequently dense hairs, usually on the underside of the metasoma, the hind legs, or the propodeal sides of many *Andrena*, where pollen is entangled, and (2) fiscinae and corbiculae with fringes of hairs enclosing a space in which the pollen is carried [87–89]. In the latter, pollen are often packed moistened, while the arrangement of the scopa depends on the pollen type collected.

The density and plumosity of scopal hairs are presumably related to the size and structure of the pollen grains. Pollen sizes vary from <10 µm to more than 100 µm, and come in a plethora of spherical morphologies, sometimes held together by viscin threads, and enclosed by an outer exine layer and an inner intine layer [90]. The ornamentation is specific to different plant taxa, sometimes at the species level, and is extremely variable. Examples include (but are not limited to) species of Eucerini that have independently evolved specialization (i.e. oligolecty) on Malvaceae which produce remarkably large pollen grains; the scopae of female bees exhibit significantly larger spaces among individual scopal hairs than in closely related species visiting host plants in other families [91]. Differences in scopal hair densities resulting in more ‘closed’ versus ‘open’ scopae have been observed in various bee lineages, e.g. [92], but remain to be more fully explored. However, as a general rule it seems that large pollen grains can therefore only efficiently be collected and transported by bees with stout, unbranched scopal hairs, such as those found in the genus *Xenoglossa* (Apidae) specialized on pollen from gourds and squashes and *Andrena* (*Onagrandrena*) on Onagraceae [68,93]. This phenomenon is further documented by examining morphological specializations of bees tied to particular host plants with unusually small pollen grains: for example, while examining pollen loads from different bees, researchers found that scopal hairs on the hind legs of bees that collect small pollen grains, like *Ptiloglossa* and *Caupolicana* (Colletidae), have an extraordinary fluffy appearance, increasing the effectiveness of picking up extremely small particles [93,94]. Similar scopal hairs, with a dense network of multi-branched hairs, are also found in the family Andrenidae (*Oxaea*) [93]. Other bees possess smoother, more numerous, and slender hairs with many closely spaced branches in a scopal network. Once the pollen grain size reaches above 100 µm, most bees are unable to pack and force the large pollen grains into the network of branched hairs for transport [93].

A morphological specialization for extracting and transporting pollen involves the presence of modified, long hairs, usually hooked or waxy at the tips, near the mouthparts or on the proboscis, on the forelegs, or even on the vertex [68,95,96]. This allows bees to extract pollen from anthers located deep in a narrow corolla and are features that occur in various unrelated bee genera and families [97,98], such as in different species of Apidae collecting pollen from flowers of Pontederiaceae [99].

A distinct challenge for bees is the collection and transportation of floral oils. It has been known since Vogel [100] that solitary female oil bees collect fatty floral oils from specialized oil-secreting plants with the aid of specialized hairs on either their legs or abdomen, a reward used as food for their larvae and/or to line their brood cells. Branched hairs to restrain the oil have evolved independently in several different lineages of bees [93,101]: *Macropis* (Melittidae) collect floral oils from species in the family Primulaceae in the northern temperate regions of the Old and the New World (Figure 2A) [102]; *Rediviva* (Melittidae) in Africa from representatives in the Scrophulariaceae and Orchidaceae [102], while Ctenoplectrini (Apidae) collect oils from species of Cucurbitaceae in Borneo, Sumatra, Java, and Sulawesi and possibly also in Africa [103]; in the New World tropics, *Centris*, *Epicharis*, and *Chalepogenus* (Apidae) are some of the best known oil-gathering bees from taxa in the families Malphiaceae and Scrophulariaceae.

Figure 2. Oil bees and oil-flowers.

(A) A female of the oil-collecting bee *Macropis fulvipes* (Melittidae) foraging for floral oils on *Lysimachia* sp., Primulaceae (Belgium), photograph by N. Vereecken; (B) Foreleg of *Centris neffi* (Apidae) (Peru), an oil-collecting specialist from *Calceolaria*, Scrophulariaceae with modified setae on the basitarsus; (C). Closeup and frontal view of the same species, with the comb on the left and the few giant spatulate setae on the right, in the middle the stout setae that may serve to open the floral oil-glands, the elaiophores (SEM image by Claus Rasmussen).

