

Cheaters and liars: chemical mimicry at its finest^{1,2}

N.J. Vereecken and J.N. McNeil

Abstract: Chemical mimicry is an essential part of certain interspecific interactions, where the outcome for both species may depend on the degree to which the original signals are mimicked. In this review, we discuss a number of specific cases relating to pollination and obtaining nutrient resources that we believe exemplify recent advances in our understanding of chemical mimicry. Subsequently, we suggest avenues for future ecological and chemical research that should allow us to gain further insight into the evolution of chemical mimicry.

Résumé : Le mimétisme chimique est une composante essentielle de certaines interactions entre les espèces, dans lesquelles l'issue pour les deux espèces peut dépendre du degré de mimétisme des signaux d'origine. Dans notre rétrospective, nous discutons de plusieurs cas spécifiques reliés à la pollinisation et à l'obtention des ressources en nutriments qui, à notre avis, illustrent bien les progrès récents dans la compréhension du mimétisme chimique. Nous proposons ensuite des avenues de recherche écologiques et chimiques pour le futur qui devraient permettre des perspectives plus approfondies sur l'évolution du mimétisme chimique.

[Traduit par la Rédaction]

Introduction

Organisms may obtain information through an array of auditory, visual, mechanical, and (or) chemical cues, and in recent years, there have been a number of major publications examining animal communication channels (Bradbury and Vehrencamp 1998; Hauser and Konishi 1999; Espmark et al. 2000; Maynard-Smith and Harper 2003; Searcy and Nowicki 2005). The recent advent of more sophisticated analytical and molecular techniques has resulted in significant advances in our understanding of chemical cues, not only with respect to the identification and role of infochemicals in intraspecific interactions (pheromones) but also of those modulating interspecific interactions within and between trophic levels (allomones). This has resulted in the discovery of some rather fascinating cases of both eavesdropping and mimicry. In the case of eavesdropping, receivers exploit chemical cues that play an important role in a totally different context. For example, traces of the sex pheromone that a female insect emits to attract potential males may remain on her eggs and subsequently act as a kairomone for egg para-

sitoids (Noldus 1988; Noldus et al. 1991; Hilker et al. 2000; Milonas et al. 2009). Similarly, the feces or honeydew from aphids and other sap-feeding insects may be exploited as foraging cues, as well as alternate food, by the parasitoids and predators that feed on the herbivore (Bouchard and Cloutier 1984; Budenberg 1990; Wäckers 2005; Wäckers et al. 2008). In addition, it is also exploited by some hyperparasitoids that in turn attack parasitized aphids (Buitenhuis et al. 2004). However, the costs associated with natural enemies exploiting these cues are lower than the benefits accrued from their production.

In contrast, in cases of chemical mimicry (Fig. 1), the mimicking species gains while the dupe species does not (Wickler 1968). For many years, descriptions of such systems have been reported in the literature; however, it really is only in the last decade or so that we have started to gain real insight into the chemistry modulating these interactions. This represents a significant step forward, as it opens up avenues that will allow us to address broader ecological and evolutionary questions about chemical mimicry. Here we first review a number of fascinating cases of chemical mimi-

Received 1 February 2010. Accepted 27 May 2010. Published on the NRC Research Press Web site at cjz.nrc.ca on 16 July 2010.

N.J. Vereecken.³ 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.

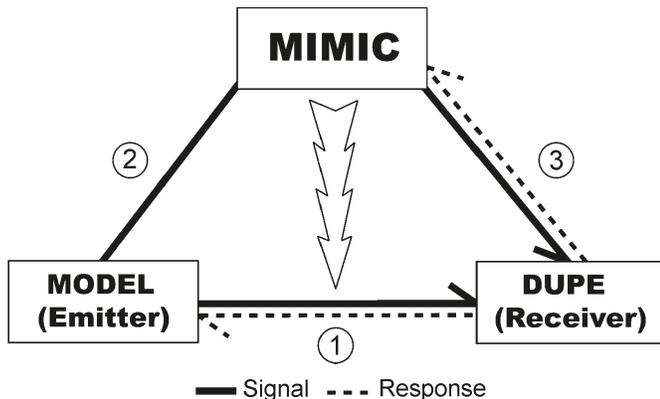
J.N. McNeil. Department of Biology, The University of Western Ontario, London ON N6A 5B7, Canada.

¹The present review is one in the special series of reviews on animal-plant interactions.

²In memory of Jan Tengö (1939–2010), who made exceptional contributions to our understanding of the chemical ecology of solitary bees, including chemical mimicry.

³Corresponding author (e-mail: nicolas.vereecken@ulb.ac.be).

Fig. 1. A schematic view of signals and responses involved in a simple, theoretical mimicry system composed of a “model”, a “mimic”, and a “dupe”. (1) The model organism emits a signal (solid line) that triggers a stereotyped response (broken line) in the receiver. (2) The mimic hijacks the pre-existing communication channel between the emitter and the receiver by imitating the signal of interest (solid line) emitted by the model organism. (3) The signal emitted by the mimic triggers a stereotyped response in the dupe organism because it is perceived as an instance of the model organism.



cry involving insects and then offer a number of suggestions for future research in a field that offers many exciting possibilities from both fundamental and applied perspectives.

Chemical mimicry in pollination and spore dispersal

Contrary to animals, the sexual reproduction of most outcrossing plant species involves the intervention of an external agent such as wind or third-party animal vectors (Proctor and Yeo 1972; Bristow 1978; Meeuse and Morris 1984). Animal-pollinated plants largely outnumber wind-pollinated ones, and it has been shown that wind pollination is a derived dispersal strategy that has evolved on multiple independent occasions, presumably as a direct outcome of pollinator limitation (Linder 2000; Culley et al. 2002; Friedman and Barrett 2008). From the plants' perspective, successful reproduction requires the adequate manipulation of animal vectors that will unwittingly move their gametes to another compatible, conspecific individual plant. Over time, a considerable proportion of animal-pollinated plants have therefore evolved combining suites of different signals (colour, scent, shapes, etc.) that are commonly interdependent and combine to enhance pollination efficiency (see, e.g., Roy and Raguso 1997; Chittka et al. 1999; Gumbert and Kunze 2001; Raguso and Willis 2002, 2005; Goyret et al. 2007 and references therein; but see Odell et al. 1999).

Most plants species are generalized, i.e., they achieve cross-pollination by attracting more than one pollen vector species (Herrera 1996; Ollerton 1996; Waser et al. 1996; Johnson and Steiner 2000; Bascombe et al. 2003; Herrera et al. 2006) by providing floral rewards such as pollen, nectar, oil, perfumes, etc., in return for pollen transfer (Simpson and Neff 1981). However, several groups of plants in different families benefit from pollinator services, although they never provide any collectible or edible reward to their pollen

vectors, a phenomenon known as pollination by deception (Dafni 1984; Renner 2006). Classic examples of this category of plants include food-deceptive orchids (van der Pijl and Dodson 1966; Ackerman 1986; Jersáková et al. 2006), whose flowers are pollinated by a relatively wide range of food-seeking insects (e.g., Cozzolino et al. 2005) that are apparently not capable of discriminating between rewarding and deceptive flowers and species. Food-deceptive orchids sometimes mimic the floral signals of specific plants, particularly the flower spectral reflectance, through Batesian mimicry (Nilsson 1983; Johnson 1994; Gigord et al. 2002; Anderson et al. 2005; Galizia et al. 2005; Peter and Johnson 2008), or else emit general visual and perhaps chemical signals that evoke the presence of a reward to the pollinators. Although it is known that the flowers of food-deceptive orchids are scented (Nilsson 1979, 1980, 1983, 1984; Bergström et al. 1992; Moya and Ackerman 1993; Ackerman et al. 1997; Barkman et al. 1997; Andersson et al. 2002; Salzmann et al. 2006, 2007a, 2007b; Salzmann and Schiestl 2007), the study of the role of floral fragrances and how they combine with visual signals to trigger pollinator attraction is still in its infancy in food-deceptive plants (reviewed by Jersáková et al. 2009).

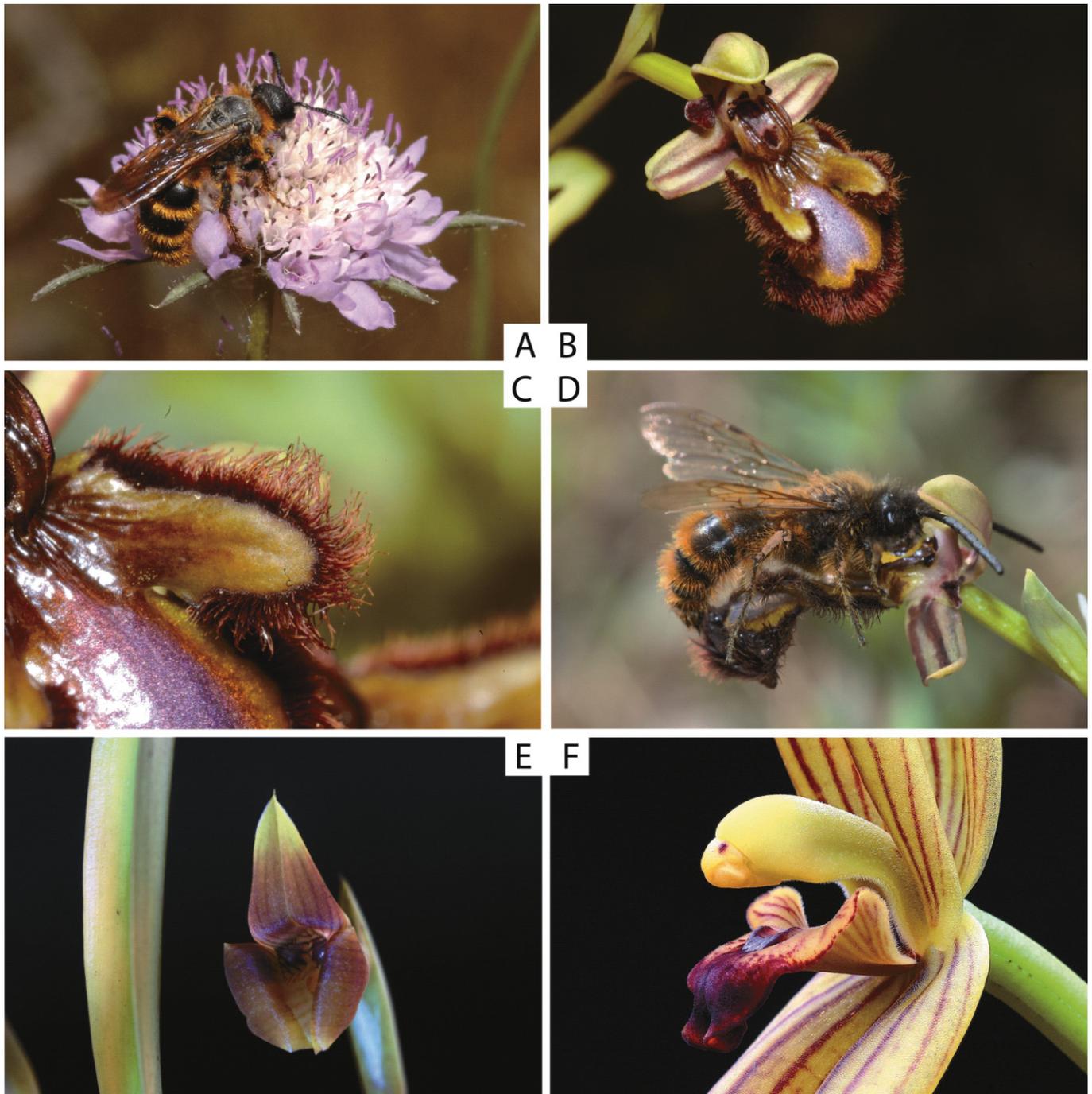
Plants do not only lure insects in search of food. In fact, manifold plant species have taken another evolutionary road to the sensory exploitation of insects, namely by mimicking signals that are hard-wired to other basic needs of the targeted insects, such as finding mates or appropriate egg-laying substrates. In the following sections, we will summarize the current state of knowledge on different insect–plant interactions based on deceit that have received attention in recent years, and for which there is evidence that the chemical signals play a major role (or even suffice) in the attraction of the targeted insects. We will first focus on sexually deceptive orchids, starting with an historical account of the discovery of sexual deception in orchids and a review of the milestone contributions in this field. This section will be followed by an overview of selected studies on the chemical basis of substrate mimicry involving not only flowering plants, but also mosses and fungi that attract insects for spore dispersal by mimicking flowers.

Orchid pollination by sexual deceit

The discovery of pollination by sexual deception

The visual similarity between the flowers of some orchids and insects has intrigued botanists and ecologists for centuries. Many hypotheses have been suggested to account for this resemblance, and even Darwin, in his long treatise *On the various contrivances by which British and foreign orchids are fertilized by insects*, published in 1862, just 3 years after the *Origin of species*, failed to provide an explanation based on natural selection for the insectiform flowers found in the European orchid genus *Ophrys* L. (Orchidaceae). In the early 20th century, Maurice-Alexandre Pouyanne, a naturalist and President of the Court of Appeal in Sidi-Bel-Abbès, Algeria, performed detailed observations on the fertilization of several *Ophrys* orchids in his home region of North Africa. In his studies, Pouyanne reported on the behaviour of the pollinators (Figs. 2A) of the mirror orchid (*Ophrys ciliata* Biv. = *Ophrys speculum* Link.) (Figs. 2B–

Fig. 2. (A) A female of *Dasyscolia* (= *Campsoscolia*) *ciliata* scoliid wasp, the model species of the mirror orchid, on an inflorescence of the genus *Scabiosa* L. (Dipsacaceae). (B) Detail of a flower of the mirror orchid (*Ophrys ciliata* = *Ophrys speculum*) showing the “mirror” in the median area of the lip and the reddish hairs on the margin of the labellum. (C) Close up on the marginal hairs of the labellum of the mirror orchid. Photographs A–C by N.J. Vereecken. (D) A male of *D. ciliata* pseudocopulating on the labellum of the mirror orchid (photograph by C.E. Hermosilla). (E) Detail of a flower of *Trigonidium obtusum* (photograph by L.P. Varella). (F) Detail of a flower of *Mormolyca ringens* (photograph by T. Ditlevsen). Images appear in colour on the Journal’s Web site and are reproduced with permission of the photographers.



2D) with an astonishing level of detail, revealing for the first time that the flowers of several orchid species do not produce nectar or any form of collectible or edible reward, but instead imitate the mating signals of female insects, thereby triggering flower visitation by the males of the tar-

geted species. He shared his observations with Henri Correvon, a member of the French Horticultural Society, which resulted in the publication of several papers (Correvon and Pouyanne 1916, 1923; Pouyanne 1917). These observations were first met with disbelief by their contem-

poraries, but several parallel observations (Godfrey 1922, 1929; Wolff 1950) confirmed these early findings and paved the way for a long series of investigations, not only in Europe, but on other continents as well.

Since Pouyanne's milestone contributions to the field, pollination by sexual deceit has been further confirmed and reported from independent orchid lineages and on different continents, with extant representatives found across Australia (10 genera; Coleman 1928; Stoutamire 1975; Peakall et al. 1987; Jones 1988; Peakall 1990; Bower 1996), Central and South America (7 genera; 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* Bergius (Orchidaceae); Steiner et al. 1994), and Europe (Delforge 2005; Schiestl 2005; Ayasse 2006; Jersáková et al. 2006). In all cases described so far, patrolling male insects (mostly solitary bees, but also solitary wasps and occasionally beetles; see Tyteca et al. 2006) attempt copulation, a phenomenon also termed "pseudocopulation", or a precopulatory courtship with the orchid flowers. The male insects sometimes display high levels of sexual stimulation on the flowers, erecting their genital capsule during convulsive movements, and rubbing it against areas on the flower lip where the density of hairs presumably adds to the initial olfactory stimulation (Agren et al. 1984; N.J. Vereecken, unpublished data). In the case of the Australian ichneumonid *Lissopimpla excelsa* (Costa, 1864) and its associated orchids *Cryptostylis erecta* F. Muell. ex Benth and *Cryptostylis leptochila* F. Muell. ex Benth, the males are excited to the point of ejaculating in the flowers during pseudocopulations (Coleman 1928; Gaskett et al. 2008). Whether other "pseudo-female" orchids are capable of such an extreme sexual stimulation of the pollinator is not known. Given the absence of any reward on flowers of sexually deceptive orchids, the interactions between these plants and their pollen vectors should best be viewed as one-sided or parasitic in nature. Indeed, although the orchids are exclusively dependent upon pollinator visits to ensure their reproductive success, the insects gain nothing in return from the time and the energy (and sometimes the sperm; see Gaskett et al. 2008) that they spend when attempting to copulate with the flowers. From the insect perspective, visiting these orchid flowers instead of searching to access freshly emerged females during the peak reproductive season might negatively affect their reproductive success, causing them to miss out on mating opportunities with genuine females (Vereecken 2009).

The chemistry of sexual deception in orchids — pre-1990 studies

Detailed studies on the pollination biology of these orchids have allowed identifying an array of pollinator attractants or stimulants, including visual, tactile, and olfactory floral signals (Kullenberg 1961). Of all these signals, the floral scent has been shown to be the major pollinator attractant (reviewed by Schiestl 2005; Ayasse 2006), a finding consistent with the species-specificity and the pivotal importance of chemical signals in the mating behaviour of solitary bees and wasps (Kullenberg 1956; Kullenberg and Bergström 1976; Alcock et al. 1978; Bergström 1978; Eickwort and Ginsberg 1980; Bergmark et al. 1984; Ayasse et al.

1999, 2000, 2001; Paulmier et al. 1999; Wyatt 2003; Schiestl et al. 2003; Simmons et al. 2003; Schiestl and Peakall 2005; Fraberger and Ayasse 2007), the major group of pollinators of these orchids. Investigations into the chemistry of orchid-pollinator interactions were initiated by Kullenberg (1956), who noticed that the females of the pollinators released odours detectable by the human nose. Hence, Kullenberg and his collaborators focused their investigations on the composition of the glands that produce these highly volatile compounds (monoterpene and sesquiterpene alcohols and aldehydes, as well as straight-chained alcohols). The research group eventually identified several such compounds from mandibular glands of the female insects, including linalool, citronellal, farnesol, and nerolidol. Then by performing bioassays, it was shown that these substances indeed triggered approaching flights of patrolling males in a manner reminiscent to their approach to emerging, virgin females. During these bioassays, Kullenberg observed "quick approaches", "persistent approaches", or "quick visits" (terms coined in Kullenberg 1956) by the patrolling males, but the experiments failed to reproduce genuine copulation attempts with the scented dummies. Still, several techniques for the collection, isolation, and enrichment of *Ophrys* floral volatiles had been investigated in the hope of characterizing the full spectrum of compounds produced by individual flowers (Bergström et al. 1980). For example, Borg-Karlson et al. (1985) concluded after analysing the compounds contained in the mandibular gland of *Andrena fuscipes* (Kirby, 1802), a summer-active male *Andrena* Fabricius, 1775 (Andrenidae), and comparing the gland composition with solvent extracts of an unrelated and nonassociated spring-flowering *Ophrys* flower, that "[...] attention should be paid to aliphatic alcohols and oxygenated terpenes, as they are found also in the mandibular gland secretion or head extracts of many species of *Andrena*" (Borg-Karlson et al. 1985, p. 285).

All these early studies were motivated by the idea of describing instances of chemical mimicry between the orchids and the female bees as suggested by behavioural observations (Bergström 1978). However, despite the considerable efforts and chemical analyses performed, no strict correspondence in odour (chemical mimicry) has ever been reported between the floral odour of the *Ophrys* species investigated and the mandibular or Dufour's gland secretions of the associated pollinator species (see Borg-Karlson and Groth 1986; Borg-Karlson and Tengö 1986; Borg-Karlson et al. 1987). This led the researchers to speculate on the existence of "general attractants" (Borg-Karlson and Tengö 1986), "of multicomponent nature" (in Tengö 1979), or "second class attractivity compounds" (Borg-Karlson 1990). By the mid-1980s, the only evidence for chemical mimicry between *Ophrys* flowers and their model organisms had come in the form of a partial qualitative match between the patterns of compounds found in (male!) bees and the floral scent of the *Ophrys* investigated. This led these authors to conclude (Borg-Karlson et al. 1985, p. 293): "[...] It seems not to be possible for the plant to release an exact qualitative and quantitative copy of the components in the females odour to attract and excitate (*sic*) the corresponding male bees." This last excerpt somehow contradicts the results of several parallel experiments,

such as those by Kullenberg (1973) and Kullenberg et al. (1984), which showed that solvent (*n*-hexane) extracts of *Ophrys* flowers, which were capable of triggering copulation attempts of male bees with the scented dummies, contained large amounts of low volatile odour compounds such as cuticular hydrocarbons and their derivatives.

