REVIEW

Insect Antennal Morphology: The Evolution of Diverse Solutions to Odorant Perception

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Chemical communication involves the production, transmission, and perception of odors. Most adult insects rely on chemical signals and cues to locate food resources, oviposition sites or reproductive partners and, consequently, numerous odors provide a vital source of information. Insects detect these odors with receptors mostly located on the antennae, and the diverse shapes and sizes of these antennae (and sensilla) are both astonishing and puzzling: what selective pressures are responsible for these different solutions to the same problem — to perceive signals and cues? This review describes the selection pressures derived from chemical communication that are responsible for shaping the diversity of insect antennal morphology. In particular, we highlight new technologies and techniques that offer exciting opportunities for addressing this surprisingly neglected and yet crucial component of chemical communication.

INTRODUCTION

Antennae are crucial for insects, the majority of whom live in a sensory world dominated by odors. The antennae support numerous sensilla that contain receptors capable of perceiving these odors [1]. The diverse shapes and sizes of insect antennae (Figure 1), ranging from the short antennae of dragonflies to the impossibly long antennae of longicorn beetles, or from the simple antennae of butterflies to the exquisite, feathery antennae of moths and beetles, is both marvelous and puzzling. What selective pressures are responsible for these diverse solutions to the same problem – to perceive signals and cues? While antennae can process information from a range of sensory modalities, the focus of this review is on olfactory communication. In particular, we outline why morphological features of insect antennae are likely to be subject to both natural and sexual selection; how applying modelling techniques from physics can help understand the significance of antennal shape, and; how particular selection pressures may act on the micro-morphology of antennae.

The majority of adult insects rely on volatile and non-volatile odors to provide information about food resources, oviposition sites, reproductive partners, and, for social species, their social environment [2]. There is a remarkable diversity of insect pheromones, odors produced by individuals that are detected by conspecifics [3], and possibly an even greater number of chemical cues that insects utilize as a source of information. In all cases, insects perceive these odors when they physically interact with chemo-receptors located on the sensilla, the majority of which are found on the antennae. For most insects, antennae provide the means to perceive these

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†Abbreviation: FSI, Fluid-Structure-Interaction.

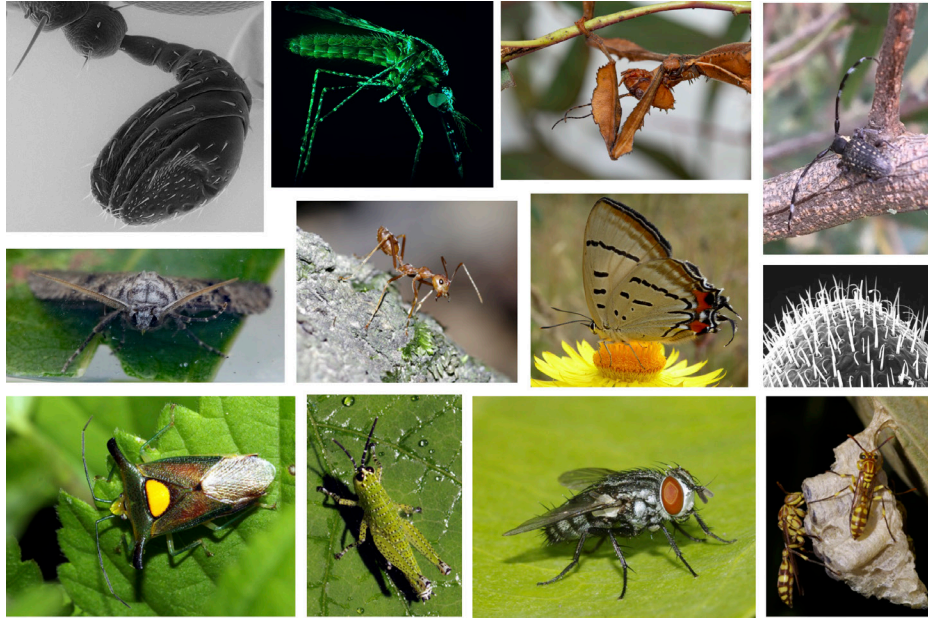Keywords: antennae, insects, chemical communication, receiver morphology, signal perception