As an example of this morphological specialization, most species of *Centris* collect floral oils with modified setae on the fore- and midlegs (Figure 2B,C) [101,104,105]. The female foreleg typically includes a row of 30 to 40 enlarged, flattened, and apically curved setae — the comb — on the basitarsus. The curved setae overlap slightly and, depending on the size of the bee, measure from 0.6 mm to 2.1 mm in length [104]. Opposite to the foreleg comb is a series of two to five giant spatulate setae, forming, together with the comb, the ‘kaputzorgane’ (sensu [20]). These latter setae are only found within females of *Centris*, although it is not clear whether these serve to collect oil more efficiently when appressed to the surface of the elaiophore. That is, the giant spatulate setae extend the scraping margin, thus increasing the oil-uptake rate by forming a continuation of the scraping movement, when the individual setae of the primary comb bend over [104]. Between the giant setae and, or just posterior to, the comb, a series of up to three stout setae is found, the setae may be large and hooked inward [104]. In some species, similar setae are found also on the midleg. It has been hypothesized that the stout setae may serve to open the cuticula of the epithelial elaiophores by ripping it up [104]. Furthermore, many species of *Centris* have a smaller and shorter compound comb anterior to the primary one [104]. The above-described comb pattern is found on most *Centris*, and on virtually all that are known to collect oil from epithelial

elaiophores. Modifications in other groups of oil-gathering bees include a dense pad that is used to sop up oil, while the comb is more or less reduced [106].

Naturally, the bee-flower biological association is much more diverse than highlighted herein, but the above overview serves as a brief account of the range of associations encompassing bee-floral specialization in terms of diet, behavior, and morphology.

Summary

- Bee-mediated pollination is one of the most fundamental and vital functions in healthy terrestrial ecosystems and yet remains poorly appreciated.
- Diet specialization, bees foraging only from a narrow range of pollen sources, secure larval provisions with optimal protein quality for growth.
- Behavioral specializations may act as a pacemaker of evolution, and frequently include daily timing of floral visits, moistening and packing of pollen grains for return flights to the nest, or the vibration of flowers (buzzing) for an effective release of pollen grains.
- Morphological specialization includes both the density and type of hair for collection of different sized of pollen grains, flattened spatulate hairs for gathering oil, and extremely elongate mouthparts to gain access to hidden nectar sources.
- Future work should further explore the behavior, physiology, and morphology of a greater breadth of individual bee species in association with their floral hosts, and give precedence to understanding host shifts at the operational level of species relative to broader, coarsely characterized ecological generalizations at higher taxonomic ranks.
- A promising avenue for future research into the evolution of host plants by bees relates to the impact of host plant shifts on diversification rates in different groups of wild bees.

Competing Interests

The authors declare that there are no competing interests associated with the manuscript.

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Author Contribution

C.R. drafted and contributed to the manuscript, M.S.E. and N.J.V. contributed to the manuscript.

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References

- 1 Simpson, B.B. and Neff, J.L. (1981) Floral rewards: alternatives to pollen and nectar. *Ann. Mo. Bot. Gard.* **68**, 301–322 <https://doi.org/10.2307/2398800>
- 2 Proctor, M.C.F. and Yeo, P.F. (1979) *The Pollination of Flowers*, Collins, London
- 3 Proctor, M.C.F., Yeo, P.F. and Lack, A.J. (1996) *The Natural History of Pollination*, Timber Press, Portland, OR

