

# The chemical ecology and evolution of bee–flower interactions: a review and perspectives<sup>1</sup>

S. Dötterl and N.J. Vereecken

**Abstract:** Bees and angiosperms have shared a long and intertwined evolutionary history and their interactions have resulted in remarkable adaptations. Yet, at a time when the “pollination crisis” is of major concern as natural populations of both wild and honey bees (*Apis mellifera* L., 1758) face alarming decline rates at a worldwide scale, there are important gaps in our understanding of the ecology and evolution of bee–flower interactions. In this review, we summarize and discuss the current knowledge about the role of floral chemistry versus other communication channels in bee-pollinated flowering plants, both at the macro- and micro-evolutionary levels, and across the specialization–generalization gradient. The available data illustrate that floral scents and floral chemistry have been largely overlooked in bee–flower interactions, and that pollination studies integrating these components along with pollinator behaviour in a phylogenetic context will help gain considerable insights into the sensory ecology and the evolution of bees and their associated flowering plants.

**Résumé :** Les abeilles et les angiospermes partagent une grande partie de leur histoire évolutive, et leurs interactions ont produit de remarquables exemples d’adaptations mutuelles. Cependant, à une époque où la « crise de la pollinisation » devient une préoccupation majeure et où les populations d’abeilles sauvages et mellifères (*Apis mellifera* L., 1758) font face à des déclin massifs à l’échelle mondiale, notre compréhension de l’écologie et de l’évolution des relations abeilles–plantes demeure fragmentaire. Dans cet article, nous fournissons une synthèse de l’état de nos connaissances relatives au rôle de la communication chimique par rapport aux autres signaux floraux chez les plantes à fleurs pollinisées par les abeilles, tant à l’échelle macro- que micro-évolutive, et le long du gradient spécialisation–généralisation. Les données disponibles illustrent que les parfums floraux et la chimie florale ont largement été ignorés dans l’étude des interactions abeilles–fleurs, et que l’intégration de ces composantes ainsi que du comportement des pollinisateurs dans un contexte phylogénétique permettrait de réaliser des avancées significatives dans notre compréhension de l’écologie sensorielle et de l’évolution des abeilles et des plantes à fleurs auxquelles elles sont associées.

## Introduction

Although it took almost until the invention of the steam engine to discover that flowering plants owe their reproduction to visits from their insect pollinators (Proctor and Yeo 1972), there is now wide agreement in the scientific community that insects actively mediate the pollination of most flowering plants worldwide. Bees (Hymenoptera, Apoidea), in particular, are commonly regarded as highly important pollinators, as much for their unusual diversity (ca. 20 000 species worldwide; Michener 2007) as for their tight codependence with flowering plants. Foraging bees move pollen from one flower to the next while collecting the floral rewards (pollen, nectar, oils, resins) upon which they depend

during both the larval and the adult stages (Eickwort and Ginsberg 1980; Simpson and Neff 1981; Wcislo and Cane 1996; but for an exception see Roubik 1982). Angiosperms and bees have a long-standing relationship that is thought to have originated between 70 and 130 million years ago (Michener and Grimaldi 1988; Engel 2000; Poinar and Danforth 2006). Flowering plants are associated with a broad spectrum of animal pollinators, of which bees constitute an important but not exclusive subset and whose sensory and learning capabilities have been explored in recent reviews (Weiss 2001; Dobson 2006). However, we have chosen to focus this review on bees and their flowers, with a desire to promote a greater appreciation for their chemical ecology, given (i) the preponderance of recent studies on their eco-

Received 15 February 2009. Accepted 3 May 2010. Published on the NRC Research Press Web site at [cjz.nrc.ca](http://cjz.nrc.ca) on 6 July 2010.

S. Dötterl<sup>2,3</sup> Department of Plant Systematics, University of Bayreuth, D-95440 Bayreuth, Germany.

N.J. Vereecken<sup>3,4</sup> Evolutionary Biology and Ecology, Free University of Brussels/Université Libre de Bruxelles, avenue FD Roosevelt 50 CP 160/12, B-1050 Brussels, Belgium; Institute of Systematic Botany, University of Zürich, Zollikerstrasse 107, CH-8008 Zürich, Switzerland.

<sup>1</sup>The present review is one in the special series of reviews on animal–plant interactions.

<sup>2</sup>Corresponding author (e-mail: [stefan.doetterl@uni-bayreuth.de](mailto:stefan.doetterl@uni-bayreuth.de)).

<sup>3</sup>Both authors contributed equally and are listed in alphabetical order.

<sup>4</sup>Corresponding author (e-mail: [nicolas.vereecken@ulb.ac.be](mailto:nicolas.vereecken@ulb.ac.be)).

system services (Kremen et al. 2004; Steffan-Dewenter et al. 2005), (ii) rising worries about mass declines of their natural populations (Steffan-Dewenter et al. 2005; Williams 2005; Biesmeijer et al. 2006; Fitzpatrick et al. 2007; Colla and Packer 2008; Goulson et al. 2008), and (iii) colony collapse disorder (CCD) of *Apis mellifera* L., 1758 (domesticated honey bee) (Cox-Foster et al. 2007; Anderson et al. 2008; see also Benjamin and McCallum 2008; Schacker 2008). Recent reports have stressed that the global crop production is largely dependent upon pollinator services (Buchmann and Nabhan 1996; Klein et al. 2007), and that the total economic value of pollination worldwide for the 100 crops used directly for human food (as listed by the Food and Agriculture Organization of the United Nations) amounts to ~153 billion per year (Gallai et al. 2009). Hence, the decline of bees would not only cause dramatic changes in habitat diversity but also could jeopardize the considerable share of human food supply derived from insect-pollinated crops.

Understanding the causes of parallel declines of bees and their host plants requires identifying the various components that make bee–flower interactions both complex and fragile, the extent of their mutual dependence, and the signals that mediate their interactions. The works of Karl von Frisch on the sensory ecology and communication of the honey bee (von Frisch 1919, 1923) pioneered the study of floral signals used by a broad spectrum of solitary to social bees for finding host plants. We have long known that bees use combinations of visual, olfactory, and tactile floral cues to find appropriate host plants (von Frisch 1919; Lacher 1964; Vareschi 1971; Kevan and Lane 1985; Menzel 1985; Dobson 1994; Giurfa et al. 1996; Whitney et al. 2009), and that they are capable of learning floral signals during their foraging bouts (Menzel et al. 1974; Smith 1991; Kaiser and De Jong 1993; Hill et al. 1997; Beekman 2005; Zhang et al. 2006). The general pattern emerging from such studies is that bees rely primarily on olfactory cues during their early foraging trips and that visual cues become more important in host-plant location as bees become more experienced (Dobson 1994 and see below). More recently, Dobson (2006) has reviewed all available data on the use of floral scent by food-seeking bees and found that flowers visited by bees emit odour bouquets which, taken as a group, encompass a huge variety of compounds and compound blends. However, their roles in bee–plant interactions remain poorly understood.

A major breakthrough in filtering biologically relevant fractions from the spectra of odour compounds emitted by flowers was achieved by coupling gas chromatographic (GC) analyses with electroantennographic detection (EAD) (see Arn et al. 1975). This method (GC–EAD) facilitates the screening of complex odour blends for EAD-active compounds, i.e., those compounds that stimulate antennal olfactory receptor neurons (Schiestl and Marion-Poll 2001). Not all electrophysiologically active compounds trigger behavioural responses (e.g., Ômura et al. 1999; Dötterl et al. 2006), however, when paired with behavioural bioassays, GC–EAD screening helps not only to identify the subset of odour compounds detected (or smelled) by bees, but also those that influence the behaviour of bees, including their attraction to flowers (Thiery et al. 1990; Henning and Teuber 1992; Henning et al. 1992; Dobson 1994; Dötterl et al.

2005; see below). This screening approach has provided many of the case studies discussed in this review and will serve as a methodological touchstone in the discussions below. A related technique consists of coupling gas chromatography with behavioural assays and (or) EAD (Wadhams et al. 1994; Blight et al. 1997; Le Métayer et al. 1997; Pham-Delègue et al. 1997). Here, the signals measured by the flame ionization detector on the gas chromatograph (GC–FID) are recorded in parallel with proboscis extension responses (GC–PER) (and with antennal recordings; GC–EAD–PER) in response to the compounds of headspace or solvent extract samples by stimulating the bees' antennae with the effluent of the GC (see also below). Collectively, the integration of these analytical approaches into studies at the interface of plant and insect ecology has an enormous potential to yield conceptual advances in our understanding of the ecology of bees and their flowers (see Schiestl and Schlüter 2009).

In this review, we take an evolutionary approach to outline the current state of knowledge about the importance of floral scent and related aspects of chemical ecology in the foraging behaviour of host-specialized and host-generalized solitary bees, as well as social bees. We discuss the importance of floral scent for (i) long- and short-distance attraction of bees to flowers; (ii) discrimination, within species, between rewarding and nonrewarding flowers; (iii) host plant finding in specialized bees; (iv) the foraging success not only of individual bees but also of entire colonies of social bees; and (v) attracting bees to globally important crops. We ask whether intra- and inter-specific differences in host-plant use can be explained by sensory bias in the way bees detect and process floral scents, and whether scent manipulations might contribute to improving the yield of bee-pollinated crops.

## Macroevolutionary origins of bees: specialized or generalized ancestors?

We begin with an evolutionary question: Was the ancestral bee a host-limited specialist or was it a broadly generalized, opportunistic forager? Fossil evidence and molecular phylogenetic hypotheses produced in recent years suggest that bees and flowering plants have flourished with extraordinary diversity through parallel and successive “explosive” radiations and that these intimate plant–insect relationships have presumably fuelled each other's diversification since the onset of their interactions (Danforth and Ascher 1999; Grimaldi 1999; Wikström et al. 2001; Soltis et al. 2005). Students of the evolution of niche differentiation have often postulated that the founders of adaptive radiations were trophic generalists and that these ancestors subsequently differentiated into more specialized descendants (Mayr 1942; Simpson 1953). Examples that illustrate this concept have been described in different groups of organisms, including phytophagous insects (Nosil 2002; Nosil and Mooers 2005). However, recent analyses of niche evolution in groups of closely related insect species which differ in their host breadth have shown that common ancestors were frequently reconstructed as niche specialists (Schluter 2000; Janz et al. 2001; Morse and Farrell 2005; Weingartner et al. 2006).

Testing the generalists-to-specialists hypothesis at a mac-

roevolutionary scale in bees has not been possible until the recent resolution of a longstanding debate around the interpretation of family-level relationships in this group. In brief, the bulk of the controversy crystallized around the question of whether the Colletidae should be considered as the earliest branch of the phylogeny, partly because these bees are unique in having a bifid tongue (the glossa), a trait also found in the spheciform wasps, which is the closest relatives of bees (Michener 1944; Malyshev 1968). The adequate understanding of this morphological character state had deep implications because it yielded two highly contrasting topologies for the phylogeny of bees that led to mutually exclusive interpretations of several aspects of the evolutionary history of bees, including interactions with their host plants (Alexander and Michener 1995). The scientific community reached a consensus with the recent publications of robust family-level relationships based on a combination of molecular and morphological markers, reporting that colletid bees are in fact a derived group and that the family Dasypodidae (in Melittidae s.l.) occupies a basal position within the phylogeny of bees (Danforth et al. 2006a, 2006b) (Figs. 1A, 1B). This re-interpretation of the evolutionary history of bees suggests that the earliest bees were host-plant specialists (Danforth et al. 2006b), a hypothesis that has subsequently received support from several reconstructions of ancestral states by mapping the degree of host-plant specialization on molecular phylogenies. Collectively, these studies have reported that pollen specialization dominates several groups of bees and is also the most probable ancestral trait both in basal genera (Stage 1966; Müller 1996; Cane et al. 1997; Michener 1981, 2007; Michez et al. 2004, 2008; Michez and Patiny 2005; Patiny et al. 2007) and in more derived ones (Sipes and Wolf 2001; Sipes and Tepedino 2005; Larkin et al. 2008; Sedivy et al. 2008).

If the common ancestor of bees (the “proto-bee”) was indeed a pollen specialist, how did these proto-bees overcome the radical changes associated with a shift in their larval diet, from the typical carnivorous diet of their digger wasp ancestors to larval provisions mainly based on pollen and nectar? The mechanisms that have driven this evolutionary transition remain obscure, but we may, nevertheless, formulate the following hypothesis based on our current understanding of the nutritional requirements of bees and wasps. To begin with, it is widely acknowledged that the pollen of flowering plants is usually very rich in nitrogen, and that it also contains vitamins, starch, proteins, and amino acids which provide all the daily nutritional requirements for most animal species (Roulston and Cane 2000; Roulston et al. 2000). However, the proto-bees, much like the wasps from which they are derived, are not capable of producing *de novo* the essential sterols needed to synthesize hormones like ecdysone, the major insect molting hormone (Blum 1985). Consequently, a major constraint in the shift from carnivory to phytophagy might have been the need to find accessible sources of sterols. Flowering plants synthesize several of these essential sterols, which are found in the pollen, independent of the means of pollination. For example, cholesterol is a main pollen constituent (90%) of the insect-pollinated herb *Hypochoeris radicata* L. (catsear) (Devys and Barbier 1965, 1966; Barbier 1970), as well as of the wind-pollinated tree *Populus fremontii* S. Wats. (cotton-

wood) (Standifer et al. 1968; Barbier 1970). Other sterols, such as 24-methylene-cholesterol,  $\beta$ -sitosterol, and to a lesser extent, stigmasterol, have also been identified from pollens of various flowering plant species in different families (Barbier 1970). The unusually high concentrations of cholesterol in the pollen of Asteraceae is intriguing, because this group of plants has been suggested as the putative hosts of the common ancestor of all extant Dasypodidae, the most basal group of bees (Michez et al. 2004, 2008).

The family Asteraceae is thought to have originated during the Eocene ( $55.8 \pm 0.2$  to  $33.9 \pm 0.1$  million years ago) (Scott et al. 2006), a period that coincides with an outburst of diversification in bees (Michener and Grimaldi 1988), after they originated ca. 100 million years ago (Poinar and Danforth 2006). However, the presence of cholesterol and related essential sterols in the pollen of the early angiosperms might have facilitated the shift towards “beehood” for the proto-bees, once they had evolved the physiological capacity to tolerate and metabolize the various other compounds, and perhaps toxins, contained in the pollenkitt (sensu Knoll 1930) of these plants (e.g., Williams 2003; Praz et al. 2008a). The contemporary Asteraceae are ubiquitous on Earth, and the plate-like structure of their inflorescences presumably allowed easy access to their floral rewards by the early bees, much like it does to a wide taxonomical range of extant specialized bee species that currently use them as preferred pollen hosts (e.g., Westrich 1989; Larkin et al. 2006, 2008; Müller and Kuhlmann 2008). As pointed out by Müller and Kuhlmann (2008), the paradox that the Asteraceae host so few generalist species but so many specialists at the same time calls for further studies on the mechanisms that drive the acquisition of physiological adaptation of bees to the pollen of these plants, and how the capacity to detoxify can be retained within and among groups of closely related species.

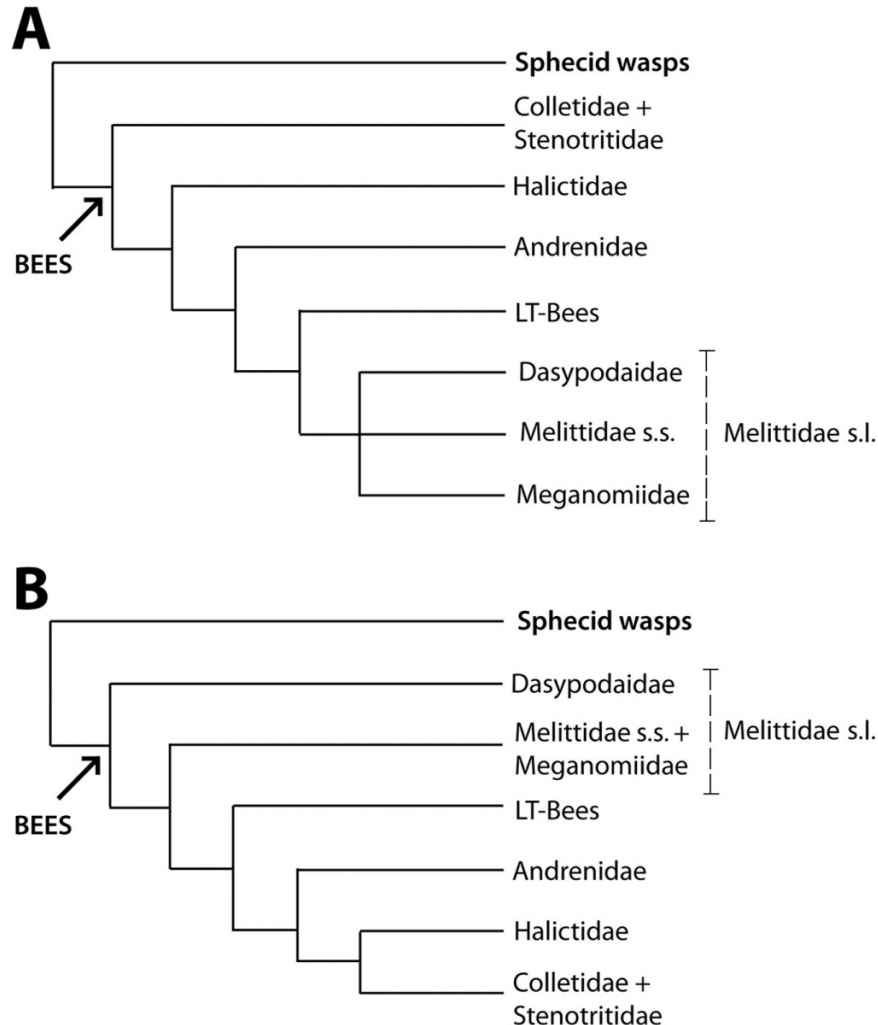
We now take a closer look at the proximate and ultimate mechanisms by which floral scent and other factors influence the foraging behaviour of bees.

## Floral scent and the foraging behaviour of bees

### Visual vs. olfactory stimuli in reward-based pollination systems

It has long been known that bees utilize not only visual but also olfactory flower cues for finding suitable host plants. This is true for bees visiting flowers for nectar and (or) pollen (e.g., von Frisch 1919; Butler 1951; Bogdany and Taber 1979), their resins (de L. Nogueira et al. 2001), or fatty floral oils (Dötterl and Schäßler 2007). Flower scent is generally considered an important long-distance signal in poorly lit habitats with dense vegetation (e.g., in rainforest understories), where coloured objects cannot be seen from far away (Knudsen et al. 1999), and for naïve bees searching for their first floral meal or for new food sources or patches (von Frisch 1919; Heinrich et al. 1977; Roy and Raguso 1997; Dötterl et al. 2005). This may particularly apply where the floral scent is emitted in high absolute amounts (Butler 1951; von Frisch 1965). On the other hand, when scent functions at scales closer to the floral resources (from a few centimetres to 1 m), innate and learned responses are

**Fig. 1.** Family-level relationships in bees. (A) The “Colletidae + Stenotritidae basal” phylogenetic hypothesis suggested by Alexander and Michener (1995). (B) The “Melittidae basal” typology suggested by Alexander and Michener (1995) as an alternative scenario and recently confirmed as the most parsimonious scenario by Danforth et al. (2006a, 2006b), who combined morphological traits and five molecular markers. The arrows indicate the common ancestor of all bees, with the sphecid wasp ancestors used as the outgroup. The LT-Bees are long-tongued bees. The Melittidae s.l. comprises the families Dasypodaidae, Melittidae, and Meganomiidae. Colletids and melittids have contrasting floral choices, with the first family encompassing much more pollen generalists (see e.g., Müller and Kuhlmann 2008) than the second family (Michez et al. 2008). The results by Danforth et al. (2006a, 2006b) therefore strongly support that pollen specialization is probably an ancestral condition in bees. (Modified from Danforth et al. 2006a and reproduced with permission of Mol. Phylogenet. Ecol., vol. 39, issue 2, p. 359, ©2006 Elsevier Limited.)



often elicited by an interplay between visual and olfactory cues (e.g., Butler 1951; Lunau 1991, 1992b; Dobson and Bergström 2000), and the odours emitted may be relatively weak to the human nose (e.g., Ashman et al. 2005). In contrast to olfactory cues, the importance of visual cues for bees appears to be limited to close proximity (a few centimetres to a few metres) to the flowers (Giurfa et al. 1996; Dafni et al. 1997), despite the long-held belief (von Frisch 1919, 1965; Kevan and Baker 1983) that visual floral stimuli are important for long-distance attraction of bees and that floral scent only plays a role close to the flowers. If flowers are arranged in large inflorescences or flowering plants occur in dense patches, however, visual cues also should be sufficient to attract bees from longer distances (Giurfa et al. 1996). For distance vision, bees rely on achromatic signals provided by green receptor contrasts (differences between

background and target) and not on coloured signals, which are important close to the flowers (Giurfa and Lehrer 2001; Spaethe et al. 2001), but e.g., honey bees cannot detect a 1 cm diameter flower from distances of more than 11.5 cm (Chittka and Raine 2006). Therefore, bees should only distinguish flower colours from background or differentiate between colours when close to the flowers, at a point where they already are immersed in floral odours. The long-range attraction of bees to colors that contrast with the background environment is exploited in the framework of surveys on the diversity of wild bees for which arrays of water-filled, UV – bright coloured pan traps are regularly used (Aizen and Feinsinger 1994; Leong and Thorp 1999; Cane et al. 2000; Bartholomew and Prowell 2005; Stephen and Rao 2005; Thomas 2005; Westphal et al. 2008; Wojcik et al. 2008; Moretti et al. 2009). The bees are drawn to these traps that



they probably associate with giant flowers and drown in the soapy water from which they are collected. This passive sampling method has proven to have the highest sample coverage, as well as a negligible bias on the species and sexes collected, compared with other techniques (transects, malaise traps, etc.) (Aizen and Feinsinger 1994; Roulston et al. 2007; Westphal et al. 2008). It is possible that coloured pan traps act as a supranormal stimulus to flower-visiting bees that otherwise rely often on a combination of visual and olfactory signals and cues to find their host plants.

For experienced bees revisiting rewarding flower patches, flower scents may also be less important for distance attraction, as bees learn to use landmarks and other contextual cues to remember the specific locality that they visited before (e.g., Reinhard et al. 2004b). However, floral scent remains an important stimulus when bees land on flowers (Pernal and Currie 2002; Wright and Schiestl 2009). von Frisch (1919) showed that when honey bees are trained to an odour-colour combination at a feeding station, and are subsequently forced to choose between these two cues by spatially separating them, the bees primarily landed at the scented feeder. Finally, floral scent remains important for experienced bees to recognize previously visited flowers and contributes significantly to the phenomenon of flower constancy (Wright and Schiestl 2009 and references therein).

Ironically, the literature on the use of floral odours by bees is dominated by accounts of the fragrance-based attraction of male orchid bees, which are, arguably, the most derived species of the Apidae (see Table 1). Male euglossine bees visit flowers of orchids and other angiosperms to collect scent compounds (Dodson et al. 1969), along with other odour sources that contribute to male sexual display (Eltz et al. 2003, 2005, 2008). Male euglossine bees are easily attracted by scent baits impregnated with single compounds or simple blends of compounds typically found in the plants visited by these bees. Through the use of such baiting experiments, more than 50 compounds have been found to attract male euglossine bees (reviewed by Williams and Whitten 1983). In this unusual pollination system, the number of attracted individuals and species decreases with increasing blend complexity of odour compounds, which also explains why some of the plants are pollinated only by one or a few euglossine species (Dodson et al. 1969; Williams and Dodson 1972; Williams and Whitten 1983). The distance from which euglossines can be attracted to flowers is enormous. Fragrance baits on a boat 1 km offshore from an island in Panama attracted 7 of the 28 euglossine species encountered at control bait sites on the island (Ackerman 1986). Although the baits were presumably more concentrated than the scent of most flowers pollinated by euglossines (J. Ackerman, personal communication), this phenomenon highlights the importance of floral scent in the attraction of euglossines from long distances, and their potential to mediate long-range pollen flow in the orchids that they pollinate (Janzen 1971).