The chemistry of sexual deception in orchids — post-1990 studies

In the late 1990s, a research team based in Vienna (Austria) extended the investigations by focusing their analyses and behavioural experiments on the low volatile compounds of the orchids and the female bees and they documented the first conclusive case of chemical mimicry in an *Ophrys*–pollinator species pair (Schiestl et al. 1999, 2000). They used as model the early spider orchid (*Ophrys sphegodes* Mill.), which is pollinated by males of the mining bee (*Andrena nigroaenea* (Kirby, 1802)). Their results show that both the virgin female bees (i.e., the model) and the fresh, unpollinated *Ophrys* flowers (i.e., the mimic) use identical odour compounds, particularly long and straight-chained monounsaturated hydrocarbons (alkenes), in similar proportions to attract the males of *A. nigroaenea*. Their bioassays provide evidence that these less volatile compounds are capable of triggering not only “quick approaches” or “quick visits”, but genuine copulation attempts with the scented dummies as well (Schiestl et al. 1999, 2000; Ayasse et al. 2000). These results contradict the statement made by Borg-Karlson et al. (1985) and show that odour compounds that had been initially overlooked in the analyses of *Ophrys* floral scents, perhaps because of their presumed low volatility and relatively basic chemical structure, might in fact be the key pollinator attractants in *Ophrys* and the source of the sex pheromone in the female bees investigated (Schiestl et al. 1999). These studies have paved the way for a series of studies that followed and renewed the interest in *Ophrys*–pollinator interactions as a model system to investigate the ecological and evolutionary basis of signals involved in this mimicry system.

Since then it has become apparent that the active odour compounds triggering stereotyped mating behaviour—including copulation attempts—by the targeted males are long-chain fatty acids and their derivatives found on the females’ cuticle, not in mandibular or Dufour’s gland secretions as it was previously assumed. Further experiments on *O. sphegodes* and *A. nigroaenea* have shown that female bees change their odour bouquets after mating and release antiaphrodisiac compounds, particularly the active compounds all-*trans*-farnesyl hexanoate and all-*trans*-farnesol, that inhibit male mating behaviour (Schiestl and Ayasse 2000). These compounds are produced by the females’ Dufour’s glands in this and other bee species (Tengö and Bergström 1975), together with other chemicals that the females use for lining their underground brood cells (Cane 1981). Interestingly, Schiestl and Ayasse (2001) reported that flowers of *O. sphegodes* also release significantly higher absolute and relative amounts of *trans*-farnesyl hexanoate after pollination. They interpreted this finding as a mechanism that might direct pollinators towards fresh, unpollinated flowers that, in turn, may ultimately maximize the overall reproduc-

tive success in this pollinator-limited orchid (Schiestl and Ayasse 2001).

Following from these studies, the female sex pheromone of *Colletes cunicularius* (L., 1761) and *Andrena morio* Brullé, 1832 have been described by Mant et al. (2005a) and Stökl et al. (2008), respectively. For these bee species, the alkenes found in the solvent (*n*-hexane) extracts of virgin females were shown to be the most attractive to patrolling males, which confirmed the results on *A. nigroaenea* (Schiestl et al. 1999, 2000). Investigations into the model bee *C. cunicularius* and the orchid mimic *Ophrys exaltata* Ten. have shown that this orchid attracts the male bees by using precisely the same set of odour compounds produced by the virgin female bees, namely (*Z*)-7-heneicosene, (*Z*)-7-tricosene, and (*Z*)-7-pentacosene (Mant et al. 2005a; Vereecken and Schiestl 2009). However, although the absolute amounts in the female bee and orchid extracts were similar, their proportions (in percentage of the total blend) differed significantly between the model and the mimic. Contrary to theoretical expectations that a Batesian mimic should resemble its specific model organism as closely as possible if the trickery is to work at all, the orchid, with its slightly “imperfect” floral scent, was shown to be even more attractive to patrolling males of *C. cunicularius* than the real females (Vereecken and Schiestl 2008). These authors suggested that the imperfect mimicry has evolved in *O. exaltata* because males of *C. cunicularius* actively prefer the slightly different scent of allopatric females over sympatric ones (Vereecken et al. 2007). Over time selection imposed by the male bees has driven the scent of the orchids towards “exoticism” and not towards a perfect copy of the local female bees.

The chemistry of sexual deception in Neotropical orchids has not been investigated to any great extent and requires in-depth investigations, especially in the genera *Geoblasta* Barb. Rodr., *Hofmeisterella* Rchb. f., *Lepanthes* Sw., *Mormolyca* Fenzl (+ *Chrysocynis* Linden & Rchb. f.), *Telipogon* Kunth (+ *Stellilabium* Schltr.), *Trichoceros* Kunth, and *Trigonidium* Lindl. (all in the family Orchidaceae). Until now, the only species that have been investigated for their floral scent are *Trigonidium obtusum* Lindl. (Fig. 2E), a species pollinated by sexually deceiving the patrolling drones of the stingless bee *Plebeia droryana* (Friese, 1900) (Singer 2002), and *Mormolyca ringens* (Lindl.) Schltr. (Fig. 2F), which is pollinated by drones of the stingless bees *Nannotrigona testaceicornis* (Lepeletier, 1836) and *Scaptotrigona* Moure, 1942 (Apidae) (van der Pijl and Dodson 1966). The floral scent of *T. obtusum* appears to be largely dominated by a single cuticular hydrocarbon, pentadecane, that failed to elicit behavioural responses by the pollinators in bioassays (Flach et al. 2004). In contrast, investigations on *M. ringens* have reported a total of 31 odour compounds in its floral scent (Singer et al. 2004), including 2-heptanol and several straight-chained hydrocarbons (e.g., tricosane, pentacosane, heptacosane, nonacosane, and their associated 9-alkenes). These have been identified both in the epicuticular waxes of the flowers of the orchid mimic and the virgin queens of *Scaptotrigona* sp. (Flach et al. 2006). Field observations and preliminary chemical analyses indicate that drones of *N. testaceicornis* also might be attracted by floral volatiles of *M. ringens* (Flach et al. 2006), and that male fungus gnats that pollinate *Lepanthes* flowers track the floral

scent upwind to its source, suggesting that floral scent is indeed likely to be the primary attractant (M. Blanco, personal communication). With their several hundreds, if not thousands, of orchid species, the Neotropics secretly hold a considerable share of fascinating orchid–pollinator interactions that call for greater scrutiny.

Not all sexually deceptive orchids have evolved the use of alkenes as pollinator attractants. For example, in the case of the European mirror orchid (*O. ciliata* = *O. speculum*), the patterns of cuticular hydrocarbons and their unsaturated derivatives identified in both the female scoliid wasps and the orchid flowers failed to trigger mating behaviour in males of *Dasyscolia* (= *Campsoscolia*) *ciliata* (Fabricius, 1787). Instead, it was discovered that oxygenated carboxylic acids ((ω -1)-hydroxy and (ω -1)-oxo acids, especially 9-hydroxydecanoic) were the key compounds in the female sex pheromone of *D. ciliata* and that they were also produced by the flowers of the mirror orchid (Ayasse et al. 2003; see also Gögler et al. 2009). In Australia, species of the genus *Chiloglottis* R. Br. (Orchidaceae) attract their pollinators, male thynnine wasps, by emitting variations on the theme of a single odour compound, 2-ethyl-5-propylcyclohexan-1,3-dione (aka chiloglottone), that also also used by the female wasps as the source of their sex pheromone (Schiestl et al. 2003; Schiestl and Peakall 2005; Poldy et al. 2008; Franke et al. 2009; Peakall et al. 2010). Here too, the sexually deceptive orchids are reported to be more attractive than the thynnine females, but the reason for this “supernormal stimulation” lies in the higher absolute amounts of chiloglottone released by the orchid species compared with the female wasps (Schiestl 2004).

Collectively, even though the chemical characterization of pollinator attractants in sexually deceptive orchids is still in its infancy, these milestone contributions have pinpointed the signal basis for the mimicry of female insects by the orchid flowers. The chemical analyses performed suggest that the patterns of the odour compounds released by the flowers might be species-specific (see Schiestl et al. 2004), a finding that is consistent with the species-specificity of insect sex pheromones (e.g., Wyatt 2003; but see Schiestl and Peakall 2005). Schiestl and Ayasse (2002) have tested this hypothesis indirectly by investigating two sister orchid species in the *Ophrys fusca* group. Their results provide evidence for species-specific patterns of odour compounds between two orchid species that are reproductively isolated through the species-specific attraction of different pollinator taxa. The compounds involved in the specific attraction of the male bees comprised a small set of cuticular hydrocarbons, particularly monounsaturated ones (alkenes) identical in nature to those identified in *A. nigroaenea* and *O. sphegodes* by Schiestl et al. (1999), and the authors have shown that the floral scent differences between the two orchid species investigated concern mainly the patterns of alkenes (Schiestl and Ayasse 2002). A next step in these investigations was performed by Stöckl et al. (2005) and Cortis et al. (2009) who, based on the study by Schiestl and Ayasse (2002), have enlarged the systematic framework to encompass a selection of *Ophrys* species pollinated specifically by several male bees. Their results show that the *Ophrys* species associated with the same pollinator taxa, independent of their phylogenetic relatedness, use similar patterns of identical

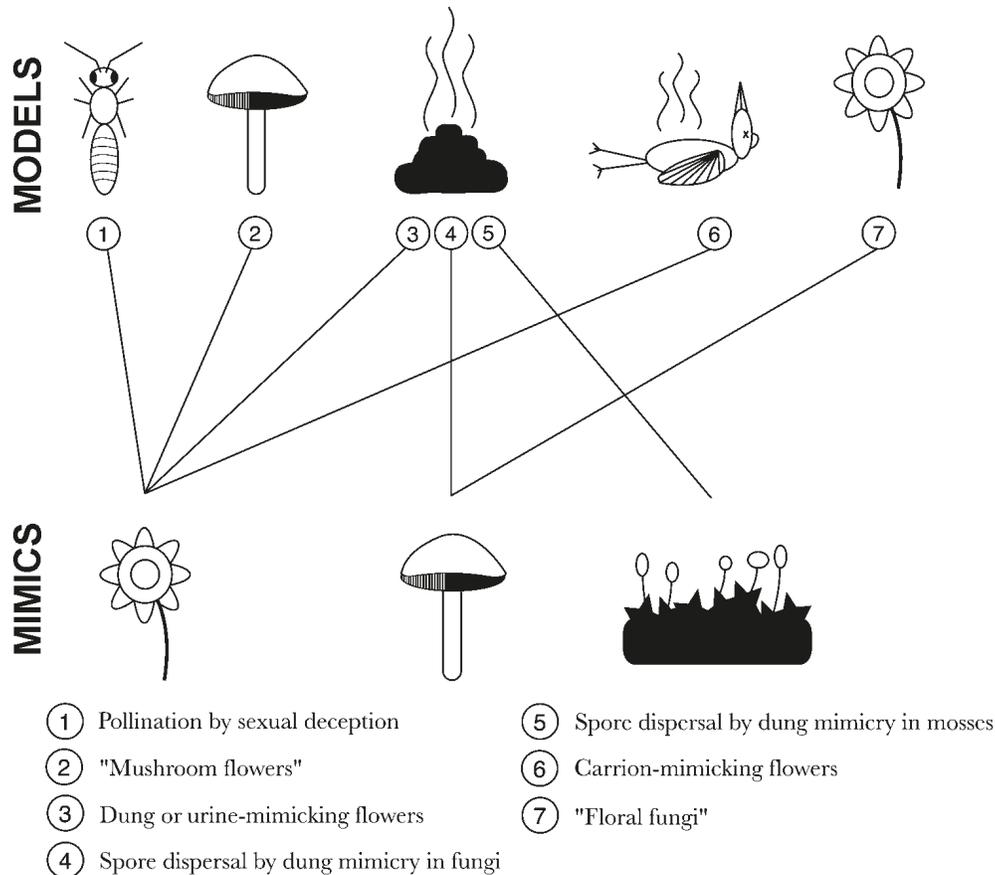
odour compounds as pollinator attractants (Stöckl et al. 2005; Cortis et al. 2009). These studies provide illustrative examples of the phenotypic consequences of convergent evolution towards the specific attraction of the same insect species that uses a specific chemical communication channel, and it shows that pollinators can impose selection on the patterns of specific sets of odour compounds. The latter point has been specifically addressed by Mant et al. (2005b), who found important levels of floral odour differentiation among allopatric populations within species, among allopatric species, and among sympatric species in their investigation of several *Ophrys* taxa in southern Italy. Furthermore, they found that the patterns of active compounds from *C. cunicularius* (Mant et al. 2005a), especially of alkenes, were more strongly differentiated among conspecific populations than nonactive compounds in the floral scent, which suggests that pollinator preferences for certain odour bouquets can drive the divergence of floral scents among populations and species in sexually deceptive orchids (Mant et al. 2005b).

Dispersal by substrate mimicry

Carrion and dung mimicry in angiosperms

To most people, plants are usually stereotyped as having beautiful, bright coloured flowers, emitting delicate odour bouquets such as that of jasmine, rose, and ylang, which have become key ingredients in today’s fragrance industry (Kaiser 1993, 2006a, 2006b). However, several groups of plants have adopted radically different olfactory standards that challenge the popular notion of floral scents. They are called sapro(myo)philous plants: their flowers are often dark, with an appearance similar to meat, and they give off strong odours that are, to the human nose, reminiscent of faeces, rotting meat, over-ripe cheese, and urine (Fig. 3). These odours may appear disagreeable to many animals and it has been proposed that they may deter herbivores and florivores (Lev-Yadun et al. 2009). However, they are powerful attractants for scavenging insects, mostly carrion or blow flies, but also a range of carrion and dung beetles that live on putrefying organic remains (Knoll 1926, 1956; Proctor and Yeo 1972; Bristow 1978; Dafni 1984; Barth 1991; Bänziger and Pape 2004). Once drawn to the flowers by the putrid odour, these insects serve as pollinators. Usually the diurnal insects are trapped in a chamber containing clusters of female flowers, at least in the aroid-type plant species, and are prevented from escaping by a barrier of spines. Consequently, any pollen the insect is carrying from a previous flower visit is likely to be delivered onto the stigmatic surface of the female flowers. During the following night, the spines degenerate allowing the insect to escape. However, at this time the male flowers start liberating pollen and they are positioned in a way that forces the pollinator to come into contact with the pollen grains as it leaves (Knoll 1926; Dormer 1960; Proctor and Yeo 1972; Bristow 1978). The presence of fly eggs in the floral chamber of several saprophilous species supports the hypothesis that the pollinators do not discriminate between the model and the mimic, as sensory stimulation by the flowers results in a full behavioural sequence, including oviposition (Fig. 4A). This parallels the observations that male insects may be sufficiently stimu-

Fig. 3. A schematic view of interactions based on chemical mimicry discussed in the section on pollination and spore dispersal.



lated by the flowers of sexually deceptive orchids to the point of ejaculating (Coleman 1928; Gaskett et al. 2008). These findings suggest that depending on the species pairs, the intensity of behavioural responses triggered by the deceptive plants range from a brief stimulation or visit to more intense responses (e.g., by provoking egg-laying or high sexual arousal and ejaculation; see Vereecken 2009) that could potentially jeopardize the pollinators' reproductive output (see Wong and Schiestl 2002).

Species with carrion and dung flowers have been described from different plant families, mostly in the Apocynaceae, Araceae, Aristolochiaceae, Brumanniaceae, Hydnoraceae, Orchidaceae, Rafflesiaceae, and Taccaceae (Proctor and Yeo 1972; Faegri and van der Pijl 1979; Endress 1994; Kaiser 2006a, 2006b). This pollination strategy has not only become famous for its floral odour chemistry, but also because some of its representatives have evolved inflorescences out of scale with any other plant species in their habitat, let alone their ancestors with tiny flowers (Davis et al. 2007, 2008; Davis 2008). They include the stinking corpse lily (*Rafflesia arnoldii* R.Br.) with the largest single flower on Earth (up to 1 m across), the giant inflorescence of the titan arum (*Amorphophallus titanum* (Becc.) Becc. ex Arcang) (on average, higher than a tall human; Fig. 4B), the Brazilian Dutchman's pipe (*Aristolochia gigantea* Mart. & Zucc.) (Fig. 4C), and the dead horse arum (*Helicodiceros muscivorus* (L.f.) Engl.) (Fig. 4D). The mechanisms that have driven the evolution of such unusually large flowers and inflorescences remain obscure, but

Davis et al. (2008) have hypothesized that extreme size may help mimicking large animal carcasses and thereby enhance the plant's attractiveness towards pollinators.

Several of these flowers, particularly in the family Araceae, have also evolved the production of floral heat that may reach up to 20 °C above the ambient air temperature (Meeuse 1975; references in Dafni 1984; Lamprecht et al. 1991, 2002; Seymour and Schultze-Motel 1997, 1999; see also Patino et al. 2002), a phenomenon that presumably enhances the volatilization of the odours over greater distances. In the case of the skunk cabbage (*Symplocarpus foetidus* (L.) Salisb. ex W.P.C. Barton), a species that inhabits cold regions of the northern hemisphere, the production of heat can have the extreme side effect of melting of the snow around the plants in their natural habitat (Meeuse 1978). The dynamics of floral heat production in *H. muscivorus* have been characterized by Seymour et al. (2003a, 2003b), and Angioy et al. (2004) discovered that the production and temporal variation of floral heat in this species (the mimic) parallels the patterns observed in gull carcasses decaying through microbial processes (the model) on which the blow fly pollinators develop. Their results also provide evidence for an interplay between floral heat and odour in pollinator attraction, which shows that mimicry refinement in this species involves not only scent but also heat and possibly tactile stimulation, because the flowers of *H. muscivorus* are covered with hairs (Angioy et al. 2004).

The floral scent composition of carrion- and dung-mimicking species has been investigated for a wide range

Fig. 4. Some textbook examples of substrate mimicry by plants and fungi. (A) Blow flies laying eggs (see arrow) in a flower of the starfish cactus (*Stapelia grandiflora* Masson) (photograph by O. Rumény). (B) Inflorescence of the titan arum (*Amorphophallus titanum*) (photograph by B. Kusler). (C) Flower of the Brazilian Dutchman's pipe (*Aristolochia gigantea*) (photograph by L. De Volder). (D) Flower of the dead horse arum (*Helicodiceros muscivorus*) (photograph by M. Stensmyr). (E) A colony of *Splachnum luteum* Hedw., a fly-dispersed moss from North America (photograph by B. Goffinet). (F) Detail of the pointed end of the common stinkhorn (*Phallus impudicus*) visited by a female of *Calliphora vicina* eating the gleba, a spore-containing jelly that is the source of the carrion odour (photograph by N.J. Vereecken). (G) Pseudoflower formed by the rust fungus (*Puccinia monoica*) complex on the genus *Boechera* A. Love & D. Love (Brassicaceae) (photograph by D. Waylett). (H) Detail of a flower of frog's skin (*Dracula chesteronii*) (photograph by T. Ditlevsen). Images appear in colour on the Journal's Web site and are reproduced with permission of the photographers.

of species (reviewed by Dobson 2006). The typical odours of rotting flesh (see Brown 1982) produced by a range of Araceae contain dimethyl oligosulfides that are also produced by decaying meat (Kite and Hetterscheid 1997; Stránský and Valterová 1999; Stensmyr et al. 2002). There also may be other compounds in these bouquets, such as monoterpenoids (e.g., linalool, *Z/E*-ocimene, nerol, limonene, β -citronellene), benzenoids (benzaldehyde, *p*-cresol, phenylacetaldehyde, 2-phenylethyl acetate, and methyl salicylate) (Kaiser 1993, 2006a, 2006b; Kite 1995; Kite et al. 1998; Diaz and Kite 2002; Gibernau et al. 2004a; Jürgens et al. 2006, 2008). Jürgens et al. (2008) performed extensive chemical analyses of the floral scents of Apocynaceae and suggested that although we tend to merge all these rather "unpleasant" odours under the concept of sapro(myo)phily, some patterns emerge and different subclasses of substrate mimicry may exist (see Table 1). This subdivision is as debatable as the concept of pollination syndromes (see Herrera 1996; Waser et al. 1996; Fenster et al. 2004), as many substrate-mimicking species emit a large and diverse spectrum of odour compounds (sometimes up to 100 or more; Dobson 2006; Jürgens et al. 2008), and hence will not strictly match any of the categories, such as strong cheese, spent firecrackers, or dead freshwater fish (mentioned by Smith and Meeuse 1966; Chen and Meeuse 1971; Kite and Hetterscheid 1997). However, this classification provides a preliminary touchstone with a relatively strong predictive value that can be used in future attempts to uncover the details of the pollination biology and the odour convergence of flowering plants to different adaptive peaks in the olfactory landscape of saprophily (see Raguso 2003; Ollerton and Raguso 2006). To date, the studies by Stensmyr et al. (2002) and Angioy et al. (2004) on *H. muscivorus* (Fig. 4D) represent the most detailed account on the pollination biology in this mimicry system. By coupling gas chromatographic analyses to electroantennographic detection (GC-EAD), Stensmyr et al. (2002) have identified a trio of biologically active oligosulfides in the floral scent (dimethyl mono-, di-, tri-sulfides) that are also produced by decaying gull carcasses and used by the pollinators, calliphorid blow flies (*Calliphora vicina* Robineau-Desvoidy, 1830 and *Lucilia caesar* (L., 1758)), to locate appropriate egg-laying substrates (Stensmyr et al. 2002).

Although there is strong evidence that dipterans predominate in pollinator lists of carrion- and dung-mimicking species (Proctor and Yeo 1972; Ollerton and Liede 1997; Gibernau et al. 2004b), the particular adaptations of most species towards their associated insects and the extent to which these pollination systems are specialized or generalized remain obscure. For example, although the floral scent

of *Aristolochia gigantea* (Fig. 4C) has been shown to have approximately 100 odour compounds, there are still no pollinator records for this species, which hinders further studies on the chemical ecology of this spectacular species (R.A. Raguso, personal communication). Likewise, the floral scent of 18 *Amorphophallus* species has been investigated (Kite and Hetterscheid 1997), but the pollinators of most of these species, including the *Amorphophallus titanum* (Fig. 4B), are still virtually unknown.