- 4 Neff, J.L. and Simpson, B.B. (1993) Bees, pollination systems and plant diversity. In *Hymenoptera and Biodiversity* (La Salle, J. and Gauld, I.D., eds), pp. 143–167, CAB International, Wallingford
- 5 Ollerton, J., Winfree, R. and Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos* **120**, 321–326 <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- 6 Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. et al. (2007) Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. Lond. Ser. B* **274**, 303–313 <https://doi.org/10.1098/rspb.2006.3721>
- 7 Gallai, N., Salles, J.-M., Settele, J. and Vaissière, B.E. (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* **68**, 810–821 <https://doi.org/10.1016/j.ecolecon.2008.06.014>
- 8 Garibaldi, L.A., Carvalheiro, L.G., Vaissière, B.E., Gemmill-Herren, B., Hipolito, J., Freitas, B.M. et al. (2016) Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science* **351**, 388–391 <https://doi.org/10.1126/science.aac7287>
- 9 Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A. et al. (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science* **339**, 1608–1611 <https://doi.org/10.1126/science.1230200>
- 10 Klein, A.-M., Steffan-Dewenter, I. and Tschamtkke, T. (2003) Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. Lond. Ser. B* **270**, 955–961 <https://doi.org/10.1098/rspb.2002.2306>
- 11 Woodcock, B.A., Garratt, M.P.D., Powney, G.D., Shaw, R.F., Osborne, J.L., Soroka, J. et al. (2019) Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. *Nat. Commun.* **10**, 1481 <https://doi.org/10.1038/s41467-019-09393-6>
- 12 Klatt, B.K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E. et al. (2014) Bee pollination improves crop quality, shelf life and commercial value. *Proc. R. Soc. B Biol. Sci.* **281**, 20132440 <https://doi.org/10.1098/rspb.2013.2440>
- 13 Gajc-Wolska, J., Kowalczyk, K., Mikas, J. and Drajski, R. (2011) Efficiency of cucumber (*Cucumis sativus* L.) pollination by bumblebees (*Bombus terrestris*). *Acta Sci. Pol. Hortorum Cultus* **10**, 159–169
- 14 Al-Attal, Y.Z., Kasrawi, M.A. and Nazer, I.K. (2003) Influence of pollination technique on greenhouse tomato production. *Agric. Mar. Sci.* **8**, 21–26
- 15 Michener, C.D. (2007) *The Bees of the World*, second edition, Johns Hopkins University Press, Baltimore
- 16 Danforth, B.N., Minckley, R.L. and Neff, J.L. (2019) *The Solitary Bees: Biology, Evolution, Conservation*, Princeton University Press
- 17 Dobson, H.E.M. and Peng, Y.-S. (1997) Digestion of pollen components by larvae of the flower-specialist bee *Chelostoma florissomne* (Hymenoptera: Megachilidae). *J. Insect Physiol.* **43**, 89–100 [https://doi.org/10.1016/S0022-1910\(96\)00024-8](https://doi.org/10.1016/S0022-1910(96)00024-8)
- 18 Cane, J.H. (2016) Adult pollen diet essential for egg maturation by a solitary *Osmia* bee. *J. Insect Physiol.* **95**, 105–109 <https://doi.org/10.1016/j.jinsphys.2016.09.011>
- 19 Cane, J.H., Dobson, H.E.M. and Boyer, B. (2017) Timing and size of daily pollen meals eaten by adult females of a solitary bee (*Nomia melanderi*) (Apiformes: Halictidae). *Apidologie* **48**, 17–30 <https://doi.org/10.1007/s13592-016-0444-8>
- 20 Vogel, S. (1974) Ölblumen und ölsammelnde Bienen. *Trop. Subtrop. Pflwelt* **7**, 1–267
- 21 Roubik, D.W. (1982) Obligate necrophagy in a social bee. *Science* **217**, 1059–1060 <https://doi.org/10.1126/science.217.4564.1059>
- 22 Mateus, S. and Noll, F.B. (2004) Predatory behavior in a necrophagous bee *Trigona hypogaea* (Hymenoptera; Apidae, Meliponini). *Naturwissenschaften* **91**, 94–96 <https://doi.org/10.1007/s00114-003-0497-1>