Figure 1. The diversity of insect antennae (by rows, top to bottom, left to right): scarab beetle, *Phyllotocus macleaya* antenna (Scarabidae, Coleoptera; image: Christopher Freelance); mosquito *Anopheles* (Culicidae, Diptera; image: Qike Wang); stick insect, *Extatosoma tiaratum* (Phasmatidae, Phasmatodea; image: Christopher Freelance); Australian longicorn beetle (Cerambycidae, Coleoptera; image: Mark Elgar); moth, *Uraba lugens* (Nolidae, Lepidoptera; image: Christopher Freelance); ant worker, *Oecophilla* (Formicidea, Hymenoptera; image Zheng-yan Zhou); butterfly, *Jalmenus eva*goras (Lycaenidae, Lepidoptera; image: Mark Elgar); bloomed furrow bee, *Lasioglossum albipes* antenna (Halictidae, Hymenoptera; image: Bernadette Wittwer); shield bug *Anaxandra* (Acanthosomatidae, Hemiptera; image Zheng-yan Zhou); grasshopper (Orthoptera; image Zheng-yan Zhou); tachinid fly (Tachinidae, Diptera; image Zheng-yan Zhou); paper wasp, *Polistes* (Vespidae, Hymenoptera; image: Zheng-yan Zhou).

odors, although with varying degrees of difficulty: some forms of chemical information can be secured by simply brushing or tapping the antennae over the substrate, while some species, like moths, can perceive minute quantities of these chemical signals over vast distances [2]. The insect antenna is not exclusively involved in signal perception: some male Galerucinine chrysomelid beetles have unusual processes on the length of their antennae that are apparently used to grasp the female during copulation [4]; and the antennae of ant workers can be both a source and receptor of signature odors indicating colony membership [5].

Olfactory Communication

There is a specific challenge for olfactory sensory systems, which differ from other sensory modalities in a crucial manner: the odorant, or odor molecules, must come into physical contact with the odor receptor [6]. This raises the question of how the morphology of insect antennae has been shaped by natural selection to optimize odorant-receptor interactions – in other words, the likelihood that volatile chemical molecules arrive in the vicinity of specific receptors located on the receiver's antenna

(Figure 2). The observed antennal morphology is likely to "optimize" [7], rather than "maximize" odorant-receptor interactions simply because the size and shape of the antennae will also be subject to selection associated with aerodynamic and resource constraints.

The insect antenna typically comprises three distinct structures, which are broadly conserved across insects and allow almost omnidirectional movement [8]. A single segment forms the basal structure, or scape, that is attached to a membranous antennal socket on the cranium and is often supported, rather like a ball joint, by a pivot termed the antennifer. The second structure is the pedicel, a single segment that is attached to the scape by membranous cuticle and articulates as a hinge joint. The third, distal structure is the flagellum, which shows the greatest variation in length and shape within sexes, between sexes, and between species [8-10]. The types of flagella range from the relatively simple thread-like setaceous and filiform, through the more elaborate club-like (clavate and capitate), lamellate, pectinate and plumose forms (Figure 3). The greatest density and diversity of sensilla occur along the length of the flagellum, with the greatest densities typically found toward the distal end and on the lateral extensions to the flagella [8-10]. The
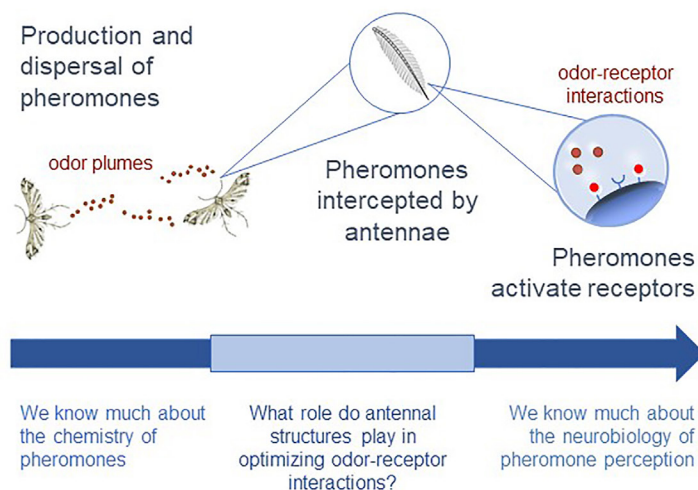
Figure 2. Schematic of the process of chemical communication, from odor production through to odorant perception, highlighting the role of antennae in bringing the odorant to the vicinity of the receptors. (Moth illustration by Sander van der Molen).

majority of these sensilla are involved in the detection of odors, temperature and humidity, while the sensilla located on the scape and pedicel are mostly mechano-receptors, allowing the individual to monitor the movement of the antennae (but see also [11]).

Research on chemical communication in insects has largely focused on either of the two ends of the process [*e.g.*, 2,12], as illustrated in Figure 2. Most research in chemistry and chemical ecology aims to characterize the chemical composition of the odors that are released as cues and signals [13], and the movement of these variously volatile odors through the environment [14,15]. More recently, phylogenetic comparative studies attempt to make sense of the evolution of both the diversification and convergence of pheromones [3]. At the other end, research on odor perception has focused on the genetic and neurobiological processes that occur once the odor molecules enter the pores of the sensilla and activate specific receptors that allow the individual to react appropriately [16-19]. The process of odor perception seems remarkably conserved, despite the considerable diversity of chemical signals and cues [17].