In the male euglossine pollination system, bees rely on flower scent for long-distance attraction, whereas visual signals (e.g., colour, size, shape of flowers, or inflorescences) appear to elicit close range attraction and landing. For example, male euglossine bees were attracted to an inflorescence of the Amazonian palm *Geonoma macrostachys* Mart. con-

cealed within a bag of cheese cloth but never alighted on it, presumably owing to the absence of the appropriate visual cues displayed by real inflorescences or flowers (Knudsen et al. 1999). In this case, it seems that bees have linked the visual and olfactory advertisements of this plant so that the strength of the behavioural response elicited is decreased when one dimension of the floral advertisement is changed (see also Bogdany 1978). On the other hand, male euglossine bees often show the complete behavioural sequence (landing, followed by collection of volatiles) after being attracted by synthetic scent compounds, or mixtures thereof, on simple rubber septa or blotting paper. The compounds offered represent simplified mixtures of the compounds emitted from the natural fragrance sources, and the bees, therefore, did not have a chance to learn them previously in combination with a specific visual advertisement. Therefore, “naïve” male euglossines may rely primarily on scents for attraction to floral fragrance sources, and these scents also elicit landing and fragrance collection behaviour. Specific visual stimuli are subsequently learned, and as a consequence, appear to be more important cues in the behaviour of experienced bees. The unusual shapes of some male euglossine pollinated orchids are well documented as integrated phenotypes that may manipulate the bees into appropriate pollen placement (e.g., orchid *Coryanthes marcantha* Hook.; Darwin 1877) or mimic the appearance of nests of euglossine bees (e.g., *Catasetum* spp.; Lunau 1992a). However, the dazzling visual displays of some of these orchids (e.g., *Stanhopea tigrina* Bateman ex Lindl.) require further inquiries into the possible roles that bright colour patterns might play in pollination.

What is the relative importance of specific odour compounds in the attraction of more typically encountered, generalized bees? Despite a large and growing literature about bee behaviour and pollination, little is known about the importance of individual floral scent compounds for the attraction of non-euglossine bees to flowers (Dobson 2006). The data presented in Table 1 summarize the current knowledge but do not include compounds known to elicit behavioural responses in standard conditioning experiments (e.g., conditioned proboscis extension reflex tests: cPER), as (honey) bees can be trained almost to any volatile organic molecule including those not produced by flowering plants (von Frisch 1919). Instead, we include compounds that elicited spontaneous responses in proboscis extension reflex experiments in at least 10% of tested bees, and that are additionally known as typical floral scent in bee-pollinated plants (Dobson 2006).

Most of the compounds presented in Table 1 elicited behavioural responses from experienced bees or from bees whose previous experience was undetermined. In general, very little is known about the innate olfactory “search image” of bees (Menzel 1985), and which compounds are important for host-plant finding (i.e., innate biases) in naïve, inexperienced bees. While the innate search image may be very important for solitary bees, it seems to be less so for social bees, such as *Apis mellifera*. Worker honey bees foraging in the field for their first time already may have learned many odours in the hive (see “Floral scent and communication in honey bee hives and bumble bee colonies” below). However, some compounds (e.g., linalool, geraniol)

**Table 1.** Floral scent compounds eliciting positive behavioural responses in bees.

Compound	Bee species	References
<i>p</i> -Anisaldehyde	<i>Apis mellifera</i> , <i>Lasioglossum</i> Curtis, 1833	Theis 2006
Anethole	<i>Apis mellifera</i> , <i>Bombus</i> spp.	Ladd et al. 1974; Ladd and Tew 1983; Allsopp and Cherry 1991
Benzyl acetate	<u>Euglossini</u>	Williams and Whitten 1983
Benzyl alcohol	<i>Apis mellifera</i>	Wadhams et al. 1994
3-Carene	<i>Apis mellifera</i>	Blight et al. 1997
( <i>E</i> )-Carvone oxide	<u>Euglossini</u>	Whitten et al. 1986
1,8-Cineole	<u>Euglossini</u> , <i>Bombus terrestris</i>	Williams and Whitten 1983; Mena Granero et al. 2005b
( <i>E</i> )-Cinnamaldehyde	<i>Peponapis pruinosa</i>	Andrews et al. 2007
( <i>Z</i> )-Citral	<i>Apis mellifera</i>	Williams et al. 1981b; Wells et al. 1993
<i>p</i> -Cresol	<u>Euglossini</u>	Williams and Whitten 1983
<i>p</i> -Cresyl acetate	<u>Euglossini</u>	Williams and Whitten 1983
<i>p</i> -Cymene	<i>Apis mellifera</i>	Blight et al. 1997
1,4-Dimethoxybenzene	<u>Euglossini</u> , <i>Andrena vaga</i>	Williams and Whitten 1983; Dötterl et al. 2005; present study
Eugenol	<u>Euglossini</u> , <i>Bombus</i> spp.	Ladd et al. 1974; Williams and Whitten 1983; Dobson et al. 1999
( <i>E,E</i> )- $\alpha$ -Farnesene	<i>Apis mellifera</i> , <i>Andrena vaga</i>	Blight et al. 1997; Laloi et al. 2001; present study
( <i>E,E</i> )-Farnesol	<i>Apis mellifera</i>	Williams et al. 1981b
Geranial	<i>Apis mellifera</i>	Williams et al. 1981b
Geraniol	<i>Apis mellifera</i> , <i>Bombus</i> spp.	Hamilton et al. 1970; Ladd et al. 1974; Williams et al. 1981b; Wells et al. 1993; Laloi et al. 2001
Ipsdienol	<u>Euglossini</u>	Whitten et al. 1988
Linalool	<i>Apis mellifera</i> , <i>Andrena</i> spp.*, <u><i>Colletes cunicularius</i></u> <sup>†</sup>	Henning et al. 1992; Wadhams et al. 1994; Borg-Karolson et al. 1996; Blight et al. 1997; Laloi et al. 2001; Meagher 2002; Borg-Karolson et al. 2003; Chaffiol et al. 2005; Theis 2006
Linalool oxide furanoid	<u><i>Colletes cunicularius</i></u>	Borg-Karolson et al. 1996
Methyl benzoate	<u>Euglossini</u>	Williams and Whitten 1983
Methyl cinnamate	<u>Euglossini</u>	Williams and Whitten 1983
Methyl salicylate	<u>Euglossini</u> , <i>Andrena vaga</i>	Williams and Whitten 1983; present study
Nerol	<i>Apis mellifera</i>	Williams et al. 1981b; Wells et al. 1993
( <i>Z</i> )-Ocimene	<i>Bombus terrestris</i>	Mena Granero et al. 2005b
Phenylacetaldehyde	<i>Apis mellifera</i> , Halictidae	Blight et al. 1997; Meagher 2002; Theis 2006
2-Phenylethanol	<u>Euglossini</u> , <i>Andrena vaga</i> , <i>Apis mellifera</i>	Williams and Whitten 1983; Wadhams et al. 1994; Blight et al. 1997; present study
2-Phenylethyl acetate	<u>Euglossini</u>	Williams and Whitten 1983
$\alpha$ -Pinene	<u>Euglossini</u> <sup>‡</sup> , <i>Apis mellifera</i>	Williams and Whitten 1983; Blight et al. 1997
Protoanemonin	<i>Chelostoma florissomme</i>	Dobson and Bergström 2000
Skatole	<u>Euglossini</u>	Williams and Whitten 1983
$\alpha$ -Terpinene	<i>Apis mellifera</i>	Blight et al. 1997
4-Terpineol	<u>Euglossini</u>	Williams and Whitten 1983
Tetradecyl acetate	<i>Bombus terrestris</i>	Dobson et al. 1999
1,2,4-Trimethoxybenzene	<i>Peponapis pruinosa</i>	Andrews et al. 2007
Vanillin	<u>Euglossini</u>	Williams and Whitten 1983

**Note:** Bee species responding without prior experience to floral volatiles are in boldface type. Bees are underlined if only males responded. Compounds known to be attractive to Euglossini only were listed if they are good attractants according to Williams and Whitten (1983).

\*Only the (+)-enantiomer was tested.

<sup>†</sup>The (+)-enantiomer is most attractive.

<sup>‡</sup>Euglossini only respond to the (-)-enantiomer.

also seem to elicit innate responses in honey bees, as individuals respond spontaneously to these compounds in PER experiments (Smith 1991; Bhagavan et al. 1994; Sandoz et al. 1995; Laloi et al. 2001). However, these bees were free-flying before the experiment, or were at least fed with pollen, so it is unclear whether bees were exposed to the compounds of interest before they were tested. Anethole (1-

methoxy-4-(1-propenyl) benzene) is an important beetle sex pheromone, and baited beetle traps attracted several honey bees and (or) bumble bees (Hamilton et al. 1970; Ladd et al. 1974; Ladd and Tew 1983; Allsopp and Cherry 1991) even though it is not a common floral scent component (Knudsen et al. 2006). Thus, it is unclear whether anethole plays an important role in bee–plant interactions. In beetle

trapping experiments, honey bees and (or) bumble bees were also attracted by a mixture of 2-phenylethyl propionate, eugenol, and geraniol (Allsopp and Cherry 1991), as well as by eugenol and geraniol when offered as single compounds or as a mixture (Hamilton et al. 1970; Ladd et al. 1974). However, unlike anethole, eugenol and geraniol are widespread floral scent compounds in bee-pollinated plants (Dobson 2006; Knudsen et al. 2006) and are therefore potential candidates for mediating interactions between honey bees or bumble bees and plants. Indeed, evidence suggests that eugenol is used by bumble bees to assess pollen availability in certain rose species (Dobson et al. 1999). Other compounds (e.g., neral, geraniol, geraniol) are both widespread glandular constituents in bees (Blum 1966; Bergström and Tengö 1974; Hefetz et al. 1979; Pickett et al. 1980; Wheeler et al. 1985) and typical floral scent compounds in bee-pollinated plants (Dobson 2006; Knudsen et al. 2006) (see sections “Floral scent and communication in honey bee hives and bumble bee colonies” and “Floral scent and crop pollination” below).

#### Discrimination of rewarding from nonrewarding flowers within species

In addition to finding suitable nectar- or pollen-host species, bees also use floral volatiles to discriminate rewarding from nonrewarding flowers within a conspecific patch. Scent often varies between different flower parts in bee-pollinated flowers (Dobson et al. 1990, 1996; Bergström et al. 1995; Dobson and Bergström 2000; Ashman et al. 2005) at levels that bees can detect (Bolwig 1954; Lex 1954; von Aufsess 1960; Lunau 1992b). Pollen-specific odours are of special interest for bees visiting flowers to forage for pollen. Although pollen scent is, in many cases, much weaker than the scent of whole flowers (Dobson and Bergström 2000), it is routinely detected by bees, for whom it provides an important signal (Pernal and Currie 2002; Cook et al. 2005). Pollen often emits odours that are clearly different from those emitted from other floral parts and organs, and these differences can be used by bees to detect the presence of pollen from a distance and possibly to assess the amount of pollen available before landing (Ribbands 1949; Dobson and Bergström 2000). For example, a distinct pollen volatile profile was described from *Rosa rugosa* Thunb. (rugosa rose), which is pollinated by bumble bees. The scent of whole flowers was dominated by the monoterpenoids citronellol, nerol, and geraniol, as well as the benzenoid 2-phenylethanol, whereas the pollen was characterized by high relative amounts of the fatty acid derivatives 2-tridecanone, tetradecanal, and tetradecyl acetate, the terpenoid geranyl acetate, and the phenylpropanoids eugenol (see Table 1) and methyleugenol (Dobson et al. 1990). To determine if bumble bees use pollen odours to assess availability, Dobson et al. (1999) removed the anthers of newly opening flowers and augmented these flowers with single compounds or a blend characteristic of pollen odours. Observations of free-flying bumble bees revealed that some pollen volatiles (2-tridecanone, geranyl acetate) reduced landing responses, whereas others (eugenol and to a lesser extent tetradecyl acetate) increased landing responses and elicited “buzzing”, the vibratile pollen-collecting behaviour (see Buchmann 1983). These results suggest that

*Bombus* do indeed use pollen-specific odours to assess pollen availability.

Recently, Howell and Alarcón (2007) demonstrated that bees of the genus *Osmia* Panzer, 1806 similarly use nectar volatiles to assess the availability of hidden floral nectar. Free-flying bees visited flowers of *Penstemon caesius* Gray (San Bernardino beardtongue) containing nectar more often than nectar-depleted ones. To test whether bees detect the nectar by its odour before landing on the flowers, the authors blocked the olfactory capabilities of some of the bees by coating their antennae with silicone and compared the floral preferences of these bees with control bees (bees with uncovered antennae). Control bees visited flowers containing nectar more frequently than empty flowers or flowers containing water instead of nectar, whereas bees with covered antennae visited all treatments equally. Given that flowers of the different treatments could not be differentiated visually and that humidity gradients within the flowers were not used by the bees, this study nicely demonstrates that bees use nectar volatiles to discriminate between nectar-rewarding flower and nectarless flowers at a distance. The compounds used by the bees to discriminate against nectar-depleted flowers in Howell and Alarcón’s (2007) study were not identified. However, it is known from other studies that the nectaries of several flowers (or petal regions with the nectaries) differ from other floral (petal) parts in their scent (Lex 1954; Bergström et al. 1995; Dötterl and Jürgens 2005), and also that floral nectars often have characteristic scents (Raguso 2004). Indeed, in some flowers, nectar may be the primary source of scent emission (Mena Granero et al. 2005a).

We might argue from our previous studies (Dötterl et al. 2005; Mant et al. 2005a) that a functional analysis of nectar volatiles in *Penstemon caesius*, in combination with electrophysiological (GC-EAD) and behavioural tests with antennally active compounds (or blends thereof), would reveal the chemical basis for the behaviour of *Osmia* bees observed by Howell and Alarcón (2007). Because it has been shown that carbon dioxide is perceived and utilized by the hawkmoth *Manduca sexta* (L., 1763) (tobacco hornworm) as a proxy to the presence of floral nectar, it might be worthwhile to track the temporal relationship between nectar presence and the emission of carbon dioxide from flowers. It is not yet well understood whether floral CO<sub>2</sub> is always a reliable indicator of floral nectar, or whether all flower-visiting insects perceive and utilize concentration gradients in CO<sub>2</sub> to assess nectar availability, as has been shown for *Manduca sexta* visiting night blooming flowers of *Datura wrightii* Regel (sacred datura) (Guerenstein et al. 2004; Thom et al. 2004; Goyret et al. 2008; Guerenstein and Hildebrand 2008). In sphingids, CO<sub>2</sub>-sensitive receptors are located in the sensilla of the labial-palp pit organ (Stange and Stowe 1999), whereas bees also have them on their antennae (sensilla ampullacea) (Lacher 1964; Stange and Stowe 1999). Honey bees measure CO<sub>2</sub> within the hive and actively regulate concentrations by wing-fanning (Seeley 1974) to avoid dangerously high levels of CO<sub>2</sub> (Guerenstein and Hildebrand 2008). It is unknown whether bees respond to CO<sub>2</sub> while foraging to assess nectar availability in flowers, and whether floral CO<sub>2</sub> influenced the result of the *Penstemon*–*Osmia* study. The localization of floral CO<sub>2</sub> emission during nectar



production has not yet been studied in detail. However, because it was suggested that high CO<sub>2</sub> emission in flowers is correlated with high metabolic activity during nectar production (Goyret et al. 2008), CO<sub>2</sub> may emanate from the nectaries and may be dissolved in nectar (a minority of it being converted into carbonic acid), from which it could be emitted subsequently. Therefore, CO<sub>2</sub> could be an honest signal for nectar-foraging insects, especially in short-lived flowers. On the other hand, longer lived flowers infested with yeasts may have dramatically modified nectar sugar composition owing to fermentation (Herrera et al. 2008), which should be accompanied by an increase in local CO<sub>2</sub>. Further experiments are needed to determine whether the unwitting bee vectors of floral yeasts (e.g., *Bombus terrestris* (L., 1758) (buff-tailed bumblebee); Canto et al. 2008) perceive and respond to floral CO<sub>2</sub> and other fermentation volatiles.

### Floral scent and communication in honey bee hives and bumble bee colonies

In social bees, floral scent is not only important for host-plant finding during foraging but also influences the behaviour of successful foragers in the hive (von Frisch 1919, 1965; Lindauer 1949; Kaschef 1957). Floral odours are known to impact the interaction, communication, and recruitment between returning workers and inactive workers in the colony of honey bees, bumble bees, and stingless bees (Ribbands 1954; Lindauer and Kerr 1960; Johnson 1967; Free 1969; Koltermann 1969; Wenner et al. 1969; Getz and Smith 1987; Jakobsen et al. 1995; Dornhaus and Chittka 1999; Reinhard et al. 2004a, 2004b; Arenas et al. 2007, 2008; Díaz et al. 2007; Grüter et al. 2008; Molet et al. 2009), and may also contribute to nest mate recognition in honey bees. Each colony might forage on different flowers and thereby acquire different odours that will ultimately result in the development of colony-specific patterns of floral odours (Smith and Breed 1995).

The likelihood that a bee dances in the hive after returning from a foraging trip (as well as the dance duration) is increased when scent, as well as sugar, is available at the feeding source (Kaschef 1957; Lindauer 1949). Furthermore, the frequency of trophallactic (mouth-to-mouth) nectar transfers between dancers and nest mates increases when dancers forage from a scented food source compared with a nonscented food source (Díaz et al. 2007). Together, these within-hive responses of honey bees to floral odours result in an increased number of bees recruited to the task of foraging. Nest mates in the hive that come in contact with the odour of the dancer (e.g., during trophallaxis) learn this odour (Farina et al. 2007; Grüter et al. 2006), and during subsequent foraging bouts they prefer food sources (flowers) that emit this odour over other odours or over scentless food sources (Koltermann 1969). Interestingly, a similar pattern has recently been documented for bumble bees (Dornhaus and Chittka 1999; Molet et al. 2009). In *Bombus terrestris*, nest mates learn the scent brought back to the colony by a successful forager, and when recruited by the forager (which performs an excitatory run), strongly prefer this odour over other odours encountered during their own foraging activity. However, the recruitment effect itself is independent of the scent introduced to the colony and is due to a pheromone produced in an abdominal gland (Dornhaus et al. 2003;

Mena Granero et al. 2005b). Interestingly, this pheromone contains compounds known to be widespread in floral scents (1,8-cineole, (*E,E*)-farnesol, (*Z*)- $\beta$ -ocimene), with 1,8-cineole shown to be the most important in recruiting bumble bees (Mena Granero et al. 2005b). It is unknown whether these compounds also play a role in host-plant finding in bumble bees when they emanate from flowers rather than from nest mates.

In honey bees, the presence of floral scent on a successful forager returning to the hive (independent of whether this forager is dancing or not) not only influences the behaviour of inexperienced foragers but can also induce experienced foragers to (re)visit scented sources emitting identical compound(s) (von Frisch 1965). Recently, it was demonstrated that when scent to which bees were trained at a feeder is blown into the hive, it induces bees to recall navigational and visual memories associated with that odour. Bees flew to the location where they were trained to the scent even if no feeders (and therefore no scent) were present (Reinhard et al. 2004a, 2004b), demonstrating the importance of scent in recruiting experienced bees.

In conclusion, these results demonstrate that floral scent contributes not only to the foraging success of individual bees, but also helps to increase the foraging efficiency and thus the growth and reproductive fitness of bee colonies by guiding recruited bees to rewarding resources (see Mattila and Seeley 2007). In nature, nectar and pollen odours, as well as floral odours adsorbed to the bees' bodies, are important in the communication between successful foragers and nest mates and for recruiting bees (Lindauer and Kerr 1960; von Frisch 1965). These plant products are often only weakly scented (Dobson and Bergström 2000; Raguso 2004) and further studies are needed to determine to what extent nectar and pollen scent directly influence the communication of bees in the hive, as well as the recruitment of flower-experienced and flower-naïve bees in a natural setting (where bees visit flowers rather than artificial feeders). In this respect, it also would be necessary to test the importance of nonvolatile characteristics of nectar or pollen (e.g., amino acid composition, phenolic content, pollen lipids), which may be detected by nest mates during trophallaxis and licking the pollen that is attached to successful foragers (see Afik et al. 2006).

### Floral scent and host-plant use by specialized bees

#### Host-plant specialization in bees — definitions

Contrary to popular belief, female bees do not venture into the floral market randomly when it comes to collecting pollen that will be stored in brood cells for their developing young. In fact, observational evidence suggests that a wide array of bee species restrict their pollen-collecting bouts to a narrow taxonomic range of plant species (Müller et al. 1997, 2006; Minckley and Roulston 2006). This taxonomic specialization can be divided into two subcategories, namely constancy and oligolecty. Floral “constancy” concerns the transient focus of an individual bee on a host-plant species during a foraging bout despite the availability of alternative hosts in the habitat; this phenomenon has been particularly well documented from experienced foragers in different spe-



cies of social (e.g., Wilson and Stine 1996) and solitary (e.g., Rust 1990) bees. On the other hand, “oligolecty” describes (in the widest acknowledged sense) the taxonomic fidelity of female bees to a consistent and sometimes narrow spectrum of host-plant species throughout their life, their geographic range, and across generations. This specialization finds an extreme in so-called “monolectic” species, for which females gather pollen from only one plant species. By contrast, “polylectic” taxa are characterized by a wide taxonomic spectrum of pollen hosts. By coining these terms associated with pollen specialization in bees, Robertson (1925, 1926) provided the first theoretical framework to investigate the ecology of bee–flower interactions in a more systematic approach, by defining host specificity in bees by pollen collection, rather than simply by range of flowers visited. Robertson’s (1925, 1926) studies paved the way for more in-depth investigations on the identification of pollens from brood cells, as well as those contained in pollen pellets transported by female bees.

A substantial body of work on this topic has accumulated over the 20th century, culminating in the recent publications by Cane and Sipes (2006) and Müller and Kuhlmann (2008) that offer revised lexicons on pollen specialization by bees (for a historical perspective, definitions, and examples see Table 2). These two recent studies have redefined and subdivided the classification of Robertson (1925, 1926) in an attempt to provide a better picture of how monolecty (extreme specialization) grades into polylecty (generalization), and how the degree of dietary specialization can be characterized by measurements of the taxonomic composition of pollen loads (in percentage by pollen grain number or percentage by pollen grain volume) for any bee species. Despite the relative coherence of these two recent lexicons of pollen specialization and the apparent ease of use of their associated methods, four factors may occasionally make their application more difficult.

First, the question of monolecty. Although this category has been suggested by Robertson (1925), possibly based on too little evidence (see Cane and Sipes 2006), there is a general agreement that monolecty *sensu stricto* is extremely rare in nature. Indeed, several species described as strictly monolectic have later been found to collect pollen on alternative hosts when their preferred host plant was not available. One such example is *Colletes hederæ* Schmidt and Westrich, 1993 (European ivy plasterer bee), which was previously thought to be monolectic on *Hedera helix* L. (English ivy) (Schmidt and Westrich 1993) (Fig. 2A) but has since then been described as “polylectic with a strong preference for ivy” (Müller and Kuhlmann 2008; Westrich 2008). Ascribing a bee species to the category monolecty requires that the bee switch onto a taxonomically or ecologically isolated host plant, such as the various bee species that have specialized on *Larrea tridentata* (Sessé & Moc. ex DC.) Coville (creosote bush) in southwestern USA (Hurd and Linsley 1975). Another route to monolecty is the evolution of a specialized pollen-collecting behaviour exclusive to the plant species visited and incompatible with sister species of the preferred host plant found in sympatry. One such case would be *Anthemurgus passifloræ* Robertson, 1902 (passionflower bee), whose only known pollen host is *Passiflora lutea* L. (wild yellow passionflower). The pollen collection behav-

our of females of *A. passifloræ* is indeed adapted to their host plant and apparently incompatible with other sympatric passionflowers like *Passiflora incarnata* L. (purple passionflower). Furthermore, the geographic range of *A. passifloræ* does not seem to reach habitats where other potentially compatible *Passiflora* species occur (Neff and Rozen 1995; Neff 2003).