- 23 Bänziger, H. (2018) Congregations of tear drinking bees at human eyes: foraging strategies for an invaluable resource by *Lisotrigona* in Thailand (Apidae, Meliponini). *Nat. Hist. Bull. Siam Soc.* **62**, 161–193
- 24 Bänziger, H., Boongird, S., Sukumalanand, P. and Bänziger, S. (2009) Bees (Hymenoptera: Apidae) that drink human tears. *J. Kans. Entomol. Soc.* **82**, 135–150 <https://doi.org/10.2317/JKES0811.17.1>
- 25 Blagoveshchenskaya, N. N. (1995) Гнездование *Macropis labiata* F. (Apoidea, Melittidae) в Среднем Поволжье [The nesting of *Macropis labiata* F. (Apoidea, Melittidae) in the Middle Volga basin]. In: Naumov RV (ed) Любичевские чтения, 1995 г. (Тезисы докладов) [The Reading to the Memory of Prof. A. A. Lyubishchev]. Ульяновский государственный педагогический институт, Ulyanovsk, Russia, pp 47–48
- 26 Steffan, S.A. and Dharampal, P.S. (2019) Undead food-webs: Integrating microbes into the food-chain. *Food Webs* **18**, e00111 <https://doi.org/10.1016/j.fooweb.2018.e00111>
- 27 Steffan, S.A., Dharampal, P.S., Danforth, B.N., Gaines-Day, H.R., Takizawa, Y. and Chikaraishi, Y. (2019) Omnivory in bees: elevated trophic positions among all major bee families. *Am. Nat.* **194**, 414–421 <https://doi.org/10.1086/704281>
- 28 Steffan, S.A., Chikaraishi, Y., Currie, C.R., Horn, H., Gaines-Day, H.R., Pauli, J.N. et al. (2015) Microbes are trophic analogs of animals. *Proc. Natl Acad. Sci. U.S.A.* **112**, 15119–15124 <https://doi.org/10.1073/pnas.1508782112>
- 29 Dharampal, P.S., Carlson, C., Currie, C.R. and Steffan, S.A. (2019) Pollen-borne microbes shape bee fitness. *Proc. R. Soc. B Biol. Sci.* **286**, 20182894 <https://doi.org/10.1098/rspb.2018.2894>
- 30 Cane, J.H. and Sipes, S.D. (2006) Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty. In *Plant-pollinator Interactions: From Specialization to Generalization* (Waser, N.M. and Ollerton, J., eds), pp. 99–122, University of Chicago Press, Chicago
- 31 Gathmann, A. and Tschamtkke, T. (2002) Foraging ranges of solitary bees. *J. Anim. Ecol.* **71**, 757–764 <https://doi.org/10.1046/j.1365-2656.2002.00641.x>
- 32 Greenleaf, S.S., Williams, N.M., Winfree, R. and Kremen, C. (2007) Bee foraging ranges and their relationship to body size. *Oecologia* **153**, 589–596 <https://doi.org/10.1007/s00442-007-0752-9>
- 33 Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S. and Dorn, S. (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biol. Conserv.* **143**, 669–676 <https://doi.org/10.1016/j.biocon.2009.12.003>
- 34 Zurbuchen, A., Cheesman, S., Klaiber, J., Müller, A., Hein, S. and Dorn, S. (2010) Long foraging distances impose high costs on offspring production in solitary bees. *J. Anim. Ecol.* **79**, 674–681 <https://doi.org/10.1111/j.1365-2656.2010.01675.x>
- 35 Madsen, H.B. (2009) Humlebie. In *Den Danske Rødliste, Aarhus, Fagdatacenter for Biodiversitet og Terrestrisk Natur (B-FDC)* (Wind, P., ed.), Aarhus Universitet, Danmarks Miljøundersøgelser
- 36 Madsen, H.B. (2019) Bier. In *Den Danske Rødliste 2019* (Moeslund, J.E., Nygaard, B., Erjnæs, R., Bell, N., Bruun, L.D., Bygebjerg, R. et al., eds), Aarhus Universitet, DCE – Nationalt Center for Miljø og Energi, Aarhus
- 37 Donovan, B.J. (2007) *Apoidea (Insecta: Hymenoptera)*, Manaaki Whenua Press, Lincoln, New Zealand
- 38 Russo, L. (2016) Positive and negative impacts of non-native bee species around the world. *Insects* **7**, 1–22 <https://doi.org/10.3390/insects7040069>