It may seem logical to refer to this mimicry system as a case of pollination by deceit, as flowers are unlikely to support the full development of fly eggs and maggots in most cases (but see Wiens 1978; Simpson and Neff 1981). However, it is tempting to ask if the pollinators could derive benefits from their interactions with these plants and if other classes of pollinators could be attracted by the flowers. As mentioned above, floral scents in these species is often accompanied by the production of floral heat and the inevitable by-product, CO₂. Floral heat itself has been suggested as a reward for insect pollinators (Kevan 1975; Cooley 1995; Seymour et al. 2003a, 2003b; Sapir et al. 2006; Rands and Whitney 2008; but see Knoll 1926), because as exotherms their body temperature is markedly affected by ambient temperatures. This scenario would make sense in cold habitats, but no study has investigated this aspect for carrion- and dung-mimicking species and it seems unlikely in these cases that floral heat could represent a reward for their pollinators. The production of CO₂ during heat outbursts also raises the question of whether this could widen the range of pollinators by attracting blood-sucking or nectar-seeking insects. CO₂ is a major attractant for blood-sucking insects in other contexts (see Lehane 1991; Barrozo and Lazzari 2004) and could explain their attraction to *Arum rupicola* Boiss. (= *Arum conophalloides* Kotschy ex Schott), *Arum jacquemontii* Blume, and other species (e.g., Thien 1969; but see Jhumur et al. 2007). The production of floral nectar is also sometimes paralleled by the emission of CO₂ (Goyret et al. 2008), and a fraction of the gas could dissolve in nectar (for the accumulation of odour compounds in nectar see Raguso 2004) and ultimately represent a reliable indicator of the presence of nectar for foraging insects such as bees. A recent study by Diaz and Kite (2006) has provided further evidence (see references in Dafni 1984) challenging the idea that all *Arum* species are saprophilous. They found that the most effective pollinator and outcrossing vectors of *Arum creticum* Boiss. & Heldr. were not flies or beetles searching for oviposition sites, but rather female bees of *Lasioglossum marginatum* (Brullé, 1832) that collect pollen and store it in their underground cell as food for their developing young. It seems that even the "duped" pollinators of saprophilous



A B
C D
E F
G H

Table 1. Floral scent composition and categories of saprophilous mimicry proposed by Jürgens et al. (2008).

Trends in floral scents	Syndromes (or adaptive peaks in the olfactory landscape) of saprophily
High amounts of <i>p</i> -cresol, low amounts of polysulfides	Mimicry of herbivore dung
Low amounts of <i>p</i> -cresol, high amounts of (dimethyl) oligosulfides	Mimicry of carnivore or omnivore carrion or dung
High amounts of heptanal and octanal	Mimicry of carnivore or omnivore carrion or dung
High amounts of hexanoic acid	Mimicry of urine

species occasionally eat pollen grains or nectar produced by the flowers (Meeuse 1978; Dafni 1984; Gottsberger and Amaral 1984 and references therein) so that at least some reward—albeit presumably not the one expected by the insect—is available. A similar disconnect between the rewards offered and what the advertisement made by the flowers is found in the European orchids broadleaf helleborine (*Epipactis helleborine* (L.) Crantz) and violet helleborine (*Epipactis purpurata* Sm.). These orchids attract social wasps of the genera *Dolichovespula* Rohwer, 1916 and *Vespula* Thomson, 1869 as pollinators (Darwin 1862; Müller 1873; Knuth 1909; Judd 1972; Proctor and Yeo 1972) by emitting green-leaf volatiles. These compounds are released by cabbage leaves following herbivory by caterpillars of the cabbage white butterfly (*Pieris brassicae* (L., 1758)), which the wasps use as an olfactory cue when foraging for their prey (Brodmann et al. 2008). Obviously, in the orchids there are no caterpillar prey for the wasps, but the flowers' hypochile (a cup-like, basal part of the lip) is filled with a large amount of nectar containing narcotic compounds such as 3-{2-[3-(3-(benzyloxy)propyl)-3-indole, 7,8-didehydro-4,5-epoxy-3,6-D-morphinan, and oxycodone (Jakubska et al. 2005) that might promote constancy or addiction in the insects as well.

Spore dispersal in dung mosses

About one half of extant representatives of the moss family Splachnaceae are known to develop on decaying organic matter, particularly animal dung (Koponen and Koponen 1978; Cameron and Wyatt 1986; Marino 1988, 1991a, 1991b, 1997; Koponen 1990). These so-called dung mosses have evolved unique suites of morphological and chemical adaptations to insect-mediated spore dispersal. Entomophily (or more precisely “entomochory”, meaning dispersal by insects) is thought to be a derived condition with multiple independent origins in this group of seedless terrestrial plants whose spores are otherwise dispersed by wind, although entomophily may be the ancestral condition followed by multiple losses (see Goffinet et al. 2004; Marino et al. 2009). The sporophytes (the spore-producing structures) of these mosses display species-specific combinations of colours (Fig. 4E) and odours that are not found in wind-dispersed relatives (Pyysalo et al. 1978, 1983). The various combinations of capsule colour and volatile chemical emanating from them entice a relatively large taxonomical range of spore-carrying flies that visit the sporophytes. Visitation time is brief, as rewards are consistently lacking (Cameron and Troilo 1982; Marino 1997). This phenomenon suggests that these mosses exploit their associated insects to transport their asexual spores to suitable substrates for germination, drawing interesting parallels between this system and the deceptive pollination of flowering plants described above.

Several authors have investigated the chemistry of the dung-moss odours in the late 1970s and early 1980s (Koponen and Koponen 1978; Pyysalo et al. 1978, 1983). These studies have shown that the sporophytes emit odour compounds typically found in faeces and urine. These include trimethylamine (Koponen and Koponen 1978), but also octane derivatives, sour-smelling organic acids such as phenylacetic acid, benzoic acid (Pyysalo et al. 1978, 1983), and benzyl alcohol (Pyysalo et al. 1983). Recently, Marino et al. (2009) characterized the role of the odour and visual signals involved in the attraction of flies by the sporophytes. Their results largely confirm the early findings mentioned above, and headspace trapping combined with gas chromatography and mass spectrometry (GC-MS) has allowed the identification of a selection of compounds typical of mushrooms (1-octene-3-ol), rotting flesh (dimethyl disulfide and trisulfide), herbivore dung (cresol, indole, and phenol), and even mammalian urine (cyclohexane carboxylic acid esters and heptanal). Marino et al. (2009) suggested that contrary to colour signals, which are found in unrelated anemophilous taxa, the sporophyte odours in this group of mosses should be considered a key innovation for spore dispersal by insects, although colour and odour seems to be required to attract the full range of spore-dispersing flies in natural environments. Trapping experiments performed in situ have revealed that the attraction of flies by the sporophytes shows only little taxonomic overlap among sympatric moss species, which suggests that the differences observed in moss substrate specificity may be the direct outcome of resource constancy or specialization in the guilds of fly species that visit the sporophytes (Marino 1991b; Marino et al. 2009).

Fungi, “mushroom flowers”, and their insect vectors

Flowering plants and fungi may belong to different kingdoms, but nonetheless they share many characteristics of their life cycle. Like plants, most fungi have a vegetative phase followed by a reproductive one (except in the Deuteromycetes) during which a special reproductive structure or a fruiting body analogous to the flowers and inflorescences produces sexual spores for dissemination. The fungal spores are usually dispersed by wind, aided by the turbulence of the air in their surrounding environment, and sexual reproduction is generally achieved when contact is made between the nuclei of two mating types (Deacon 2005; Webster and Weber 2007). Like plants, several groups of fungi have also evolved highly elaborate interactions with different groups of insects that feed on their reproductive structure and also help in dispersing their spores. One such group comprises the so-called fungus gnats, dipterans of the families Bolitophilidae, Diadocidiidae, Ditomyiidae, Keroplatidae, Mycetophilidae, and Sciaridae, which are common pests of seedlings, houseplants, and ornamentals. The role of fungus

Table 2. Floral scent compounds used by “rust fungi” to attract their “pollinators”.

Species pair investigated	Odour compounds emitted by the pseudoflowers	References
Common barberry (<i>Berberis vulgaris</i> L.) – <i>Puccinia arrhenatheri</i> (Kleb.) Erikss.	Indole, methyl nicotinate, jasmine lactone, γ -jasmolactone, carvacryl methyl ether	Naef et al. 2002
Canada thistle (<i>Cirsium arvense</i> (L.) Scop.) – creeping thistle rust (<i>Puccinia punctiformis</i> (F. Strauss) Röhl.)	Indole, phenylacetaldehyde, 2-phenylacetyl alcohol	Connick and French 1991
<i>Puccinia monoica</i> complex and their Brassicaceae hosts (<i>Arabis</i> sp. and others)	Phenylacetaldehyde, 2-phenylethyl alcohol, benzaldehyde, methylbenzoate	Roy and Raguso 1997; Raguso and Roy 1998
Cypress spurge (<i>Euphorbia cyparissias</i> L.) – pea rust (<i>Uromyces pisi</i> (Pers.) de Bary) complex	Indole, jasmine lactone, 1-pyrroline	Kaiser 2006a, 2006b
<i>Uromyces verrucosae-craccae</i> Mayor	(<i>E,Z</i>)-5,7-Decadien-4-olide (derived from linolenic acid)	Kaiser 2006a, 2006b

gnats as pollinators of flowering plants seems quite limited (Vogel 1978; Okuyama et al. 2004, 2008 and references therein; Goldblatt et al. 2004; Blanco and Barboza 2005). However, a series of recent studies on the genus *Epichloë* (Fr.) Tul. & C. Tul. (Clavicipitaceae) has shown that the flies of the genus *Botanophila* Lioy, 1864, which “pollinate” this obligate outcrossing fungus (Schardl 1996), are attracted primarily by two uncommon odour compounds, namely the sesquiterpene alcohol (chokol K) and methyl (*Z*)-3-methyldodec-2-enoate (Schiestl et al. 2006; Steinebrunner et al. 2008a, 2008b, 2008c). These two compounds are thought to be specific to *Epichloë*, and Steinebrunner et al. (2008a, 2008b, 2008c) have hypothesized that chokol K is an antimicrobial compound that has evolved secondarily as a pollinator attractant.

More parallels between flowering plants and fungi can be made when considering the sexual reproduction of stink-horns, a group of fungi that are renowned for the shape of their fruiting bodies, which are similar in shape to an erect penis. This resemblance is so obvious that one of the stink-horns was even named *Phallus impudicus* L. (the “shameless penis”). The odour bouquet emitted by its reproductive structure is particularly dominated by dimethyl disulphide and dimethyl trisulphide, which as we have seen above (Table 1), are characteristic of carrion and dung mimicry (Borg-Karlson et al. 1994), although Borg-Karlson et al. (1994) have also identified linalool, *trans*-ocimene, and phenylacetaldehyde in the scent of this species. Thus, not surprisingly, this stinkhorn species exploits carrion flies for the dispersal of its spores. The attractive compounds are emitted by the gleba, a slimy jelly covering the knob of the reproductive structure that contains the spores, on which the flies feed, sometimes several individuals at a time (Fig. 4F).

At the other end of the olfactory spectrum, some representatives of the “rust” fungi (Basidiomycota, Uredinales) have evolved the production of floral odour compounds to attract their spore vectors (Kaiser 2006a, 2006b; Ngugi and Scherm 2006). These fungi are obligate parasites and cause systemic infections in their host plants that result in the formation of “pseudoflowers”. For example, leaves of different host species infected by rust fungi in the genus *Puccinia* Pers. (Pucciniaceae) turn into a relatively accurate impersonation of yellow flower petals found in the Brassicaceae and Ranunculaceae (Fig. 4G). Several studies have shown that the scent and colours of infected leaves indeed lure insects that mediate spore dispersal during their visits and take up

some droplets of sugar water produced by the fungus in the process (Gäumann 1959; Roy 1993; Pfunder and Roy 2000; Naef et al. 2002). The chemistry of this interaction has been investigated by several authors and the results show that the infections by the rust fungi tend to produce very similar odour blends, often composed of indole, phenylacetaldehyde, jasmine lactone, 2-phenylethyl alcohol, and other compounds in varying proportions (see Table 2 and references therein). These compounds are ubiquitous in floral scents (Knudsen et al. 2006) and are renowned attractants, sometimes with a pheromonal function (El-Sayed 2008), for a wide taxonomic range of insects. It is interesting to note that the scent emitted by the pseudoflowers differ both quantitatively and qualitatively from the scent of the infected host plants and that of other uninfected co-blooming plants (Roy and Raguso 1997; Raguso and Roy 1998; Kaiser 2006a, 2006b). In bioassays with the “pollinators” of *Puccinia monoica* Arthur, Roy and Raguso (1997) have shown that among the visitors, halictid bees were attracted by a blend of the major compounds in the same relative concentrations as in pseudoflowers, suggesting that the scent emitted by the latter was sufficient to attract insects. However, the relative role of visual versus olfactory cues in triggering visits by either halictid bees or flies (the other group of visitors) appears largely dependent upon the interacting species under consideration. Many other examples of insect–fungus interactions are known, but only few of them have received attention, particularly with respect to the “pollinator” attractants and the pollinators’ preferences.

This hijacking of plant–pollinator interactions by fungi species to enhance their reproductive output by co-opting insects as spore-dispersal agents is spectacular, but “reverse” scenarios also have been reported in some flowering plants and the best known cases, at least from a chemical perspective, are endemic to the Neotropics. For example, the rainforests of the Colombian Andes are home to frog’s skin (*Dracula chestertonii* (Rchb. f.) Luer), an orchid whose lip mimics the fruiting body of small fungi with lamella-like structures, pore imitations (Fig. 4H), and by emitting a typical “mushroom” scent composed of oct-1-en-3-ol, oct-1-en-3-one, octan-3-ol, and octan-3-one (Kaiser 1993, 2006a, 2006b). This combination of characters appears irresistible to fungus gnats that visit and pollinate these orchid flowers as they lay eggs on the involutions of the flowers’ pseudo-lamella. However, much like the situation observed in the carrion- and dung-mimicking species described above, the

flowers of *D. chestertonii* do not support the larval development of the insect pollinators (Vogel 1978; Stowe 1988; van der Cingel 2001). A similar pollination strategy is apparently found in *Aristolochia arborea* Linden, a small tree native to Central America. Its flowers and the small bogus fruiting body found deep inside them have a weak scent that contains α -pinene, camphene, β -pinene, sabinene, limonene, β -cedrene, caryophyllene, germacrene D, bicyclogermacrene, germacrene A, and germacrene-1(10),5-dien-4-ol (Kaiser 2006a, 2006b). Many more plant species in different families, including the orchid genera *Corybas* Salisb. (Orchidaceae) and *Cypripedium* L. (Orchidaceae), seem to use this fungus gnat pollination syndrome (Vogel 1978), but the details of their floral odour chemistry and pollination biology remain unknown.

Mimicry in predation and parasitism

The chemical ecology of nest invaders

Cuckoo bees and their hosts

Tengö and Bergström (1975, 1976, 1977) investigated the chemistry of host–parasite interactions, using species of the cuckoo bee genus *Nomada* Scopoli, 1770 (Apidae) and their associated hosts, species of the bee genera *Andrena* (Andrenidae) and *Melitta* Kirby, 1802 (Melittidae). Their results show an important qualitative correspondence between the major odour compounds produced by the mandibular glands of the *Nomada* males and the abdominal Dufour's gland of their hosts' females. These volatile lipids (geranyl octanoate or farnesyl hexanoate in *Nomada–Andrena* and octadecyl butyrate in *Nomada–Melitta*) have not been identified in the mandibular glands of the female host bees (Tengö and Bergström 1977). Compounds identified in the Dufour's gland secretions of nonparasitic female bees have waterproof and antimicrobial properties when used by the female to coat her underground brood cells (Hefetz et al. 1979; Cane 1981). J. Tengö and G. Bergström suggested that the *Nomada* males transfer these “host-mimetic” odour compounds to their conspecific females during mating. According to their scenario, this chemical camouflage presumably helps the gravid cuckoo females to invade their hosts' nests undetected, thus avoiding fights with host females by having the scent of a conspecific (for a review see Bergström 2008).

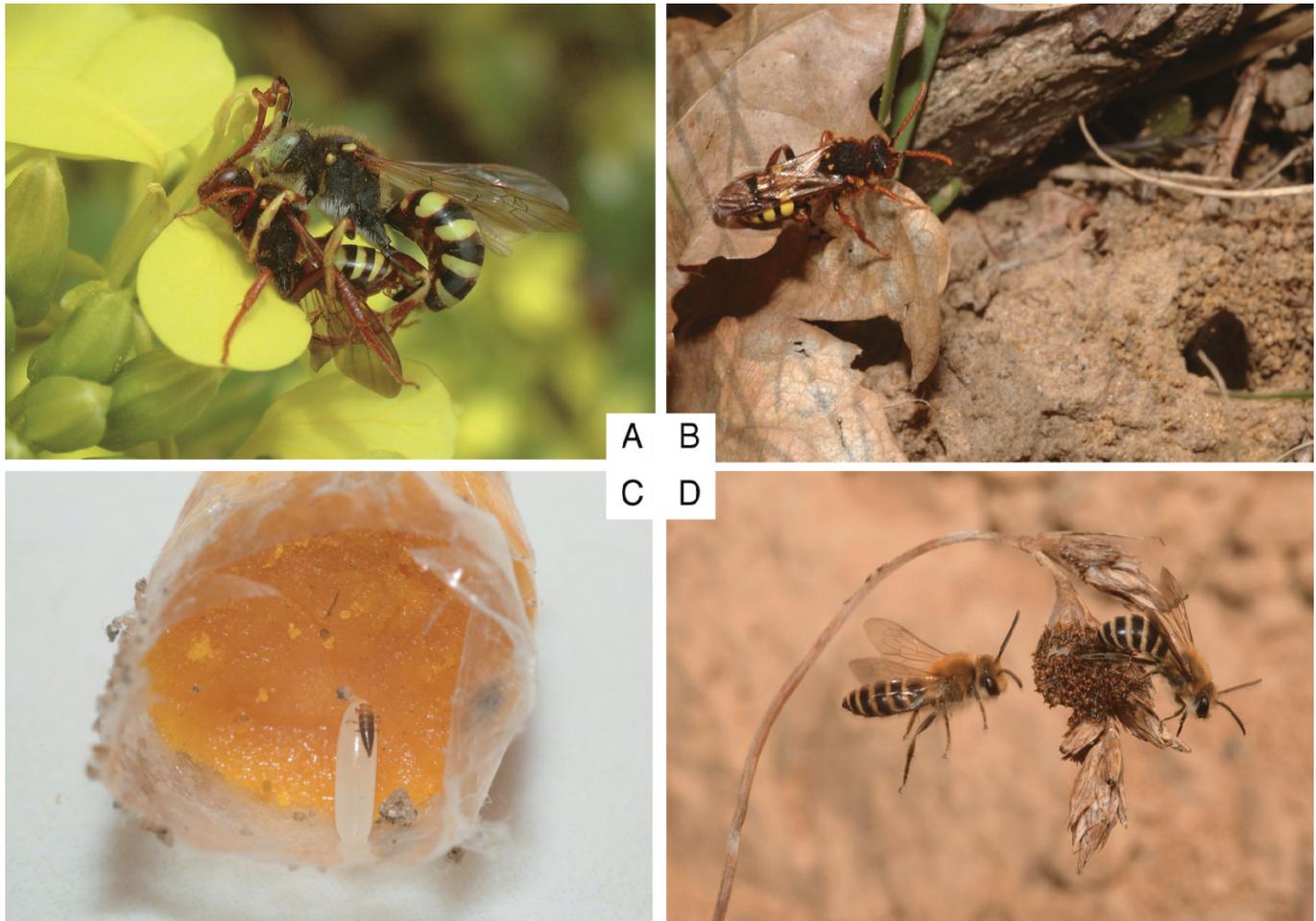
Although the evidence for a chemical similarity between the *Nomada* males and the females of their associated hosts is indisputable, behavioural evidence and experimental studies remain to be done. Observational evidence suggest that this camouflage, or “wolf in sheep's clothing” strategy of *Nomada* females might not be the prevailing mechanism by which the parasites slip into their hosts' nests. First, observations of antagonistic interactions between *Andrena* females at nest entrances indicate that fights do occur among conspecifics: in noncommunal nesting species, each female actively protects its nest to the point of attacking intruders, including conspecifics (N.J. Vereecken, personal observation). Second, antagonistic interactions between *Nomada* females and their hosts have been regularly observed, both within the nest (Mohra et al. 1999; Schindler 2005) and at the nest entrance (Eickwort and Abrams 1980; Cane 1983; Schindler 2005). Third, parallel studies on the composition

of natural extracts have failed to provide evidence for congruence in odour between the *Nomada* females and their associated hosts (Duffield et al. 1984), except in one study on *Nomada marshamella* (Kirby, 1802) and its communal host *Andrena carantonica* (= *Andrena scotica*) Pérez 1902 (Fleck 1995). Finally, recent investigations into the mating behaviour of *Nomada fucata* Panzer, 1798 and *Nomada lathburi-ana* (Kirby, 1802) have shown that a male typically winds his antennal flagellae around the female's during courtship and then pulls them upwards so that they glide over the female's (Fig. 5A). Males of different *Nomada* species have specialized antennal glands that may secrete sex pheromones onto the female antennae during mating (Schindler 2005). This stereotyped behavioural sequence differs from the courtship behaviour described by Tengö and Bergström (1977) and the apparent contradiction between their mimicry hypothesis and these recent observations on the behavioural ecology of *Andrena–Nomada* certainly merit further investigations. A particularly promising research avenue would be to compare the similarity in odour signals between *Nomada* species and their associated host species, contrasting those that associated with communal versus solitary nesting species. *Nomada* females that parasitize solitary nesting *Andrena* bees are often found patrolling nesting sites and inspecting nest entrances of their hosts; the cuckoos sometimes wait in ambush for several minutes close to the nest (Fig. 5B) until the female host leaves for a foraging bout before infiltrating the burrow to lay their eggs. In contrast, cuckoo bees associated with communal nesters face a more important challenge: there will always be one or more females inside the nest, or at least close to the nest entrance, to contest the entry of intruders. Under such circumstances, *Nomada* species may have evolved adaptations such as mimicry or camouflage to help them gain access to the underground brood cells without being attacked by the hosts inside the nests. The modern analytical techniques available for the study of odour compounds (e.g., Blomquist and Vogt 2003; Tholl and Röse 2006), combined with breeding experiments of the host bees and their associated cuckoo species (Schindler 2005), should now permit a rigorous testing of J. Tengö and G. Bergström's mimicry hypothesis in *Andrena–Nomada* interactions. However, it must be remembered that when testing the hypothesis through in-depth behavioural and experimental studies, the results from such studies may differ substantially from one host–parasite interaction to the next. For example, Sick et al. (1994) found evidence for intranest antagonistic behaviour between several cuckoo bees of the genus *Sphecodes* Latreille, 1804 (Halictidae) and their associated solitary or social bee hosts. Furthermore, they found that the Dufour's gland volatiles from the cuckoos and their associated hosts are not similar, so these findings do not lend support to the mimicry hypothesis. However, recent work on the European beewolf (*Philanthus triangulum* (Fabricius, 1775)) showed that the patterns of cuticular hydrocarbons are similar to those of the host female, and thus would support J. Tengö and G. Bergström's hypothesis (Strohm et al. 2008).