Second, the question of incorporation of the geographic and temporal context in the ecology of bees. A more detailed picture of host-plant specialization in bees will be sketched when the breadth of their dietary “niche” will be thoroughly explored at different spatial scales (e.g., across populations in their home range), as well as during successive years. To date, the pollen host records of most bee species are largely based on the analysis of pollen pellets extracted from small numbers of pollen-laden female bees curated in entomological collections. Surely, investigating pollen hosts in bees on a wide geographic scale requires labour-intensive samplings and might prove difficult to organize in practice, as several bee species are locally rare and nests are not readily found amid the vegetation. However, such data would provide important insights on the predictability of pollen hosts in bees and may help resolve equivocal cases of pollen specialization in bees.

Third, the question of purity of pollen pellets. Although a large proportion of bees often rely exclusively on specific plant species for their development, the plants visited are pollinated by a wide taxonomical range of pollinators that have themselves evolved towards generalization (e.g., Herrera 1996, 2005; Ollerton 1996; Waser et al. 1996). It is, therefore, expected that the alternative visitors or pollinators could mediate secondary deposition of nonhost pollen on flowers of the host plant, particularly if the flowers are easily accessible and displayed in open inflorescence like in the ubiquitous family Asteraceae. Consequently, caution should be taken when quantifying the purity of pollen pellets collected by a bee on flowers, because nonhost pollen grains might have been incorporated by mistake, although the specialized females might have restricted their foraging bouts to their predicted host plant (see the discussion in Müller 1996; Cane and Sipes 2006)

Finally, the question of biological relevance of taxonomically diverse pollen hosts. One aspect of pollen specialization concerns the number of potential pollen hosts for a given bee taxon. Part of the ongoing debate concerns the extent to which oligolectic bees that specialize on plant species in relatively small families (i.e., Campanulaceae) should be ascribed to the same category of pollen specialization as bees that use plant species in extremely diverse lineages (i.e., Asteraceae). This ambiguity is reflected in the differences of nomenclature used by Cane and Sipes (2006) compared with Müller and Kuhlmann (2008) (see Table 2).

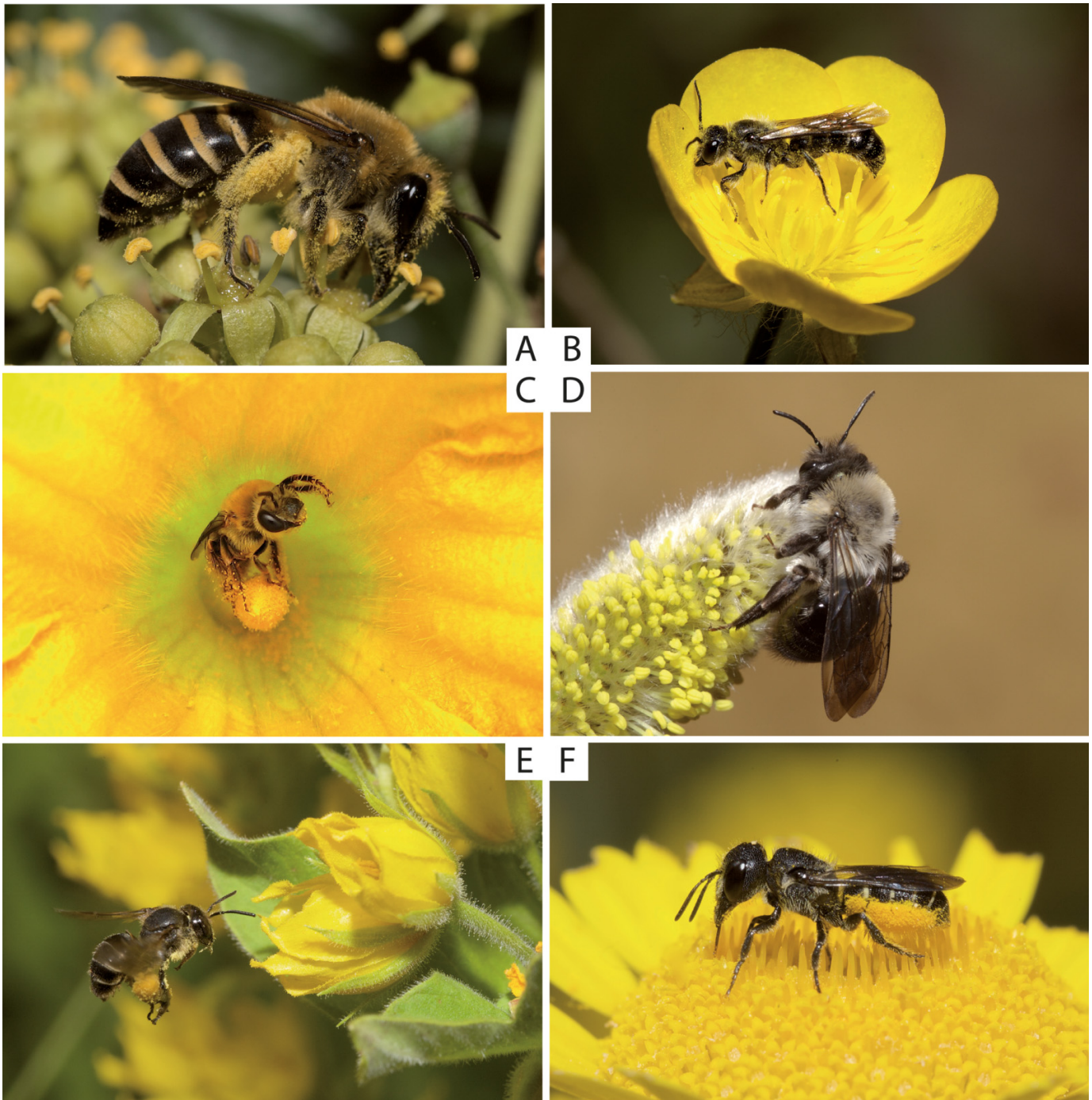
In light of these important factors for the study of bee–flower interactions, future studies should attempt to uncover the underlying mechanisms of dietary specialization in bees. Such projects should be coupled with parallel efforts to improve the current methods of pollen identification, which will ultimately provide opportunities to test whether some of the categories are redundant, which criteria should be used in the future, and if all contemporary categories of pol-

**Table 2.** Evolution of categories of pollen-host range in wild bees (after Robertson 1925, 1926; Cane and Sipes 2006; Müller and Kuhlmann 2008).

Category of pollen-host range			Number of plants visited			Examples from Westrich (1989); Müller (1996); Cane and Sipes (2006); Michener (2007); Müller and Kuhlmann (2008)
Robertson (1925, 1926)	Cane and Sipes (2006)	Müller and Kuhlmann (2008)	Species	Genera	Families	
Monolecty	Monolecty	Monolecty	1	1	1	<i>Anthemurgus passiflorae</i>
Oligolecty	Narrow oligolecty	Narrow oligolecty	>1	1	1	<i>Andrena apicata</i> Smith, 1847; <i>Andrena curvungula</i> Thomson, 1870; <i>Andrena florea</i> Fabricius, 1793; <i>Andrena potentillae</i> Panzer, 1809; <i>Andrena ventralis</i> Imhoff, 1832; <i>Bombus gerstaeckeri</i> ; <i>Chelostoma campanularum</i> (Kirby, 1802); <i>Colletes hylaeiformis</i> Eversmann, 1852; <i>Colletes sierrensis</i> Frey-Gessner, 1903; <i>Hoplitis anthocopoides</i> (Schenck, 1853); <i>Macropis europaea</i> Warncke, 1973; <i>Macropis fulvipes</i> ; <i>Melitta tricincta</i> Kirby, 1802; <i>Melitta haemorrhoidalis</i> (Fabricius, 1775); <i>Osmia cerinthidis</i> Morawitz, 1876; <i>Systropha planidens</i> Giraud, 1861
	Oligolecty	Broad oligolecty	>1	>1	1	<i>Andrena fuscipes</i> (Kirby, 1802); <i>Andrena hattorfiana</i> (Fabricius, 1775); <i>Andrena lagopus</i> Latreille, 1809; <i>Andrena lapponica</i> Zetterstedt, 1838; <i>Andrena lathyri</i> Alfken, 1899; <i>Andrena marginata</i> Fabricius, 1776; <i>Colletes halophilus</i> Verhoeff, 1944; <i>Colletes similis</i> Schenck, 1853; <i>Dasygoda hirtipes</i> (Fabricius, 1793) (= <i>Dasygoda altercator</i> (Harris, 1780)); <i>Panurgus banksianus</i> (Kirby, 1802); <i>Rophites algirus</i> Pérez, 1895; <i>Rophitoides canus</i> (Eversmann, 1852)
	Eclectic oligolecty	Eclectic oligolecty	>1	2–4	2–3	<i>Diadasia</i> spp.; <i>Calliopsis andreniformis</i> Smith, 1853; <i>Osmia ribifloris</i> Cockerell, 1900
Polylecty	Mesolecty	Polylecty with strong preference	Wide taxonomical range, but one plant species, genus, or family generally predominates			<i>Andrena labiata</i> Fabricius, 1781; <i>Anthidium punctatum</i> Latreille, 1809; <i>Colletes carinatus</i> Radoszkowski, 1891; <i>Colletes impunctatus</i> Nylander, 1852; <i>Colletes hederæ</i> Schmidt and Westrich, 1993; <i>Colletes succinctus</i> (L., 1758); <i>Colletes albomaculatus</i> (Lucas, 1849); <i>Colletes dorsalis</i> Morawitz, 1888
	Polylecty	Mesolecty	>1	>4	2–3	<i>Anthidium manicatum</i> (L., 1758); <i>Colletes intricatus</i> Smith, 1879; <i>Colletes acutus</i> Pérez, 1903
	Broad polylecty	Polylecty sensu stricto	>1	>4	4 or more	<i>Andrena fulva</i> Viereck, 1916; <i>Colletes brevigena</i> Noskiewicz, 1936; <i>Colletes cunicularius</i> ; <i>Colletes maidli</i> Noskiewicz, 1936; <i>Osmia bicolor</i> (Schrank, 1781); <i>Osmia caerulea</i> (L., 1758); <i>Osmia rufa</i> (L., 1758)



**Fig. 2.** Representative solitary bees that have evolved pollen specialization: (A) *Colletes hederæ* (European ivy plasterer bee) on *Hedera helix* (English ivy); (B) *Chelostoma florissomne* (sleepy carpenter bee) on *Ranunculus* sp. (buttercup); (C) *Peponapis* sp. in an inflorescence of *Cucurbita* sp. (gourd); (D) *Andrena vaga* on an inflorescence of *Salix* sp. (willow); (E) *Macropis fulvipes* on *Lysimachia punctata* (large yellow loosestrife); (F) *Heriades truncorum* on *Anthemis tinetoria* L. (yellow chamomile). All individuals are females except for the individual in B. All photographs by N.J. Vereecken except for C, which is by J. Forman Orth (reproduced with permission).



len specialization in bees are biologically and ecologically relevant.

#### How specialized bees find their pollen hosts

How do flower odours impact the proximate choices made by specialized bees of which flowers to visit? To date, remarkably few studies have been conducted on the ol-

factory capabilities of bees and the signals that they use for finding their preferred pollen hosts. In fact, the role of whole-flower and pollen volatiles has been investigated for only seven specialized bee taxa in total, six of which were found to be attracted by the odour sources in bioassays (Dobson 1987; Bergström et al. 1995; Dobson and Bergström 2000; Dötterl et al. 2005; Andrews et al. 2007; Dötterl

and Schäffler 2007; Dötterl 2008; Burger et al. 2009, 2010). The attractive scent compounds have only been identified in three cases thus far and these are discussed with the context of our nascent understanding of pollen-host specialization in bees.

The chemical basis of specialized bee–flower interactions was first elucidated by Dobson and Bergström (2000), who investigated the floral scents of the genus *Ranunculus* L. (Ranunculaceae; buttercup), the preferred host plants of the narrow oligolectic *Chelostoma florissomne* (L., 1758) (Westrich 1989; Sedivy et al. 2008) (Fig. 2B). They found that foraging inexperienced adult female bees that had been exposed to pollen and nectar of *Ranunculus* during the larval stages were attracted by protoanemonine (5-methylene-2(5H)-furanone), an uncommon floral scent compound often found in high concentrations in pollen of *Ranunculus* spp. (Bonora et al. 1988; Bergström et al. 1995; Jürgens and Dötterl 2004). This volatile lactone, which is particularly toxic to insects and mammals and has renowned antibiotic properties (Tocan and Baron 1969; Didry et al. 1991), occurs in a wide range of Ranunculaceae and may owe its evolutionary origin to defense against florivory or pathogens because they often grow in moist habitats. The females of *C. florissomne* may use this compound to discriminate Ranunculaceae from non-Ranunculaceae, but there are likely to be additional features (e.g., morphological or other chemical cues) of *Ranunculus* used by *Chelostoma* to discriminate hosts from nonhosts within Ranunculaceae, as protoanemonin also occurs in nonhost Ranunculaceae growing with *Ranunculus*. Low-volatility compounds may be especially important in pollen-host recognition, as *Chelostoma* bees only responded to pollen odours when they were within 1 cm of their source (Dobson and Bergström 2000). Experienced *Chelostoma* bees recognized host plants based on whole-flower odours rather than pollen odours, but the compounds important in this process remain unknown (Dobson and Bergström 2000).

In another study, Andrews et al. (2007) showed that the females of *Peponapis pruinosa* (Say, 1837) (North American squash bee), a narrow oligolectic species specialized on *Cucurbita* spp. (Fig. 2C), are attracted to flower volatiles emitted by flowers of their pollen hosts. Volatiles were offered in yellow traps at a concentration 100-fold higher than that emitted naturally by *Cucurbita* flowers. The authors used 1,2,4-trimethoxybenzene and indole, which had been identified in headspace samples collected from *Cucurbita* flowers (Andersen and Metcalf 1987; Mena Granero et al. 2005a; Ferrari et al. 2006), and (*E*)-cinnamaldehyde, which was identified in cucurbit floral steam distillates (Andersen 1987). Behavioural experiments using yellow traps baited with these compounds at concentrations 100× higher than natural emissions revealed that female bees used 1,2,4-trimethoxybenzene and (*E*)-cinnamaldehyde, but not indole. Recently it was found that 1,2,4-trimethoxybenzene is emitted mainly by the nectar and indole by the petals of *Cucurbita pepo* L. (field pumpkin) (Mena Granero et al. 2005a). So, we suggest that this compound may be used by females of *P. pruinosa* to discriminate between nectar-rich and nectarless flowers. This study calls for several follow-up experiments, notably (i) to confirm whether (*E*)-cinnamaldehyde is also found in headspace samples of *Cucurbita* flowers, (ii) to investigate whether both flower naïve and experienced

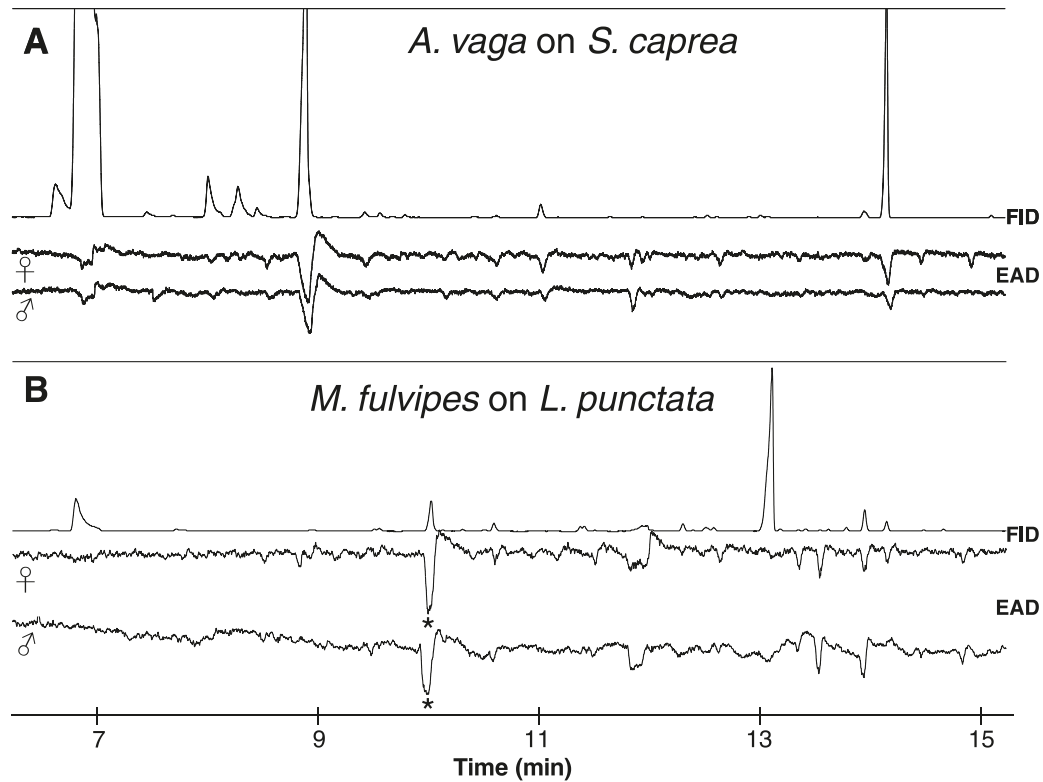
female bees are attracted by these compounds, and finally (iii) to examine whether the attraction of female bees would differ significantly if the experimental stimuli were scaled down to match the emission patterns of individual *Cucurbita* flowers. It would also be of interest to test the extent to which linalool influences the attraction of females of *Peponapis*, because this compound is usually emitted in high amounts not only by the petals but also by the anthers of *Cucurbita* flowers. The detection of this compound could, therefore, be used by the bees to quantify the amount of pollen available in flowers.

Dötterl et al. (2005) recently have shown that 1,4-dimethoxybenzene, another volatile aromatic compound structurally similar to 1,2,4-trimethoxybenzene, mediates the attraction of *Andrena vaga* Panzer, 1799, another narrowly oligolectic bee that collects pollen only from *Salix* inflorescences (Bischoff et al. 2003) (Fig. 2D). Their GC–EAD analyses revealed that both female and male bees can detect several odour compounds emitted from the inflorescences of *Salix caprea* L. (goat willow) and *Salix atrocinerea* Brot. (= *Salix cinerea* ssp. *oleifolia* (Sm.) Macreight) (large gray willow), but the strongest antennal response to headspace extracts was elicited by 1,4-dimethoxybenzene (Fig. 3A). This compound was subsequently found to attract females of *Andrena vaga* early after their emergence when assayed on their nesting site (Dötterl et al. 2005). Another series of experiments revealed that this compound also attracted males, and that other biologically active compounds (except eugenol) were equally attractive to males and females of *A. vaga* (Fig. 4). These studies have highlighted that the bees were only attracted to the scent stimuli early after emergence (S. Dötterl, unpublished results), which suggests that flower-naïve bees might rely on innate preferences for floral or pollen odours during their first visits to their pollen hosts, whereas experienced bees might be less attracted by the odour signals and instead use other cues (e.g., landmarks) to return to specific host-plant patches. The volatile compounds identified as attractants for *A. vaga* have also been found in the scents of diverse flowering plants other than willows (Knudsen et al. 2006). Furthermore, several of these compounds are absent in other willow species visited by *A. vaga* (Westrich 1989; Füssel et al. 2007; S. Dötterl, unpublished results), which suggests that other odours, including less volatile and perhaps more *Salix*-specific compounds, could attract females of *A. vaga* at close range and allow final host-plant recognition.

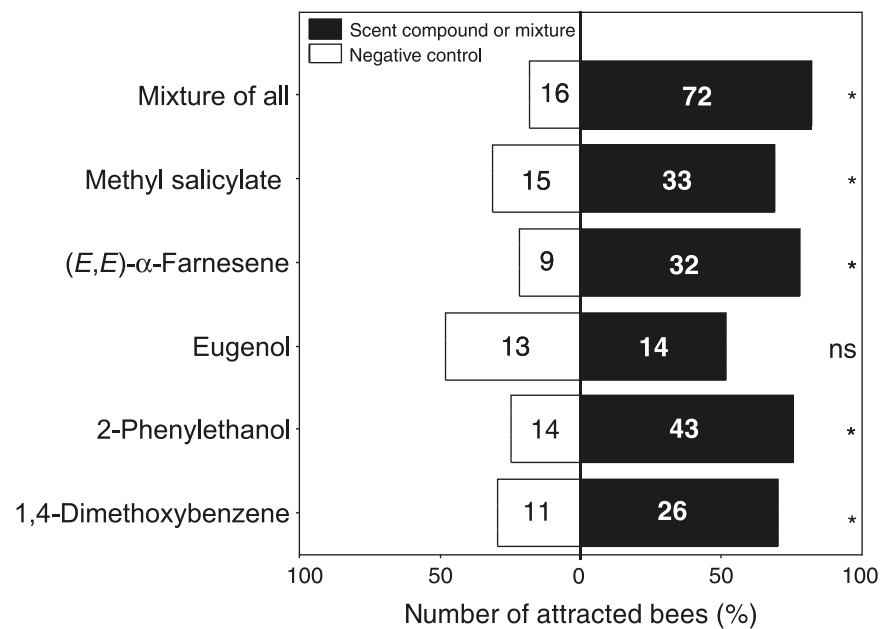
Collectively, these three case studies demonstrate that specialized bees have olfactory receptors for some floral volatiles emitted by their host plants but most likely not for others, and that these bees also have evolved innate preferences for some of these compounds. Considering the results of the behavioural assays conducted so far, it seems reasonable to hypothesize that adults of specialized bees might initially rely on an innate olfactory “search image” (sensu Tinbergen 1960; Gegear and Laverty 2001) that might be changed through experience into a learned multimodal “search image”, which could include floral colour, shape, location, and other cues (see also Menzel 1985). However, the chemical basis for host-plant finding in oligolectic bees is not fully understood in any of these systems. The current state of knowledge calls for more research on the role of



**Fig. 3.** Antennal responses of female and male bees to floral scent headspace samples of host plants of the oligolectic female bees. (A) *Andrena vaga* tested on *Salix caprea* (from Dötterl et al. 2005 and reproduced with permission of J. Chem. Ecol., vol. 31, issue 12, p. 2996, ©2005 Springer-Verlag). (B) *Macropis fulvipes* tested on *Lysimachia punctata*. In *Andrena* and *Macropis* species, both sexes responded similarly to the scent samples, but floral visitation behaviour differed strongly between the sexes. This result suggests that sexual dimorphism in foraging behaviour results from central processing (rather than peripheral screening) of olfactory stimuli. \*Response to 1-hydro-1-phenyl-2-propanone.



**Fig. 4.** Attraction of female and male *Andrena vaga* bees to different floral scent compounds and a mixture thereof compared with a negative control. The compounds were diluted 10-fold (in paraffin) and presented to the bees on impregnated gas chromatograph (GC) septa. The total number of bees attracted is given in the bars. The asterisks indicate that bees significantly preferred the compound (or mixture) over the control (observed vs. expected  $\chi^2$  test,  $\alpha = 0.05$ ); ns indicates that the odour stimuli and the control did not differ significantly in attractiveness.



chemical signals used by specialized bees for host-plant finding or recognition and the extent to which responses to visual vs. olfactory signals are modified by experience. The results obtained from such studies will undoubtedly add important pieces to the puzzle and challenge our current understanding of bee-flower interactions. For example, Dötterl and Schäßler (2007) have reported that experienced females of *Macropis fulvipes* (Fabricius, 1804), a narrow oligolectic species that collects pollen and floral oil on *Lysimachia* spp. (Westrich 1989; Michez and Patiny 2005) (Fig. 2E), can be attracted to flower extracts of one of its hosts (*Lysimachia punctata* L. (large yellow loosestrife)) from up to a few metres, which emphasizes the importance of flower scent for host-plant finding in this group of specialist bees (Dötterl and Schäßler 2007). Some uncommon benzenoid volatiles have been found in the floral scents of flowers of *L. punctata*, including the biologically active 1-hydroxy-1-phenyl-2-propanone (Dötterl and Schäßler 2007; Dötterl 2008) (see also Fig. 3B). However, this compound failed to attract flower inexperienced, as well as experienced, female bees from a distance, even when the enantiomeric composition found in the pollen hosts was assayed (S. Dötterl, unpublished results). Other EAD-active compounds also did not attract the bees, suggesting that different approaches will be necessary to uncover the cues mediating this pollination system. It seems unlikely that a colour cue, which is needed in several oligolectic species for triggering behavioural responses to scents (Dobson and Bergström 2000), is essential for host-plant finding in *Macropis*, as both inexperienced and experienced bees responded to the host scent without an additional visual floral stimuli (S. Dötterl, unpublished results).