- 39 Cane, J.H. (2003) Exotic non-social bees (Hymenoptera: Apoidea) in North America: Ecological implications. In *For Non-Native Crops, Whence Pollinators of the Future?* (Strickler, K.L. and Cane, J.H., eds), pp. 113–126, Thomas Say Publications, Entomological Society of America, Lanham, Maryland
- 40 Andrieu-Ponel, V., Ponel, P., Féon, V.L., Geslin, B. and Duvallet, G. (2018) À propos du comportement de butinage de *Megachile sculpturalis* Smith, 1853, en France méditerranéenne (Nîmes et Montpellier) (Hymenoptera, Megachilidae). *Bull. Soc. Entomol. Fr.* **123**, 49–54 https://doi.org/10.32475/bsef_1984
- 41 Vereecken, N.J. and Barbier, E. (2009) Premières données sur la présence de l'abeille asiatique *Megachile (Callomegachile) sculpturalis* Smith (Hymenoptera, Megachilidae) en Europe. *Osmia* **3**, 4–6
- 42 Rasmussen, C., Carrion, A.L., Castro-Urgal, R., Chamorro, S., Gonzalez, V.H., Griswold, T.L. et al. (2012) *Megachile timberlakei* Cockerell (Hymenoptera: Megachilidae): yet another adventive bee species to the Galápagos Archipelago. *Pan-Pacific Entomol.* **88**, 98–102 <https://doi.org/10.3956/2012-04.1>
- 43 Kevan, P.G. and Baker, H.G. (1983) Insects as flower visitors and pollinators. *Annu. Rev. Entomol.* **28**, 407–453 <https://doi.org/10.1146/annurev.en.28.010183.002203>
- 44 Rojas-Nossa, S.V., Sánchez, J.M. and Navarro, L. (2016) Nectar robbing: a common phenomenon mainly determined by accessibility constraints, nectar volume and density of energy rewards. *Oikos* **125**, 1044–1055 <https://doi.org/10.1111/oik.02685>
- 45 Grimaldi, D.A. (1999) The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Ann. Mo. Bot. Gard.* **86**, 373–406 <https://doi.org/10.2307/2666181>
- 46 Murray, E.A., Bossert, S. and Danforth, B.N. (2018) Pollinivory and the diversification dynamics of bees. *Biol. Lett.* **14**, 20180530 <https://doi.org/10.1098/rsbl.2018.0530>
- 47 Franz, N.M. and Engel, M.S. (2010) Can higher-level phylogenies of weevils explain their evolutionary success? A critical review. *Syst. Entomol.* **35**, 597–606 <https://doi.org/10.1111/j.1365-3113.2010.00534.x>
- 48 Roulston, T.H., Cane, J.H. and Buchmann, S.L. (2000) What governs protein content of pollen: pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecol. Monogr.* **70**, 617–643 [https://doi.org/10.1890/0012-9615\(2000\)070\[0617:WGPCOP\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2000)070[0617:WGPCOP]2.0.CO;2)
- 49 Bolick, M.R. and Vogel, S. (1992) Breaking strengths of pollen grain walls. *Plant Syst. Evol.* **181**, 171–178 <https://doi.org/10.1007/BF00937442>
- 50 Dötterl, S. and Vereecken, N.J. (2010) The chemical ecology and evolution of bee-flower interactions: a review and perspectives. *Can. J. Zool.* **88**, 668–697 <https://doi.org/10.1139/Z10-031>
- 51 Wcislo, W.T. and Cane, J.H. (1996) Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annu. Rev. Entomol.* **41**, 257–286 <https://doi.org/10.1146/annurev.en.41.010196.001353>
- 52 Larkin, L.L., Neff, J.L. and Simpson, B.B. (2008) The evolution of a pollen diet: host choice and diet breadth of *Andrena* bees (Hymenoptera: Andrenidae). *Apidologie* **39**, 133–145 <https://doi.org/10.1051/apido:2007064>
- 53 Sedivy, C., Praz, C.J., Müller, A., Widmer, A. and Dorn, S. (2008) Patterns of host-plant choice in bees of the genus *Chelostoma*: the constraint hypothesis of host-range evolution in bees. *Evolution* **62**, 2487–2507 <https://doi.org/10.1111/j.1558-5646.2008.00465.x>
- 54 Sipes, S.D. and Tepedino, V.J. (2005) Pollen-host specificity and evolutionary patterns of host switching in a clade of specialist bees (Apoidea: *Diadasia*). *Biol. J. Linn. Soc.* **86**, 487–505 <https://doi.org/10.1111/j.1095-8312.2005.00544.x>