Meloid beetles and their bee hosts

Another group of insect parasites associated with solitary bees are meloids (also called blister beetles or oil beetles;

Fig. 5. (A) A mating pair of the cuckoo bee *Nomada lathburiana*. (B) A female of *N. lathburiana* inspecting the nest entrance of its host, the mining bee (*Andrena vaga* Panzer, 1799). (C) A triungulin of the oil beetle (*Stenoria analis*) in a brood cell of a bee species belonging to the *Colletes succinctus* (L., 1758) group. Once inside the brood cell, the highly mobile triungulin will feed on the egg of its host, and then transforms into a grub-like larva that will go through a total of six metamorphoses leading to the pupal stage. (D) Two males of the European ivy plasterer bee (*Colletes hederæ*) attracted to a mass of triungulins of *S. analis* on a dried grass. All photographs by N.J. Vereecken except A, which was by M. Clénot. Images appear in colour on the Journal's Web site and are reproduced with permission of the photographers.



Meloidae), a large group of approximately 2500 species with a worldwide distribution (Bologna and Pinto 2001, 2002; Bologna et al. 2008). These beetles are unique in having a hypermetabolous larval development, which the French entomologist Jean-Henri Fabre termed “hypermetamorphoses” (Fabre 1857). Each meloid beetle larva develops through a series of instars, the first being the highly mobile “triungulin” which possesses adaptations that facilitate such activities as displacement, food seeking, grasping their hosts, and entering underground burrows. (Bologna and Pinto 2002). Some species parasitize bees and it is the triungulins (Fig. 5C) that invade the underground brood cells where the larvae feed on bee host larvae, as well as on the provisions (pollen, nectar) accumulated in the nest.

Although both the morphology and systematics of meloids have received considerable interest, the details of their ecology, in particular the modus operandi by which those that parasitize bees actually gain access to the resources of their

hosts, remain relatively obscure. Only very little is known beyond the name of one or a few host species for each meloid species. In some species, the triungulins are highly mobile and disperse after hatching to investigate their nearby environment for food (e.g., genus *Cysteodemus* LeConte, 1851 (Meloidae)), whereas in others (e.g., genera *Sitaris* Latreille, 1802 and *Hornia* Riley, 1877 (Meloidae)), the eggs are laid close to the nest entrance of their hosts, which facilitates the access of the underground burrows to these parasites. Finally, there are groups of species (e.g., in the genera *Meloe* L., 1758 (Meloidae) and *Stenoria* Mulsant, 1857 (Meloidae)) that cling onto the setae of their host and access the nest through “phoresy”, i.e., they are being transported onto the body of their host without directly parasitizing the latter (Clausen 1976). The phoretic triungulins typically climb on nearby flowers and inflorescences upon hatching, and attach to passing female bees that come to the plant to collect nectar and pollen. The triungulins are then ultimately trans-

ported to the host nest as the female bees discharge their loads in their underground brood cells. Fossil evidence suggest that the origin of such highly specialized host–parasite interactions can be traced as far back in time as the early Miocene (23.8–16.4 million years ago) (Poinar 1992) or the middle Eocene (48.6–37.2 million years ago) (Engel 2005), and molecular phylogenetic studies have reported that phoresy has evolved multiple times independently in the family Meloidae (Bologna and Pinto 2001).

At least two unrelated species of meloids that show adaptations for grasping their host in the first instar have evolved a means of attracting males of their solitary bee hosts by sexual deception instead of “patiently” waiting on flowers until a suitable bee host passes by. The first known case involves *Meloe franciscanus* Van Dyke, 1928 and its host, the digger bee (*Habropoda pallida* (Timberlake, 1937)), described from the Mojave desert in California, USA (Hafernik and Saul-Gershenz 2000), whereas the second concerns *Stenoria analis* (Schaum, 1859) and its host, the plasterer bee (*Colletes hederæ* Schmidt and Westrich, 1993), in France (Vereecken and Mahé 2007). In both instances, the freshly emerged triangulins actively aggregate on dead stems or twigs in the vegetation to form discrete, compact clusters. These masses of triangulins deceive patrolling males of the targeted host species in search of females into landing on the clusters and even attempting copulation with them (Fig. 5D). In the process, subgroups of triangulins attach to the male bees and are then either transferred onto the female bees during real copulations (Hafernik and Saul-Gershenz 2000) or brought back directly because the males regularly fly back to the nest during the day (Vereecken and Mahé 2007).

The interaction between *H. pallida* and *M. franciscanus* has received the most attention to date, including the chemical analyses of odour extracts made from the clusters of triangulins and the receptive female bees, along with behavioural bioassays in the extreme conditions of the Mojave Desert (Saul-Gershenz and Millar 2006). Their results show that the triangulins attract the patrolling males of their host by emitting odour compounds, particularly alkenes ((*Z*)-9-C23, (*Z*)-11-C23, (*Z*)-9-C25 and (*Z*)-11-C25) that correspond to a subset of key sex attractants also emitted by the receptive female bees. Several other species of solitary bees are known to use alkenes as the source of their sex pheromone, including *Amegilla dawsoni* (Rayment, 1951) (Simmons et al. 2003), *Andrena flavipes* Panzer, 1799 (Schiestl and Ayasse 2002; N.J. Vereecken, unpublished data), *A. morio* (Stöckl et al. 2007), *A. nigroaenea* (Schiestl et al. 1999), *C. cunicularius* (Mant et al. 2005a), alfalfa leafcutting bee (*Megachile rotundata* (Fabricius, 1793)) (Paulmier et al. 1999), and *Osmia rufa* (L., 1758) (Ayasse et al. 2000). Preliminary studies on the sex pheromone chemistry of *C. hederæ* indicate that alkenes are also present in solvent extracts of virgin females, as well as larval clusters of *S. analis*, and that these compounds are capable of triggering copulation attempts by the males on scented dummies (N.J. Vereecken, unpublished data). These data suggest that the two sexually deceptive meloid beetles have independently evolved towards the emission of alkenes, perhaps even identical compounds, as a mechanism to attract the male bees and, thereby, facilitate the infiltration of their host’s nest.

Whether this host exploitation strategy has evolved in other meloid beetle species is an open question, but we may hypothesize that in light of these recent discoveries, other cases are likely to be uncovered in the future. The degree of specificity of these mimicry systems also remains to be investigated, addressing questions like “do the triangulins attract males of only one species”, “how similar are the key odour compounds of the models and their mimics, or how “perfect” is the chemical mimicry”, and “what are the odour preferences of the dupes” (see Vereecken and Schiestl 2008; Vereecken 2009). Such studies will add important insights into the understanding of chemical mimicry in meloid beetles and they will help shed light on the selection pressures driving the evolution of sexually deceptive signals in this large group of insects.

Lycaenid caterpillars and ants

There are many thousands insect species whose life history involves either facultative or obligatory associations with ants (Holldobler and Wilson 1990). For the most part these associations are mutualistic, with ants gaining resources such as essential nutrients, whereas the partner species may suffer lower levels of predation or parasitism owing to the intervention of their attendant “body guards”. Myrmecophily has certainly been well documented for many lycaenid butterflies, with the caterpillar or pupal stages deploying a number of different means to ensure that they are attended rather than attacked by ants. These include specialized myrmecophilous glands that produce nutrient rewards and (or) chemical cues that serve as adoption or appeasement signals (see Fiedler et al. 1996; Pierce et al. 2002 and references therein). There is also evidence that lycaenids may actively recruit ants using chemical and mechanical signals (e.g., DeVries 1990; Axén et al. 1996; Travassos and Pierce 2000).

Many studies have examined the relative costs and benefits for both species involved in these mutualistic interactions (see Wagner 1993; Fiedler et al. 1996; Pierce et al. 2002 and references therein). However, mutualistic interactions may breakdown for several different reasons; the most obvious being local or widespread extinctions when perturbations significantly disrupt obligate mutualistic interactions (Sachs and Simms 2006). One of the means by which mutualism may break down is a shift from a mutualistic to a parasitic or predatory relationship (Sachs and Simms 2006), and a number of well-documented cases have been reported for lycaenid species, especially in the European large blue butterflies (*Maculinea* van Eecke, 1915 (Lycaenidae)) and in the Asian genus *Phengaris* Doherty, 1891 (Lycaenidae) (see Als et al. 2004 and references therein). Females of parasitic or predatory species lay their eggs on specific host plants and the young instar larvae develop as typical herbivores. However, once they reach the fourth instar, they fall to the ground; at which time they are located by foraging ants (usually genus *Myrmica* Latreille, 1804 (Formicidae)) and are carried back to the nest where they switch to a parasitic mode of development. Once in the ant nest, the majority of lycaenid species are true predators that feed on the ant colony, whereas a few are cuckoo species that are generally cared for by worker ants (see Als et al. 2001, 2004; Thomas and Settele 2004, as well as references therein).

The *Maculinea* larvae on the ground may be located and transported back to the nest by a number of different *Myrmica* species, many of which are unsuitable for the normal development of the parasitic larvae. For example, as shown for populations of *Maculinea rebeli* (Hirschke, 1904) in France and Spain, although more than two-thirds of all caterpillars are retrieved by nonhost ant species, more than 95% of all adults emerge from nests of one specific ant (*Myrmica schencki* Viereck, 1903) (Elmes et al. 1991; Thomas and Elmes 1998). Holldobler and Wilson (1990), suggested that the social parasites of ants would use a different array of cues, including chemical mimicry and (or) camouflage, to access host colonies. However, the fact that many “unsuitable” ant species collect *M. rebeli* larvae when they fall to the ground would suggest that if chemical cues are involved, they do not perfectly mimic *M. schencki*. The pre-adoption cuticular hydrocarbon profile of the caterpillars was relatively simple and resembled that of *M. rebeli* than other *Myrmica* species, although there was enough similarity to explain why larvae would be collected by other ant species in the genus (Akino et al. 1999; Schlick-Steiner et al. 2004; Schönrogge et al. 2004).

However, once retrieved and brought into the nest, a moderate chemical similarity to the host ant would most probably be insufficient to avoid detection as an intruder, an idea supported by the finding that within 2 days the acceptance of caterpillars was significantly higher in a colony of *M. schencki* than in the nonhosts *Myrmica sabuleti* Meinert, 1861 and *Myrmica rubra* (L., 1758) (Schönrogge et al. 2004). Thus, caterpillars would have to camouflage themselves through the acquisition of chemicals from the attendant hosts and (or) by synthesizing additional cuticular compounds that allow them to mimic their host. In their study, Akino et al. (1999) found that there was a significant change in the cuticular profile of caterpillars 7 days after adoption, with evidence that at least one compound was actively synthesized. A subsequent study by Schönrogge et al. (2004) found that 3 weeks after adoption, *M. rebeli* caterpillars had a similarity index of about 40% with *M. schencki* ants and retained this difference even when held for an additional 4 days without attendant ants. Interestingly, larvae that were held with nonhosts actually have a higher similarity with their attendant ants than those held with *M. schencki*, supporting the idea that *M. rebeli* uses camouflage when with nonhost ants. This would permit the caterpillars to survive in nonhost colonies when food resources are abundant (Schönrogge et al. 2004). However, Schönrogge et al. (2004) found that under conditions of food stress caterpillar survival was significantly lower in nonhost than host colonies and proposed that the marked decline in the similarity index when caterpillars were held alone for 4 days, accompanied with the synthesis of compounds that mimic their preferred host, *M. schencki*, would identify them as nest intruders and explain why *M. rebeli* larvae were eliminated.

It has been recognised for some time that lycaenid caterpillars and pupae produce sounds and that these auditory signals may play a role in the recruitment of attendant ants in mutualistic interactions (see DeVries 1990; Travassos and Pierce 2000; Pierce et al. 2002). Barbero et al. (2009) reported that queens of *M. schencki* produce specific auditory

signals that result in the higher expression of benevolent worker behaviours, particularly guarding, than those produced by conspecific workers. They also demonstrated that the larvae and pupae of *M. rebeli* produce auditory signals very similar to those of the ant queen. Thus, auditory mimicry combines with the abovementioned chemical mimicry to help *M. rebeli* exploit its ant host and could explain why, even under stressful conditions, these parasitic caterpillars retain their high position within the hierarchy of the nest.

A case of specific chemical caste mimicry has recently been reported in another lycaenid, *Niphanda fusca* (Bremer and Grey, 1852) (Hojo et al. 2009). In this cuckoo species, the caterpillars exploit colonies of the ant *Camponotus japonicus* Mayr, 1866, where they are tended preferentially by their hosts. There is a marked change in the cuticular chemical profile following adoption and this, in part, may result from the passive acquisition of hydrocarbons from attendant worker ants. However, discriminant analysis of the cuticular profiles of *N. fusca* and the different castes of *C. japonicus* show that the caterpillars most closely resemble adult males. This finding strongly supports the idea that the caterpillars also have the ability to synthesis specific cuticular hydrocarbons, as they normally would not come into contact with male ants. Hojo et al. (2009) note that males are present in the colony for many months and are very competitive when it comes to acquiring food through trophallaxis, and propose that caterpillars would, therefore, benefit from this specific chemical mimicry. This increased ability to attract attendant workers could work in conjunction with the caterpillar's glucose secretion that contains glycine, the latter lowering the threshold concentration for feeding and may permit the parasites to manipulate the worker ants (Wada et al. 2001),

Many of the *Maculinea* species are now endangered and is one group of Lepidoptera that have been highlighted for butterfly conservation efforts (Thomas and Settele 2004), so the greater our understanding of these specialized, multispecies interactions, the greater the probability of successful conservation program. Clearly, additional information on different aspects related to population and community ecology, such as relative importance of the distribution of the host plants on which early instars develop, as well as the distribution and diversity of potential ant colonies, at different spatial scales are required (e.g., Hochberg et al. 1992; van Dyck et al. 2000; Thomas and Elmes 2001; Mouquet et al. 2005; Anton et al. 2008). Furthermore, there is now increasing evidence that the number of ant species parasitized by a given lycaenid species may vary geographically (Als et al. 2001, 2004; Pech et al. 2007; Tartally and Varga 2008; Tartally et al. 2008; Witek et al. 2008). Consequently, more experimental studies are needed to provide a better understanding of the various steps of chemical mimicry that modulate the adoption and integration of a given parasite species into the nests of different host ants (e.g., Als et al. 2001; Schlick-Steiner et al. 2004).

The intensity of the chemical arms race between host and parasite could be modulated by the intensity of parasitism. Geographic mosaic models predict that there will hot spots and cold spots of coevolution, and in ant-lycaenid systems, it will only be advantageous for the ant at a given site to change its cuticular profile to facilitate discrimination between nest mates and nest parasites if the associated costs

are less than those resulting from parasitism. Nash et al. (2008) provided clear experimental evidence that this could occur in interactions with *Maculinea alcon* (Denis and Schiffermüller, 1775) and *M. rubra*, but not for *M. alcon* and *Myrmica ruginodis* Nylander, 1846, even though both host ants occurred sympatrically. They postulated that changes in the cuticular hydrocarbon profiles of *M. rubra* arose in response to high predation pressure because of hot spots that arose owing to the low level of gene flow between ant populations. In contrast, a higher level of gene flow between populations of *M. ruginodis* resulted in lower selection pressure and thus the absence of such chemical arms race hot spots. The authors suggested that these species-specific *M. ruginodis* cold spots might permit *M. alcon* to survive in areas where *M. rubra* nests are under strong pressure to chemically discriminate between nest mates and parasitic caterpillars. Thus, chemical mimicry scenarios may vary markedly both spatially and temporally and underscore the need to have a greater knowledge of these systems to improve the chances for successful conservation program.

Aggressive chemical mimicry in bolas spiders

Many parasitoids and predators eavesdrop on their potential prey using an array of direct and indirect chemical cues (Stowe et al. 1995), but a small number use deceitful chemical cues to attract prey. Several spider species are known to actually lure prey by imitating the female sex pheromone of different moth species (Stowe 1988; Yeargan 1994; Haynes and Yeargan 1999) and the best documented cases are those examining the bolas spiders, particularly the temperate, monovoltine species in the genus *Mastophora* Holmberg, 1876 (Araneidae) (Yeargan 1994). However, not a great deal is known even for these species, as they are both cryptic and nocturnal.

When foraging the immature bolas spiders remain motionless on leaf edges with their front two pairs of legs up in air, and feed primarily on adults of small Diptera (Yeargan 1994). Yeargan and Quate (1996) tested the hypothesis that the spiderlings attract prey with chemical cues using *Mastophora hutchinsoni* Gertsch, 1955, *Mastophora bisaccata* (Emerton, 1884), and *Mastophora phrynosoma* Gertsch, 1955, which are three North American species with similar hunting strategies. For each species, they baited sticky traps with either young male or female spiderlings and blank traps were used as controls. They found that, for each species, traps baited with spiderlings, regardless of sex, captured significantly higher numbers of the fly genus *Psychoda* Latreille, 1796 (Psychodidae) than controls. Furthermore, over the 2-year trial, >95% of all the adult *Psychoda* flies captured were male, strongly supporting the idea that aggressive mimicry of a female sex pheromone was being used. A detailed examination of the prey captured strongly suggested that although they all selectively prey on male *Psychoda* flies, each of the bolas spider species exploits different prey species. Spiderlings of *M. phrynosoma* caught mostly *Psychoda phalaenoides* (L., 1758), whereas those of *M. hutchinsoni* attracted mainly *Psychoda trinodulosa* Tonnoir, 1922. The situation was less clearcut for *M. bisaccata*. In the first year, the traps baited with spiderlings also captured *P. phalaenoides* and *P. trinodulosa*. However, in the

second year, the majority of moth flies captured in traps baited with *M. bisaccata* were *Psychoda satchelli* Quate, 1955, a species that was not attracted by the spiderlings of the other two species. Although the interyear differences may, in part, be due to different climatic conditions, the authors also raise the possibility that what is considered to be *M. bisaccata* may actually be more than one species (Yeargan and Quate 1996). Subsequently, Levi (2003) divided *M. bisaccata* into three species (*Mastophora bisaccata*, *Mastophora stowei* Levi, 2003, and *Mastophora yeargani* Levi, 2003). Overall, the data strongly suggest that the spiderlings of the different species are producing species-specific chemical cues to attract their prey.

Using the same experimental design, Yeargan and Quate (1997) also tested the hypothesis that the small male bolas spiders use the same hunting strategy as the spiderlings. In this 3-year study, they baited traps with individual *M. phrynosoma* and caught mainly *P. phalaenoides* and >96% of all *Psychoda* flies captured were male. Thus, adult bolas males would appear to use the same aggressive mimicry as spiderling stages, attracting male prey species by mimicking the female sex pheromone of the prey species that they exploit. The only pheromones identified in the Psychodidae have been from the genus *Lutzomyia* França, 1924, which serve as vectors of the parasite causing leishmaniasis in the New World. However, in these species of sand fly, the sex pheromones are produced by males (Hamilton et al. 2002; Brazil et al. 2009). Thus, if the foraging of young spiderlings and adult male bolas spiders is based on aggressive mimicry using olfactory cues that resemble female sex pheromones, it is clear that the chemical ecology of moth flies (subfamily Psychodinae) is very different than those of sand flies (subfamily Phlebotominae).