### Host plant inheritance: chemical legacy vs. genetic imprinting

How might floral odours contribute to host choice in a more ultimate context? Like all phytophagous insects, bees face the major challenge that the host plants supporting their larval development are selected at the adult stage over a range of potential hosts by the pollen-collecting female bees. Linsley (1958) first suggested that the chemosensory environment provided by pollen odours stored in the brood cells represents the only chemical “search image” a freshly emerged female bee can use to find a suitable host plant. This theory of “chemical legacy”, also termed Hopkins’ host-selection principle (HHSP), has been formulated based on the observation that insects actively prefer the host species that supported their larval development when given a choice among different co-occurring hosts (reviewed by Barron 2001). The concept continues to be widely debated in the literature and remains far from resolved at present (see van Emden et al. 1996; Rietdorf and Steidle 2002; Facknath and Wright 2007; Niklas et al. 2009).

To test the effect of larval experience on adult conditioning and host-plant preference, Dobson and Ayasse (2000) reared larvae of the polylectic bee *Osmia bicornis* (L., 1758) (= *Osmia rufa* (L., 1758)) on pollen of *Brassica napus* L. (turnip rape), but their results showed no effect of larval experience on the preferences of the next-generation female bees for *B. napus*. By contrast, Praz et al. (2008b) tested the HHSP with the solitary bee *Heriades truncorum* (L., 1758)

(Fig. 2F) that is broadly oligolectic on Asteraceae but can also develop on pollen of nonhost plants such as *Campanula* L. (Campanulaceae; bellflower), *Echium* L. (Boraginaceae; vipersbugloss), and *Sinapis* L. (Brassicaceae; mustard). Their results showed unambiguously that the newly emerged females consistently collected pollen from their preferred host plants (Asteraceae), irrespective of the pollen types that they had been fed with during larval development (Praz et al. 2008b). These results suggest that genetically determined factors predominate in host-plant recognition in this species, but the extent to which the conclusions from this study apply to other specialized bee species remains unclear.

### The dynamics and patterns of host-plant use by bees

Although a wide range of bee species are specialized on certain pollen hosts (Cane and Sipes 2006; Minckley and Roulston 2006; see above) and the preference of female bees for these hosts seems—at least in some cases—to have a relatively strong genetic basis (see above), changes in host plants do occur among closely related species of bees. Overall, the most frequently observed patterns are shifts by oligolectic species from one plant taxon to another. The host plants used tend to be related in most cases (Sipes and Tepedino 2005; Patiny et al. 2007; Michez et al. 2008), which is consistent with the patterns observed in other groups of phytophagous insects (see Mitter and Farrell 1991) and could be partially explained by the phylogenetic conservatism of the host plants’ secondary chemistry (Smith 1976). However, some specialist bee species have also undergone shifts between unrelated host plants (e.g., Müller 1996; Michez et al. 2008; Müller and Kuhlmann 2008), for which one possible explanation is that these broad taxonomic “jumps” might have been facilitated by a shared chemistry of the preferred host plants.

When changes are detected in the breadth of host-plant use, most transitions concern shifts from oligolecty to polylecty; that is, an increase in host breadth or generalization (Müller 1996; Sipes and Tepedino 2005; Patiny et al. 2007; Michez et al. 2008). That being said, independent shifts from generalization to specialization also have been described in the family Halictidae (Danforth et al. 2003; McGinley 2003). Similarly, *Bombus consobrinus* Dahlbom, 1832 and *Bombus gerstaeckeri* Morawitz, 1881, two European bumble bee species, have independently evolved specialization on *Aconitum* L. (monkshood) and other closely related species in the Ranunculaceae (Löken 1961; Müller et al. 1997; Westrich 1989; Mahé 2007; for the phylogeny of the genus *Bombus* see Cameron et al. 2007).

What is the relative importance of floral chemistry, compared with floral colour, flower morphology, and pollen morphology, in mediating evolutionary host shifts by specialized bees? It has been assumed in these cases that the patterns of host-plant evolution might be driven by the floral morphology of the targeted host plants (Sipes and Tepedino 2005; Michez et al. 2008). For example, some bee lineages in the North American deserts have shifted between distantly related but morphologically similar species in the family Cactaceae and Malvaceae that grow in close vicinity (Minckley and Roulston 2006, and references therein). Another morphological trait of importance might be pollen size (Pernal and Currie 2002), especially in cases where oli-

golectic bees are adapted to plants (e.g., *Convolvulus* L. (Convolvulaceae; morning glories) or *Malva* L. (Malvaceae; mallows)) producing extraordinarily large pollen grains (Thorp 1979; Minckley and Roulston 2006). Flower colour, which is one dimension of the visual display of flowers, seems to play a minor role in host-plant switches in bees. However, though most bees have three visual receptors (UV, blue, green), one bee species (the andrenid *Callonychium petuniae* Cure and Wittman, 1990) that is specialized on purple flowers of the *Petunia* Juss. (Solanaceae; nightshades) evolved an additional red receptor, which may have been an important prerequisite in effectively detecting the purple flowers and using *Petunia* as host plants (Peitsch et al. 1992). Pollen nutrient content appears to be less important for bee foraging and host-use evolution (Roulston et al. 2000), in contrast to the presence of defensive compounds that may act as a strong barrier to host-plant switches, because the pollen of some taxonomic groups might possess protective chemicals that hamper digestion by bees (see Williams 2003; Praz et al. 2008a). Pollen defensive compounds, therefore, seem to act as a floral filter (for a discussion on floral filters see Johnson et al. 2006) in bees, and not only attraction but also repellence may, therefore, be an important dimension for host-plant evolution of bees.

Considering the information reviewed above, flower or pollen odour appears to contribute significantly to the evolution of host-plant use in bees. Several oligolectic bees use floral volatiles to find and discriminate host plants from nonhosts (Dobson and Bergström 2000). The olfactory preference of oligolectic bees for their pollen hosts seem to have an important genetic basis in the few species investigated so far, when females were not influenced by pollen or nectar odours to which they were exposed during their larval development or as emerging adults (Praz et al. 2008a). Similar experiments should now be performed on a wider range of species. In particular, analyses of the attractive scent compounds used by specialist and generalist bees in combination with the determination of their olfactory capabilities should be performed to increase our understanding of the mechanisms of host-plant use and switches in oligolectic bee species. For example, it could be hypothesized that host-plant switches are due to changes in the bees' capacity to detect floral scents (e.g., gain or loss of olfactory antennal receptors) correlated with changes in behavioural responses to scents (see Menken and Roessingh 1998). However, rather than argue for the primacy of one sensory modality over another, we urge bee biologists to design balanced studies in which several dimensions of floral traits (odour, colour, iridescence, tactile cues, shape, size, and composition of pollen and whole flowers), as well as the community context in which they are presented, are assayed simultaneously.

### Male bees and their "pseudofemale" orchids

Thus far, we have concentrated on the odour-mediated foraging behaviours of female solitary and social bees and on the cues used by specialized solitary bees for host-plant finding. Interestingly, the males of many of the bee lineages discussed above (e.g., genera *Andrena* Fabricius, 1775 and *Colletes* Latreille, 1802) also visit flowers for a diversity of

reasons that are only now beginning to be fully appreciated. Male bees are undoubtedly the neglected gender in scientific studies (Koeniger 2005), particularly on the ecology and evolution of bee-flower associations. Surely, co-opting male insects as pollinators should be regarded as an exception in the pollination biology of flowering plants. Males are usually short lived and have traditionally been caricatured as investing their time and energy only transiently to mate with emerging females, spending the rest of their adult life moving leisurely amid the nearby vegetation and probing flowers for nectar. If this were true, it would be fair to consider that male bees contribute very little to their offspring and virtually nothing to the pollination of flowers in their habitat. But in reality, we find that male bees, particularly in non-*Apis* species, patrol for mating partners throughout the day and during the whole mating period, literally using up all their resources searching for emerging females (Alcock et al. 1978; Paxton 2005). Moreover, the reproduction—and hence the survival—of hundreds of orchid species relies exclusively on the attraction of male bees and wasps as pollinators through sexual deception, i.e., the false promise of sex.

Unlike the vast majority of flowering plants, but similar to approximately one third of all 30 000 orchid species described to date, the flowers of "sexually deceptive" orchids provide no reward of any kind to their pollinators (Dafni 1984; Jersáková et al. 2006; Renner 2006). For example, it has been suggested that these orchids might achieve unusually high degrees of pollinator specificity in pollen transfer and low rates of pollen loss through the assiduous focus of males on finding conspecific mates throughout their reproductive season (Alcock et al. 1978; Paxton 2005). Besides, the movement patterns of males during the reproductive season differ strikingly from those of conspecific females, many of whom are central-place foragers bound physically by proximity to their nests (Eickwort and Ginsberg 1980). In particular, the capacity of males to patrol for mating partners over long distances (Williams and Dodson 1972; Peakall 1990; Peakall and Beattie 1996) could potentially help the orchids maximize outcrossing distances and promote genetic mixing within and among populations via long-distance dispersal of pollen masses (see Johnson et al. 2004).

Pollination by sexual deceit has evolved several times independently in different genera across Australia (e.g., Coleman 1928; Stoutamire 1975; Peakall et al. 1987; Jones 1988; Peakall 1990; Bower 1996, 2006), the Neotropics (van der Pijl and Dodson 1966; Dod 1976; Singer 2002; Singer et al. 2004; Blanco and Barboza 2005; Ciotek et al. 2006), South Africa (genus *Disa* P.J. Bergius (Orchidaceae); Steiner et al. 1994), and Europe (Schiestl 2005; Ayasse 2006; Delforge 2006; Jersáková et al. 2006; Vereecken 2009). Cross-pollination in sexually deceptive orchids is brought about through a process termed "pseudocopulation", whereby the male bees unwittingly transfer the orchids' pollen masses from one flower to the next as they successively attempt copulation with the flower labellum as a female decoy. The floral signals involved in this mimicry remained a mystery until the second half of the 20th century when based on behavioural experiments with the pollinators and comparative analyses of floral traits of the

orchid *Ophrys* L. (Orchidaceae), Bertil Kullenberg proposed that floral odours were the key to the attraction of the male insects as pollinators (Kullenberg 1956, 1961). In *Ophrys* orchids, it has been shown that out of the 100+ compounds emitted by the individual flowers (Schiestl et al. 1999, 2000; Ayasse et al. 2000), only a subset of them, in particular straight-chained, monounsaturated alkenes 21–29 carbons long, are also used by the female bees in similar proportions and effectively constitute the female sex pheromone signal (Schiestl et al. 1999; Mant et al. 2005a; Stöckl et al. 2007). Sympatric *Ophrys* species that are adapted to different pollinators are usually reproductively isolated through the species-specific patterns of alkenes emitted by their flowers (Schiestl and Ayasse 2002; Stöckl et al. 2005) (ethological isolation, but see Stöckl et al. 2008). When the sympatric *Ophrys* species have converged towards the attraction of the pollinator species, cross-pollination is usually prevented by the species-specific orientations of the hairs covering the labellum of each species, leading the attachment of the orchids' pollen masses on different body parts of the insect (e.g., head vs. abdomen tip) during pseudocopulations (Kullenberg 1961; Ågren et al. 1984; Borg-Karlson 1990; see also Pauw 2006; but see Gögler et al. 2009). Mechanical and ethological isolation barriers help maintain strong reproductive isolation, especially when they act in concert (Johnson 2006; but see Cortis et al. 2009).

In-depth studies into the reproductive behaviour of the plasterer bee *Colletes cunicularius* (L., 1761) have led to insights on the mechanisms that drive the evolution of sexual deception in *Ophrys* orchids. In a first series of experiments that combined chemical analyses of floral scents with behavioural bioassays in a subtractive design, Mant et al. (2005a) successfully narrowed down the whole spectrum of several tens of odour compounds to just three alkenes ((*Z*)-7-heneicosene, (*Z*)-7-tricosene, (*Z*)-7-pentacosene) that were as attractive as the whole blend and used by the emerging females as sex pheromones. This finding paved the way for further experiments on a multiple-population scale that assessed the spatial variation of sex pheromone signals and floral scents in this *Ophrys*-bee interaction. These follow-up studies found evidence for population-specific patterns of the key odour compounds in a manner reminiscent of “dialects” (Mant et al. 2005b; Vereecken et al. 2007). Although it was expected that the orchids' floral odour bouquet should mimic the female sex pheromone of its pollinator as closely as possible to attract the targeted males, Vereecken and Schiestl (2008) found that the proportions of the three alkenes emitted by the orchids in sympatry were significantly different from the bees'. Ensuing behavioural bioassays using natural extracts of the bees and the orchids showed that the “imperfect” orchid mimics were in fact actively preferred by males over their own females. The authors suggested that because males of *C. cunicularius* have a clear preference for exotic female signals (see Vereecken et al. 2007), their preferences might have transferred into selection on the floral scent of the orchids towards similar but not identical proportions of the odour compounds found in the local females' sex pheromone (Vereecken and Schiestl 2008).

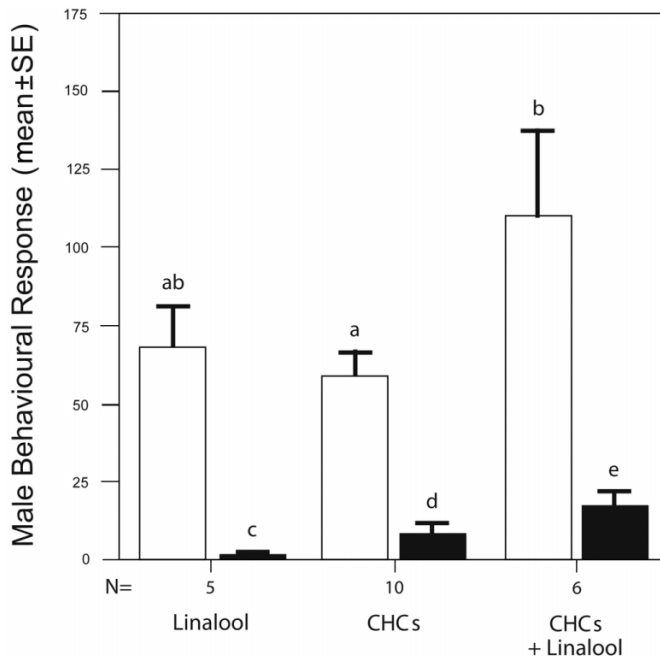
The abovementioned studies have largely focused on flo-

ral scent, particularly the low-volatile compounds, because they proved to be capable of triggering attraction 2–3 m from the odour source, landing and stereotyped copulatory behaviour in the male insects, even when assayed on visually neutral dummies such as small plastic beads (see Mant et al. 2005a, 2005b; Vereecken et al. 2007; Vereecken and Schiestl 2008). Conversely, the highly volatile compounds that have been the focus of earlier investigations on the chemistry of *Ophrys*-pollinator interactions only triggered “quick approaches”, “persistent approaches”, or “quick visits” (terms coined by Kullenberg 1956) by the patrolling males and failed to reproduce genuine copulation attempts of the male insects with the scented dummies (Kullenberg 1956; Tengö 1979; Bergström et al. 1980; Borg-Karlson et al. 1985; Borg-Karlson and Tengö 1986). The results depicted in Fig. 5 show that linalool, a highly volatile compound emitted by females of *C. cunicularius* (Bergström and Tengö 1978; Cane and Tengö 1981; Borg-Karlson et al. 2003) and by the flowers of *Ophrys exaltata* Tenore (Borg-Karlson 1990; Borg-Karlson and Groth 1986; Mant et al. 2005a) acts as a long-range attractant for males of *C. cunicularius*. However, this compound is not capable of triggering copulation attempts by the males when assayed alone (Fig. 5). Because the cuticular hydrocarbons used in these bioassays are less-volatile compounds secreted on the cuticle surface of females of *C. cunicularius*, Mant et al. (2005a) suggested that the sex pheromone of *C. cunicularius* should be considered a multicomponent blend, with linalool acting as long-range mate attractant, whereas the epicuticular compounds elicit male mating behaviour at short range.

Although there is a general agreement that floral chemistry holds the key to the mechanism of sexual deception in *Ophrys* orchids, parallel investigations have studied the role (if any) of visual cues in the attractiveness of flowers of *Ophrys* orchids, driven by the obvious fact that flowers of *Ophrys* orchids display spectacular colours and look remarkably like insects to the human eye (see Figs. 6C, 6D). Kullenberg (1961) and Paulus (1988, 2007) showed that male bees and wasps could be attracted to the flowers of their associated *Ophrys* species by a combination of visual and olfactory signals. However, Spaethe et al. (2007) pioneered the quantification of the relative contribution of olfactory vs. visual signals in pollinator attraction in *Ophrys* orchids by performing dual-choice bioassays with intact flowers vs. flowers deprived of their perianth, using *Ophrys heldreichii* Schlechter, a species from Crete with a large pinkish perianth surrounding the “pseudofemale” labellum. The authors reported that the presence of the perianth triggered an increase in the visitation rates by males of *Tetralonia berlandi* Dusmet, 1926 (the long-horned bee), thus acting in synergy with the odour signals of the labellum (Fig. 6D). Furthermore, the authors showed that the overall perianth colour of *O. heldreichii* coincides precisely with the spectral reflectance of sympatric “rendez-vous” flowers, i.e., other plant species on which mating takes place shortly after males and females emerge from their underground nest (Spaethe et al. 2007). This study illustrates that although chemical mimicry of female cuticular pheromones might be the primary strategy to attract male bees as pollinators in *Ophrys* orchids, some species also might include visual contextual signals along with their sex pheromone mimicry to enhance their at-



**Fig. 5.** Relative contribution of the highly volatile linalool (racemic mixture) vs. a synthetic mixture of the low-volatility cuticular hydrocarbons (CHCs) in the long-range attraction (number of inspecting flights; open bars) and landing or copulation (number of contacts; solid bars) of males of *Colletes cunicularius* with a scented dummy during 3 min behavioural bioassays. Values are mean  $\pm$  SE. Different letters above the bars indicate significant differences at  $\alpha = 0.05$  (modified after Mant et al. 2005a).



tractiveness and thereby maximize their reproductive success (see also Streinzer et al. 2009). No other such report has been made so far in the genus *Ophrys* except by Vereecken and Schiestl (2009), who showed that the polymorphic coloured perianth of *Ophrys arachnitiformis* Gren. & M. Philippe does not influence visitation rates of males of *C. cunicularius*, its main pollinator. The role of colour signals in pollination of *Ophrys* orchids is still largely unexplored, and we assume that floral colour might play a role in other species such as in the narrow endemic *Ophrys aveyronensis* (Wood) from southern France, which also displays a large white and pink perianth that is not found in closely related species (Fig. 6C). This orchid is pollinated by males of the mining bee *Andrena hattorfiana* (Fabricius, 1775) (Paulus and Gack 1999), the females of which are oligolectic on the white or pinkish inflorescences of *Knautia* spp. and *Scabiosa* spp. (Dipsacaceae) (Figs. 6A, 6B) (Westrich 1989). Early in the reproductive season, the males patrol these “rendez-vous” flowers in search of freshly emerged females and attempt copulation with the latter as they collect pollen and nectar (Fig. 6B). This *Ophrys*–pollinator pair might represent another instance of multi-component floral mimicry that supports the findings by Spaethe et al. (2007). The genus *Ophrys* promises a multitude of other examples in which visual stimuli, labellum texture, and other contextual cues modify the chemical mimicry of female sex pheromone to maximize the flowers’ attractiveness towards patrolling males (Vereecken 2009).

## Floral scent and crop pollination

Bees have a great impact on the productivity of at least 50 of the leading agricultural crops in the world. In some of these crops such as the watermelon, melon, pumpkin, squash, zucchini, and kiwifruit (*Actinidia deliciosa* (A. Chev.) C.F. Liang & A.R. Ferguson), bees are essential pollinators (Klein et al. 2007). Honey bees, especially *Apis mellifera* and to a minor extent other *Apis* species (e.g., *Apis cerana* Fabricius, 1793), are important pollen vectors for many crop plants, but other social bees (bumble bees, stingless bees) and solitary bees (e.g., megachilids, anthophorids, halictids) also contribute to crop yield. In some crops (e.g., passionfruit), productivity is ensured only through the pollination service of solitary bees. Although the pollination of crops by bees is acknowledged to be a critical ecosystem service (Daily 1997; Kremen et al. 2002, 2004), little is known about the attraction of bees to the flowers of crop plants or about the extent to which floral scent contributes to pollinator attraction, discrimination, and constancy in agricultural settings. In crops such as tomato, mango, almond, and Robusta coffee, the compounds emitted from the flowers remain unknown. However, some knowledge is available in cucurbits (Andersen 1987; Mena Granero et al. 2004, 2005a; Ferrari et al. 2006; Theis et al. 2009), different *Prunus* L. species, such as sweet cherry and apricot (Baraldi et al. 1999), apple (Loughrin et al. 1990; Buchbauer et al. 1993; Baraldi et al. 1999), pear (Baraldi et al. 1999), raspberry (Robertson et al. 1995), turnip rape (Tollsten and Bergström 1988; Ômura et al. 1999), roses (e.g., Dobson et al. 1990), fennel (Chung et al. 2003), and kiwi (Tatsuka et al. 1990; Crowhurst et al. 2008). In all these crops at least one compound known to be attractive to at least one bee species has been found (see Table 1), and several species pollinated by the honey bee *A. mellifera* emit compounds known to elicit behavioural responses from them. Moreover, cucurbit flowers emit scents that have already been shown to attract a specialized cucurbit pollinator, *Peponapis pruinosa* (Andrews et al. 2007). These results emphasize the importance of flower scent in attracting generalized, as well as specialized, bee pollinators to the major crops and point to floral scent as an important (indirect) factor in world-crop production.

For many years agriculturalists have sought to increase the yield of many different crops by manipulating odours that mediate the behaviour of bees. Honey bees were fed inside or outside the hive with sugar water containing the scent of the crops or placed close to crop flowers (according to protocols described by von Frisch (1944, 1965) and references therein). When feeding in the hive, bees were conditioned to the scent, and if they were recruited by a dancer, were more likely to visit the crop whose scent was presented in the hive. Similarly, visitation rates to specific crops could be increased when feeding the bees outside the hive. Foragers feeding from the scented feeding stations that were placed in the crop fields effectively recruited nest mates in the hive by dancing and these recruited bees subsequently visited flowers emitting the odour that they learned from the dancer. These scent guidance methods have promoted increased yield in clover (genus *Trifolium* L.), oilseed rape (*Brassica napus* var. *oleifera* Delile) and turnip rape (*B. rapa*), but not in horsebean (*Vicia faba* L.) or buckwheat

**Fig. 6.** Examples of the interaction between visual and odour signals in the reproductive biology of solitary bees and in the pollination biology of *Ophrys* orchids. (A) The females of the mining bee *Andrena hattorfiana* are oligolectic on different *Scabiosa* species. (B) The photograph shows a male of *A. hattorfiana* that had just attempted to mate with a female foraging on the “rendez-vous” flowers (a *Scabiosa* species) and that returned a few seconds later, although the female was still on its back. (C) Detail of a flower of *Ophrys aveyronensis*, a narrow endemic species that is pollinated exclusively by males of *A. hattorfiana*. The spectral similarity between the large white and pink perianth and the *Scabiosa* inflorescences might enhance the flower attractiveness. (D) Behavioural bioassay in dual-choice design illustrating the experiments by Spaethe et al. (2007) on the relative role of visual vs. olfactory signals in *Ophrys*–pollinator interactions. The photograph depicts a male of *Tetralonia berlandi* attempting to copulate with a flower of *Ophrys heldreichii*. In their study, Spaethe et al. (2007) showed that the coloured perianth of the flowers of *O. heldreichii* significantly increases the attractiveness of the flowers to their pollinator. All photos by N.J. Vereecken except for D, which is by P.M. Schlüter (reproduced with permission).