- 55 Praz, C.J., Müller, A. and Dorn, S. (2008) Specialized bees fail to develop on non-host pollen: do plants chemically protect their pollen? *Ecology* **89**, 795–804 <https://doi.org/10.1890/07-0751.1>
- 56 Vanderplanck, M., Vereecken, N.J., Grumiau, L., Esposito, F., Lognay, G., Wattiez, R. et al. (2017) The importance of pollen chemistry in evolutionary host shifts of bees. *Sci. Rep.* **7**, 43058 <https://doi.org/10.1038/srep43058>
- 57 Moldenke, A.R. (1976) Evolutionary history and diversity of the bee faunas of Chile and Pacific North America. *Wasmann J. Biol.* **34**, 147–178
- 58 Westrich, P. (1990) *Die Wildbienen Baden-Württembergs. Teil 1: Lebensräume, Verhalten, Ökologie und Schutz*, Ulmer, Stuttgart
- 59 Pekkarinen, A. (1998) Oligolectic bee species in Northern Europe (Hymenoptera, Apoidea). *Entomol. Fennica* **8**, 205–214 <https://doi.org/10.33338/ef.83945>
- 60 Michez, D., Eardley, C.D., Timmermann, K. and Danforth, B.N. (2010) Unexpected polylecty in the bee genus *Meganomia* (Hymenoptera: Apoidea: Melittidae). *J. Kans. Entomol. Soc.* **83**, 221–230 <https://doi.org/10.2317/JKES0911.20.1>
- 61 MacIvor, J.S., Cabral, J.M. and Packer, L. (2014) Pollen specialization by solitary bees in an urban landscape. *Urban Ecosyst.* **17**, 139–147 <https://doi.org/10.1007/s11252-013-0321-4>
- 62 Laroca, S., Michener, C.D. and Hofmeister, R.M. (1989) Long mouthparts among 'short-tongued' bees and the fine structure of the labium in *Niltonia* (Hymenoptera, Colletidae). *J. Kans. Entomol. Soc.* **62**, 400–410
- 63 Rozen, J.G. and Ruz, L. (1995) South American Panurgine bees (Andrenidae: Panurginae), part II. Adults, immature stages, and biology of *Neffapis longilingua*, a new genus and species with an elongate glossa. *Am. Mus. Novit.* **3136**, 1–15
- 64 Neff, J.L. (2003) The passiflower bee: *Anthemurgus passiflorae*. *Passiflora* **13**, 7–9
- 65 González-Varo, J.P., Ortiz-Sánchez, F.J. and Vilà, M. (2016) Total bee dependence on one flower species despite available congeners of similar floral shape. *PLoS ONE* **11**, e0163122 <https://doi.org/10.1371/journal.pone.0163122>
- 66 Mayr, E. (1960) The emergence of evolutionary novelties. In *Evolution After Darwin* (Tax, S., ed.), pp. 349–380, University of Chicago Press, Chicago
- 67 Linsley, E.G. (1962) Ethological adaptations of solitary bees for the pollination of desert plants. In *Proceedings of the First International Symposium on Pollination* (Mittler, T.E., ed.), pp. 189–197, Swedish Seed Growers Association, Copenhagen, Denmark
- 68 Thorp, R.W. (1979) Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. *Ann. Mo. Bot. Gard.* **66**, 788–812 <https://doi.org/10.2307/2398919>
- 69 Buchmann, S.L. (1985) Bees use vibration to aid pollen collection from non-poroid flowers. *J. Kans. Entomol. Soc.* **58**, 517–525
- 70 Dedej, S. and Delaplane, K.S. (2003) Honey bee (Hymenoptera: Apidae) pollination of rabbiteye blueberry *Vaccinium ashei* var. 'Climax' is pollinator density-dependent. *J. Econ. Entomol.* **96**, 1215–1220 <https://doi.org/10.1603/0022-0493-96.4.1215>
- 71 Gogala, A. and Surina, B. (2011) Foraging behaviour of the bee *Osmia apicata* Smith, 1853 (Hymenoptera: Megachilidae). *Acta Entomol. Slovenica* **19**, 139–144
- 72 Dukas, R. and Dafni, A. (1990) Buzz-pollination in three nectariferous Boraginaceae and possible evolution of buzz-pollinated flowers. *Plant Syst. Evol.* **169**, 65–68 <https://doi.org/10.1007/BF00935985>
- 73 Torchio, P.F. (1990) *Osmia ribifloris*, a native bee species developed as a commercially managed pollinator of highbush blueberry (Hymenoptera: Megachilidae). *J. Kans. Entomol. Soc.* **63**, 427–436