Clearly, additional work needs to be carried out to experimentally confirm that, as hypothesized, allomones are actually being produced. In addition, if present, it would be of interest to determine the pathways for the synthesis of such compounds and to what extent, both within and between species, their production varies as a function prevailing climatic conditions and (or) host availability. Such information would certainly help in our understanding of these specific predator-prey interactions, especially with respect to the extent that different bolas species mimic different prey species.

There also is a need for further research to determine where such chemicals are released. Both sexes of young spiderlings and the adult males have a row of bristles on the prolateral side of the first two legs, whereas females lose theirs during the later stages of immature development (Yeargan 1988, 1994). It is possible that these bristles only serve as a mechanical means of handling prey, but additional research should investigate whether they are involved in the production and (or) release of the allomones that attract male *Psychoda* flies. Lopez et al. (1985) have implicated the legs in the release of allomones by adult female *Mastophora*, and Stowe et al. (1987) noted that neither the bolas nor the webbing contain pheromone components. However, Lopez et al. (1986) reported that ampullate glands of the silk-forming apparatus of *Kaira alba* (Hentz, 1850) (which also attracts male pyralids as prey; see Levi 1993) contain adenocytes very similar to those found the pheromone producing glands of many insects.

Table 3. Volatile compounds emitted by hunting females of the bolas spiders *Mastophora cornigera* and *Mastophora hutchinsoni* (data from Stowe et al. 1987; Stowe et al. 1995; Gemeno et al. 2000).

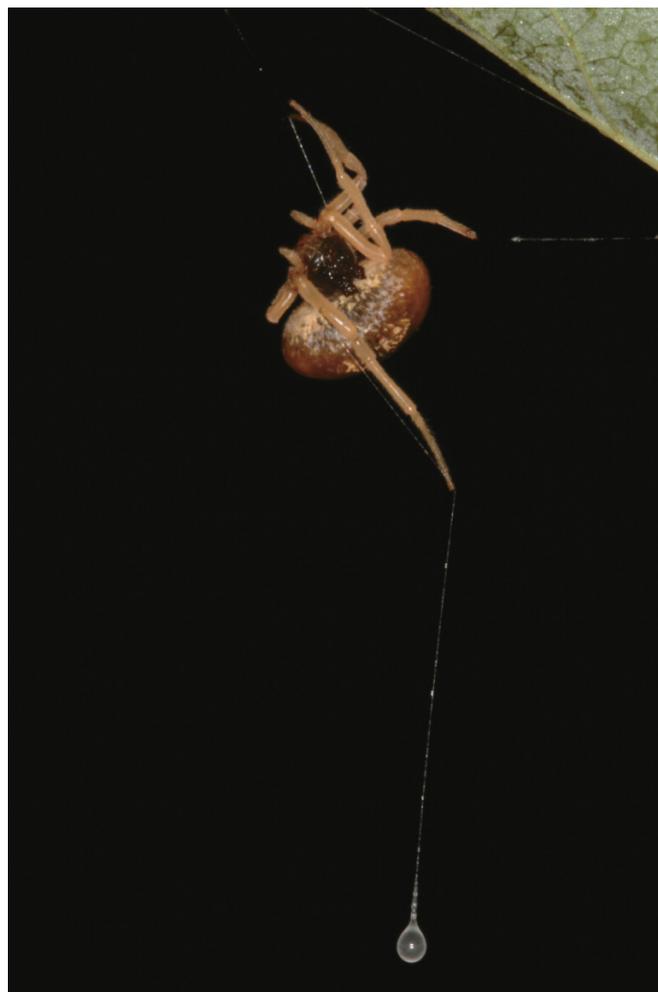
Compound	Abbreviation	Emitter
(Z)-9-Tetradecenyl acetate	Z9-14:Ac	<i>Mastophora cornigera</i> , <i>Mastophora hutchinsoni</i>
(Z)-9-Tetradecnal	Z9-14:Al	<i>Mastophora cornigera</i>
(Z)-11-Hexadecenal Z11-16:Al	Z11-16:Al	<i>Mastophora cornigera</i>
(Z)-11-Hexadecenyl acetate	Z11-16:Ac	<i>Mastophora cornigera</i> *
(Z,E)-9,12-Tetradecadienyl acetate	(Z,E)-9,12-14:Ac	<i>Mastophora hutchinsoni</i>

*Detected but not confirmed in subsequent analyses.

Advanced immature and adult female bolas spiders do not feed on dipterans but rather prey on the males of a few moth species, the large majority being noctuids (Stowe et al. 1987, 1995; Yeargan 1988). However, they still deploy a form of aggressive chemical mimicry, using components of female sex pheromones to attract potential prey. As in the case of spiderlings, the majority of detailed work on the chemical mimicry of female bolas spiders has been done on *M. hutchinsoni* and *Mastophora cornigera* (Hentz, 1850). All of the volatiles identified from hunting females of these two species are well-known components of female moth sex pheromones (Stowe et al. 1987, 1995; Gemeno et al. 2000; Table 3).

Male moths, attracted by these compounds, fly upwind to the hunting female and are captured with the sticky droplet at the end of the bolas (Fig. 6), at which time they are paralysed by biting and then generally wrapped in silk for later consumption. Females are able to detect the wing vibrations of an approaching male moth and use these cues to flick the bolas towards the potential prey. Interestingly, females in the hunting position (front legs extended) but with no bolas also emit moth pheromone components and use the auditory cues of an approaching moth to initiate bolas formation. This process takes about 2 min, so although the first approaching male moth is not likely to be captured, the female spider obtains information about the surrounding availability of prey (Haynes et al. 2001). Again the fact that females with the legs raised release significantly more allomones than those in a resting position or feeding supports the idea that the legs may be the release point of these infochemicals.

Stowe et al. (1987, 1995) reported considerable variability in the airborne volatiles from individual females and have suggested that females could produce different blends, as several prey species were captured by individual females. They noted that a total of 19 different prey species had been recorded for *M. cornigera*, with up to 9 different moth species being captured by one female. Z9-14:Ac, and possibly Z11-16:Ac, in the volatile emissions of *M. cornigera* are components of the female sex pheromones from six of the different prey species captured. Interestingly, although the production of Z11-16:Ac was not confirmed in the volatile emissions from *M. cornigera*, it is the major component of the armyworm (*Pseudaletia unipuncta* (Haworth, 1809)) and has proven effective as a lure for this species (Turgeon et al. 1983a, 1983b). *Pseudaletia unipuncta* is only one of three prey species captured by different species of bolas spider: by *M. cornigera* in California and *M. bisaccata* in Kentucky (Yeargan 1994). Thus, relying on common compounds

Fig. 6. A female spider of *Mastophora yeargani* with a bolas (photograph by and reproduced with permission of K. Haynes). Images appear in colour on the Journal's Web site.

found in an array of moth species could offer both temporal and spatial flexibility for hunting females.

The prey of *M. hutchinsoni* in Kentucky is composed of four moth species: bristly cutworm (*Lacinipolia renigera* (Stephens, 1829)), smoky tetanolita (*Tetanolita mynesalis* Walker, 1859), bronzed cutworm (*Nephelodes minians* Guenée, 1852), and bluegrass webworm (*Parapediasia teterella* (Zincken, 1821)) (Yeargan 1988). These moth species have very different female sex pheromones and (or) are attracted to very different lures (Clark and Haynes 1990; Haynes 1990; Haynes et al. 1996; Zhu and Haynes 2004; Table 4).

Table 4. Components identified in the sex pheromones of the smoky tetanolita (*Tetanolita mynesalis*), bristly cutworm (*Lacinipolia renigera*), and bronzed cutworm (*Nephalodes minians*), which are three noctuid moth species frequently captured by hunting females of the bolas spider *Mastophora hutchinsoni* (data from Haynes 1990; Haynes et al. 1996; Zhu and Haynes 2004).

Compound	Abbreviation	Emitter
3Z,9Z-6S,7R-Epoxy-heneicosadiene	3Z,9Z-6S,7R-epoxy-21:H	<i>Tetanolita mynesalis</i>
3Z,6Z,9Z-Henecosatriene	3Z,6Z,9Z-21:H	<i>Tetanolita mynesalis</i>
(Z)-9-Tetradecenyl acetate	(Z)-9-14:Ac	<i>Lacinipolia renigera</i>
(Z,E)-9,12-Tetradecadienyl acetate	(Z,E)-9,12-14:AC	<i>Lacinipolia renigera</i>
(Z)-11-Hexadecenal	Z11-16:Al	<i>Nephalodes minians</i>
(Z)-11-hexadecenyl acetate	Z11-16:Ac	<i>Nephalodes minians</i>

The first two species composing >90% of all moths captured and there is considerable seasonal overlap in their flight periods, although *L. renigera* is active early in the scotophase, whereas *T. mynesalis* flies later in the night (Yeargan 1988).

Haynes and collaborators used this system to investigate how such a temporal switch in the use of different prey species could be achieved using chemical mimicry when the moths use such very different pheromones. Gemeno et al. (2000) found the emissions of hunting females of *M. hutchinsoni* contained Z11-16:Ac and (Z,E)-12-14:AC, the two compounds of *L. renigera* (Haynes 1990), in ratios similar to those of the calling female moth. However, they did not find evidence of 3Z,9Z-6S,7R-epoxy-21:H or 3Z,6Z,9Z-21:H, the pheromone components of *T. mynesalis*. In a subsequent study, Haynes et al. (2002) found that the diel flight patterns of the moths coincided with the periods that *M. hutchinsoni* captured males of the two prey species. Furthermore, they found that males of neither species were captured in pheromone traps baited with heterospecific blends, but whereas the presence of *T. mynesalis* pheromone did not affect the response of males of *L. renigera* to their conspecific blend, the inverse was not true. The presence of the *L. renigera* pheromone was behaviorally antagonistic for the response of males of *T. mynesalis* to their conspecific blend in a positive-dose-dependent manner (Haynes et al. 2002). Through a series of elegant experiments shifting the male response windows of both prey species, they provided evidence that *M. hutchinsoni* continuously produce the pheromone components of *L. renigera* and *T. mynesalis*. However, they also clearly demonstrated that the production of *L. renigera* pheromone declines significantly in the latter part of the scotophase, coinciding with the onset of the flight period of *T. mynesalis*. Thus, through the differential temporal production of Z9-14:Ac and (Z,E)-9,12-14:AC, female bolas spiders are able to circumvent behaviorally antagonism of these compounds on males of *T. mynesalis*, and as a result can effectively exploit two different prey species within the same scotophase. It would be of interest to know whether the late immature stage female also produce the sex pheromones of both prey species, for at the time of the year when they are present *T. mynesalis* is the only prey species flying (Yeargan 1988).

Conclusions and perspectives

For more than a century, the literature on mimicry has been largely dominated by studies on the adaptive resem-

blance of animals to other organisms with a strong focus on the comparative analysis of visual signals. The gaudy colour patterns of unpalatable *Heliconius* butterflies that are mimicked by unrelated and otherwise palatable species have become prime examples of mimicry that are used recurrently in textbooks, but the past few decades of research into the chemical communication of insect–insect and insect–plant interactions have revealed a growing body of examples that include not only animals, but also seedless plants, angiosperms, and even fungi that resort to “chemical” mimicry to reproduce or, more generally, to complete their life cycle.

As we have shown in this review, we are only just beginning to scratch the surface when it comes to our understanding of chemical mimicry, and the taxonomic diversity of organisms involved in this particular form of deception offers promising avenues for future research. Each group of interacting organisms will of course bring series of questions that are unique to the biology of the species involved, but there are also more general questions to be addressed that will provide greater insight into specific cases of mimicry. Orchid chemical mimicry has received the most attention so far by independent teams of researchers that have worked on several genera with representatives in different parts of the globe, and spectacular new examples of chemical mimicry are regularly described (see Brodmann et al. 2008, 2009). Several of the more general questions on the ecology and evolution of chemical mimicry in other systems that have been discovered more recently can, therefore, be drawn from past studies on the chemistry of orchid pollination as follows.

Which compounds are responsible for the attraction of the dupe species?

Different sampling techniques (e.g., solvent versus headspace extraction), the chemical composition of the extracts should be carefully analysed and natural extracts should be tested for their attractiveness towards the dupe species to determine the chemical nature of the attractants. A second step involves the use of GC–EAD to help filter through the range of odour compounds emitted and pinpoint a subset of so-called “biologically active compounds” that are detected by the duped species.

Which selection pressures drive the evolution of chemical signals?

Performing bioassays with the dupe species using dummies scented with natural extracts or blends of synthetic bio-

logically active compounds from both the model and the mimic are an essential prerequisite to test whether the operators show a preference for one kind of chemical signal or another. Multivariate statistical analyses of the chemical signals used by both the model and the mimic can also help track the footprints of selection when comparative analyses are carried out using biologically active versus nonactive compounds. This approach can reveal contrasting patterns of differentiation and, e.g., highlight overlapping patterns in compounds that are involved in the attraction of the dupe species, whereas nonactive compounds could be more strongly differentiated (e.g., Mant et al. 2005b; Cortis et al. 2009).

The convergence in chemical signals between the model and the mimic might not always be perfect. There are several situations where other selection pressures than that of the mimetic refinement might drive the evolution of the chemical signals involved. For example, the mimic might influence the evolution of the chemical signals of the model species when the mimic has a high fitness impact on the dupe (e.g., high predation by bolas spiders, sperm wastage and female avoidance in orchid pollinators, the intensity of parasitism in lycaenid–ant interactions). Imperfect chemical mimicry could also be maintained in instances where a mimic is involved in interactions with multiple model species (e.g., for visual signals see Edmunds 2006), or where the cognitive processes of the operator allow for phenotypic dissimilarities between models and mimics (e.g., for visual signals see Chittka and Osorio 2007). Finally, as we have described above, there also may be cases where an apparently imperfect chemical mimicry is maintained through the active preferences of the operators for slightly dissimilar chemical signals (Vereecken and Schiestl 2008).

How do signals evolve among populations, seasons, and species?

Several other factors might influence the evolution of chemical signals, both at the intra- and inter-specific level. Within species, chemical signals of the model can vary among distant populations (Vereecken et al. 2007) and also among seasons when either the model or the mimic has an active control over the composition or rates of emission of the chemical signals used to attract the operators. Quantifying how specific is the interaction between the mimic and the operators is key to understanding how evolutionary flexible mimicry systems are. For example, it seems quite clear now that *Ophrys* orchids are capable of attracting alternative pollinator species, which occasionally leads to the production of natural hybrids when male bees come and go from one *Ophrys* species to the next, delivering pollen masses in the process. This phenomenon obviously makes the mimicry system much more flexible because it might allow the orchids to ensure their reproductive success by overcoming seasonal or annual fluctuations in local pollinator populations. The bolas spiders and their preys raise similar and related questions such as (i) to what degree is there species specificity in the mimicry of prey pheromones; (ii) is, as suggested by the existing literature, this more tightly controlled in spiderlings and males than in females once they switch to the use of the bolas as a means of predation; (iii) to what extent are the marked adult interfemale differences observed by Stowe et al. (1987, 1995) governed ge-

netically and (or) by daily and season climatic cues; and (iv) are the spiders able to change the allomones produced to cope with changes in the availability of different potential prey species?

Investigating differences in chemical signals among closely related species represents a first important step towards integrating the study of chemical signals in a phylogenetic context. The comparative method applied to the evolution of signals also offers unique opportunities to uncover the mechanisms of speciation and reproductive isolation between model and mimic species that have evolved highly specialized interactions with their operators (Harvey and Pagel 1991; Maynard-Smith and Harper 2003; Oller and Griebel 2004).

Obviously, answers to these and a host of other questions will not only provide greater insight into specific cases of chemical mimicry but will also open avenues for future research. The study of chemical mimicry is still in its infancy and its future will depend on active collaborations between naturalists, evolutionary biologists, and organic chemists to unravel the often extraordinary cases of adaptive resemblance between unrelated species armed with extraordinary repertoires of chemical disguises in the struggle for life.

Acknowledgements

Thanks are due to James H. Cane (Utah State University, Logan, Utah, USA), Matthias Schlinder (University of Bonn, Bonn, Germany), Marco Bologna (University of Roma, Rome, Italy), Bernard Goffinet (University of Connecticut, Storrs, Connecticut, USA), Mario Blanco (University of Florida, Gainesville, Florida, USA), and Ken Haynes (University of Kentucky, Lexington, Kentucky, USA) for their comments that helped improve the review article. We are grateful to Michel Clémot, Patrick Coin, Thomas Ditlevsen, Bernard Goffinet, Ken Haynes, Carlos Hermsilla, Brian Kusler, Linda De Volder, Luiz Filipe Varella, Marcus Stensmyr, Olaf Rumeny, and Doug Waylett for providing photographs to illustrate the review. 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 and J.N.M. is supported by a Discovery Grant from the Natural Sciences and Engineering Research Council of Canada.

References

- Ackerman, J.D. 1986. Mechanisms and evolution of food-deceptive pollination systems in orchids. *Lindleyana*, **1**: 108–113.
- Ackerman, J.D., Méléndez-Ackerman, E.J., and Salguero-Faria, J. 1997. Variation in pollinator abundance and selection on fragrance phenotypes in an epiphytic orchid. *Am. J. Bot.* **84**(10): 1383–1390. doi:10.2307/2446136.
- Agren, 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 Series V, C*, **3**: 15–25.
- Akino, T., Knapp, J.J., Thomas, J.A., and Elmes, G.W. 1999. Chemical mimicry and host specificity in the butterfly, *Maculina rebeli*, a social parasite of *Myrmica* ant colonies. *Proc. R. Soc. Lond. B Biol. Sci.* **266**(1427): 1419–1426. doi:10.1098/rspb.1999.0796.