(*Fagopyrum esculentum* Moench) (von Frisch 1965; Silva et al. 2003), and appear not to do so for garden onion (*Allium cepa* L.) (Silva et al. 2003).

Because scent augmentation techniques are time consuming, do not work with all bee-pollinated crops, and need to be adjusted for each crop individually, researchers have sought to develop a general bee attractant that might increase crop visitation rate and yield independent of the target plant and its blooming phenology. Two important candidates were the honey bee Nasonov pheromone (Williams et al. 1981a, 1981b; Wells et al. 1993) and queen mandibular pheromone (QMP) (Currie et al. 1992a; Higo et al. 1995). Nasonov pheromone is made up of seven compounds (neral and geranial, the corresponding alcohols and acids, and (*E,E*)- $\alpha$ -farnesol) and is released by worker bees to attract other workers (Pickett et al. 1980). It is useful in several contexts; for example, it helps workers find the entrance to their hive, sources of water, or artificial food, and

is important during swarming (Slessor et al. 2005). A spraying reagent containing synthetic Nasonov compounds has been developed for this purpose (Elmstrom and Maynard 1991; Schultheis et al. 1994) and is now commercially available as BeeScent<sup>®</sup>. The QMP, which consists of five compounds ((*2E*)-9-oxodec-2-enoic acid, (*R*)-(*2E*)-9-hydroxydec-2-enoic acid, (*S*)-(*2E*)-9-hydroxydec-2-enoic acid, methyl-4-hydroxybenzoate, 4-hydroxy-3-methoxyphenylethanol); Keeling et al. 2004), has many functions, including the attraction of drones (Gary 1962; Butler and Fairey 1964) and workers (especially members of the retinue) to the queen (Slessor et al. 2005). Spraying crops with synthetic Nasonov pheromone and QMP increased visitation rate and (or) crop production in some cases (Elmstrom and Maynard 1991; Currie et al. 1992a, 1992b; Higo et al. 1995), but not in others (Schultheis et al. 1994; Winston 1995). Several reasons have been proposed as to why these pheromone blends were not universally effective, one of



which is that pheromones were used out of the natural context and that not only flowers but whole plants were sprayed, which might ultimately confuse the bees (Wells et al. 1993; Winston 1995; Paldi 2004). Interestingly, with the exception of the acids, all compounds occurring in the Nasonov pheromone are well known and widespread floral scent compounds occurring also in plants pollinated by bees (Dobson 2006; Knudsen et al. 2006). These compounds therefore may not only have pheromonal functions but also may be mediators in bee–plant interactions, depending upon their concentrations and combinatorial relationships with other compounds. However, the importance of these compounds in attracting honey bees to flowers in a natural setting begs further study. A promising model system for this is the domestic apple (*Malus × domestica* Borkh.), whose flowers emit three of the Nasonov compounds and several others known to be attractive for honey bees (e.g., linalool). Assessing the importance of the single compounds and mixtures thereof may help to understand the relative importance of Nasonov compounds in comparison with other compounds in the attraction of bees to (apple) flowers.

Since the 1990s, coupled GC–EAD (Thiery et al. 1990; Henning and Teuber 1992) and behavioural measurements (Wadhams et al. 1994; Blight et al. 1997; Le Métayer et al. 1997; Pham-Delègue et al. 1997) have increased our understanding of the chemical basis for honey bee–crop interactions. By using these combined methods, individual components that are electrophysiologically active, as well as those that are behaviourally active, were identified from complex scent mixtures emitted from alfalfa (*Medicago sativa* L.) (Henning et al. 1992; Henning and Teuber 1992), sunflower (Thiery et al. 1990), and oilseed rape flowers (Wadhams et al. 1994; Blight et al. 1997; Le Métayer et al. 1997; Pham-Delègue et al. 1997). In alfalfa, bees responded in the GC–EAD measurements to all 10 common alfalfa volatiles tested (Henning and Teuber 1992), and 5 of these compounds were subsequently used in behavioural experiments (Henning et al. 1992). Only linalool was found to be attractive, (*E*)- $\beta$ -ocimene and (*Z*)-3-hexenyl acetate were neutral, and methyl salicylate and 3-octanone were repellent in comparison with an odourless source (control). The authors suggested that alfalfa breeders should select for varieties emitting high amounts of linalool and low amounts of methyl salicylate and 3-octanone (but see Waller et al. 1974).

Although sunflowers emit a highly complex volatile blend with up to 250 compounds (Pham-Delègue et al. 1989), a series of chemical (including fractionations), electrophysiological, and behavioural experiments have pinpointed a small subset of six floral scent compounds (including bornyl acetate, vanillin, propiovanillone) as major attractants to the honey bee (Pham-Delègue et al. 1986, Thiery et al. 1990).

Finally, studies with honey bees and flower volatiles from oilseed rape identified the compounds used by experienced bees (individuals were either fed with pollen or allowed to forage freely before testing) to recognize the flowers (Wadhams et al. 1994; Blight et al. 1997; Le Métayer et al. 1997; Pham-Delègue et al. 1997). Eight compounds ( $\alpha$ -pinene,  $\alpha$ -terpinene, 3-carene, linalool, (*E,E*)- $\alpha$ -farnesene, phenylacetaldehyde, *p*-cymene, 2-phenylethanol) were learned by the

bees, and among these eight compounds, linalool, (*E,E*)- $\alpha$ -farnesene, and phenylacetaldehyde were identified as key compounds used by bees in recognizing the flowers (Blight et al. 1997).

The identification of volatiles emitted by crop plants and their flowers, along with behavioural and electrophysiological screening to determine their importance in attracting bee pollinators, should be prioritized during the next few years if we are to advance our understanding of the olfactory basis of bee–crop interactions. Furthermore, comparing the chemical signals of crops with those of their wild relatives may reveal why cultivated plants are often less attractive to pollinators than wild types (Young and Severson 1994). Similarly, comparisons among crop varieties will uncover why some varieties are more attractive to bees than others (Boren et al. 1962; Loper et al. 1974). Recently, it was shown that inbreeding level is a factor influencing floral scent chemistry, which might likewise affect bee–crop interactions. In *Cucurbita pepo*, experimental self-pollination resulted in both reduced emissions of floral scent and different chemical composition (particularly different relative contributions by individual compounds) detectable in first-generation selfed progeny compared with outcrossed progeny (Ferrari et al. 2006). Similarly, artificial selection for specific floral or plant traits during the course of plant breeding and domestication often has pleiotropic effects on floral scent composition (Dudareva and Pichersky 2006), and honey bees have been shown to distinguish between cultivars owing to their odours alone (Wright et al. 2005). Thus, our growing knowledge of the chemical ecology of bee–crop interactions could serve as a guide to the transgenic manipulation of the scent emitted by crop flowers or whole-crop plants to increase their attractiveness to bee pollinators, which might in some cases result in higher yield (Pichersky and Dudareva 2007).

## Conclusions and perspectives

We have outlined our current knowledge of the chemical ecology of bee–flower interactions, contrasting female and male bee responses to different floral odours along a spectrum of highly host-specialized to highly generalized floral foragers. Three themes have emerged from our review and deserve further attention.

First, there are alarmingly few cases in which the floral scent attractants (and their relative importance compared with visual cues) have been identified for ANY bee–flower interactions, running the gamut from host-specialized to generalized bees. Indeed, there is a strong disconnect between the community-scale studies of bee pollination that dominate the recent literature (e.g., Kremen et al. 2004; Ricketts et al. 2004) and the patch- or flower-scale behavioural studies with single bee species outlined in our review. This gap reflects a historical “anosmia” endemic to pollination biology (see Raguso 2008), and more importantly, a dearth of studies that bridge different spatial scales in pollinator behaviour, from migration or dispersal to habitat selection to individual flower choice.

Second, several floral scent compounds known from bee-pollinated plants play a role in the bees’ sexual or social biology (e.g., Mena Granero et al. 2005*b*). However, we still

do not know whether these compounds are mediators in bee–plant interactions, as well as pheromones. We urgently need a well-designed phylogenetic study of innate odour preference and social pheromones among congeneric bees, something akin to the phylogeographic study of colour vision among Mediterranean *Bombus* spp. by Chittka et al. (2001).

Third, apart from the cases of genetic predisposition for host odors, sensory flexibility and learned modification of responses to odours are apparent across the spectrum of bees discussed here. This finding suggests that studies narrowly focused on single sensory modalities or bees of a single age class are likely to miss the more nuanced reality of floral foraging that includes, but is not limited to, foraging experience and olfactory signalling.

## Acknowledgements

We dedicate this review to Heidi E.M. Dobson, whose pioneering works on oligolectic bees have been—and still are—a constant source of inspiration for students investigating the chemical ecology of bee–flower interactions. Special thanks are due to R.A. Raguso for his invaluable and constant support and editorial suggestions throughout the preparation of this review, and many thanks go to an anonymous reviewer for comments that greatly helped improve the text. N.J.V. is grateful to B.N. Danforth, J.H. Cane, D. Michez, A. Müller, J. Neff, and S.P.M. Roberts for their constructive comments on an earlier version of the manuscript and the figures, as well as to J. Forman Orth and P.M. Schlüter for providing photo material used to illustrate this review. S.D. thanks J. Ackerman, H. Dobson, T. Eltz, W. Farina, A. Mattich, and N. Theis for fruitful discussions or for making unpublished data available, and S. Emmrich for providing bioassay data. N.J.V. received financial support from the Belgian Fonds National pour la Recherche Scientifique through a Fonds de la Recherche Scientifique – Fonds National pour la Recherche Scientifique (FRS–FNRS) Postdoctoral Fellowship.

## References

- Ackerman, J.D. 1986. Coping with the epiphytic existence: pollination strategies. *Selbyana*, **9**: 52–60.
- Afik, O., Dag, A., Kerem, Z., and Shafir, S. 2006. Analyses of avocado (*Persea americana*) nectar properties and their perception by honey bees (*Apis mellifera*). *J. Chem. Ecol.* **32**(9): 1949–1963. doi:10.1007/s10886-006-9120-1. PMID:16902825.
- Ågren, L., Kullenberg, B., and Sensenbaught, T. 1984. Congruences in pilosity between three species of *Ophrys* (Orchidaceae) in their hymenopteran pollinators. *Nova Acta Regiae Societatis Scientiarum Upsaliensis Ser. 3*: 15–25.
- Aizen, M.A., and Feinsinger, P. 1994. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentina “Chaco Serrado”. *Ecol. Appl.* **4**(2): 378–392. doi:10.2307/1941941.
- Alcock, J., Barrows, E.N., Gordh, G., Hubbard, J., Kirkendall, L., Pyle, D.W., Ponder, T.L., and Zalom, F.G. 1978. The ecology and evolution of male reproductive behaviour in the bees and wasps. *Zool. J. Linn. Soc.* **64**(4): 293–326. doi:10.1111/j.1096-3642.1978.tb01075.x.
- Alexander, B.A., and Michener, C.D. 1995. Phylogenetic studies of the families of short-tongued bees (Hymenoptera: Apoidea). *Univ. Kansas Sci. Bull.* **55**: 377–424.
- Allsopp, P.G., and Cherry, R.H. 1991. Attraction of *Apis mellifera* L. (Hymenoptera, Apidae) to volatile compounds. *J. Aust. Entomol. Soc.* **30**: 219–220.
- Andersen, J.F. 1987. Composition of the floral odor of *Cucurbita maxima* Duchesne (Cucurbitaceae). *J. Agric. Food Chem.* **35**(1): 60–62. doi:10.1021/jf00073a014.
- Andersen, J.F., and Metcalf, R.L. 1987. Factors influencing distribution of *Diabrotica* spp. in blossoms of cultivated *Cucurbita* spp. *J. Chem. Ecol.* **13**(4): 681–699. doi:10.1007/BF01020152.
- Anderson, D., East, I.J., Cox-Foster, D., Conlan, S., Holmes, E.C., Palacios, G., Kalkstein, A., Evans, J.D., Moran, N.A., Quan, P.-L., Geiser, D., Briese, T., Hornig, M., Hui, J., Vanengelsdorp, D., Pettis, J.S., and Lipkin, W.I. 2008. The latest buzz about colony collapse disorder. *Science* (Washington, D.C.), **319**(5864): 724–725, author reply 724–725. doi:10.1126/science.319.5864.724c. PMID:18258878.
- Andrews, E.S., Theis, N., and Adler, L.S. 2007. Pollinator and herbivore attraction to *cucurbita* floral volatiles. *J. Chem. Ecol.* **33**(9): 1682–1691. doi:10.1007/s10886-007-9337-7. PMID:17659427.
- Arenas, A., Fernández, V.M., and Farina, W.M. 2007. Floral odor learning within the hive affects honeybees’ foraging decisions. *Naturwissenschaften*, **94**(3): 218–222. doi:10.1007/s00114-006-0176-0. PMID:17119909.
- Arenas, A., Fernández, V.M., and Farina, W.M. 2008. Floral scents experienced within the colony affect long-term foraging preferences in honeybees. *Apidologie*, **39**(6): 714–722. doi:10.1051/apido:2008053.
- Arn, H., Städler, E., and Rauscher, S. 1975. The electroantennographic detector: a selective and sensitive tool in the gas chromatographic analysis of insect pheromones. *Z. Naturforsch. Sect. C Biosci.* **30**: 722–725.
- Ashman, T.L., Bradburn, M., Cole, D.H., Blaney, B.H., and Raguso, R.A. 2005. The scent of a male: the role of floral volatiles in pollination of a gender dimorphic plant. *Ecology*, **86**(8): 2099–2105. doi:10.1890/04-1161.
- Ayasse, M. 2006. Floral scent and pollinator attraction in sexually deceptive orchids. *In* *Biology of floral scent*. Edited by N. Dudareva and E. Pichersky. CRC Press, Boca Raton, Fla. pp. 219–241.
- Ayasse, M., Schiestl, F.P., Paulus, H.F., Löfstedt, C., Hansson, B.S., Ibarra, F., and Francke, W. 2000. Evolution of reproductive strategies in the sexually deceptive orchid *Ophrys sphegodes*: how does flower-specific variation of odor signals influence reproductive success? *Evolution*, **54**(6): 1995–2006. doi:10.1111/j.0014-3820.2000.tb01243.x. PMID:11209776.
- Baraldi, R., Rapparini, F., Rossi, F., Latella, A., and Ciccioli, P. 1999. Volatile organic compound emissions from flowers of the most occurring and economically important species of fruit trees. *Phys. Chem. Earth B Hydrol. Oceans Atmos.* **24**: 729–732. doi:10.1016/S1464-1909(99)00073-8.
- Barbier, M. 1970. Chemistry and biochemistry of pollens. *Prog. Phytochem.* **2**: 1–34.
- Barron, A.B. 2001. The life and death of Hopkins’ host selection principle. *J. Insect Behav.* **14**(6): 725–737. doi:10.1023/A:1013033332535.
- Bartholomew, C.S., and Prowell, D. 2005. Pan compared to malaise trapping for bees (Hymenoptera: Apoidea) in a longleaf pine savanna. *J. Kans. Entomol. Soc.* **78**(4): 390–392. doi:10.2317/0409.24.1.
- Beekman, M. 2005. How long will honey bees (*Apis mellifera* L.) be stimulated by scent to revisit past-profitable forage sites? *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **191**(12): 1115–1120. doi:10.1007/s00359-005-0033-1.



- Benjamin, A., and McCallum, B. 2008. A world without bees. Guardian Books, London.
- Bergström, G., and Tengö, J. 1974. Studies on natural odoriferous compounds. IX. Farnesyl esters and geranyl esters as main volatile constituents of secretion from dufour's gland in six species of *Andrena* (Hymenoptera, Apidae). *Chem. Scr.* **5**: 28–38.
- Bergström, G., and Tengö, J. 1978. Linalool in mandibular gland secretion of *Colletes* bees (Hymenoptera: Apoidea). *J. Chem. Ecol.* **4**: 447–449. doi:10.1007/BF00989500.
- Bergström, G., Appelgren, M., Borg-Karlson, A.-K., Groth, I., Strömberg, S., and Strömberg, S. 1980. Studies on natural odoriferous compounds. XXII. Techniques for the isolation/enrichment of plant volatiles in the analyses of *Ophrys* orchids (Orchidaceae). *Chem. Scr.* **16**: 173–180.
- Bergström, G., Dobson, H.E.M., and Groth, I. 1995. Spatial fragrance patterns within the flowers of *Ranunculus acris* (Ranunculaceae). *Plant Syst. Evol.* **195**(3–4): 221–242. doi:10.1007/BF00989298.
- Bhagavan, S., Benatar, S., Cobey, S., and Smith, B.H. 1994. Effect of genotype but not of age or caste on olfactory learning performance in the honey bee, *Apis mellifera*. *Anim. Behav.* **48**(6): 1357–1369. doi:10.1006/anbe.1994.1372.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., and Kunin, W.E. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* (Washington, D.C.), **313**(5785): 351–354. doi:10.1126/science.1127863. PMID:16857940.
- Bischoff, I., Feltgen, K., and Breckner, D. 2003. Foraging strategy and pollen preferences of *Andrena vaga* (Panzer) and *Colletes cunicularius* (L.) (Hymenoptera: Apidae). *J. Hym. Res.* **12**: 220–237.
- Blanco, M.A., and Barboza, G. 2005. Pseudocopulatory pollination in *Lepanthes* (Orchidaceae: Pleurothallidinae) by fungus gnats. *Ann. Bot. (Lond.)*, **95**(5): 763–772. doi:10.1093/aob/mci090.
- Blight, M.M., Le Métayer, M., Pham-Delègue, M.-H., Pickett, J.A., Marion-Poll, F., and Wadhams, L.J. 1997. Identification of floral volatiles involved in recognition of oilseed rape flowers, *Brassica napus*, by honeybees, *Apis mellifera*. *J. Chem. Ecol.* **23**(7): 1715–1727. doi:10.1023/B:JOEC.0000006446.21160.c1.
- Blum, M.S. 1966. Chemical releasers of social behavior. VIII. Central in mandibular gland secretion of *Lestrimelitta limao* (Hymenoptera: Apoidea: Melittidae). *Ann. Entomol. Soc. Am.* **59**: 962–964.
- Blum, M.S. 1985. Fundamentals of insect physiology. John Wiley, New York.
- Bogdany, F.J. 1978. Linking of learning signals in honeybee orientation. *Behav. Ecol. Sociobiol.* **3**(4): 323–336. doi:10.1007/BF00303198.
- Bogdany, F.J., and Taber, S., III. 1979. Significance of odor for bees orienting across a canyon. *Apidologie*, **10**(1): 55–62. doi:10.1051/apido:19790107.
- Bolwig, N. 1954. The role of scent as a nectar guide for honeybees on flowers and an observation on the effect of colour and recruits. *Br. J. Anim. Behav.* **2**(3): 81–83. doi:10.1016/S0950-5601(54)80042-6.
- Bonora, A., Botta, B., Menziani-Andreoli, E., and Bruni, A. 1988. Organ-specific distribution and accumulation of protoanemonin in *Ranunculus ficaria* L. *Biochem. Physiol. Pflanz.* **183**: 451–455.
- Boren, R.B., Parker, R.L., and Sorensen, E.L. 1962. Foraging behavior of honey bees on selected alfalfa clones. *Crop Sci.* **2**: 185–188.
- Borg-Karlson, A.-K. 1990. Chemical and ethological studies of pollination in the genus *Ophrys* (Orchidaceae). *Phytochemistry*, **29**(5): 1359–1387. doi:10.1016/0031-9422(90)80086-V.
- Borg-Karlson, A.-K., and Groth, I. 1986. Volatiles from the flowers of four species in the sections Arachnitiformes and Araniferae of the genus *Ophrys* as insect mimetic attractants. *Phytochemistry*, **25**(6): 1297–1299. doi:10.1016/S0031-9422(00)81276-5.
- Borg-Karlson, A.-K., and Tengö, J. 1986. Odor mimetism? Key substances in *Ophrys lutea*–*Andrena* pollination relationship (Orchidaceae: Andrenidae). *J. Chem. Ecol.* **12**(9): 1927–1941. doi:10.1007/BF01041856.
- Borg-Karlson, A.-K., Bergström, G., and Groth, I. 1985. I. Volatile compounds of *Ophrys lutea* and *O. fusca* as insect mimetic attractants/excitants. *Chem. Scr.* **25**: 283–294.
- Borg-Karlson, A.K., Unelius, C.R., Valterová, I., and Nilsson, L.A. 1996. Floral fragrance chemistry in the early flowering shrub *Daphne mezereum*. *Phytochemistry*, **41**(6): 1477–1483. doi:10.1016/0031-9422(95)00801-2.
- Borg-Karlson, A.-K., Tengö, J., Valterová, I., Unelius, C.R., Taghizadeh, T., Tolasch, T., and Francke, W. 2003. (S)-(+)-Linalool, a mate attractant pheromone component in the bee *Colletes cunicularius*. *J. Chem. Ecol.* **29**(1): 1–14. doi:10.1023/A:1021964210877. PMID:12647849.
- Bower, C.C. 1996. Demonstration of pollinator-mediated reproductive isolation in sexually deceptive species of *Chiloglottis* (Orchidaceae: Caladeniinae). *Aust. J. Bot.* **44**(1): 15–33. doi:10.1071/BT9960015.
- Bower, C.C. 2006. Specific pollinators reveal a cryptic taxon in the bird orchid, *Chiloglottis valida sensu lato* (Orchidaceae), in south-eastern Australia. *Aust. J. Bot.* **54**(1): 53–64. doi:10.1071/BT05043.
- Buchbauer, G., Jirovetz, L., Wasicky, M., and Nikiforov, A. 1993. Headspace and essential oil analysis of apple flowers. *J. Agric. Food Chem.* **41**(1): 116–118. doi:10.1021/jf00025a025.
- Buchmann, S.L. 1983. Buzz pollination in angiosperms. In *Handbook of experimental pollination biology*. Edited by C.E. Ones and R.J. Little. Academic Press, New York. pp. 73–113.
- Buchmann, S.L., and Nabhan, G.P. 1996. The forgotten pollinators. Island Press, Washington, D.C.
- Burger, H., Dötterl, S., and Ayasse, M. 2009. Importance of olfactory and visual cues of *Echium* for host-plant finding of the oligolectic bee *Osmia adunca* (Megachilidae). *Mitt. Dtsch. Ges. Allg. Angew. Entomol.* **6**: 163–166.
- Burger, H., Dötterl, S., and Ayasse, M. 2010. Host plant finding and recognition by visual and olfactory floral cues in an oligolectic bee. *Funct. Ecol.* In press. doi:10.1111/j.1365-2435.2010.01744.x.
- Butler, C.G. 1951. The importance of perfume in the discovery of food by the worker honeybee (*Apis mellifera* L.). *Proc. R. Soc. Lond. B Biol. Sci.* **138**(892): 403–413. doi:10.1098/rspb.1951.0032.
- Butler, C.G., and Fairey, E.M. 1964. Pheromones of the honeybee: biological studies of the mandibular gland secretion of the queen. *J. Apic. Res.* **3**: 65–76.
- Cameron, S.A., Hines, H.M., and Williams, P.H. 2007. A comprehensive phylogeny of the bumble bees (*Bombus*). *Biol. J. Linn. Soc.* **91**(1): 161–188. doi:10.1111/j.1095-8312.2007.00784.x.
- 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*. Edited by N.M. Waser and J. Ollerton. University of Chicago Press, Chicago. pp. 99–122.
- Cane, J.H., and Tengö, J. 1981. Pheromonal cues direct mate seeking behaviour of male *Colletes cunicularius* (Hymenoptera, Colletidae). *J. Chem. Ecol.* **7**(2): 427–436. doi:10.1007/BF00995765.
- Cane, J.H., Snelling, R.R., and Kervin, L.J. 1997. A new monolec-