- 74 Cane, J.H. (2014) The oligolectic bee *Osmia brevis* sonicates *Penstemon* flowers for pollen: a newly documented behavior for the Megachilidae. *Apidologie* **45**, 678–684 <https://doi.org/10.1007/s13592-014-0286-1>
- 75 Cardinal, S., Buchmann, S.L. and Russell, A.L. (2018) The evolution of floral sonication, a pollen foraging behavior used by bees (Anthophila). *Evolution* **72**, 590–600 <https://doi.org/10.1111/evo.13446>
- 76 Rozen, J.G. and Ugarte-Peña, A. (1999) Notes on the seasonality, geographic distribution, and floral preferences of the bee *Alocandrena porteri* (Hymenoptera: Andrenidae). *J. Kans. Entomol. Soc.* **72**, 335–338
- 77 Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. and Totland, Ø. (2009) How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* **12**, 184–195 <https://doi.org/10.1111/j.1461-0248.2008.01269.x>
- 78 Schenk, M., Krauss, J. and Holzschuh, A. (2018) Desynchronizations in bee-plant interactions cause severe fitness losses in solitary bees. *J. Anim. Ecol.* **87**, 139–149 <https://doi.org/10.1111/1365-2656.12694>
- 79 Riveros, A.J., Hernández, E.J. and Wcislo, W.T. (2009) Nesting biology of *Euglossa dodsoni* Moure (Hymenoptera: Euglossinae) in Panama. *J. Kans. Entomol. Soc.* **82**, 210–214 <https://doi.org/10.2317/JKES808.15.1>
- 80 Bronstein, J.L., Gouyon, P.-H., Gliddon, C., Kjellberg, F. and Michaloud, G. (1990) The ecological consequences of flowering asynchrony in monoecious figs: a simulation study. *Biol. J. Linn. Soc.* **71**, 2145–2156
- 81 Robbirt, K.M., Roberts, D.L., Hutchings, M.J. and Davy, A.J. (2014) Potential disruption of pollination in a sexually deceptive orchid by climatic change. *Curr. Biol.* **24**, 2845–2849 <https://doi.org/10.1016/j.cub.2014.10.033>
- 82 Kehrberger, S. and Holzschuh, A. (2019) Warmer temperatures advance flowering in a spring plant more strongly than emergence of two solitary spring bee species. *PLoS ONE* **14**, e0218824 <https://doi.org/10.1371/journal.pone.0218824>
- 83 Miller-Struttmann, N.E., Geib, J.C., Franklin, J.D., Kevan, P.G., Holdo, R.M., Ebert-May, D. et al. (2015) Functional mismatch in a bumble bee pollination mutualism under climate change. *Science* **349**, 1541–1544 <https://doi.org/10.1126/science.aab0868>
- 84 Schmidt, N.M., Mosbacher, J.B., Nielsen, P.S., Rasmussen, C., Høye, T.T. and Roslin, T. (2016) An ecological function in crisis? – the temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms. *Ecography* **39**, 1250–1252 <https://doi.org/10.1111/ecog.02261>
- 85 Ferrari, R.R. (2015) A new species of *Geodiscelis* Michener & Rozen (Hymenoptera: Colletidae: Xeromelissinae) from Peru. *Zootaxa* **4033**, 293–300 <https://doi.org/10.11646/zootaxa.4033.2.10>
- 86 Engel, M.S. (2000) Classification of the bee tribe Augochlorini (Hymenoptera: Halictidae). *Bull. Am. Mus. Nat. Hist.* **250**, 1–89 [https://doi.org/10.1206/0003-0090\(2000\)250<0001:COTBTA>2.0.CO;2](https://doi.org/10.1206/0003-0090(2000)250<0001:COTBTA>2.0.CO;2)
- 87 Michener, C.D. (1999) The corbiculae of bees. *Apidologie* **30**, 67–74 <https://doi.org/10.1051/apido:19990108>
- 88 Braue, A. (1913) Die Pollensammelapparate der beinsammelnden Bienen. *Jenaische Zeitschrift für Naturwissenschaft.* **50**, 1–96
- 89 Engel, M.S. (2001) A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). *Bull. Am. Mus. Nat. Hist.* **259**, 1–192 [https://doi.org/10.1206/0003-0090\(2001\)259<0001:AMOTBA>2.0.CO;2](https://doi.org/10.1206/0003-0090(2001)259<0001:AMOTBA>2.0.CO;2)