- 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. Zool. J. Linn. Soc.* **64**(4): 293–326. doi:10.1111/j.1096-3642.1978.tb01075.x.
- Als, T.D., Nash, D., and Boomsma, J.J. 2001. Adoption of parasitic *Maculinaalcon* caterpillars (Lepidoptera: Lycaenidae) by three *Myrmica* ant species. *Anim. Behav.* **62**(1): 99–106. doi:10.1006/anbe.2001.1716.
- Als, T.D., Vila, R., Kandul, N.P., Nash, D.R., Yen, S.-H., Hsu, Y.-F., Mignault, A.A., Boomsma, J.J., and Pierce, N.E. 2004. The evolution of alternative parasitic life histories in large blue butterflies. *Nature (London)*, **432**(7015): 386–390. doi:10.1038/nature03020. PMID:15549104.
- Anderson, B., Johnson, S.D., and Carbutt, C. 2005. Exploitation of a specialized mutualism by a deceptive orchid. *Am. J. Bot.* **92**(8): 1342–1349. doi:10.3732/ajb.92.8.1342.
- Andersson, S., Nilsson, L.A., Gröth, I., and Bergström, G. 2002. Floral scents in butterfly-pollinated plants: possible convergence in chemical composition. *Bot. J. Linn. Soc.* **140**(2): 129–153. doi:10.1046/j.1095-8339.2002.00068.x.
- Angioy, A.-M., Stensmyr, M.C., Urru, I., Puliafito, M., Collu, I., and Hansson, B.S. 2004. Function of the heater: the dead horse arum revisited. *Biol. Lett.* **271**: 13–15.
- Anton, C., Musche, M., Hula, V., and Settele, J. 2008. *Myrmica* host-ant limit the density of ant-predatory large blue, *Maculinae nausithous*. *J. Insect Conserv.* **12**(5): 511–517. doi:10.1007/s10841-007-9091-8.
- Axén, A.H., Leimar, O., and Hoffman, V. 1996. Signalling in a mutualistic interaction. *Anim. Behav.* **52**(2): 321–333. doi:10.1006/anbe.1996.0178.
- 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, Taylor & Francis Group, Boca Raton, Fla. pp. 219–241.
- Ayasse, M., Engels, W., Lübke, G., Taghizadeh, T., and Francke, W. 1999. Mating expenditures reduced via female sex pheromone modulation in the primitively eusocial halictine bee, *Lasioglossum (Evylyaeus) malachurum* (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **45**: 95–106. doi:10.1007/s002650050543.
- Ayasse, M., Dutzler, G., Schiestl, F.P., Ibarra, F., and Francke, W. 2000. Identification of female and male sex pheromone in the solitary bee *Osmia rufa* (Hymenoptera: Megachilidae). In *Proceedings of the XXI International Congress of Entomology and XVIII Brazilian Congress of Entomology (Chemistry and Physiological Ecology Symposium and Poster Session)*, Iguassu Falls, Brazil, 20–26 August 2000. Sociedade Entomológica do Brasil, Ministério da Agricultura e do Abastecimento, Embrapa Soja, Londrina, PR, Brazil. Abstract Book II, pp. 21.
- Ayasse, M., Paxton, R.J., and Tengö, J. 2001. Mating behavior and chemical communication in the order Hymenoptera. *Annu. Rev. Entomol.* **46**(1): 31–78. doi:10.1146/annurev.ento.46.1.31. PMID:11112163.
- Ayasse, M., Schiestl, F.P., Paulus, H.F., Ibarra, F., and Francke, W. 2003. Pollinator attraction in a sexually deceptive orchid by means of unconventional chemicals. *Proc. R. Soc. Lond. B Biol. Sci.* **270**(1514): 517–522. doi:10.1098/rspb.2002.2271.
- Bänziger, H., and Pape, T. 2004. Flowers, feces and cadavers: natural feeding and laying habits of flesh flies in Thailand (Diptera: Sarcophagidae, *Sarcophaga* spp.). *J. Nat. Hist.* **38**(13): 1677–1694. doi:10.1080/0022293031000156303.
- Barbero, F., Thomas, J.A., Bonelli, S., Balletto, E., and Schönrogge, K. 2009. Queen ants make distinctive sounds that are mimicked by a butterfly social parasite. *Science (Washington, D.C.)*, **323**(5915): 782–785. doi:10.1126/science.1163583. PMID:19197065.
- Barkman, T.J., Beaman, J.H., and Gage, D.A. 1997. Floral fragrance variation in *Cypripedium*: implications for evolutionary and ecological studies. *Phytochemistry*, **44**(5): 875–882. doi:10.1016/S0031-9422(96)00614-0.
- Barrozo, R.B., and Lazzari, C.R. 2004. The response of the blood-sucking bug *Triatoma infestans* to carbon dioxide and other host odours. *Chem. Senses*, **29**(4): 319–329. doi:10.1093/chemse/bjh035. PMID:15150145.
- Barth, F.G. 1991. *Insects and flowers: the biology of a partnership*. Princeton University Press, Princeton, N.J.
- Bascompte, J., Jordano, P., Melián, C.J., and Olesen, J.M. 2003. The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci. U.S.A.* **100**(16): 9383–9387. doi:10.1073/pnas.1633576100. PMID:12881488.
- Bergmark, L., Borg-Karlson, A.-K., and Tengö, J. 1984. Female characteristics and odour cues in mate recognition in *Dasypoda alterator* (Hym., Melittidae). *Nova Acta Regiae Societatis Scientiarum Upsaliensis Series V, C, 3*: 137–143.
- Bergström, G. 1978. Role of volatile chemicals in *Ophrys*–pollinator interactions. In *Biochemical aspects of plant and animal coevolution*. Edited by G. Harborne. Academic Press, London. pp. 207–230.
- 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, L.G.W. 2008. Chemical communication by behaviour-guiding olfactory signals. *Chem. Commun. (Camb.)*, 2008(34): 3959–3979. doi:10.1039/b712681f.
- Bergström, L.G.W., Birgersson, G., Gröth, I., and Nilsson, L.A. 1992. Floral fragrance disparity between three taxa of lady's slipper *Cypripedium calceolus* L. (Orchidaceae). *Phytochemistry*, **31**(7): 2315–2319. doi:10.1016/0031-9422(92)83271-Y.
- 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.
- Blomquist, G.J., and Vogt, R.G. 2003. Biosynthesis and detection of pheromones and plant volatiles — introduction and overview. In *Insect pheromone biochemistry and molecular biology — the biosynthesis and detection of pheromones and plant volatiles*. Edited by G.J. Blomquist and R.G. Vogt. Elsevier, New York. pp. 3–18.
- Bologna, M.A., and Pinto, J.D. 2001. Phylogenetic studies of Meloidae (Coleoptera), with emphasis on the evolution of phoresy. *Syst. Entomol.* **26**(1): 33–72. doi:10.1046/j.1365-3113.2001.00132.x.
- Bologna, M.A., and Pinto, J.D. 2002. The Old World genera of Meloidae (Coleoptera): a key and synopsis. *J. Nat. Hist.* **36**(17): 2013–2102. doi:10.1080/00222930110062318.
- Bologna, M.A., Oliverio, M., Pitzalis, M., and Mariottini, P. 2008. Phylogeny and evolutionary history of the blister beetles (Coleoptera, Meloidae). *Mol. Phylogenet. Evol.* **48**(2): 679–693. doi:10.1016/j.ympev.2008.04.019. PMID:18514547.
- 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-Karolson, 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-Karolson, A.-K., Bergström, G., and Kullenberg, B. 1987. II. Volatile compounds of *O. insectifera* and *O. speculum* as insect mimetic attractants/excitants. *Chem. Scr.* **27**: 303–311.
- Borg-Karolson, A.-K., Englund, F.O., and Unelius, C.R. 1994. Dimethyl oligosulphides, major volatiles released from *Sauromatum guttatum* and *Phallus impudicus*. *Phytochemistry*, **35**(2): 321–323. doi:10.1016/S0031-9422(00)94756-3.
- Bouchard, Y., and Cloutier, C. 1984. Honeydew as a source of host-searching kairomones for the aphid parasitoid *Aphidius nigripes* (Hymenoptera: Aphidiidae). *Can. J. Zool.* **62**(8): 1513–1520. doi:10.1139/z84-220.
- 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.
- Bradbury, J.W., and Vehrencamp, S.L. 1998. Principles of animal communication. Sinauer Associates, Inc. Sunderland, Mass.
- Brazil, R.P., Caballero, N.N., and Hamilton, J.G.C. 2009. Identification of the sex pheromone of *Lutzomyia longipalpis* (Lutz & Neiva, 1912) (Diptera: Psychodidae) from Asunción, Paraguay. *Parasit. Vectors*, **2**(1): 51. doi:10.1186/1756-3305-2-51. PMID:19883505.
- Bristow, A. 1978. The sex life of plants. New English Library Ltd., London.
- Brodmann, J., Twele, R., Francke, W., Hölzler, G., Zhang, Q.-H., and Ayasse, M. 2008. Orchids mimic green-leaf volatiles to attract prey-hunting wasps for pollination. *Curr. Biol.* **18**(10): 740–744. doi:10.1016/j.cub.2008.04.040. PMID:18472423.
- Brodmann, J., Twele, R., Francke, W., Yi-bo, L., Xi-qiang, S., and Ayasse, M. 2009. Orchid mimics honey bee alarm pheromone in order to attract hornets for pollination. *Curr. Biol.* **19**(16): 1368–1372. doi:10.1016/j.cub.2009.06.067. PMID:19664924.
- Brown, M.H. 1982. Meat microbiology. Applied Science Publishers Ltd., London.
- Budenberg, W.J. 1990. Honeydew as a contact kairomone for aphid parasitoids. *Entomol. Exp. Appl.* **55**(2): 139–148. doi:10.1007/BF00352575.
- Buitenhuis, R., McNeil, J.N., Boivin, G., and Brodeur, J. 2004. The role of honeydew in host searching of aphid hyperparasitoids. *J. Chem. Ecol.* **30**(2): 273–285. doi:10.1023/B:JOEC.0000017977.39957.97. PMID:15112724.
- Cameron, R.G., and Troilo, D. 1982. Fly-mediated spore dispersal in *Splachnum ampullaceum* (Musci). *Mich. Bot.* **21**: 59–65.
- Cameron, R.G., and Wyatt, R. 1986. Substrate restriction in entomophilous Splachnaceae: role of spore dispersal. *Bryologist*, **89**(4): 279–284. doi:10.2307/3243199.
- Cane, J.H. 1981. Dufour's gland secretion in the cell linings of bees (Hymenoptera: Apoidea). *J. Chem. Ecol.* **7**(2): 403–410. doi:10.1007/BF00995762.
- Cane, J.H. 1983. Olfactory evaluation of *Andrena* host nest suitability by kleptoparasitic *Nomada* bees (Hymenoptera: Apoidea). *Anim. Behav.* **31**(1): 138–144. doi:10.1016/S0003-3472(83)80181-X.
- Chen, J., and Meeuse, B.J.D. 1971. Production of free indole by some arum lilies. *Acta Bot. Neerl.* **20**: 627–635.
- Chittka, L., and Osorio, D. 2007. Cognitive dimensions of predator responses to imperfect mimicry. *PLoS Biol.* **5**(12): e339. doi:10.1371/journal.pbio.0050339. PMID:18162048.
- Chittka, L., Thomson, J.D., and Waser, N.M. 1999. Flower constancy, insect psychology and plant evolution. *Naturwissenschaften*, **86**(8): 361–377. doi:10.1007/s001140050636.
- 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 bistrimacula* (Hymenoptera, Scoliidae). *Flora*, **201**: 365–369.
- Clarke, J.D., and Haynes, K.F. 1990. Sex attractant for the bluegrass webworm (Lepidoptera: Pyralidae). *J. Econ. Entomol.* **83**: 856–859.
- Clausen, C.P. 1976. Phoresy among entomophagous insects. *Annu. Rev. Entomol.* **21**(1): 343–368. doi:10.1146/annurev.en.21.010176.002015.
- Coleman, E. 1928. Pollination of *Cryptostylis leptochila*. *Vic. Nat.* **44**: 333–340.
- Connick, W.J., and French, R.C. 1991. Volatiles emitted during the sexual stage of the Canada thistle rust fungus and by thistle flowers. *J. Agric. Food Chem.* **39**(1): 185–188. doi:10.1021/jf00001a037.
- Cooley, J.R. 1995. Floral heat rewards and direct benefits to insect pollinators. *Ann. Entomol. Soc. Am.* **88**: 576–579.
- Correvon, H., and Pouyanne, M. 1916. Un curieux cas de mimétisme chez les ophrydées. *J. Soc. Nat. Hortic. Fr.* **4**: 29–47.
- Correvon, H., and Pouyanne, M. 1923. Nouvelles observations sur le mimétisme et la fécondation chez les *Ophrys speculum* et *lutea*. *J. Soc. Nat. Hortic. Fr.* **4**: 372–377.
- 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.
- Cozzolino, S., Schiestl, F.P., Müller, A., De Castro, O., Nardella, A.M., and Widmer, A. 2005. Evidence for pollinator sharing in Mediterranean nectar-mimic orchids: absence of pre-mating barriers? *Proc. R. Soc. Lond. B Biol. Sci.* **272**(1569): 1271–1278. doi:10.1098/rspb.2005.3069.
- Culley, T.M., Weller, S.G., and Sakai, A.K. 2002. The evolution of wind pollination in angiosperms. *Trends Ecol. Evol.* **17**(8): 361–369. doi:10.1016/S0169-5347(02)02540-5.
- Dafni, A. 1984. Mimicry and deception in pollination. *Annu. Rev. Ecol. Syst.* **15**(1): 259–278. doi:10.1146/annurev.es.15.110184.001355.
- Darwin, C. 1862. On the various contrivances by which British and foreign orchids are fertilised by insects. John Murray, London, UK.
- Davis, C.C. 2008. Floral evolution: dramatic size change was recent and rapid in the world's largest flowers. *Curr. Biol.* **18**(23): R1102–R1104. doi:10.1016/j.cub.2008.10.011.
- Davis, C.C., Latvis, M., Nickrent, D.L., Wurdack, K.J., and Baum, D.A. 2007. Floral gigantism in Rafflesiaceae. *Science (Washington, D.C.)*, **315**(5820): 1812. doi:10.1126/science.1135260. PMID:17218493.
- Davis, C.C., Endress, P.K., and Baum, D.A. 2008. The evolution of floral gigantism. *Curr. Opin. Plant Biol.* **11**(1): 49–57. doi:10.1016/j.pbi.2007.11.003. PMID:18207449.
- Deacon, J. 2005. Fungal biology. 4th ed. Wiley, Blackwell, N.J.
- Delforge, P. 2005. Guide des orchidées d'Europe, d'Afrique du Nord et du Proche-Orient. Delachaux & Niestlé, Paris, France.
- DeVries, P.J. 1990. Enhancement of symbiosis between butterfly caterpillars and ants by vibrational communication. *Science (Washington, D.C.)*, **248**(4959): 1104–1106. doi:10.1126/science.248.4959.1104. PMID:17733373.
- Diaz, A., and Kite, G.C. 2002. A comparison of pollination ecology of *Arum maculatum* and *A. italicum* in England. *Watsonia*, **24**: 171–181.
- Diaz, A., and Kite, G.C. 2006. Why be a rewarding trap? The evolution of floral rewards in *Arum* (Araceae), a genus character-

- ized by saprophilous pollination systems. *Biol. J. Linn. Soc.* **88**(2): 257–268. doi:10.1111/j.1095-8312.2006.00612.x.
- 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, Taylor & Francis Group, Boca Raton, Fla. pp. 147–198.
- Dod, D.D. 1976. *Oncidium henekenii*: bee orchid pollinated by bee. *Am. Orchid Soc. Bull.* **45**: 792–794.
- Dormer, K.J. 1960. The truth about pollination in *Arum*. *New Phytol.* **59**(3): 298–301. doi:10.1111/j.1469-8137.1960.tb06224.x.
- Duffield, R.M., Wheeler, J.W., and Eickwort, G.C. 1984. Sociochemicals of bees. *In* *Chemical ecology of insects*. Edited by W.J. Bell and R.T. Cardé. Chapman and Hall, London. pp. 387–428.
- Edmunds, M. 2006. Do Malaysian Myrmarachne associate with particular species of ant? *Biol. J. Linn. Soc.* **88**(4): 645–653. doi:10.1111/j.1095-8312.2006.00649.x.
- Eickwort, G.C., and Abrams, J. 1980. Parasitism of sweat bees in the genus *Agapostemon* by cuckoo bees in the genus *Nomada*. *Pan-Pac. Entomol.* **56**: 144–152.
- 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.
- El-Sayed, A.M. 2008. The Pherobase: database of insect pheromones and semiochemicals [online]. Available from <http://www.pherobase.com> [accessed 20 November 2009].
- Elmes, G.W., Wardlaw, J.C., and Thomas, J.A. 1991. Larvae of *Maculinea rebeli*, a large-blue butterfly and their *Myrmica* host ants: patterns of caterpillar growth and survival. *J. Zool. (Lond.)*, **224**(1): 79–92. doi:10.1111/j.1469-7998.1991.tb04789.x.
- Endress, P.K. 1994. *Diversity and evolutionary biology of tropical flowers*. Cambridge University Press, Cambridge.
- Engel, M.S. 2005. An Eocene ectoparasite of bees: the oldest definitive record of phoretic meloid triungulins (Coleoptera: Meloidae; Hymenoptera: Megachilidae). *Acta Zool. Cracov.* **48**(3): 43–48. doi:10.3409/173491505783995635.
- Espmark, Y., Anumdsen, T., and Rosenqvist, G. (Editors). 2000. *Animal signals: signaling and signal design in animal communication*. Tapir Academic Press, Trondheim, Norway.
- Fabre, J.-H. 1857. Mémoire sur l'hypermétamorphose et les moeurs des méloïdes. *Annales des Sciences Naturelles et de Zoologie*, Paris.
- Faegri, K., and van der Pijl, L. 1979. *The principles of pollination biology*. 3rd ed. Pergamon, Oxford.
- Fenster, C.B., Armbruster, S.W., Wilson, P., Dudash, M.R., and Thomson, J.D. 2004. Pollination syndromes and floral specialization. *Annu. Rev. Ecol. Syst.* **35**(1): 375–403. doi:10.1146/annurev.ecolsys.34.011802.132347.
- Fiedler, K., Holldobler, B., and Seufert, P. 1996. Butterflies and ants: the communicative domain. *Experientia (Basel)*, **52**: 14–24.
- Flach, A., Dondon, R.C., Singer, R.B., Koehler, S., Amaral, M.C., and Marsaioli, A.J. 2004. The chemistry of pollination in selected Brazilian Maxillariinae orchids: floral rewards and fragrance. *J. Chem. Ecol.* **30**(5): 1045–1056. doi:10.1023/B:JOEC.0000028466.50392.ed. PMID:15274447.
- Flach, A., Marsaioli, A.J., Singer, R.B., Amaral, M.C., Menezes, C., Kerr, W.E., Batista-Pereira, L.G., and Corrêa, A.G. 2006. Pollination by sexual mimicry in *Mormolyca ringens*: a floral chemistry that remarkably matches the pheromones of virgin queens of *Scaptotrigona* sp. *J. Chem. Ecol.* **32**(1): 59–70. doi:10.1007/s10886-006-9351-1. PMID:16525870.
- Fleck, O. 1995. Identifizierung und Synthese flüchtiger Inhaltsstoffe von parasitären Bienen der Gattung *Nomada*. Ph.D. dissertation, University of Hamburg, Hamburg, Germany.
- Fraberger, R.J., and Ayasse, M. 2007. Mating behavior, male territoriality and chemical communication in the European spiral-horned bees *Systropha planidens* and *S. curvicornis* (Hymenoptera, Halictidae). *J. Kans. Entomol. Soc.* **80**(4): 348–360. doi:10.2317/0022-8567(2007)80[348:MBMTAC]2.0.CO;2.
- Franke, S., Ibarra, F., Schulz, C.M., Twele, R., Poldy, J., Barrow, R.A., Peakall, R., Schiestl, F.P., and Francke, W. 2009. The discovery of 2,5-dialkylcyclohexan-1,3-diones as a new class of natural products. *Proc. Natl. Acad. Sci. U.S.A.* **106**(22): 8877–8882. doi:10.1073/pnas.0900646106. PMID:19470640.
- Friedman, J., and Barrett, S.C.H. 2008. A phylogenetic analysis of the evolution of wind pollination in angiosperms. *Int. J. Plant Sci.* **169**(1): 49–58. doi:10.1086/523365.
- Galizia, C.G., Kunze, J., Gumbert, A., Borg-Karlson, A.K., Sachse, S., Markl, C., and Menzel, R. 2005. Relationship of visual and olfactory signal parameters in a food-deceptive flower mimicry system. *Behav. Ecol.* **16**(1): 159–168. doi:10.1093/beheco/arh147.
- Gaskett, A.C., Winnick, C.G., and Herberstein, M.E. 2008. Orchid sexual deceit provokes ejaculation. *Am. Nat.* **171**(6): E206–E212. doi:10.1086/587532.
- Gäumann, E. 1959. Die Rostpilze Mitteleuropas. *Beitr. Krypt. Flora Schweiz*, **12**: 355–397.
- Gemenio, C., Yeorgan, K.V., and Haynes, K.F. 2000. Aggressive chemical mimicry by the bolas spider, *Mastophora hutchinsoni*: identification and quantification of a major prey's sex pheromone components in the spider's volatile emissions. *J. Chem. Ecol.* **26**(5): 1235–1243. doi:10.1023/A:1005488128468.
- Gibernau, M., Favre, C., Talou, T., and Raynaud, C. 2004a. Floral odor of *Arum italicum*. *Aroideana*, **27**: 142–147.
- Gibernau, M., Macquart, D., and Przetak, G. 2004b. Pollination in the genus *Arum*: a review. *Aroideana*, **27**: 148–166.
- Gigord, L.D.B., Macnair, M.R., Stritesky, M., and Smithson, A. 2002. The potential for floral mimicry in rewardless orchids: an experimental study. *Proc. R. Soc. Lond. B Biol. Sci.* **269**(1498): 1389–1395. doi:10.1098/rspb.2002.2018.
- Godfery, M. 1922. Notes on the fertilization of orchids. *J. Bot. (Lond.)*, **60**: 359–361.
- Godfery, M. 1929. Recent observations on the pollination of *Ophrys*. *J. Bot. (Lond.)*, **67**: 298–302.
- Goffinet, B., Shaw, A.J., and Cox, C.J. 2004. Phylogenetic inferences in the dung-moss family Splachnaceae from analyses of cpDNA sequence data and implications for the evolution of entomophily. *Am. J. Bot.* **91**(5): 748–759. doi:10.3732/ajb.91.5.748.
- 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.
- Goldblatt, P., Bernhardt, P., Vogan, P., and Manning, J.C. 2004. Pollination by fungus gnats (Diptera: Mycetophilidae) and self-recognition sites in *Tolmiea menziesii* (Saxifragaceae). *Plant Syst. Evol.* **244**(1–2): 55–67. doi:10.1007/s00606-003-0067-1.
- Gottsberger, G., and Amaral, A. 1984. Pollination strategies in Brazilian *Philodendron* species. *Ber. Dtsch. Bot. Ges.* **97**: 391–410.
- Goyret, J., Markwell, P.M., and Raguso, R.A. 2007. The effect of olfactory and visual stimuli decoupling on the foraging behavior of *Manduca sexta*. *J. Exp. Biol.* **209**: 1586–1593.
- Goyret, J., Markwell, P.M., and Raguso, R.A. 2008. Context- and scale-dependent effects of floral CO₂ on nectar foraging by *Manduca sexta*. *Proc. Natl. Acad. Sci. U.S.A.* **105**(12): 4565–4570. doi:10.1073/pnas.0708629105. PMID:18212123.
- Gumbert, A., and Kunze, J. 2001. Colour similarity to rewarding model plants affects pollination in a food deceptive orchid, *Orchis boryi*. *Biol. J. Linn. Soc.* **72**(3): 419–433. doi:10.1111/j.1095-8312.2001.tb01328.x.
- Hafernik, J., and Saul-Gershenz, L.S. 2000. Beetle larvae cooperate