- tic coastal bee, *Hesperapis oraria* Snelling and Stage (Hymenoptera: Melittidae), with a review of desert and neotropical disjunctives in the southeastern U.S. *J. Kans. Entomol. Soc.* **69**: 238–247.
- Cane, J.H., Minckley, R.L., and Kervin, L.J. 2000. Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. *J. Kans. Entomol. Soc.* **73**: 225–231.
- Canto, A., Herrera, C.M., Medrano, M., Pérez, R., and García, I.M. 2008. Pollinator foraging modifies nectar sugar composition in *Helleborus foetidus* (Ranunculaceae): an experimental test. *Am. J. Bot.* **95**(3): 315–320. doi:10.3732/ajb.95.3.315.
- Chaffiol, A., Laloï, D., and Pham-Delègue, M.H. 2005. Prior classical olfactory conditioning improves odour-cued flight orientation of honey bees in a wind tunnel. *J. Exp. Biol.* **208**(19): 3731–3737. doi:10.1242/jeb.01796. PMID:16169950.
- Chittka, L., and Raine, N.E. 2006. Recognition of flowers by pollinators. *Curr. Opin. Plant Biol.* **9**(4): 428–435. doi:10.1016/j.pbi.2006.05.002. PMID:16713328.
- Chittka, L., Spaethe, J., Schmidt, A., and Hickelsberger, A. 2001. Adaptation, constraint, and chance in the evolution of flower color and pollinator color vision. *In* Cognitive ecology of pollination—animal behavior and floral evolution. Edited by L. Chittka and J.D. Thomson. Cambridge University Press, Cambridge, UK. pp. 106–126
- Chung, H.-G., Bang, J.-K., Kim, G.-S., Seong, N.-S., and Kim, S.-M. 2003. Identification of the major volatile components from different plant organs of *Foeniculum vulgare* Mill. *Korean J. Med. Crop Sci.* **11**: 274–278.
- Ciotek, L., Giorgis, P., Benitez-Vieyra, S., and Cocucci, A.A. 2006. First confirmed case of pseudocopulation in terrestrial orchids of South America: pollination of *Geoblasta pennicillata* (Orchidaceae) by *Campsomeris bistrimaculata* (Hymenoptera, Scoliidae). *Flora*, **201**(5): 365–369. doi:10.1016/j.flora.2005.07.012.
- Coleman, E. 1928. Pollination of *Cryptostylis leptochila*. *Vict. Nat.* (Blackburn), **44**: 333–340.
- Colla, S.R., and Packer, L. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. *Biodivers. Conserv.* **17**(6): 1379–1391. doi:10.1007/s10531-008-9340-5.
- Cook, S.M., Sandoz, J.C., Martin, A.P., Murray, D.A., Poppy, G.M., and Williams, I.H. 2005. Could learning of pollen odours by honey bees (*Apis mellifera*) play a role in their foraging behaviour? *Physiol. Entomol.* **30**(2): 164–174. doi:10.1111/j.1365-3032.2005.00445.x.
- Cortis, P., Vereecken, N.J., Schiestl, F.P., Barone Lumaga, M.R., Scrugli, A., and Cozzolino, S. 2009. Pollinator convergence and the nature of species' boundaries in sympatric Sardinian *Ophrys* (Orchidaceae). *Ann. Bot. (Lond.)*, **104**(3): 497–506. doi:10.1093/aob/mcn219.
- Cox-Foster, D.L., Conlan, S., Holmes, E.C., Palacios, G., Evans, J.D., Moran, N.A., Quan, P.-L., Briese, T., Hornig, M., Geiser, D.M., Martinson, V., vanEngelsdorp, D., Kalkstein, A.L., Drysdale, A., Hui, J., Zhai, J., Cui, L., Hutchison, S.K., Simons, J.F., Egholm, M., Pettis, J.S., and Lipkin, W.I. 2007. A metagenomic survey of microbes in honey bee colony collapse disorder. *Science* (Washington, D.C.), **318**(5848): 283–287. doi:10.1126/science.1146498. PMID:17823314.
- Crowhurst, R.N., Gleave, A.P., MacRae, E.A., Ampomah-Dwamena, C., Atkinson, R.G., Beuning, L.L., Bulley, S.M., Chagne, D., Marsh, K.B., Matich, A.J., Montefiori, M., Newcomb, R.D., Schaffer, R.J., Usadel, B., Allan, A.C., Boldingh, H.L., Bowen, J.H., Davy, M.W., Eckloff, R., Ferguson, A.R., Fraser, L.G., Gera, E., Hellens, R.P., Janssen, B.J., Klages, K., Lo, K.R., MacDiarmid, R.M., Nain, B., McNeilage, M.A., Rassam, M., Richardson, A.C., Rikkerink, E.H.A., Ross, G.S., Schröder, R., Snowden, K.C., Souleyre, E.J.F., Templeton, M.D., Walton, E.F., Wang, D., Wang, M.Y., Wang, Y.Y., Wood, M., Wu, R.M., Yauk, Y.K., and Laing, W.A. 2008. Analysis of expressed sequence tags from *Actinidia*: applications of a cross species EST database for gene discovery in the areas of flavor, health, color and ripening. *BMC Genomics*, **9**(1): 351. doi:10.1186/1471-2164-9-351. PMID:18655731.
- Currie, R.W., Winston, M.L., Slessor, K.N., and Mayer, D.F. 1992a. Effect of synthetic queen mandibular pheromone sprays on pollination of fruit crops by honey bees (Hymenoptera: Apidae). *J. Econ. Entomol.* **85**: 1293–1299.
- Currie, R.W., Winston, M.L., and Slessor, K.N. 1992b. Effect of synthetic queen mandibular pheromone sprays on honey bee (Hymenoptera: Apidae) pollination of berry crops. *J. Econ. Entomol.* **85**: 1300–1306.
- Dafni, A. 1984. Mimicry and deception in pollination. *Annu. Rev. Ecol. Syst.* **15**(1): 259–278. doi:10.1146/annurev.es.15.110184.001355.
- Dafni, A., Lehrer, M., and Kevan, P.G. 1997. Spatial flower parameters and insect spatial vision. *Biol. Rev. Camb. Philos. Soc.* **72**(2): 239–282. doi:10.1017/S0006323196005002.
- Daily, G.C. 1997. Nature's services: social dependence on natural ecosystems. Island Press, Washington, D.C.
- Danforth, B.N., and Ascher, J. 1999. Flowers and insect evolution. *Science* (Washington, D.C.), **283**(5399): 143. doi:10.1126/science.283.5399.143a.
- Danforth, B.N., Conway, L., and Ji, S.Q. 2003. Phylogeny of eusocial *Lasios glossum* reveals multiple losses of eusociality within a primitively eusocial clade of bees (Hymenoptera: Halictidae). *Syst. Biol.* **52**(1): 23–36. doi:10.1080/10635150390132687. PMID:12554437.
- Danforth, B.N., Fang, J., and Sipes, S.D. 2006a. Analysis of family-level relationships in bees (Hymenoptera: Apiformes) using 28S and two previously unexplored nuclear genes: CAD and RNA polymerase II. *Mol. Phylogenet. Evol.* **39**(2): 358–372. doi:10.1016/j.ympev.2005.09.022. PMID:16412668.
- Danforth, B.N., Sipes, S.D., Fang, J., and Brady, S.G. 2006b. The history of early bee diversification based on five genes plus morphology. *Proc. Natl. Acad. Sci. U.S.A.* **103**(41): 15118–15123. doi:10.1073/pnas.0604033103. PMID:17015826.
- Darwin, C. 1877. The various contrivances by which orchids are fertilised by insects. 2nd ed. John Murray, London.
- Delforge, P. 2006. Orchids of Europe, North Africa and the Middle East. Timber Press, Portland, Oregon.
- de L. Nogueira, P.C., Bittrich, V., Shepherd, G.J., Lopes, A.V., and Marsaioli, A.J. 2001. The ecological and taxonomic importance of flower volatiles of *Clusia* species (Guttiferae). *Phytochemistry*, **56**(5): 443–452. doi:10.1016/S0031-9422(00)00213-2. PMID:11261577.
- Devys, M., and Barbier, M. 1965. Cholesterol, principal sterol of the pollen of a composite, the porcellanoid *Hypochoeris radicata*. *C.R. Seances Acad. Sci. Ser. D*, **261**: 4901–4903.
- Devys, M., and Barbier, M. 1966. Sur le cholestérol du pollen de la porcelle *Hypochoeris radicata*. *Phytochemistry*, **5**(5): 1031–1033. doi:10.1016/S0031-9422(00)82802-2.
- Díaz, P.C., Grüter, C., and Farina, W.M. 2007. Floral scents affect the distribution of hive bees around dancers. *Behav. Ecol. Sociobiol.* **61**(10): 1589–1597. doi:10.1007/s00265-007-0391-5.
- Didry, N., Dubreuil, L., and Pinkas, M. 1991. Activité antibactérienne des vapeurs de protoanémone [Antibacterial activity of vapors of protoanemone]. *Pharmazie*, **46**(7): 546–547. [In French.] PMID:1784621.
- Dobson, H.E.M. 1987. Role of flower and pollen aromas in host-

- plant recognition by solitary bees. *Oecologia* (Berl.), **72**(4): 618–623. doi:10.1007/BF00378991.
- Dobson, H.E.M. 1994. Floral volatiles in insect biology. *In* Insect-plant interactions. Edited by E.A. Bernays. CRC Press, London. pp. 47–81.
- Dobson, H.E.M. 2006. Relationship between floral fragrance composition and type of pollinator. *In* Biology of floral scent. Edited by N. Dudareva and E. Pichersky. CRC Press, Boca Raton, Fla. pp. 147–198.
- Dobson, H.E.M., and Ayasse, M. 2000. Does larval pollen diet influence host-flower selection in solitary bees? *Am. J. Bot.* **87**(6): 42.
- Dobson, H.E.M., and Bergström, G. 2000. The ecology and evolution of pollen odor. *Plant Syst. Evol.* **222**(1–4): 63–87. doi:10.1007/BF00984096.
- Dobson, H.E.M., Bergström, G., and Groth, I. 1990. Differences in fragrance chemistry between flower parts of *Rosa rugosa* Thunb. (Rosaceae). *Isr. J. Bot.* **39**: 143–156.
- Dobson, H.E.M., Groth, I., and Bergström, G. 1996. Pollen advertisement: chemical contrasts between whole-flower and pollen odors. *Am. J. Bot.* **83**(7): 877–885. doi:10.2307/2446264.
- Dobson, H.E.M., Danielson, E.M., and van Wesep, I.D. 1999. Pollen odor chemicals as modulators of bumble bee foraging on *Rosa rugosa* Thunb. (Rosaceae). *Plant Species Biol.* **14**(2): 153–166. doi:10.1046/j.1442-1984.1999.00020.x.
- Dod, D.D. 1976. *Oncidium henekenii*: bee orchid pollinated by bee. *Am. Orchid Soc. Bull.* **45**: 792–794.
- Dodson, C.H., Dressler, R.L., Hills, H.G., Adams, R.M., and Williams, N.H. 1969. Biologically active compounds in orchid fragrances. *Science* (Washington, D.C.), **164**(3885): 1243–1249. doi:10.1126/science.164.3885.1243. PMID:17772561.
- Dornhaus, A., and Chittka, L. 1999. Evolutionary origins of bee dances. *Nature* (London), **401**(6748): 38. doi:10.1038/43372.
- Dornhaus, A., Brockman, A., and Chittka, L. 2003. Bumble bees alert to food with pheromone from tergal gland. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **189**: 47–51.
- Dötterl, S. 2008. Antennal responses of an oligolectic bee and its cleptoparasite to plant volatiles. *Plant Signal. Behav.* **3**(5): 296–297. PMID:19841650.
- Dötterl, S., I, and Jürgens, A. 2005. Spatial fragrance patterns in flowers of *Silene latifolia*: lilac compounds as olfactory nectar guides? *Plant Syst. Evol.* **255**(1–2): 99–109. doi:10.1007/s00606-005-0344-2.
- Dötterl, S., and Schäffler, I. 2007. Flower scent of floral oil-producing *Lysimachia punctata* as attractant for the oil-bee *Macropis fulvipes*. *J. Chem. Ecol.* **33**(2): 441–445. doi:10.1007/s10886-006-0237-2. PMID:17151908.
- Dötterl, S., Füssel, U., Jürgens, A., and Aas, G. 2005. 1,4-Dimethoxybenzene, a floral scent compound in willows that attracts an oligolectic bee. *J. Chem. Ecol.* **31**(12): 2993–2998. doi:10.1007/s10886-005-9152-y. PMID:16258713.
- Dötterl, S., Jürgens, A., Seifert, K., Laube, T., Weissbecker, B., and Schütz, S. 2006. Nursery pollination by a moth in *Silene latifolia*: the role of odours in eliciting antennal and behavioural responses. *New Phytol.* **169**(4): 707–718. doi:10.1111/j.1469-8137.2005.01509.x. PMID:16441752.
- Dudareva, N., and Pichersky, E. 2006. Floral scent metabolic pathways: their regulation and evolution. *In* Biology of floral scent. Edited by N. Dudareva and E. Pichersky. CRC Press, Boca Raton, Fla. pp. 55–78.
- Eickwort, G.C., and Ginsberg, H.S. 1980. Foraging and mating behaviour in Apoidea. *Annu. Rev. Entomol.* **25**(1): 421–446. doi:10.1146/annurev.en.25.010180.002225.
- Elmstrom, G.W., and Maynard, D.N. 1991. Bee-Scent<sup>®</sup> for improved pollination of watermelon. *HortScience*, **26**: 488–489.
- Eltz, T., Roubik, D.W., and Whitten, M.W. 2003. Fragrances, male display and mating behaviour of *Euglossa hemichlora*: a flight cage experiment. *Physiol. Entomol.* **28**(4): 251–260. doi:10.1111/j.1365-3032.2003.00340.x.
- Eltz, T., Sager, A., and Lunau, K. 2005. Juggling with volatiles: exposure of perfumes by displaying male orchid bees. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **191**(7): 575–581. doi:10.1007/s00359-005-0603-2.
- Eltz, T., Zimmermann, Y., Pfeiffer, C., Pech, J.R., Twele, R., Francke, W., Quezada-Euan, J.J.G., and Lunau, K. 2008. An olfactory shift is associated with male perfume differentiation and species divergence in orchid bees. *Curr. Biol.* **18**(23): 1844–1848. doi:10.1016/j.cub.2008.10.049. PMID:19062287.
- Engel, M.S. 2000. A new interpretation of the oldest fossil bee (Hymenoptera: Apidae). *Am. Mus. Novit.* **3296**(1): 1–11. doi:10.1206/0003-0082(2000)3296<0001:ANIOTO>2.0.CO;2.
- Facknath, S., and Wright, D.J. 2007. Is host selection in leafminer adults influenced by pre-imaginal or early adult experience? *J. Appl. Entomol.* **131**(8): 505–512. doi:10.1111/j.1439-0418.2007.01195.x.
- Farina, W.M., Grüter, C., Acosta, L., and Mc Cabe, S. 2007. Honeybees learn floral odors while receiving nectar from foragers within the hive. *Naturwissenschaften*, **94**(1): 55–60. doi:10.1007/s00114-006-0157-3. PMID:17021915.
- Ferrari, M.J., Stephenson, A.G., Mescher, M.C., and De Moraes, C.M. 2006. Inbreeding effects on blossom volatiles in *Cucurbita pepo* subsp. *texana* (Cucurbitaceae). *Am. J. Bot.* **93**(12): 1768–1774. doi:10.3732/ajb.93.12.1768.
- Fitzpatrick, U., Murray, T.E., Paxton, R.J., Breen, J., Cotton, D., Santorum, V., and Brown, M.J.F. 2007. Rarity and decline in bumblebees—a test of causes and correlates in the Irish fauna. *Biol. Conserv.* **136**(2): 185–194. doi:10.1016/j.biocon.2006.11.012.
- Free, J.B. 1969. Influence of the odour of a honeybee colony's food stores on the behaviour of its foragers. *Nature* (London), **222**(5195): 778. doi:10.1038/222778a0.
- Füssel, U., Dötterl, S., Jürgens, A., and Aas, G. 2007. Inter- and intraspecific variation in floral scent in the genus *Salix* and its implication for pollination. *J. Chem. Ecol.* **33**(4): 749–765. doi:10.1007/s10886-007-9257-6. PMID:17334921.
- Gallai, N., Salles, J.-M., Settele, J., and Vaissière, B.E. 2009. Economic valuation of the vulnerability of world agriculture confronted to pollinator decline. *Ecol. Econ.* **68**(3): 810–821. doi:10.1016/j.ecolecon.2008.06.014.
- Gary, N.E. 1962. Chemical mating attractants in queen honey bee. *Science* (Washington, D.C.), **136**(3518): 773–774. doi:10.1126/science.136.3518.773. PMID:17752107.
- Gegear, R.J., and Lavery, T.M. 2001. The effect of variation among floral traits on the flower constancy of pollinators. *In* Cognitive ecology of pollination—animal behavior and floral evolution. Edited by L. Chittka and J.D. Thomson. Cambridge University Press, Cambridge, UK. pp. 1–20.
- Getz, W.M., and Smith, K.B. 1987. Olfactory sensitivity and discrimination of mixtures in the honeybee *Apis mellifera*. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **160**(2): 239–245. doi:10.1007/BF00609729.
- Giurfa, M., and Lehrer, M. 2001. Honeybee vision and floral displays: from detection to close-up recognition. *In* Cognitive ecology of pollination—animal behavior and floral evolution. Edited by L. Chittka, and J.D. Thomson. Cambridge University Press, Cambridge, UK. pp. 61–82.
- Giurfa, M., Vorobyev, M., Kevan, P., and Menzel, R. 1996. Detection of coloured stimuli by honeybees: minimum visual angles and receptor specific contrasts. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **178**: 699–709.



- Gögler, J., Stökl, J., Sramkova, A., Twele, R., Francke, W., Cozzolino, S., Cortis, P., Scrugli, A., and Ayasse, M. 2009. Ménage à trois—two endemic species of deceptive orchids and one pollinator species. *Evolution*, **63**(9): 2222–2234. doi:10.1111/j.1558-5646.2009.00712.x. PMID:19473395.
- Goulson, D., Lye, G.C., and Darvill, B. 2008. Decline and conservation of bumble bees. *Annu. Rev. Entomol.* **53**(1): 191–208. doi:10.1146/annurev.ento.53.103106.093454. PMID:17803456.
- Goyret, J., Markwell, P.M., and Raguso, R.A. 2008. Context- and scale-dependent effects of floral CO<sub>2</sub> on nectar foraging by *Manduca sexta*. *Proc. Natl. Acad. Sci. U.S.A.* **105**(12): 4565–4570. doi:10.1073/pnas.0708629105. PMID:18212123.
- Grimaldi, D.A. 1999. The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Ann. Mo. Bot. Gard.* **86**(2): 373–406. doi:10.2307/2666181.
- Grüter, C., Acosta, L.E., and Farina, W.M. 2006. Propagation of olfactory information within the honeybee hive. *Behav. Ecol. Sociobiol.* **60**(5): 707–715. doi:10.1007/s00265-006-0214-0.
- Grüter, C., Balbuena, M.S., and Farina, W.M. 2008. Informational conflicts created by the waggle dance. *Proc. R. Soc. Lond. B Biol. Sci.* **275**(1640): 1321–1327. doi:10.1098/rspb.2008.0186.
- Guerenstein, P.G., and Hildebrand, J.G. 2008. Roles and effects of environmental carbon dioxide in insect life. *Annu. Rev. Entomol.* **53**(1): 161–178. doi:10.1146/annurev.ento.53.103106.093402. PMID:17803457.
- Guerenstein, P.G., A Yopez, E., van Haren, J., Williams, D.G., and Hildebrand, J.G. 2004. Floral CO<sub>2</sub> emission may indicate food abundance to nectar-feeding moths. *Naturwissenschaften*, **91**(7): 329–333. doi:10.1007/s00114-004-0532-x. PMID:15257387.
- Hamilton, D.W., Schwartz, P.H., and Townshend, B.G. 1970. Capture of bumble bees and honey bees in traps baited with lures to attract Japanese beetles. *J. Econ. Entomol.* **63**: 1443–1445.
- Hefetz, A., Batra, S.W.T., and Blum, M.S. 1979. Linalool, neral and geraniol in the mandibular glands of *Colletes* bees—an aggregation pheromone. *Cell. Mol. Life Sci.* **35**(3): 319–320. doi:10.1007/BF01964324.
- Heinrich, B., Mudge, P.R., and Deringis, P.G. 1977. Laboratory analysis of flower constancy in foraging bumblebees: *Bombus ternarius* and *B. terricola*. *Behav. Ecol. Sociobiol.* **2**(3): 247–265. doi:10.1007/BF00299738.
- Henning, J.A., and Teuber, L.R. 1992. Combined gas chromatography–electroantennogram characterization of alfalfa floral volatiles recognized by honey bees (Hymenoptera: Apidae). *J. Econ. Entomol.* **85**(1): 226–232.
- Henning, J.A., Peng, Y.-S., Montague, M.A., and Teuber, L.R. 1992. Honey bee (Hymenoptera: Apidae) behavioral response to primary alfalfa (Rosales: Fabaceae) floral volatiles. *J. Econ. Entomol.* **85**: 233–239.
- Herrera, C.M. 1996. Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. In *Floral biology: studies on floral evolution in animal-pollinated plants*. Edited by D.G. Lloyd and S.C.H. Barrett. Chapman and Hall, New York. pp. 65–87.
- Herrera, C.M. 2005. Plant generalization on pollinators: species property or local phenomenon? *Ecology*, **92**: 13–20.
- Herrera, C.M., García, I.M., and Pérez, R. 2008. Invisible floral larcenies: microbial communities degrade floral nectar of bumble bee-pollinated plants. *Ecology*, **89**(9): 2369–2376. doi:10.1890/08-0241.1. PMID:18831156.
- Higo, H.A., Winston, M.L., and Slessor, K.N. 1995. Mechanisms by which honey bee (Hymenoptera: Apidae) queen pheromone sprays enhance pollination. *Ann. Entomol. Soc. Am.* **88**: 366–373.
- Hill, P.S.M., Wells, P.H., and Wells, H. 1997. Spontaneous flower constancy and learning in honey bees as a function of colour. *Anim. Behav.* **54**(3): 615–627. doi:10.1006/anbe.1996.0467. PMID:9299046.
- Howell, A.D., and Alarcón, R. 2007. *Osmia* bees (Hymenoptera: Megachilidae) can detect nectar-rewarding flowers using olfactory cues. *Anim. Behav.* **74**(2): 199–205. doi:10.1016/j.anbehav.2006.11.012.
- Hurd, P.D., Jr., and Linsley, E.G. 1975. The principal *Larrea* bees of the southwestern United States. *Smithson. Contrib. Zool.* **193**: 1–74.
- Jakobsen, H.B., Kristjánsson, K., Rohde, B., Terkildsen, M., and Olsen, C.E. 1995. Can social bees be influenced to choose a specific feeding station by adding the scent of the station to the hive air? *J. Chem. Ecol.* **21**(11): 1635–1648. doi:10.1007/BF02033666.
- Janz, N., Nyblom, K., and Nylin, S. 2001. Evolutionary dynamics of host-plant specialization: a case study of the tribe Nymphalini. *Evolution*, **55**(4): 783–796. doi:10.1554/0014-3820(2001)055[0783:EDOHPS]2.0.CO;2. PMID:11392396.
- Janzen, D.H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science (Washington, D.C.)*, **171**(3967): 203–205. doi:10.1126/science.171.3967.203. PMID:17751330.
- Jersáková, J., Johnson, S.D., and Kindlmann, P. 2006. Mechanisms and evolution of deceptive pollination in orchids. *Biol. Rev. (Camb.)*, **81**(2): 1–17. doi:10.1017/S1464793105006986. PMID:16677433.
- Johnson, D.L. 1967. Communication among honey bees with field experience. *Anim. Behav.* **15**(4): 487–492. doi:10.1016/0003-3472(67)90048-6. PMID:6055103.
- Johnson, S.D. 2006. Pollinator-driven speciation in plants. In *Ecology and evolution of flowers*. Edited by L.D. Harder and S.C.H. Barrett. Oxford University Press, New York. pp. 295–310.
- Johnson, S.D., Peter, C.I., and Ågren, J. 2004. The effects of nectar addition on pollen removal and geitonogamy in the non-rewarding orchid *Anacamptis morio*. *Proc. R. Soc. Lond. B Biol. Sci.* **271**(1541): 803–809. doi:10.1098/rspb.2003.2659.
- Johnson, S.D., Hargreaves, A.L., and Brown, M. 2006. Dark, bitter-tasting nectar functions as a filter of flower visitors in a bird-pollinated plant. *Ecology*, **87**(11): 2709–2716. doi:10.1890/0012-9658(2006)87[2709:DBNFAA]2.0.CO;2. PMID:17168015.
- Jones, D.L. 1988. *Native orchids of Australia*. American Orchid Society, Delray Beach, Fla.
- Jürgens, A., and Dötterl, S. 2004. Chemical composition of anther volatiles in Ranunculaceae: genera-specific profiles in *Anemone*, *Aquilegia*, *Caltha*, *Pulsatilla*, *Ranunculus*, and *Trollius* species. *Am. J. Bot.* **91**(12): 1969–1980. doi:10.3732/ajb.91.12.1969.
- Kaiser, L., and De Jong, R. 1993. Multi-odour memory influenced by learning order. *Behav. Processes*, **30**(2): 175–183. doi:10.1016/0376-6357(93)90007-E.
- Kaschef, A.H. 1957. Über die Einwirkung von Duftstoffen auf die Bienen tänze. *Z. Vgl. Physiol.* **39**(5): 562–576. doi:10.1007/BF00340378.
- Keeling, C.I., Plettner, E., and Slessor, K.N. 2004. Hymenopteran semiochemicals. *Top. Curr. Chem.* **239**: 133–177. doi:10.1007/b95452.
- Kevan, P.G., and Baker, H.G. 1983. Insects as flower visitors and pollinators. *Annu. Rev. Entomol.* **28**(1): 407–453. doi:10.1146/annurev.ento.28.010183.002203.
- Kevan, P.G., and Lane, M.A. 1985. Flower petal microtexture is a tactile cue for bees. *Proc. Natl. Acad. Sci. U.S.A.* **82**(14): 4750–4752. doi:10.1073/pnas.82.14.4750. PMID:16593582.
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., and Tscharntke, T. 2007. Importance of pollinators in changing landscapes for world crops.