- 90 Hesse, M., Halbritter, H., Zetter, R., Weber, M., Buchner, R., Frosch-Radivo, A. et al. (2009) *Pollen Terminology: An Illustrated Handbook*, Springer, Wien
- 91 Eardley, C.D. (1989) The Afrotropical species of *Eucera* Friese, *Tetralonia* Spinola and *Tetraloniella* Ashmead (Hymenoptera: Anthophoridae). *Entomol. Mem. Department of Agriculture and Water Supply* **75**, 1–62
- 92 Engel, M.S., Alquarni, A.S. and Shebl, M.A. (2017) Discovery of the bee tribe Tarsaliini in Arabia (Hymenoptera: Apidae), with the description of a new species. *Am. Mus. Novit.* **3877**, 1–28 <https://doi.org/10.1206/3877.1>
- 93 Roberts, R.B. and Vallespir, S.R. (1978) Specialization of hairs bearing pollen and oil on the legs of bees (Apoidea: Hymenoptera). *Ann. Entomol. Soc. Am.* **71**, 619–627 <https://doi.org/10.1093/aesa/71.4.619>
- 94 Robertson, C. (1925) Heterotrophic bees. *Ecology* **6**, 412–436 <https://doi.org/10.2307/1929107>
- 95 Neff, J.L. (2004) Hooked hairs and not so narrow tubes: Two new species of *Colletes* Latreille from Texas (Hymenoptera: Apoidea: Colletidae). *J. Hymenopt. Res.* **13**, 250–261
- 96 Müller, A. (1996) Convergent evolution of morphological specializations in Central European bee and honey wasp species as an adaptation to the uptake of pollen from nototribic flowers (Hymenoptera, Apoidea and Masaridae). *Biol. J. Linn. Soc.* **57**, 235–252 <https://doi.org/10.1006/bjil.1996.0013>
- 97 Parker, F.D. and Tepedino, V.J. (1982) A nest and pollen-collection records of *Osmia sculleni* Sandhouse, a bee with hooked hairs on the mouthparts (Hymenoptera: Megachilidae). *J. Kans. Entomol. Soc.* **55**, 329–334
- 98 Thorp, R.W. (2000) The collection of pollen by bees. *Plant Syst. Evol.* **222**, 211–223 <https://doi.org/10.1007/BF00984103>
- 99 Alves-dos-Santos, I. (2003) Adaptations of bee proboscides for collecting pollen from Pontederiaceae flowers. In *Apoidea Neotropica: Homenagem aos 90 Anos de Jesus Santiago Moure* (Melo, G.A.R. and Alves-dos-Santos, I., eds), pp. 257–264, Editora UNESCO, Criciúma
- 100 Vogel, S. (1969) Flowers offering fatty oil instead of nectar. *XI Int. Bot. Congr. Abstr.* **1969**, 229
- 101 Rasmussen, C. and Olesen, J.M. (2000) Oil flowers and oil-collecting bees. Det Norske Videnskaps-akademi I Matematisk Naturvidenskapelig Klasse, Skrifter. *Ny Serie* **39**, 23–31
- 102 Vogel, S. (1988) Die ölblumensymbiosen - Parallelismus und andere Aspekte ihrer Entwicklung in Raum und Zeit. *Z. Zool. Syst. Evol.forsch.* **26**, 341–362 <https://doi.org/10.1111/j.1439-0469.1988.tb00322.x>
- 103 Steiner, K.E. and Whitehead, V.B. (1988) The association between oil-producing flowers and oil-collecting bees in the Drakensberg of Southern Africa. *Monogr. Syst. Bot. Mo. Bot. Gard.* **25**, 259–277
- 104 Neff, J.L. and Simpson, B.B. (1981) Oil-collecting structures in the Anthophoridae (Hymenoptera): morphology, function, and use in systematics. *J. Kans. Entomol. Soc.* **54**, 95–123
- 105 Buchmann, S.L. (1987) The ecology of oil flowers and their bees. *Annu. Rev. Ecol. Syst.* **18**, 343–369 <https://doi.org/10.1146/annurev.es.18.110187.002015>
- 106 Roig-Alsina, A. (1997) A generic study of the bees of the tribe *Tapinotaspini*, with notes on the evolution of their oil-collecting structures. *Mitt. Münch. Ent. Ges.* **87**, 3–21