- to mimic bees. *Nature* (London), **405**(6782): 35–36. doi:10.1038/35011129. PMID:10811206.
- Hamilton, J.G., Brazil, R.P., Campbell-Lendrum, D., Davies, C.R., Kelly, D.W., Pessoa, F.A., and de Queiroz, R.G. 2002. Distribution of putative male sex pheromones among *Lutzomyia* sandflies (Diptera: Psychodidae). *Ann. Trop. Med. Parasitol.* **96**(1): 83–92. doi:10.1179/000349802125000547. PMID:11989537.
- Harvey, P.H., and Pagel, M.D. 1991. The comparative method in evolutionary biology. Oxford Series in Ecology and Evolution, Oxford University Press, Oxford.
- Hauser, M.D., and Konishi, M. (Editors). 1999. The design of animal communication. MIT Press, Cambridge, Mass.
- Haynes, K.F. 1990. Identification of the sex pheromone of bristly cutworm, *Lacinipolia renigra* (Stephens). *J. Chem. Ecol.* **16**(9): 2615–2621. doi:10.1007/BF00988073.
- Haynes, K.F., and Yeorgan, K.V. 1999. Exploitation of intraspecific communication systems: illicit signalers and receivers. *Ann. Entomol. Soc. Am.* **92**: 960–970.
- Haynes, K.F., Yeorgan, K.V., Millar, J.G., and Chastain, B.B. 1996. Identification of the sex pheromone of *Tetanolita mynesalis* (Lepidoptera: Noctuidae), a prey species of a bolas spider, *Mastophora hutchinsoni*. *J. Chem. Ecol.* **22**(1): 75–89. doi:10.1007/BF02040201.
- Haynes, K.F., Yeorgan, K.V., and Gemeno, C. 2001. Detection of prey by a spider that aggressively mimics pheromone blends. *J. Insect Behav.* **14**(4): 535–544. doi:10.1023/A:1011128223782.
- Haynes, K.F., Gemeno, C., Yeorgan, K.V., Millar, J.G., and Johnson, K.M. 2002. Aggressive chemical mimicry of moth pheromones by a bolas spider: how does this specialist predator attract more than one species of prey? *Chemoecology*, **12**(2): 99–105. doi:10.1007/s00049-002-8332-2.
- Hefetz, A., Fales, H.M., and Batra, S.W.T. 1979. Natural polyesters: Dufour's gland macrocyclic lactones form brood cell laminesters in *Colletes* bees. *Science* (Washington, D.C.), **204**(4391): 415–417. doi:10.1126/science.204.4391.415.
- 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., Castellanos, M.C., and Medrano, M. 2006. Geographical context of floral evolution: towards an improved research programme in floral diversification. In *Ecology and evolution of flowers*. Edited by L.D. Harder and S.C.H. Barrett. Oxford University Press, New York. pp. 278–294.
- Hilker, M., Blaske, V., Kobs, C., and Dippel, C. 2000. Kairomonal effects of sawfly sex pheromones on egg parasitoids. *J. Chem. Ecol.* **26**(11): 2591–2601. doi:10.1023/A:1005592930772.
- Hochberg, M.E., Thomas, J.A., and Elmes, G.W. 1992. A modeling study of the population dynamics of a large blue butterfly, *Maculinea rebeli*, a parasite of red ant nests. *J. Anim. Ecol.* **61**(2): 397–409. doi:10.2307/5331.
- Hojo, M.K., Wada-Katsumata, A., Akino, T., Yamaguchi, S., Ozaki, M., and Yamaoka, R. 2009. Chemical disguise as particular caste of host ants in the ant inquiline parasite, *Niphanda fusca* (Lepidoptera: Lycaenidae). *Proc. R. Soc. Lond. B. Biol. Sci.* **276**(1656): 551–558. doi:10.1098/rspb.2008.1064.
- Holldobler, D., and Wilson, E.O. 1990. The ants. Springer-Verlag, Berlin.
- Jakubska, A., Przado, D., Steininger, M., Aniol-Kwiatkowska, J., and Kadej, M. 2005. Why do pollinators become “sluggish”? Nectar chemical constituents from *Epipactis helleborine* (L.) Crantz (Orchidaceae). *Appl. Ecol. Environ. Res.* **3**(2): 29–38.
- Jersáková, J., Johnson, S.D., and Kindlmann, P. 2006. Mechanisms and evolution of deceptive pollination in orchids. *Biol. Rev. Camb. Philos. Soc.* **81**(2): 219–235. doi:10.1017/S1464793105006986. PMID:16677433.
- Jersáková, J., Johnson, S.D., and Jürgens, A. 2009. Deceptive behavior in plants. II. Food deception by plants: from generalized systems to specialized floral mimicry. In *Plant–environment interactions: from sensory plant biology to active behaviour*. Edited by F. Baluska. Springer-Verlag, Berlin. pp. 223–246.
- Jhumur, U.S., Dötterl, S., and Jürgens, A. 2007. Electrophysiological and behavioural responses of mosquitoes to volatiles of *Silene otites* (Caryophyllaceae). *Arthropod-Plant Interact.* **1**(4): 245–254. doi:10.1007/s11829-007-9022-3.
- Johnson, S.D. 1994. Evidence for Batesian mimicry in a butterfly pollinated orchid. *Biol. J. Linn. Soc.* **53**: 91–104.
- Johnson, S.D., and Steiner, K.E. 2000. Generalization versus specialization in plant pollination systems. *Trends Ecol. Evol.* **15**(4): 140–143. doi:10.1016/S0169-5347(99)01811-X. PMID:10717682.
- Jones, D.L. 1988. Native orchids of Australia. American Orchid Society, Delray Beach, Fla.
- Judd, W.W. 1972. Wasps pollinating *Epipactis helleborine* (L.) Crantz at Owen, Ontario. *Proc. Entomol. Soc. Ont.* **102**: 115.
- Jürgens, A., Dötterl, S., and Meve, U. 2006. The chemical nature of fetid floral odours in stapeliads (Apocynaceae–Asclepiadoideae–Ceropegieae). *New Phytol.* **172**(3): 452–468. doi:10.1111/j.1469-8137.2006.01845.x. PMID:17083676.
- Jürgens, A., Dötterl, S., Liede-Schumann, S., and Meve, U. 2008. Chemical diversity of floral volatiles in Asclepiadoideae–Asclepiadeae (Apocynaceae). *Biochem. Syst. Ecol.* **36**(11): 842–852. doi:10.1016/j.bse.2008.10.005.
- Kaiser, R. 1993. The scents of orchids: olfactory and chemical investigations. Elsevier Editions Roche, Basel, Switzerland.
- Kaiser, R. 2006a. Flowers and fungi use scents to mimic each other. *Science* (Washington, D.C.), **311**(5762): 806–807. doi:10.1126/science.1119499.
- Kaiser, R. 2006b. Meaningful scents around the world: olfactory, chemical, biological and cultural considerations. Wiley–VCH, Zürich, Switzerland.
- Kevan, P.G. 1975. Sun-tracking solar furnaces in high arctic flowers: significance for pollination and insects. *Science* (Washington, D.C.), **189**(4204): 723–726. doi:10.1126/science.189.4204.723.
- Kite, G.C. 1995. The floral odour of *Arum maculatum*. *Biochem. Syst. Ecol.* **23**(4): 343–354. doi:10.1016/0305-1978(95)00026-Q.
- Kite, G.C., and Hetterscheid, W.L.A. 1997. Inflorescence odours of *Amorphophallus* and *Pseudodraconitum* (Araceae). *Phytochemistry*, **46**(1): 71–75. doi:10.1016/S0031-9422(97)00221-5.
- Kite, G.C., Hetterscheid, W.L.A., Lewis, M.J., Boyce, P.C., Ollerton, J., Cocklin, E., Diaz, A., and Simmonds, M.S.J. 1998. Inflorescence odours and pollinators of *Arum* and *Amorphophallus* (Araceae). In *Reproductive biology*. Edited by S.J. Owens and P.J. Rudall. Royal Botanic Gardens, Kew, UK. pp. 295–315.
- Knoll, F. 1926. Insekten und Blumen. Experimentelle Arbeiten zur Vertiefung unserer Kenntnisse über die Wechselbeziehungen zwischen Pflanzen und Tieren. IV. Die *Arum*-Blütenstände und ihre Besucher. *Abh. Zool. Bot. Ges. Wien*, **12**: 379–482.
- Knoll, F. 1956. Die Biologie der Blüte. Springer-Verlag, Berlin.
- 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:DADOFS]2.0.CO;2.
- Knuth, P. 1909. Handbook of flower pollination. Clarendon Press, Oxford, UK.
- Koponen, A. 1990. Entomophily in the Splachnaceae. *Bot. J. Linn. Soc.* **104**(1–3): 115–127. doi:10.1111/j.1095-8339.1990.tb02214.x.
- Koponen, A., and Koponen, T. 1978. Evidence of entomophily in Splachnaceae (Bryophyta). *Bryophyt. Bibl.* **13**: 569–577.

- Kullenberg, B. 1956. Field experiments with chemical sexual attractants on Aculeate Hymenoptera males. *Zool. Bidr.* **31**: 253–352.
- Kullenberg, B. 1961. Studies in *Ophrys* pollination. *Zool. Bidr.*, **34**: 1–340.
- Kullenberg, B. 1973. Field experiments with chemical sexual attractants on aculeate Hymenoptera males. II. *Zoon* (Uppsala), **1**(Suppl.): 31–42.
- Kullenberg, B., and Bergström, G. 1976. *Hymenoptera Aculeata* males as pollinators of *Ophrys* orchids. *Zool. Scr.* **5**(1–4): 13–23. doi:10.1111/j.1463-6409.1976.tb00678.x.
- Kullenberg, B., Borg-Karlson, A.-K., and Kullenberg, A.-L. 1984. Field studies on the behaviour of the *Eucera nigrolabris* male in the odour flow from flower labellum extract of *Ophrys tenthredinifera*. *Nova Acta Regise Societatis Scientiarum Upsalien-sis Series V, C, 3*: 79–110.
- Lamprecht, I., Drong, K., Schaarschmidt, B., and Welge, G. 1991. Some like it hot: calorimetric investigations of voodoo lilies. *Thermochim. Acta*, **187**: 33–40. doi:10.1016/0040-6031(91)87179-Z.
- Lamprecht, I., Schmolz, E., Blanco, L., and Romero, C.M. 2002. Flower ovens: thermal investigations on heat producing plants. *Thermochim. Acta*, **391**(1–2): 107–118. doi:10.1016/S0040-6031(02)00168-5.
- Lehane, M.J. 1991. *Biology of blood-sucking insects*. Harper-Collins Academic, London.
- Levi, H.W. 1993. The orb-weaver genus *Kaira* (Araneae, Araneidae). *J. Arachnol.* **21**(3): 209–225.
- Levi, H.W. 2003. The bolas spiders of the genus *Mastophora* (Araneae: Araneidae). *Bull. Mus. Comp. Zool. Harv. Univ.* **157**: 309–382.
- Lev-Yadun, S., Ne'eman, G., and Shanas, U. 2009. A sheep in wolf's clothing: do carrion and dung odours of flowers not only attract pollinators but also deter herbivores? *Bioessays*, **31**(1): 84–88. doi:10.1002/bies.070191. PMID:19154006.
- Linder, H.P. 2000. Pollen morphology and wind pollination in angiosperms. In *Pollen and spores: morphology and biology*. Edited by M.M. Harley, C.M. Morton, and S. Blackmore. Royal Botanic Gardens, Kew, UK. pp. 73–88.
- Lopez, A., Stowe, M.K., and Bonaric, J.C. 1985. Anatomie interne de l'araignée à bolas nord-américaine *Mastophora cornigera* (Hentz, 1850) (Araneae: Araneidae) après sa sortie du cocon. *C.R. VIIIe Coll. Arachnol. Moulis, P.S.A.* **8**: 1–9.
- Lopez, A., Juberthie-Jupeau, L., and Stowe, M.K. 1986. L'appareil sericigène de *Kaira alba* (Hentz) (Araneae: Araneidae). *Mem. Soc. R. Belge. Entomol.* **33**: 119–128.
- 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.
- Marino, P.C. 1988. Coexistence on divided habitats: mosses in the family Splachnaceae. *Ann. Zool. Fenn.* **25**: 89–98.
- Marino, P.C. 1991a. Competition between mosses (Splachnaceae) in patchy habitats. *J. Ecol.* **79**(4): 1031–1046. doi:10.2307/2261096.
- Marino, P.C. 1991b. Dispersal and coexistence of mosses (Splachnaceae) in patchy habitats. *J. Ecol.* **79**(4): 1047–1060. doi:10.2307/2261097.
- Marino, P.C. 1997. Competition, dispersal and coexistence of Splachnaceae in patchy habitats. *Adv. Bryol.* **6**: 241–263.
- Marino, P.C., Raguso, R.A., and Goffinet, B. 2009. The ecology and evolution of fly dispersed dung mosses (family Splachnaceae): manipulating insect behaviour through odour and visual cues. *Symbiosis*, **47**(2): 61–76. doi:10.1007/BF03182289.
- Maynard-Smith, J., and Harper, D.G.C. 2003. *Animal signals*. Oxford University Press, Oxford.
- Meeuse, B.J.D. 1975. Thermogenic respiration in aroids. *Annu. Rev. Plant Physiol.* **26**(1): 117–126. doi:10.1146/annurev.pp.26.060175.001001.
- Meeuse, B.J.D. 1978. The physiology of some sapromyophilous flowers. In *The pollination of flowers by insects*. Edited by A.J. Richards. Academic Press, London. pp. 97–104.
- Meeuse, B., and Morris, S. 1984. *The sex life of flowers*. Facts on File Editions, New York.
- Milonas, P.G., Martinou, A.F., Kontodimas, D.Ch., Karamaouna, F., and Konstantopoulou, M.A. 2009. Attraction of different *Trichogramma* species to *Prays oleae* sex pheromone. *Ann. Entomol. Soc. Am.* **102**(6): 1145–1150. doi:10.1603/008.102.0624.
- Mohra, C., Fellendorf, M., Paxton, R.J., and Tengö, J. 1999. Agonismus und Toleranz im Verhalten der kommunalen Sandbiene *Andrena scotica* und ihres Brutparasiten *Nomda marshalli*. In *Soziale Insekten IUSI-Tagung, Hohenheim, 1999*. Edited by P. Rosenkranz and C. Garrido. Programm und Kurzfassungen, Internationale Union zum Studium der Sozialen Insekten (IUSI), Graz, Hohenheim, Würzburg. p. 68.
- Mouquet, N., Thomas, J.A., Elmes, G.W., Clarke, R.T., and Hochberg, M.E. 2005. Population dynamics and conservation of a specialised predator: a case study of *Maculinea arion*. *Ecol. Monogr.* **75**(4): 525–542. doi:10.1890/05-0319.
- Moya, S.J.D., and Ackerman, J.D. 1993. Variation in the floral fragrance of *Epidendrum ciliare* (Orchidaceae). *Nord. J. Bot.* **13**(1): 41–47. doi:10.1111/j.1756-1051.1993.tb00009.x.
- Müller, H. 1873. *Die Befruchtung der Blumen durch Insekten und die gegenseitigen Anpassungen beider* Leipzig, Germany. Engelmann Verlag, Leipzig, Germany.
- Naef, A., Roy, B.A., Kaiser, R., and Honegger, R. 2002. Insect-mediated reproduction of systemic infections by *Puccinia arrhenatheri* on *Berberis vulgaris*. *New Phytol.* **154**(3): 717–730. doi:10.1046/j.1469-8137.2002.00406.x.
- Nash, D.R., Als, T.D., Maile, R., Jones, G.R., and Boomsma, J.J. 2008. A mosaic of chemical coevolution in a large blue butterfly. *Science* (Washington, D.C.), **319**(5859): 88–90. doi:10.1126/science.1149180.
- Ngugi, H.K., and Scherm, H. 2006. Mimicry in plant-parasitic fungi. *FEMS Microbiol. Lett.* **257**(2): 171–176. doi:10.1111/j.1574-6968.2006.00168.x. PMID:16553849.
- Nilsson, L.A. 1979. Anthecological studies on the lady's slipper, *Cypripedium calceolus* (Orchidaceae). *Bot. Not.* **132**: 329–347.
- Nilsson, L.A. 1980. The pollination ecology of *Dactylorhiza sambucina* (Orchidaceae). *Bot. Not.* **133**: 367–385.
- Nilsson, L.A. 1983. Mimesis of bellflower (*Campanula*) by the red helleborine orchid *Cephalanthera rubra*. *Nature* (London), **305**(5937): 799–800. doi:10.1038/305799a0.
- Nilsson, L.A. 1984. Anthecology of *O. morio* (Orchidaceae) and its outpost in the North. *Nova Acta Regise Societatis Scientiarum Upsaliensis Series V, C, 3*: 167–180.
- Noldus, L.P.J.J. 1988. Response of the egg parasitoid *Trichogramma pretiosum* to the sex pheromone of its host *Heliothis zea*. *Entomol. Exp. Appl.* **48**(3): 293–300. doi:10.1007/BF00376410.
- Noldus, L.P.J.J., van Lenteren, J.C., and Lewis, W.J. 1991. How *Trichogramma* parasitoids use moth sex pheromones as

- kairomones: orientation behaviour in a wind tunnel. *Physiol. Entomol.* **16**(3): 313–327. doi:10.1111/j.1365-3032.1991.tb00570.x.
- Odell, E., Raguso, R.A., and Jones, K.N. 1999. Bumblebee foraging responses to variation in floral scent and color in snapdragons (*Antirrhinum*: Scrophulariaceae). *Am. Midl. Nat.* **142**(2): 257–265. doi:10.1674/0003-0031(1999)142[0257:BFRTVI]2.0.CO;2.
- Okuyama, Y., Kato, M., and Murakami, M. 2004. Pollination by fungus gnats in four species of the genus *Mitella* (Saxifragaceae). *Bot. J. Linn. Soc.* **144**(4): 449–460. doi:10.1111/j.1095-8339.2003.00259.x.
- Okuyama, Y., Pellmyr, O., and Kato, M. 2008. Parallel floral adaptations to pollination by fungus gnats within the genus *Mitella* (Saxifragaceae). *Mol. Phylogenet. Evol.* **46**(2): 560–575. doi:10.1016/j.ympev.2007.09.020. PMID:18248825.
- Oller, D.K., and Griebel, U. 2004 (*Editors*) The evolution of communication systems: a comparative approach. MIT Press, Cambridge, Mass.
- 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.
- Ollerton, J., and Liede, S. 1997. Pollination systems in the Asclepiadaceae: a survey and preliminary analysis. *Biol. J. Linn. Soc.* **62**(4): 593–610. doi:10.1111/j.1095-8312.1997.tb00324.x.
- Ollerton, J., and Raguso, R.A. 2006. The sweet stench of decay. *New Phytol.* **172**(3): 382–385. doi:10.1111/j.1469-8137.2006.01903.x. PMID:17083669.
- Patino, S., Aalto, T., Edwards, A.A., and Grace, J. 2002. Is *Rafflesia* an endothermic flower? *New Phytol.* **154**(2): 429–437. doi:10.1046/j.1469-8137.2002.00396.x.
- Paulmier, I., Bagnères, A.-G., Afonso, C.M.M., Dusticier, G., Rivière, G., and Clement, J.-L. 1999. Alkenes as sexual pheromone in the alfalfa leaf-cutter bee *Megachile rotundata*. *J. Chem. Ecol.* **25**(3): 471–490. doi:10.1023/A:1020993518226.
- 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., 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.
- Peakall, R., Ebert, D., Poldy, J., Barrow, R.A., Francke, W., Bower, C.C., and Schiestl, F.P. 2010. Pollinator specificity, floral odour chemistry and the phylogeny of Australian sexually deceptive *Chiloglottis* orchids: implications for pollinator-driven speciation. *New Phytol.* In press. doi:10.1111/j.1469-8137.2010.03308.x. PMID:20561345.
- Pech, P., Fric, Z., and Konvicka, M. 2007. Species-specificity of the *Phengaris (Maculinea)* – *Myrmica* host system: fact or myth? (Lepidoptera: Lycaenidae; Hymenoptera: Formicidae). *Sociobiology*, **50**: 983–1003.
- Peter, C.I., and Johnson, S.D. 2008. Mimics and magnets: the importance of color and ecological facilitation in floral deception. *Ecology*, **89**(6): 1583–1595. doi:10.1890/07-1098.1. PMID:18589523.
- Pfunder, M., and Roy, B.A. 2000. Pollinator-mediated interactions between a pathogenic fungus, *Uromyces pisi* (Pucciniaceae), and its host plant, *Euphorbia cyparissias* (Euphorbiaceae). *Am. J. Bot.* **87**(1): 48–55. doi:10.2307/2656684. PMID:10636829.
- Pierce, N.E., Braby, M.F., Heath, A., Lohman, D.J., Mathew, J., Rand, D.B., and Travassos, M.A. 2002. The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Annu. Rev. Entomol.* **47**(1): 733–771. doi:10.1146/annurev.ento.47.091201.145257. PMID:11729090.
- Poinar, G.O., Jr. 1992. Life in amber. Stanford University Press, Stanford, Calif.
- Poldy, J., Peakall, R., and Barrow, R.A. 2008. Pheromones and analogs from *Neozeleboria* wasps and the orchids that seduce them: a versatile synthesis of 2,5-dialkylated 1,3-cyclohexanediones. *Tetrahedron Lett.* **49**(15): 2446–2449. doi:10.1016/j.tetlet.2008.02.037.
- Pouyanne, M. 1917. La fécondation des *Ophrys* par les insectes. *Bull. Soc. Hist. Nat. Afr. Nord*, **43**: 6–7.
- Proctor, M., and Yeo, P. 1972. The pollination of flowers. Taplinger Publishing Company, New York.
- Pyysalo, H., Koponen, A., and Koponen, T. 1978. Studies on entomophily in Splachnaceae (Musci). I. Volatile compounds in the sporophytes. *Ann. Bot. Fenn.* **15**: 293–296.
- Pyysalo, H., Koponen, A., and Koponen, T. 1983. Studies on entomophily in Splachnaceae (Musci). II. Volatile compounds in the hypophysis. *Ann. Bot. Fenn.* **20**: 335–338.
- Raguso, R.A. 2003. Olfactory landscapes and deceptive pollination: signal, noise and convergent evolution in scent. *In* Insect pheromone biochemistry and molecular biology—the biosynthesis and detection of pheromones and plant volatiles. *Edited by* G.J. Blomquist and R.G. Vogt. Elsevier, New York. pp. 631–650.
- Raguso, R.A. 2004. Why are some nectars scented? *Ecology*, **85**(6): 1486–1494. doi:10.1890/03-0410.
- Raguso, R.A., and Roy, B.A. 1998. ‘Floral’ scent production by *Puccinia* rust fungi that mimic flowers. *Mol. Ecol.* **7**(9): 1127–1136. doi:10.1046/j.1365-294x.1998.00426.x. PMID:9734071.
- Raguso, R.A., and Willis, M.A. 2002. Synergy between visual and olfactory cues in nectar feeding by naïve hawkmoths, *Manduca sexta*. *Anim. Behav.* **64**(5): 685–695. doi:10.1006/anbe.2002.4010.
- Raguso, R.A., and Willis, M.A. 2005. Synergy between visual and olfactory cues in nectar feeding by wild hawkmoths, *Manduca sexta*. *Anim. Behav.* **69**(2): 407–418. doi:10.1016/j.anbehav.2004.04.015.
- Rands, S.A., and Whitney, H.M. 2008. Floral temperature and optimal foraging: is heat a feasible floral reward for pollinators? *PLoS One*, **3**(4): e2007. doi:10.1371/journal.pone.0002007. PMID:18431488.
- 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.
- Roy, B.A. 1993. Floral mimicry by a plant pathogen. *Nature (London)*, **362**(6415): 56–58. doi:10.1038/362056a0.
- 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.
- Sachs, J.L., and Simms, E.L. 2006. Pathways to mutualism breakdown. *Trends Ecol. Evol.* **21**(10): 585–592. doi:10.1016/j.tree.2006.06.018. PMID:16828927.
- Salzmann, C.C., and Schiestl, F.P. 2007. Odour and colour polymorphism in the food-deceptive orchid *Dactylorhiza romana*. *Plant Syst. Evol.* **267**(1–4): 37–45. doi:10.1007/s00606-007-0560-z.
- Salzmann, C.C., Brown, A., and Schiestl, F.P. 2006. Floral scent emission and pollination syndromes: evolutionary changes from food to sexual deception. *Int. J. Plant Sci.* **167**(6): 1197–1204. doi:10.1086/508022.
- Salzmann, C.C., Cozzolino, S., and Schiestl, F.P. 2007a. Floral scent in food-deceptive orchids: species specificity and sources of variability. *Plant Biol (Stuttg.)*, **9**(6): 720–729. doi:10.1055/s-2007-965614. PMID:17891704.
- Salzmann, C.C., Nardella, A., Cozzolino, S., and Schiestl, F.P. 2007b. Variability in floral scent in rewarding and deceptive orchids: the signature of pollinator-imposed selection? *Ann. Bot. (Lond.)*, **100**(4): 757–765. doi:10.1093/aob/mcm161.