- Proc. R. Soc. Lond. B Biol. Sci. **274**(1608): 303–313. doi:10.1098/rspb.2006.3721.
- Knoll, F. 1930. Über Pollenkitt und Bestäubungsart. Z. Bot. **23**: 610–675.
- Knudsen, J.T., Andersson, S., and Bergman, P. 1999. Floral scent attraction in *Geonoma macrostachys*, an understory palm of the Amazonian rain forest. Oikos, **85**(3): 409–418. doi:10.2307/3546690.
- Knudsen, J.T., Eriksson, R., Gershenzon, J., and Ståhl, B. 2006. Diversity and distribution of floral scent. Bot. Rev. **72**(1): 1–120. doi:10.1663/0006-8101(2006)72[1:DADOF5]2.0.CO;2.
- Koeniger, G. 2005. The neglected gender—males in bees. Apidologie, **36**(2): 143–144. doi:10.1051/apido:2005017.
- Koltermann, R. 1969. Lern- und Vergessensprozesse bei der Honigbiene? Aufgezeigt anhand von Duftdressuren. Z. Vgl. Physiol. **63**(3): 310–334. doi:10.1007/BF00298165.
- Kremen, C., Williams, N.M., and Thorp, R.W. 2002. Crop pollination from native bees at risk from agricultural intensification. Proc. Natl. Acad. Sci. U.S.A. **99**(26): 16812–16816. doi:10.1073/pnas.262413599. PMID:12486221.
- Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P., and Thorp, R.W. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecol. Lett. **7**(11): 1109–1119. doi:10.1111/j.1461-0248.2004.00662.x.
- Kullenberg, B. 1956. Field experiments with chemical sexual attractants on Aculeate Hymenoptera males. Zool. Bidr. Upps. **31**: 253–352.
- Kullenberg, B. 1961. Studies in *Ophrys* pollination. Zool. Bidr. Upps. **34**: 1–340.
- Lacher, V. 1964. Elektrophysiologische Untersuchungen an einzelnen Rezeptoren für Geruch, Kohlendioxid, Luftfeuchtigkeit und Temperatur auf den Antennen der Arbeitsbiene und der Drohne (*Apis mellifica* L.). Z. Vgl. Physiol. **48**(6): 587–623. doi:10.1007/BF00333743.
- Ladd, T.L., and Tew, J.E. 1983. Attraction of honey bees (Hymenoptera: Apidae) to traps baited with lures for Japanese beetles (Coleoptera: Scarabaeidae). J. Econ. Entomol. **76**: 769–770.
- Ladd, T.L., McGovern, T.P., and Beroza, M. 1974. Attraction of bumble bees and honey bees to traps baited with lures for Japanese beetle. J. Econ. Entomol. **67**: 307–308.
- Laloi, D., Gallois, M., Roger, B., and Pham-Delègue, M.H. 2001. Changes with age in olfactory conditioning performance of worker honey bees (*Apis mellifera*). Apidologie, **32**(3): 231–242. doi:10.1051/apido:2001125.
- Larkin, L.L., Neff, J.L., and Simpson, B.B. 2006. Phylogeny of the *Callandrena* subgenus of *Andrena* (Hymenoptera: Andrenidae) based on mitochondrial and nuclear DNA data: polyphyly and convergent evolution. Mol. Phylogenet. Evol. **38**(2): 330–343. doi:10.1016/j.ympev.2005.10.003. PMID:16343953.
- 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**(1): 133–145. doi:10.1051/apido:2007064.
- Le Métayer, M., Marion-Poll, F., Sandoz, J.C., Pham-Delègue, M.H., Blight, M.M., Wadhams, L.J., Masson, C., and Woodcock, C.M. 1997. Effect of conditioning on discrimination of oilseed rape volatiles by the honeybee: use of a combined gas chromatography – proboscis extension behavioural assay. Chem. Senses, **22**(4): 391–398. doi:10.1093/chemse/22.4.391. PMID:9279462.
- Leong, J.M., and Thorp, R.W. 1999. Colour-coded sampling: the pan trap colour preferences of oligolectic and nonoligolectic bees associated with a vernal pool plant. Ecol. Entomol. **24**(3): 329–335. doi:10.1046/j.1365-2311.1999.00196.x.
- Lex, T. 1954. Duftmale an Blüten. Z. Vgl. Physiol. **36**(2): 212–234. doi:10.1007/BF00297747.
- Lindauer, M. 1949. Über die Einwirkung von Duft- und Geschmackstoffen sowie anderer Faktoren auf die Tänze der Bienen. Z. Vgl. Physiol. **31**(3): 348–412. doi:10.1007/BF00297951. PMID:18131263.
- Lindauer, M., and Kerr, W.E. 1960. Communication between the workers of stingless bees. Bee World, **41**: 29–71.
- Linsley, E.G. 1958. The ecology of solitary bees. Hilgardia, **27**: 543–599.
- Löken, A. 1961. *Bombus consobrinus* Dahlb., an oligolectic bumble bee (Hymenoptera, Apidae). Int. Congr. Entomol. Proc. XI, **1**: 598–603.
- Loper, G.M., Waller, G.D., and Berdel, R.L. 1974. Olfactory screening of alfalfa clones for uniform honey bee selection. Crop Sci. **14**: 120–122.
- Loughrin, J.H., Hamilton-Kemp, T.R., Andersen, R.A., and Hildebrand, D.F. 1990. Volatiles from flowers of *Nicotiana sylvestris*, *N. otophora* and *Malus × domestica*: headspace components and day/night changes in their relative concentrations. Phytochemistry, **29**(8): 2473–2477. doi:10.1016/0031-9422(90)85169-G.
- Lunau, K. 1991. Innate flower recognition in bumblebees (*Bombus terrestris*, *B. lucorum*; Apidae): optical signals from stamens as landing reaction releasers. Ethology, **88**(3): 203–214. doi:10.1111/j.1439-0310.1991.tb00275.x.
- Lunau, K. 1992a. Evolutionary aspects of perfume collection in male euglossine bees (Hymenoptera) and of nest deception in bee-pollinated flowers. Chemoecology, **3**(2): 65–73. doi:10.1007/BF01245884.
- Lunau, K. 1992b. Innate recognition of flowers by bumble bees: orientation of antennae to visual stamen signals. Can. J. Zool. **70**(11): 2139–2144. doi:10.1139/z92-288.
- Mahé, G. 2007. Comportement de butinage de *Bombus gerstaeckeri* (Hymenoptera, Apidae) sur *Delphinium dubium* (Rouy & Foucaud) (Ranunculaceae) dans les Alpes Françaises. OSMIA, **1**: 16–19.
- Malyshev, S.I. 1968. Genesis of the Hymenoptera and phases of their evolution. Methuen, London.
- Mant, J., Brändli, C., Vereecken, N.J., Schulz, C.M., Francke, W., and Schiestl, F.P. 2005a. Cuticular hydrocarbons as sex pheromone of the bee *Colletes cunicularius* and the key to its mimicry by the sexually deceptive orchid, *Ophrys exaltata*. J. Chem. Ecol. **31**(8): 1765–1787. doi:10.1007/s10886-005-5926-5. PMID:16222807.
- Mant, J.G., Peakall, R., and Schiestl, F.P. 2005b. Does selection on floral odor promote differentiation among populations and species of the sexually deceptive orchid genus *Ophrys*? Evolution, **59**(7): 1449–1463. PMID:16153031.
- Mattila, H.R., and Seeley, T.D. 2007. Genetic diversity in honey bee colonies enhances productivity and fitness. Science (Washington, D.C.), **317**(5836): 362–364. doi:10.1126/science.1143046. PMID:17641199.
- Mayr, E. 1942. Systematics and the origin of species. Columbia University Press, New York.
- McGinley, R.J. 2003. Studies of Halictinae (Apoidea: Halictidae), II: Revision of *Sphcodogastra* Ashmead, floral specialists of Onagraceae. Smithsonian Contrib. Zool. **610**: 1–55.
- Meagher, R.L. 2002. Trapping noctuid moths with synthetic floral volatile lures. Entomol. Exp. Appl. **103**(3): 219–226. doi:10.1046/j.1570-7458.2002.00977.x.
- Mena Granero, A., Egea González, F.J., Garrido Frenich, A., Guerra Sanz, J.M., and Martínez Vidal, J.L. 2004. Single step determination of fragrances in *Cucurbita* flowers by coupling headspace solid-phase microextraction low-pressure gas

- chromatography–tandem mass spectrometry. *J. Chromatogr. A*, **1045**(1–2): 173–179. doi:10.1016/j.chroma.2004.06.026. PMID: 15378892.
- Mena Granero, A., Egea González, F.J., Guerra Sanz, J.M., and Martínez Vidal, J.L. 2005a. Analysis of biogenic volatile organic compounds in zucchini flowers: identification of scent sources. *J. Chem. Ecol.* **31**(10): 2309–2322. doi:10.1007/s10886-005-7103-2.
- Mena Granero, A.M., Sanz, J.M.G., Gonzalez, F.J.E., Vidal, J.L.M., Dornhaus, A., Ghani, J., Serrano, A.R., and Chittka, L. 2005b. Chemical compounds of the foraging recruitment pheromone in bumblebees. *Naturwissenschaften*, **92**(8): 371–374. doi:10.1007/s00114-005-0002-0. PMID:16049691.
- Menken, S.B.J., and Roessingh, P. 1998. Evolution of insect–plant associations: sensory perception and receptor modifications direct food specialization and host shifts in phytophagous insects. *In* *Endless forms: species and speciation*. Edited by D.J. Howard and S.H. Berlocher. Oxford University Press, New York. pp. 145–156.
- Menzel, R. 1985. Learning in honey bees in an ecological and behavioral context. *In* *Experimental behavioral ecology and socio-biology*. Edited by B. Hölldobler and M. Lindauer. Gustav Fischer Verlag, Stuttgart, Germany. pp. 55–74.
- Menzel, R., Erber, J., and Masuhr, T. 1974. Learning and memory in the honeybee. *In* *Experimental analysis of insect behaviour*. Edited by L.B. Browne. Springer-Verlag, Berlin. pp. 195–217.
- Michener, C.D. 1944. Comparative external morphology, phylogeny, and a classification of the bees. *Bull. Am. Mus. Nat. Hist.* **82**: 151–326.
- Michener, C.D. 1981. Classification of the bee family Melittidae with a review of species of Meganomiinae. *Contrib. Am. Entomol. Inst.* **18**: 1–135.
- Michener, C.D. 2007. *The bees of the World*. 2nd ed. Johns Hopkins University Press, Baltimore, Md.
- Michener, C.D., and Grimaldi, D.A. 1988. The oldest fossil bee: Apoid history, evolutionary stasis, and antiquity of social behavior. *Proc. Natl. Acad. Sci. U.S.A.* **85**(17): 6424–6426. doi:10.1073/pnas.85.17.6424. PMID:16593976.
- Michez, D., and Patiny, S. 2005. World revision of the oil-collecting bee genus *Macropis* Panzer 1809 (Hymenoptera, Apoidea, Melittidae) with a description of a new species from Laos. *Ann. Soc. Entomol. Fr.* **41**: 15–28.
- Michez, D., Terzö, M., and Rasmont, P. 2004. Phylogénie, biogéographie et choix floraux des abeilles oligolectiques du genre *Dasygoda* Latreille 1802 (Hymenoptera, Apoidea, Melittidae). *Ann. Soc. Entomol. Fr.* **40**: 421–435.
- Michez, D., Patiny, S., Rasmont, P., Timmermann, K., and Vereecken, N.J. 2008. Phylogeny and host-plant evolution in Melittidae *s.l.* (Hymenoptera: Apoidea). *Apidologie*, **39**(1): 146–162. doi:10.1051/apido:2007048.
- Minckley, R.L., and Roulston, T.H. 2006. Incidental mutualisms and pollen specialization among bees. *In* *Plant–pollinator interactions: from generalization to specialization*. Edited by N.M. Waser and J. Ollerton. The University of Chicago Press, Chicago. pp. 69–98.
- Mitter, C., and Farrell, B. 1991. Macroevolutionary aspects of insect–plant relationships. *In* *Insect–plant interactions* Edited by E.A. Bernays. CRC Press, Boca Raton, Fla. pp. 35–78.
- Molet, M., Chittka, L., and Raine, N.E. 2009. How floral odours are learned inside the bumblebee (*Bombus terrestris*) nest. *Naturwissenschaften*, **96**(2): 213–219. doi:10.1007/s00114-008-0465-x. PMID:18949450.
- Moretti, M., de Bello, F., Roberts, S.P.M., and Potts, S.G. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *J. Anim. Ecol.* **78**(1): 98–108. doi:10.1111/j.1365-2656.2008.01462.x. PMID:18705629.
- Morse, G.E., and Farrell, B.D. 2005. Ecological and evolutionary diversification of the seed beetle genus *Stator* (Coleoptera: Chrysomelidae: Bruchinae). *Evolution*, **59**(6): 1315–1333. PMID:16050108.
- Müller, A. 1996. Host-plant specialization in western Palearctic anthidiine bees (Hymenoptera: Apoidea: Megachilidae). *Ecol. Monogr.* **66**(2): 235–257. doi:10.2307/2963476.
- Müller, A., and Kuhlmann, M. 2008. Pollen hosts of western palearctic bees of the genus *Colletes* (Hymenoptera: Colletidae): the Asteraceae paradox. *Biol. J. Linn. Soc.* **95**(4): 719–733. doi:10.1111/j.1095-8312.2008.01113.x.
- Müller, A., Krebs, A., and Amiet, F. 1997. *Bienen—Mitteleuropäische Gattungen, Lebensweise, Beobachtung*. NaturBuch Verlag, Augsburg, Germany.
- Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C., and Dorn, S. 2006. Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee–flower relationships. *Biol. Conserv.* **130**(4): 604–615. doi:10.1016/j.biocon.2006.01.023.
- Neff, J.L. 2003. The Passiflora bee. *Passiflora*, **13**: 7–9.
- Neff, J.L., and Rozen, J.G., Jr. 1995. Foraging and nesting biology of the bee *Anthemurgus passiflorae* (Hymenoptera: Apoidea), descriptions of its immature stages, and observations on its floral host (Passifloraceae). *Am. Mus. Novit.* **3138**: 1–19.
- Niklas, J., Söderlind, L., and Sören, N. 2009. No effect of larval experience on adult host preferences in *Polygonia c-album* (Lepidoptera: Nymphalidae): on the persistence of Hopkins' host selection principle. *Ecol. Entomol.* **34**(1): 50–57. doi:10.1111/j.1365-2311.2008.01041.x.
- Nosil, P. 2002. Transition rates between specialization and generalization in phytophagous insects. *Evolution*, **56**(8): 1701–1706. PMID:12353763.
- Nosil, P., and Mooers, A.Ø. 2005. Testing hypotheses about ecological specialization using phylogenetic trees. *Evolution*, **59**(10): 2256–2263. PMID:16405168.
- Ollerton, J. 1996. Reconciling ecological processes with phylogenetic patterns: the apparent paradox of plant–pollinator systems. *J. Ecol.* **84**(5): 767–769. doi:10.2307/2261338.
- Ômura, H., Honda, K., and Hayashi, N. 1999. Chemical and chromatic bases for preferential visiting by the cabbage butterfly, *Pieris rapae*, to rape flowers. *J. Chem. Ecol.* **25**(8): 1895–1906. doi:10.1023/A:1020990018111.
- Paldi, N. 2004. Method of enhancing entomophilous. US Patent No. 2004/0078847 A1.
- Patiny, S., Michez, D., and Danforth, B.N. 2007. Phylogenetic relationships and host-plant evolution within the basal clade of Halictidae (Hymenoptera, Apoidea). *Cladistics*, **23**: 1–15.
- Paulus, H.F. 1988. Co-evolution and unilateral adaptations in flower–pollinator systems: pollinators as pacemakers in the evolution of flowers. *Verh. Dtsch. Zool. Ges.* **81**: 25–46.
- Paulus, H.F. 2007. Wie Insekten-Männchen von Orchideenblüten getäuscht werden—Bestäubungstricks und Evolution in der mediterranen Ragwurzgattung *Ophrys*. *Denisia*, **20**: 255–294.
- Paulus, H.F., and Gack, C. 1999. Bestäubungsbiologische Untersuchungen an der Gattung *Ophrys* in der Provence (S-Frankreich), Ligurien und Toscana (NW-Italien) (Orchidaceae und Insecta, Apoidea). *J. Eur. Orch.* **31**: 347–422.
- Pauw, A. 2006. Floral syndromes accurately predict pollination by a specialized oil-collecting bee (*Rediviva peringueyi*, Melittidae) in a guild of South African orchids (Coryciinae). *Am. J. Bot.* **93**(6): 917–926. doi:10.3732/ajb.93.6.917.

- Paxton, R.J. 2005. Male mating behaviour and mating systems of bees: an overview. *Apidologie*, **36**(2): 145–156. doi:10.1051/apido:2005007.
- Peakall, R. 1990. Responses of male *Zaspilothynnus trilobatus* Turner wasps to females and the sexually deceptive orchid it pollinates. *Funct. Ecol.* **4**(2): 159–167. doi:10.2307/2389335.
- Peakall, R., and Beattie, A.J. 1996. Ecological and genetic consequences of pollination by sexual deception in the orchid *Caladenia tentaculata*. *Evolution*, **50**(6): 2207–2220. doi:10.2307/2410692.
- Peakall, R., Beattie, A.J., and James, S.H. 1987. Pseudocopulation of an orchid by male ants: a test of two hypotheses accounting for the rarity of ant pollination. *Oecologia (Berl.)*, **73**(4): 522–524. doi:10.1007/BF00379410.
- Peitsch, D., Fietz, A., Hertel, H., de Souza, J., Ventura, D.F., and Menzel, R. 1992. The spectral input systems of hymenopteran insects and their receptor-based colour vision. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **170**(1): 23–40. PMID:1573568.
- Pernal, S.F., and Currie, R.W. 2002. Discrimination and preferences for pollen-based cues by foraging honeybees, *Apis mellifera* L. *Anim. Behav.* **63**(2): 369–390. doi:10.1006/anbe.2001.1904.
- Pham-Delègue, M.H., Masson, C., Etiévant, P., and Azar, M. 1986. Selective olfactory choices of the honeybee among sunflower aromas: a study by combined olfactory conditioning and chemical analysis. *J. Chem. Ecol.* **12**(3): 781–793. doi:10.1007/BF01012110.
- Pham-Delègue, M.H., Etiévant, P., Guichard, E., and Masson, C. 1989. Sunflower volatiles involved in honeybee discrimination among genotypes and flowering stages. *J. Chem. Ecol.* **15**(1): 329–343. doi:10.1007/BF02027794.
- Pham-Delègue, M.H., Blight, M.M., Kerguelen, V., Le Métayer, M., Marion-Poll, F., Sandoz, J.C., and Wadhams, L.J. 1997. Discrimination of oilseed rape volatiles by the honeybee: combined chemical and biological approaches. *Entomol. Exp. Appl.* **83**(1): 87–92. doi:10.1046/j.1570-7458.1997.00160.x.
- Pichersky, E., and Dudareva, N. 2007. Scent engineering: toward the goal of controlling how flowers smell. *Trends Biotechnol.* **25**(3): 105–110. doi:10.1016/j.tibtech.2007.01.002. PMID:17234289.
- Pickett, J.A., Williams, I.H., Martin, A.P., and Smith, M.C. 1980. Nasonov pheromone of the honey bee, *Apis mellifera* L. (Hymenoptera: Apidae). Part I. Chemical characterization. *J. Chem. Ecol.* **6**(2): 425–434. doi:10.1007/BF01402919.
- Poinar, G.O., Jr., and Danforth, B.N. 2006. A fossil bee from Early Cretaceous Burmese amber. *Science (Washington, D.C.)*, **314**(5799): 614. doi:10.1126/science.1134103. PMID:17068254.
- Praz, C.J., Müller, A., and Dorn, S. 2008a. Specialized bees fail to develop on non-host pollen: do plants chemically protect their pollen? *Ecology*, **89**(3): 795–804. doi:10.1890/07-0751.1. PMID:18459342.
- Praz, C.J., Müller, A., and Dorn, S. 2008b. Host recognition in a pollen-specialist bee: evidence for a genetic basis. *Apidologie*, **39**(5): 547–557. doi:10.1051/apido:2008034.
- Proctor, M., and Yeo, P. 1972. *The pollination of flowers*. Taplinger Publishing Company, New York.
- Raguso, R.A. 2004. Why are some floral nectars scented? *Ecology*, **85**(6): 1486–1494. doi:10.1890/03-0410.
- Raguso, R.A. 2008. Start making scents: the challenge of integrating chemistry into pollination ecology. *Entomol. Exp. Appl.* **128**(1): 196–207. doi:10.1111/j.1570-7458.2008.00683.x.
- Reinhard, J., Srinivasan, M.V., Guez, D., and Zhang, S.W. 2004a. Floral scents induce recall of navigational and visual memories in honeybees. *J. Exp. Biol.* **207**(25): 4371–4381. doi:10.1242/jeb.01306. PMID:15557023.
- Reinhard, J., Srinivasan, M.V., and Zhang, S.W. 2004b. Olfaction: scent-triggered navigation in honeybees. *Nature (London)*, **427**(6973): 411. doi:10.1038/427411a. PMID:14749818.
- Renner, S.S. 2006. Rewardless flowers in the angiosperms and the role of insect cognition in their evolution. In *Plant–pollinator interactions: from specialization to generalization*. Edited by N.M. Waser and J. Ollerton. University of Chicago Press, Chicago. pp. 123–144.
- Ribbands, C.R. 1949. The foraging method of individual honeybees. *J. Anim. Ecol.* **18**(1): 47–66. doi:10.2307/1581.
- Ribbands, C.R. 1954. Communication between honeybees. I: The response of crop-attached bees to the scent of their crop. *Proc. R. Entomol. Soc. Lond. Ser. A. Gen. Entomol.* **29**: 141–144.
- Ricketts, T.H., Daily, G.C., Ehrlich, P.R., and Michener, C.D. 2004. Economic value of tropical forest to coffee production. *Proc. Natl. Acad. Sci. U.S.A.* **101**(34): 12579–12582. doi:10.1073/pnas.0405147101. PMID:15306689.
- Rietdorf, K., and Steidle, J.L.M. 2002. Was Hopkins right? Influence of larval and early adult experience on the olfactory response in the granary weevil *Sitophilus granarius* (Coleoptera, Curculionidae). *Physiol. Entomol.* **27**(3): 223–227. doi:10.1046/j.1365-3032.2002.00289.x.
- Robertson, C. 1925. Heterotrophic bees. *Ecology*, **6**(4): 412–436. doi:10.2307/1929107.
- Robertson, C. 1926. Revised list of oligolectic bees. *Ecology*, **7**(3): 378–380. doi:10.2307/1929320.
- Robertson, G.W., Griffiths, D.W., Woodford, J.A.T., and Birch, A.N.E. 1995. Changes in the chemical composition of volatiles released by the flowers and fruits of the red raspberry (*Rubus idaeus*) cultivar Glen Prosen. *Phytochemistry*, **38**(5): 1175–1179. doi:10.1016/0031-9422(94)00782-O.
- Roubik, D.W. 1982. Obligate necrophagy in a social bee. *Science (Washington, D.C.)*, **217**(4564): 1059–1060. doi:10.1126/science.217.4564.1059. PMID:17839343.
- Roulston, T.H., and Cane, J.H. 2000. Pollen nutritional content and digestibility for animals. *Plant Syst. Evol.* **222**(1–4): 187–209. doi:10.1007/BF00984102.
- 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.
- Roulston, T.H., Smith, S.A., and Brewster, A.L. 2007. A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. *J. Kans. Entomol. Soc.* **80**(2): 179–181. doi:10.2317/0022-8567(2007)80[179:ACOPTA]2.0.CO;2.
- Roy, B.A., and Raguso, R.A. 1997. Olfactory versus visual cues in a floral mimicry system. *Oecologia (Berl.)*, **109**(3): 414–426. doi:10.1007/s004420050101.
- Rust, R.W. 1990. Spatial and temporal heterogeneity of pollen foraging in *Osmia lignaria propinqua* (Hymenoptera: Megachilidae). *Environ. Entomol.* **16**: 668–671.
- Sandoz, J.C., Roger, B., and Pham-Delègue, M.H. 1995. Olfactory learning and memory in the honeybee: comparison of different classical conditioning procedures of the proboscis extension response. *C.R. Acad. Sci. III Life Sci.* **318**(7): 749–755. PMID:7583763.
- Schacker, M. 2008. A spring without bees: how colony collapse disorder has endangered our food supply. The Lyons Press, Guilford, Conn.
- Schiestl, F.P. 2005. On the success of a swindle: pollination by deception in orchids. *Naturwissenschaften*, **92**(6): 255–264. doi:10.1007/s00114-005-0636-y. PMID:15931514.
- Schiestl, F.P., and Ayasse, M. 2002. Do changes in floral odor cause speciation in sexually deceptive orchids? *Plant Syst. Evol.* **234**(1): 111–119. doi:10.1007/s00606-002-0187-z.



- Schiestl, F.P., and Marion-Poll, F. 2001. Detection of physiologically active flower volatiles using gas chromatography coupled with electroantennography. *In* Molecular methods of plant analysis, 21: analysis of taste and aroma. *Edited by* J.F. Jackson, H.F. Linskens, and R.B. Inman. Springer-Verlag, Berlin. pp. 173–198.
- Schiestl, F.P., and Schlüter, P.M. 2009. Floral isolation, specialized pollination, and pollinator behavior in orchids. *Annu. Rev. Entomol.* **54**(1): 425–446. doi:10.1146/annurev.ento.54.110807.090603. PMID:19067636.
- Schiestl, F.P., Ayasse, M., Paulus, H.F., Löfstedt, C., Hansson, B.S., Ibarra, F., and Francke, W. 1999. Orchid pollination by sexual swindle. *Nature (London)*, **399**(6735): 421–422. doi:10.1038/20829.
- Schiestl, F.P., Ayasse, M., Paulus, H.F., Löfstedt, C., Hansson, B.S., Ibarra, F., and Francke, W. 2000. Sex pheromone mimicry in the early spider orchid (*Ophrys sphegodes*): patterns of hydrocarbons as the key mechanism for pollination by sexual deception. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **186**(6): 567–574. doi:10.1007/s003590000112. PMID:10947239.
- Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford.
- Schmidt, K., and Westrich, P. 1993. *Colletes hederæ* n. sp., eine bisher unerkannte, auf Efeu (*Hedera*) spezialisierte Bienenart (Hymenoptera: Apoidea). *Entomol. Die Zeit*, **103**: 89–93.
- Schultheis, J.R., Ambrose, J.T., Bambara, S.B., and Mangum, W.A. 1994. Selective bee attractants did not improve cucumber and watermelon yield. *HortScience*, **29**: 155–158.
- Scott, L., Cadman, A., and McMillan, I. 2006. Early history of Cainozoic Asteraceae along the South African west coast. *Rev. Palaeobot. Palynol.* **142**(1–2): 47–52. doi:10.1016/j.revpalbo.2006.07.010.
- 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**(10): 2487–2507. doi:10.1111/j.1558-5646.2008.00465.x. PMID:18637958.
- Seeley, T.D. 1974. Atmospheric carbon dioxide regulation in honey-bee (*Apis mellifera*) colonies. *J. Insect Physiol.* **20**(11): 2301–2305. doi:10.1016/0022-1910(74)90052-3. PMID:4424243.
- Silva, E.M., Dean, B.B., and Hiller, L.K. 2003. Honey bee (Hymenoptera: Apidae) foraging in response to preconditioning with onion flower scent compounds. *J. Econ. Entomol.* **96**(5): 1510–1513. doi:10.1603/0022-0493-96.5.1510. PMID:14650525.
- Simpson, G.G. 1953. The major features of evolution. Columbia University Press, New York.
- Simpson, B.B., and Neff, J.L. 1981. Floral rewards: alternative to pollen and nectar. *Ann. Mo. Bot. Gard.* **68**(2): 301–322. doi:10.2307/2398800.
- Singer, R.B. 2002. The pollination mechanism in *Trigonidium obtusum* Lindl (Orchidaceae: Maxillariinae): sexual mimicry and trap-flowers. *Ann. Bot. (Lond.)*, **89**(2): 157–163. doi:10.1093/aob/mcf021.
- Singer, R.B., Flach, A., Koehler, S., Marsaioli, A.J., and Amaral, M.E. 2004. Sexual mimicry in *Mormolyca ringens* (Lindl.) Schltr. (Orchidaceae: Maxillariinae). *Ann. Bot. (Lond.)*, **93**(6): 755–762. doi:10.1093/aob/mch091.
- 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**(4): 487–505. doi:10.1111/j.1095-8312.2005.00544.x.
- Sipes, S.D., and Wolf, P.G. 2001. Phylogenetic relationships within *Diadasia*, a group of specialist bees. *Mol. Phylogenet. Evol.* **19**(1): 144–156. doi:10.1006/mpev.2001.0914. PMID:11286499.
- Slessor, K.N., Winston, M.L., and Le Conte, Y. 2005. Pheromone communication in the honeybee (*Apis mellifera* L.). *J. Chem. Ecol.* **31**(11): 2731–2745. doi:10.1007/s10886-005-7623-9. PMID:16273438.
- Smith, P.M. 1976. The chemotaxonomy of plants. Contemporary Biology Series. Edward Arnold Limited, London.
- Smith, B.H. 1991. The olfactory memory of the honeybee *Apis mellifera*. 1. Odorant modulation of short-term and intermediate-term memory after single-trial conditioning. *J. Exp. Biol.* **161**: 367–382.
- Smith, B.H., and Breed, M.D. 1995. The chemical basis for nest-mate recognition and mate discrimination in social insects. *In* Chemical ecology of insects 2. *Edited by* R. T. Cardé and W. J. Bell. Chapman and Hall, New York. pp. 287–317.
- Soltis, D.E., Soltis, P.S., Endress, P.K., and Chase, M.W. 2005. Phylogeny and evolution of angiosperms. Sinauer Associates, Inc., Sunderland, Mass.
- Spaethe, J., Tautz, J., and Chittka, L. 2001. Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. *Proc. Natl. Acad. Sci. U.S.A.* **98**(7): 3898–3903. doi:10.1073/pnas.071053098. PMID:11259668.
- Spaethe, J., Moser, W.H., and Paulus, H.F. 2007. Increase of pollinator attraction by means of a visual signal in the sexually deceptive orchid, *Ophrys heldreichii* (Orchidaceae). *Plant Syst. Evol.* **264**(1–2): 31–40. doi:10.1007/s00606-006-0503-0.
- Stage, G.I. 1966. Biology and systematics of the American species of the genus *Hesperapis* Cockerell. Ph.D. dissertation, University of California, Berkeley.
- Standifer, L.N., Devys, M., and Barbier, M. 1968. Pollen sterols—a mass spectrographic survey. *Phytochemistry*, **7**(8): 1361–1365. doi:10.1016/S0031-9422(00)85638-1.
- Stange, G., and Stowe, S. 1999. Carbon-dioxide sensing structures in terrestrial arthropods. *Microsc. Res. Tech.* **47**(6): 416–427. doi:10.1002/(SICI)1097-0029(19991215)47:6<416::AID-JEMT5>3.0.CO;2-X. PMID:10607381.
- Steffan-Dewenter, I., Potts, S.G., and Packer, L. 2005. Pollinator diversity and crop pollination services are at risk. *Trends Ecol. Evol.* **20**(12): 651–652. doi:10.1016/j.tree.2005.09.004. PMID:16701452.
- Steiner, K.E., Whitehead, V.B., and Johnson, S.D. 1994. Floral and pollinator divergence in two sexually deceptive Cape orchids. *Am. J. Bot.* **81**(2): 185–194. doi:10.2307/2445632.
- Stephen, W.P., and Rao, S. 2005. Unscented color traps for non-*Apis* bees (Hymenoptera: Apiformes). *J. Kans. Entomol. Soc.* **78**(4): 373–380. doi:10.2317/0410.03.1.
- Stöckl, J., Paulus, H.F., Dafni, A., Schulz, C., Francke, W., and Ayasse, M. 2005. Pollinator attracting odour signals in sexually deceptive orchids of the *Ophrys fusca* group. *Plant Syst. Evol.* **254**(1–2): 105–120. doi:10.1007/s00606-005-0330-8.
- Stöckl, J., Twele, R., Erdmann, D.H., Francke, W., and Ayasse, M. 2007. Comparison of the flower scent of the sexually deceptive orchid *Ophrys iricolor* and the female sex pheromone of its pollinator *Andrena morio*. *Chemoecology*, **17**(4): 231–233. doi:10.1007/s00049-007-0383-y.
- Stöckl, J., Schlüter, P.M., Stuessy, T.F., Paulus, H.F., Assum, G., and Ayasse, M. 2008. Scent variation and hybridization cause the displacement of a sexually deceptive orchid species. *Am. J. Bot.* **95**(4): 472–481. doi:10.3732/ajb.95.4.472.
- Stoutamire, W.P. 1975. Pseudocopulation in Australian terrestrial orchids. *Am. Orchid Soc. Bull.* **44**: 226–233.
- Streinzer, M., Paulus, H.F., and Spaethe, J. 2009. Floral colour signal increases short-range detectability of a sexually deceptive orchid to its bee pollinator. *J. Exp. Biol.* **212**(9): 1365–1370. doi:10.1242/jeb.027482.



- Tatsuka, K., Suekane, S., Sakai, Y., and Sumitani, H. 1990. Volatile constituents of kiwi fruit flowers: simultaneous distillation and extraction versus headspace sampling. *J. Agric. Food Chem.* **38**(12): 2176–2180. doi:10.1021/jf00102a015.
- Tengö, J. 1979. Odour-released behaviour in *Andrena* bees (Apoidea, Hymenoptera). *Zoon*, **7**: 15–48.
- Theis, N. 2006. Fragrance of Canada thistle (*Cirsium arvense*) attracts both floral herbivores and pollinators. *J. Chem. Ecol.* **32**(5): 917–927. doi:10.1007/s10886-006-9051-x. PMID:16739013.
- Theis, N., Kesler, K., and Adler, L.S. 2009. Leaf herbivory increases floral fragrance in male but not female *Cucurbita pepo* subsp. *texana* (Cucurbitaceae) flowers. *Am. J. Bot.* **96**(5): 897–903. doi:10.3732/ajb.0800300.
- Thiery, D., Bluet, J.M., Pham-Delègue, M.-H., Etiévant, P., and Masson, C. 1990. Sunflower aroma detection by the honeybee — study by coupling gas chromatography and electroantennography. *J. Chem. Ecol.* **16**(3): 701–711. doi:10.1007/BF01016481.
- Thom, C., Guerenstein, P.G., Mechaber, W.L., and Hildebrand, J.G. 2004. Floral CO<sub>2</sub> reveals flower profitability to moths. *J. Chem. Ecol.* **30**(6): 1285–1288. doi:10.1023/B:JOEC.0000030298.77377.7d. PMID:15303329.
- Thomas, J.A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **360**(1454): 339–357. doi:10.1098/rstb.2004.1585. PMID:15814349.
- Thorp, R.W. 1979. Structural, behavioral, and physiological adaptations of bees (Apoidea) for collecting pollen. *Ann. Mo. Bot. Gard.* **66**(4): 788–812. doi:10.2307/2398919.
- Tinbergen, N. 1960. The natural control of insects in pine woods. I. Factors influencing the intensity of predation by songbirds. *Arch. Neerl. Zool.* **13**: 265–343.
- Tocan, V., and Baron, O. 1969. Antibiotic activity of protoanemonine from *Ranunculus oxyspermus*. *Boll. Chim. Farm.* **108**(12): 789–791. PMID:5374885.
- Tollsten, L., and Bergström, G. 1988. Headspace volatiles of whole plants and macerated plant parts of *Brassica* and *Sinapis*. *Phytochemistry*, **27**(7): 2073–2077. doi:10.1016/0031-9422(88)80099-2.
- van der Pijl, L., and Dodson, C.H. 1966. Orchid flowers — their pollination and evolution. University of Miami Press, Coral Gables, Fla.
- van Emden, H.F., Sponagl, B., Wagner, E., Baker, T., Ganguly, S., and Douloupaka, S. 1996. Hopkins' 'host-selection principle', another nail in its coffin. *Physiol. Entomol.* **21**(4): 325–328. doi:10.1111/j.1365-3032.1996.tb00873.x.
- Vareschi, E. 1971. Duftunterschiede bei der Honigbiene — Einzelzell-Ableitungen und Verhaltensreaktionen. *Z. Vgl. Physiol.* **75**: 143–173.
- Vereecken, N.J. 2009. Deceptive behavior in plants. I. Pollination by sexual deception in orchids: a host–parasite perspective. *In* Plant–environment Interactions — from sensory plant biology to active behavior. *Edited by* F. Baluska. Springer-Verlag, Berlin. pp. 203–222.
- Vereecken, N.J., and Schiestl, F.P. 2008. The evolution of imperfect floral mimicry. *Proc. Natl. Acad. Sci. U.S.A.* **105**(21): 7484–7488. doi:10.1073/pnas.0800194105. PMID:18508972.
- Vereecken, N.J., and Schiestl, F.P. 2009. On the roles of colour and scent in a specialized floral mimicry system. *Ann. Bot. (Lond.)*, **104**(6): 1077–1084. doi:10.1093/aob/mcp208.
- Vereecken, N.J., Mant, J., and Schiestl, F.P. 2007. Population differentiation in female sex pheromone and male preferences in a solitary bee. *Behav. Ecol. Sociobiol.* **61**(5): 811–821. doi:10.1007/s00265-006-0312-z.
- von Aufsess, A. 1960. Geruchliche Nahorientierung der Biene bei entomophilen und ornithophilen Blüten. *Z. Vgl. Physiol.* **43**(5): 469–498. doi:10.1007/BF00298072.
- von Frisch, K. 1919. Über den Geruchssinn der Biene und seine blütenbiologische Bedeutung. *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere*, **37**: 1–238.
- von Frisch, K. 1923. Über die “Sprache” der Bienen. *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere*, **40**: 1–186.
- von Frisch, K. 1944. Weitere Versuche über die Lenkung des Bienenfluges durch Duftstoffe. *Biol. Zentbl.* **64**: 237–266.
- von Frisch, K. 1965. *Tanzsprache und Orientierung der Bienen*. Springer-Verlag, Berlin.
- Wadhams, L.J., Blight, M.M., Kerguelen, V., Le Métayer, M., Marion-Poll, F., Masson, C., Pham-Delègue, M.H., and Woodcock, C.M. 1994. Discrimination of oilseed rape volatiles by honey bee: novel combined gas chromatographic–electrophysiological behavioral assay. *J. Chem. Ecol.* **20**(12): 3221–3231. doi:10.1007/BF02033722.
- Waller, G.D., Loper, G.M., and Berdel, R.L. 1974. Olfactory discrimination by honeybees of terpenes identified from volatiles of alfalfa flowers. *J. Apic. Res.* **13**: 191–197.
- Waser, N.M., Chittka, L., Price, M.V., Williams, N.M., and Ollerton, J. 1996. Generalization in pollination systems, and why it matters. *Ecology*, **77**(4): 1043–1060. doi:10.2307/2265575.
- 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. PMID:15012330.
- Weingartner, E., Wahlberg, N., and Nylin, S. 2006. Dynamics of host plant use and species diversity in *Polygonia* butterflies (Nymphalidae). *J. Evol. Biol.* **19**(2): 483–491. doi:10.1111/j.1420-9101.2005.01009.x. PMID:16599924.
- Weiss, M. 2001. Vision and learning in some neglected pollinators: beetles, flies, moths, and butterflies. *In* Cognitive ecology of pollination — animal behavior and floral evolution. *Edited by* L. Chittka and T.D. Thomson. Cambridge University Press, Cambridge, UK. pp. 171–190.
- Wells, P., Wells, H., Vu, V., Vadehra, N., Lee, C., Han, R., Han, K., and Chang, L. 1993. Does honey bee nasonov pheromone attract foragers? *Bull. South. Calif. Acad. Sci.* **92**: 70–77.
- Wenner, A.M., Wells, P.H., and Johnson, D.L. 1969. Honey bee recruitment to food sources: olfaction or language? *Science (Washington, D.C.)*, **164**(3875): 84–86. doi:10.1126/science.164.3875.84. PMID:5773718.
- Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S.G., Roberts, S.P.M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B.E., Woyciechowski, M., Biesmeijer, J.C., Kunin, W.E., Settele, J., and Steffan-Dewenter, I. 2008. Measuring bee diversity in different European habitats and biogeographical regions. *Ecol. Monogr.* **78**(4): 653–671. doi:10.1890/07-1292.1.
- Westrich, P. 1989. *Die Wildbienen Baden-Württembergs. Spezieller Teil: Die Gattungen und Arten*. Eugen Ulmer GmbH & Co, Stuttgart, Germany.
- Westrich, P. 2008. Flexibles Pollensammelverhalten der ansonsten streng oligolektischen Seidenbiene *Colletes hederiae* Schmidt & Westrich (Hymenoptera: Apidae). *Eucera*, **2**: 17–29.
- Wheeler, J.W., Shamim, M.T., Ekpa, O., Eickwort, G.C., and Duffield, R.M. 1985. Exocrine secretions of bees. VI. Unsaturated ketones and aliphatic esters in the dufour's gland secretion of *Dufourea novaeangliae* (Hymenoptera, Halictidae). *J. Chem. Ecol.* **11**(3): 353–361. doi:10.1007/BF01411422.
- Whitney, H.M., Kolle, M., Andrew, P., Chittka, L., Steiner, U., and Glover, B.J. 2009. Floral iridescence, produced by diffractive optics, acts as a cue for animal pollinators. *Science (Wa-*

- shington, D.C.), **323**(5910): 130–133. doi:10.1126/science.1166256. PMID:19119235.
- Whitten, W.M., Williams, N.H., Armbruster, W.S., Battiste, M.A., Streckowski, L., and Lindquist, N. 1986. Carvone oxide: an example of convergent evolution in euglossine pollinated plants. *Syst. Bot.* **11**(1): 222–228. doi:10.2307/2418960.
- Whitten, M.W., Hills, H.G., and Williams, N.H. 1988. Occurrence of ipsdienol in floral fragrances. *Phytochemistry*, **27**(9): 2759–2760. doi:10.1016/0031-9422(88)80657-5.
- Wikström, N., Savolainen, V., and Chase, M.W. 2001. Evolution of the angiosperms: calibrating the family tree. *Proc. R. Soc. Lond. B Biol. Sci.* **268**(1482): 2211–2220. doi:10.1098/rspb.2001.1782.
- Williams, N.M. 2003. Use of novel pollen species by specialist and generalist solitary bees (Hymenoptera: Megachilidae). *Oecologia (Berl.)*, **134**: 228–237.
- Williams, P. 2005. Does specialization explain rarity and decline among British bumblebees? A response to Goulson et al. *Biol. Conserv.* **122**(1): 33–43. doi:10.1016/j.biocon.2004.06.019.
- Williams, N.H., and Dodson, C.H. 1972. Selective attraction of male euglossine bees to orchid floral fragrances and its importance in long-distance pollen flow. *Evolution*, **26**(1): 84–95. doi:10.2307/2406985.
- Williams, N.H., and Whitten, W.M. 1983. Orchid floral fragrances and male Euglossine bees: methods and advances in the last sesquidecade. *Biol. Bull.* **164**(3): 355–395. doi:10.2307/1541248.
- Williams, I.H., Pickett, J.A., and Martin, A.P. 1981a. Attraction of honey bees to flowering plants by using synthetic nasonov pheromone. *Entomol. Exp. Appl.* **30**(2): 199–201. doi:10.1007/BF00300889.
- Williams, I.H., Pickett, J.A., and Martin, A.P. 1981b. The nasonov pheromone of the honeybee *Apis mellifera* L. (Hymenoptera, Apidae). Part II. Bioassay of the components using foragers. *J. Chem. Ecol.* **7**(2): 225–237. doi:10.1007/BF00995745.
- Wilson, P., and Stine, M. 1996. Floral constancy in bumble bees: handling efficiency or perceptual conditioning? *Oecologia (Berl.)*, **106**(4): 493–499. doi:10.1007/BF00329707.
- Winston, M. 1995. Things that didn't work. *Bee Culture*, **123**: 559–560.
- Wojcik, V.A., Frankie, G.W., Thorp, R.W., and Hernandez, J.L. 2008. Seasonality in bees and their floral resource plants at a constructed bee habitat in Berkeley, California. *J. Kans. Entomol. Soc.* **81**(1): 15–28. doi:10.2317/JKES-701.17.1.
- Wright, G.A., and Schiestl, F. 2009. The evolution of floral scent: the influence of olfactory learning by insect pollinators on the honest signalling of floral rewards. *Funct. Ecol.* **23**(5): 841–851. doi:10.1111/j.1365-2435.2009.01627.x.
- Wright, G.A., Lutmerding, A., Dudareva, N., and Smith, B.H. 2005. Intensity and the ratios of compounds in the scent of snapdragon flowers affect scent discrimination by honeybees (*Apis mellifera*). *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* **191**(2): 105–114. doi:10.1007/s00359-004-0576-6.
- Young, A.M., and Severson, D.W. 1994. Comparative analysis of steam distilled floral oils of cacao cultivars (*Theobroma cacao* L., Sterculiaceae) and attraction of flying insects: implications for a *Theobroma* pollination syndrome. *J. Chem. Ecol.* **20**(10): 2687–2703. doi:10.1007/BF02036201.
- Zhang, S., Schwarz, S., Pahl, M., Zhu, H., and Tautz, J. 2006. Honeybee memory: a honeybee knows what to do and when. *J. Exp. Biol.* **209**(22): 4420–4428. doi:10.1242/jeb.02522. PMID:17079712.

Copyright of Canadian Journal of Zoology is the property of Canadian Science Publishing and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.