- Sapir, Y., Shmida, A., and Ne'eman, G. 2006. Morning floral heat as a reward to the pollinators of the *Oncoclytus* irises. *Oecologia* (Berl.), **147**(1): 53–59. doi:10.1007/s00442-005-0246-6.
- Saul-Gershenz, L.S., and Millar, J.G. 2006. Phoretic nest parasites use sexual deception to obtain transport to their host's nest. *Proc. Natl. Acad. Sci. U.S.A.* **103**(38): 14039–14044. doi:10.1073/pnas.0603901103. PMID:16966608.
- Schardl, C.L. 1996. *Epichloë* species: fungal symbionts of grasses. *Annu. Rev. Phytopathol.* **34**(1): 109–130. doi:10.1146/annurev.phyto.34.1.109. PMID:15012537.
- Schiestl, F.P. 2004. Floral evolution and pollinator mate choice in a sexually deceptive orchid. *J. Evol. Biol.* **17**(1): 67–75. doi:10.1046/j.1420-9101.2003.00650.x. PMID:15000649.
- 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. 2000. Post-mating odor in females of the solitary bee, *Andrena nigroaenea* (Apoidea, Andrenidae), inhibits male mating behavior. *Behav. Ecol. Sociobiol.* **48**(4): 303–307. doi:10.1007/s002650000241.
- Schiestl, F.P., and Ayasse, M. 2001. Post-pollination emission of a repellent compound in a sexually deceptive orchid: a new mechanism for maximising reproductive success? *Oecologia* (Berl.), **126**(4): 531–534. doi:10.1007/s004420000552.
- 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 Peakall, R. 2005. Two orchids attract different pollinators with the same floral odour compound: ecological and evolutionary implications. *Funct. Ecol.* **19**(4): 674–680. doi:10.1111/j.1365-2435.2005.01010.x.
- 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.
- Schiestl, F.P., Peakall, R., Mant, J.G., Ibarra, F., Schulz, C., Franke, S., and Francke, W. 2003. The chemistry of sexual deception in an orchid-wasp pollination system. *Science* (Washington, D.C.), **302**(5644): 437–438. doi:10.1126/science.1087835. PMID:14564006.
- Schiestl, F.P., Peakall, R., and Mant, J. 2004. Chemical communication in the sexually deceptive orchid genus *Cryptostylis*. *Bot. J. Linn. Soc.* **144**(2): 199–205. doi:10.1111/j.1095-8339.2003.00249.x.
- Schiestl, F.P., Steinebrunner, F., Schulz, C., von Reuß, S., Francke, W., Weymuth, C., and Leuchtman, A. 2006. Evolution of 'pollinator'-attracting signals in fungi. *Biol. Lett.* **2**(3): 401–404. doi:10.1098/rsbl.2006.0479. PMID:17148414.
- Schindler, M. 2005. Biologie kleptoparasitischer Bienen und ihrer Wirte (Hymenoptera, Apiformes): Labor- und Freilanduntersuchungen an Arten der Gattungen *Nomada* und *Andrena*. Dissertation, Rheinische Friedrich-Wilhelms-Universität Bonn, 2004, Bonn (Selbstverlag).
- Schlick-Steiner, B.C., Steiner, F.M., Höttinger, H., Nikiforov, A., Mistrik, R., Schafellner, C., Baier, P., and Christian, E. 2004. A butterfly's chemical key to various ant forts: intersection-odour or aggregate-odour multi-host mimicry? *Naturwissenschaften*, **91**(5): 209–214. doi:10.1007/s00114-004-0518-8. PMID:15146266.
- Schönrogge, K., Wardlaw, J.C., Peters, A.J., Everett, S., Thomas, J.A., and Elmes, G.W. 2004. Changes in chemical signature and host specificity from larval retrieval to full social integration in the myrmecophilous butterfly *Maculinea rebeli*. *J. Chem. Ecol.* **30**(1): 91–107. doi:10.1023/B:JOEC.0000013184.18176.a9. PMID:15074659.
- Searcy, W.A., and Nowicki, S. 2005. The evolution of animal communication: reliability and deception in signaling systems. Princeton University Press, Princeton, N.J.
- Seymour, R.S., and Schultze-Motel, P. 1997. Heat-producing flowers. *Endeavour*, **21**(3): 125–129. doi:10.1016/S0160-9327(97)80222-0.
- Seymour, R.S., and Schultze-Motel, P. 1999. Respiration, temperature regulation and energetics of thermogenic inflorescences of the dragon lily *Dracunculus vulgaris* (Araceae). *Proc. R. Soc. Lond. B Biol. Sci.* **266**(1432): 1975–1983. doi:10.1098/rspb.1999.0875.
- Seymour, R.S., Gibernau, M., and Ito, K. 2003a. Thermogenesis and respiration of inflorescences of the dead horse lily *Heliconia muscivora*, a pseudo-thermoregulatory aroid associated with fly pollination. *Funct. Ecol.* **17**(6): 886–894. doi:10.1111/j.1365-2435.2003.00802.x.
- Seymour, R.S., White, C.R., and Gibernau, M. 2003b. Environmental biology: heat reward for insect pollinators. *Nature* (London), **426**(6964): 243–244. doi:10.1038/426243a. PMID:14628037.
- Sick, M., Ayasse, M., Tengö, J., Engels, W., Lübke, G., and Francke, W. 1994. Host-parasite relationships in six species of *Sphecodes* bees and their halictid hosts: nest intrusion, intranidal behavior, and Dufour's gland volatiles (Hymenoptera: Halictidae). *J. Insect Behav.* **7**(1): 101–117. doi:10.1007/BF01989830.
- Simmons, L.W., Alcock, J., and Reeder, A. 2003. The role of cuticular hydrocarbons in male attraction and repulsion by female Dawson's burrowing bee, *Amegilla dawsoni*. *Anim. Behav.* **66**(4): 677–685. doi:10.1006/anbe.2003.2240.
- Simpson, B.B., and Neff, J.L. 1981. Floral rewards: alternatives 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.
- Smith, B.N., and Meeuse, B.J.D. 1966. Production of volatile amines and skatole at anthesis in some arum lily species. *Plant Physiol.* **41**(2): 343–347. doi:10.1104/pp.41.2.343. PMID:16656260.
- Steinebrunner, F., Schiestl, F.P., and Leuchtman, A. 2008a. Variation of insect attracting odor in endophytic *Epichloë* fungi: phylogenetic constrains versus host influence. *J. Chem. Ecol.* **34**(6): 772–782. doi:10.1007/s10886-008-9476-5. PMID:18463800.
- Steinebrunner, F., Schiestl, F.P., and Leuchtman, A. 2008b. Ecological role of volatiles produced by *Epichloë*: differences in antifungal toxicity. *FEMS Microbiol. Ecol.* **64**(2): 307–316. doi:10.1111/j.1574-6941.2008.00452.x. PMID:18328083.
- Steinebrunner, F., Twele, R., Francke, W., Leuchtman, A., and Schiestl, F.P. 2008c. Role of odour compounds in the attraction of gamete vectors in endophytic *Epichloë* fungi. *New Phytol.* **178**(2): 401–411. doi:10.1111/j.1469-8137.2007.02347.x. PMID:18194147.

- 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.
- Stensmyr, M.C., Urru, I., Collu, I., Celander, M., Hansson, B.S., and Angioy, A.-M. 2002. Pollination: rotting smell of dead-horse arum florets. *Nature (London)*, **420**(6916): 625–626. doi:10.1038/420625a. PMID:12478279.
- Stökl, J., Paulus, H., 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.
- Stökl, 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.
- Stökl, 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.
- Stowe, M.K. 1988. Chemical mimicry. In *Chemical mediation of coevolution*. Edited by K. Spencer. Academic Press, San Diego, Calif. pp. 513–580.
- Stowe, M.K., Tumlinson, J.H., and Heath, R.R. 1987. Chemical mimicry: bolas spiders emit components of moth prey species sex pheromones. *Science (Washington, D.C.)*, **236**(4804): 964–967. doi:10.1126/science.236.4804.964. PMID:17812752.
- Stowe, M.K., Turlings, T.C.J., Loughrin, J.H., Lewis, W.J., and Tumlinson, J.H. 1995. The chemistry of eavesdropping, alarm, and deceit. *Proc. Natl. Acad. Sci. U.S.A.* **92**(1): 23–28. doi:10.1073/pnas.92.1.23. PMID:7816823.
- Stránský, K., and Valterová, I. 1999. Release of volatiles during the flowering period of *Hydrosme rivieri* (Araceae). *Phytochemistry*, **52**(8): 1387–1390. doi:10.1016/S0031-9422(99)00247-2.
- Strohm, E., Kroiss, J., Herzner, G., Laurien-Kehnen, C., Boland, W., Schreier, P., and Schmitt, T. 2008. A cuckoo in wolves' clothing? Chemical mimicry in a specialized cuckoo wasp of the European beewolf (Hymenoptera, Chrysididae and Crabronidae). *Front. Zool.* **5**(1): 2. doi:10.1186/1742-9994-5-2. PMID:18190702.
- Tartally, A., and Varga, Z. 2008. Host and use by *Maculinea teleius* in the Carpathian Basin (Lepidoptera: Lycaenidae). *Acta Zool. Acad. Sci. Hung.* **54**(3): 257–268.
- Tartally, A., Nash, D.R., Lengyel, S., and Varga, Z. 2008. Patterns of host ant use by sympatric populations of *Maculinea alcon* and *M. 'rebeli'* in the Carpathian Basin. *Insectes Soc.* **55**(4): 370–381. doi:10.1007/s00040-008-1015-4.
- Tengö, J. 1979. Odour-released behaviour in *Andrena* bees (Apoidea, Hymenoptera). *Zoon*, **7**: 15–48.
- Tengö, J., and Bergström, G. 1975. All-*trans*-farnesyl hexanoate and geranyl octanoate in the Dufour gland secretion of *Andrem* (Hymenoptera, Apidae). *J. Chem. Ecol.* **1**(2): 253–268. doi:10.1007/BF00987874.
- Tengö, J., and Bergström, G. 1976. Odor correspondence between *Melitta* females and males of their nest parasite *Nomada flavo-picta* K. (Hymenoptera: Apoidea). *J. Chem. Ecol.* **2**(1): 57–65. doi:10.1007/BF00988024.
- Tengö, J., and Bergström, G. 1977. Cleptoparasitism and odor mimicry in bees: do *Nomada* males imitate the odor of *Andrena* females? *Science (Washington, D.C.)*, **196**(4294): 1117–1119. doi:10.1126/science.196.4294.1117. PMID:17778551.
- Thien, L.B. 1969. Mosquito pollination of *Habenaria obtusata* (Orchidaceae). *Am. J. Bot.* **56**(2): 232–237. doi:10.2307/2440711.
- Tholl, D., and Röse, U.S.R. 2006. Detection and identification of floral scent compounds. In *Biology of floral scent*. Edited by N. Dudareva and E. Pichersky. CRC Press, Taylor & Francis Group, Boca Raton, Fla. pp. 3–26.
- Thomas, J.A., and Elmes, G.W. 1998. Higher productivity at the cost of increased host-specificity when *Maculinea* butterfly larvae exploit ant colonies through tropholaxis rather than by predation. *Ecol. Entomol.* **23**(4): 457–464. doi:10.1046/j.1365-2311.1998.00153.x.
- Thomas, J.S., and Elmes, G.W. 2001. Food-plant niche selection rather than the presence of ants nests explains oviposition patterns of the myrmecophilous butterfly genus *Maculinea*. *Proc. R. Soc. Lond. B. Biol. Sci.* **268**(1466): 471–477. doi:10.1098/rspb.2000.1398.
- Thomas, J.A., and Settele, J. 2004. Evolutionary biology: butterfly mimics of ants. *Nature (London)*, **432**(7015): 283–284. doi:10.1038/432283a. PMID:15549080.
- Travassos, M.A., and Pierce, N.E. 2000. Acoustics, context and function of vibrational signalling in a lycaenid butterfly–ant mutualism. *Anim. Behav.* **60**(1): 13–26. doi:10.1006/anbe.1999.1364. PMID:10924199.
- Turgeon, J.J., McNeil, J.N., and Roelofs, W.L. 1983a. Responsiveness of *Pseudaletia unipuncta* males to the female sex pheromone. *Physiol. Entomol.* **8**(3): 339–344. doi:10.1111/j.1365-3032.1983.tb00366.x.
- Turgeon, J.J., McNeil, J.N., and Roelofs, W.L. 1983b. Evaluation of sex pheromone traps for the armyworm, *Pseudaletia unipuncta* (Haw.) (Lepidoptera: Noctuidae). *Environ. Entomol.* **12**: 891–894.
- Tyteca, D., Róis, A.S., and Vereecken, N.J. 2006. Observations on the pollination of *Ophrys fuciflora* by pseudocopulating males of *Phyllopertha horticola* in northern France. *Journal Europäischer Orchideen*, **38**: 203–214.
- van der Cingel, N.A. 2001. An atlas of orchid pollination: America, Africa, Asia and Australia. Balkema, Rotterdam, the Netherlands.
- van der Pijl, L., and Dodson, C.H. 1966. *Orchid flowers — their pollination and evolution*. University of Miami Press, Coral Gables, Fla.
- van Dyck, H., Oostermeijer, J.G.B., Talloen, W., Feenstra, V., van der Hidde, A., and Wynhoff, I. 2000. Does the presence of ants matter for oviposition to a specialized myrmecophilous *Maculinea* butterfly? *Proc. R. Soc. Lond. B Biol. Sci.* **267**: 861–866. doi:10.1098/rspb.2000.1082.
- 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 behaviour*. Edited by F. Baluska. Springer-Verlag, Berlin. pp. 203–222.
- Vereecken, N.J., and Mahé, G. 2007. Larval aggregations of the blister beetle *Stenoria analis* (Schaum) (Coleoptera: Meloidae) sexually deceive patrolling males of their host, the solitary bee *Colletes hederiae* Schmidt & Westrich (Hymenoptera: Colletidae). *Ann. Soc. Entomol. Fr.* **43**: 493–496.
- 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.
- Vogel, S. 1978. Pilzmückenblumen als Pilzmimeten I. Erster teil. *Flora*, **167**: 329–366.
- Wäckers, F.L. 2005. Suitability of (extra-)floral nectar, pollen and honeydew as insect food sources. In *Plant-provided food for car-*

- nivorous insects: a protective mutualism and its applications. Edited by F.L. Wäckers, P.C.J. van Rijn, and J. Bruin. Cambridge University Press, Cambridge. pp. 17–74.
- Wäckers, F.L., van Rijn, P.C.J., and Heimpel, G.E. 2008. Honeydew as a food source for natural enemies: making the best of a bad meal? *Biol. Control*, **45**(2): 176–184. doi:10.1016/j.biocontrol.2008.01.007.
- Wada, A., Isobe, Y., Yamaguchi, S., Yamaoka, R., and Ozaki, M. 2001. Taste-enhancing effects of glycine on the sweetness of glucose: a gustatory aspect of symbiosis between the ant, *Camponotus japonicus*, and the larvae of the lycaenid butterfly, *Niphanda fusca*. *Chem. Senses*, **26**(8): 983–992. doi:10.1093/chemse/26.8.983. PMID:11595675.
- Wagner, D. 1993. Species-specific effects of tending ants on the development of lycaenid butterfly larvae. *Oecologia (Berl.)*, **96**(2): 276–281. doi:10.1007/BF00317742.
- 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.
- Webster, J., and Weber, R. 2007. Introduction to fungi. 3rd ed. Cambridge University Press, Cambridge, UK.
- Wickler, W. 1968. Mimicry in plants and animals. Weidenfeld and Nicolson, London.
- Wiens, D. 1978. Mimicry in plants. *Evol. Biol.* **11**: 365–403.
- Witek, M., Sliwinska, E.B., Skorka, P., Nowichi, P., Wantuch, M., Vrabec, V., Settele, J., and Woyciechowski, M. 2008. Host and specificity of large blue butterflies *Phengaris (Maculinea)* (Lepidoptera: Lycaenidae) inhabiting humid grasslands in East-central Europe. *Eur. J. Entomol.* **105**: 871–877.
- Wolff, T. 1950. Pollination and fertilization of the fly ophrys, *Ophrys insectifera* L. in Allindellille Fredskov, Denmark. *Oikos*, **2**(1): 20–59. doi:10.2307/3564661.
- Wong, B.B.M., and Schiestl, F.P. 2002. How an orchid harms its pollinator. *Proc. R. Soc. Lond. B Biol. Sci.* **269**(1500): 1529–1532. doi:10.1098/rspb.2002.2052.
- Wyatt, T.D. 2003. Pheromones and animal behaviour: communication by smell and taste. Cambridge University Press, Cambridge.
- Yeagan, K.V. 1988. Ecology of a bolas spider, *Mastophora hutchinsoni*: phenology, hunting tactics, and evidence for aggressive chemical mimicry. *Oecologia (Berl.)*, **74**(4): 524–530. doi:10.1007/BF00380049.
- Yeagan, K.V. 1994. Biology of bolas spiders. *Annu. Rev. Entomol.* **39**(1): 81–99. doi:10.1146/annurev.en.39.010194.000501.
- Yeagan, K.V., and Quate, L.W. 1996. Juvenile bolas spiders attract psychodid flies. *Oecologia (Berl.)*, **106**(2): 266–271. doi:10.1007/BF00328607.
- Yeagan, K.V., and Quate, L.W. 1997. Adult male bolas spiders retain juvenile hunting tactics. *Oecologia (Berl.)*, **112**(4): 572–576. doi:10.1007/s004420050347.
- Zhu, J., and Haynes, K.F. 2004. Sex pheromone components of the bronzed cutworm, *Nephelodes minians*, a prey species of a bolas spider, *Mastophora hutchinsoni*. *J. Chem. Ecol.* **30**(10): 2047–2056. doi:10.1023/B:JOEC.0000045594.72243.b2. PMID:15609836.

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.