Signals, Cues, and Odor Detection

It is useful to distinguish odors as signals or cues, since their production and perception can involve different evolutionary processes. Following [20,21], an odor is a signal if it "influences the behavior of other organisms (receivers), and which evolved specifically because of that effect" [21, p. 75], whereas a cue is an incidental source of information that may influence the behavior of the receiver, despite not having evolved under selection for that end [21]. Thus, the sex pheromones of moths, beetles, and other insects are signals because they evolved to attract members of the opposite sex, whereas the release of CO_2 by breathing mammals did not evolve as a signal to feeding mosquitoes, but rather mosquitoes use CO_2 as a cue for locating their victims [20]. The evolution of a signal often, but not always, involves co-evolutionary processes in olfactory sensory systems because particular odorant molecules require specific receptors, although combinatorial processes of odorant perception allow individuals to extract considerable diversity of information, including from novel sources [2].

Theoretical and empirical studies of the evolutionary significance of animal signals retain a strong focus on the adaptive value of the signal, and especially the relationship between the signal and the signaler [20-25]. To behave, an animal requires an effective mechanism to perceive signals and cues, and yet any reference to the receiver is typically couched in terms of how the signal is distinguished from the background [23]. Far fewer studies acknowledge how selection may shape morphological and physiological traits that optimize signal or cue detection [3,26]. The evolutionary significance of the diversity of antennal morphology, including the abundance and variation in sensilla, is poorly understood despite the critical role of antennae for survival and reproduction. Antennae are often used as diagnostic characters for taxonomic and systematic studies, and there are numerous studies that provide detailed descriptions of the gross and fine structure of insect antennae [1,8-10]. However, surprisingly few ask how antennal morphology influences the efficiency with which chemical odors are detected [27], contrasting rather strikingly with our understanding
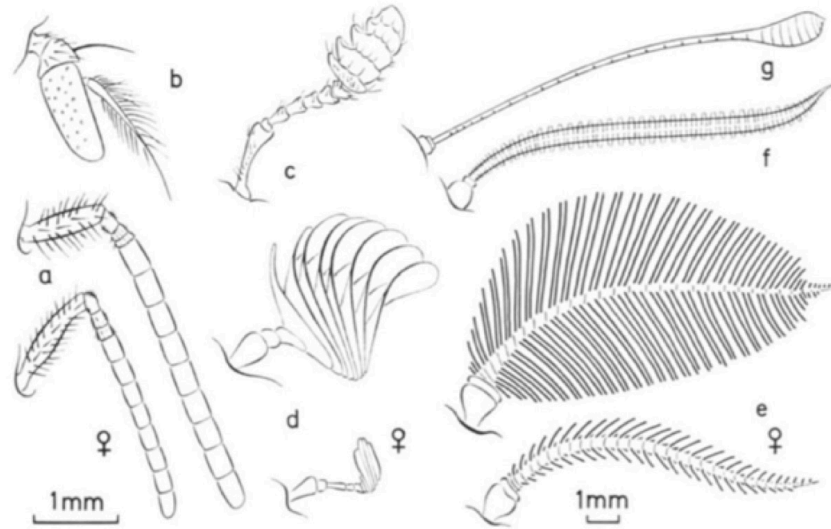
Figure 3. Antennae of male and female insects with well-developed olfactory sense: (**a**) honey bee (*Apis mellifera* L.); (**b**) flesh fly (genus *Sarcophaga*); (**c**) cariion beetle (genus *Necrophorus*); (**d**) scarabid beetle (genus *Rhopaea*); (**e**) saturniid moth (genus *Antheraea*); (**f**) hawk-moth (sphingidae, genus *Pergesa*) (**g**) butterfly (genus *Vanessa*). Common scale (1 mm) for **a-d** and **e-g**. Reproduced from [10].

of other key features of insect morphology, such as wings [28].

COSTS AND BENEFITS OF ANTENNAL MORPHOLOGY

In theory, we expect the size and structure of insect antennae to be shaped by natural selection so that the morphology optimizes [*sensu* 7] the benefits of improved signal perception against the costs of developing and maintaining these structures. Nervous tissue is among the most expensive of animal tissues [29] and resources are required to both construct the antennae and maintain neural activity [29,30]. While measuring how those costs vary with the size and structure of antennae are technically challenging, the facultative changes in the investment in sensilla number with life-history changes are consistent with that view (see below).

A widely held, but largely untested, premise is that odorant-receptor interactions are enhanced primarily by the size of the antennae, simply because larger antennae can support larger numbers of sensilla (Figure 4). The striking sexual dimorphism in antennal size and shape in many groups of insects, but especially moths and beetles (Figure 1) is often used to illustrate this point: the impressively ornate antennae of males allows them to detect the typically minute quantities of sex pheromones released by females [*e.g.*, 31]. Indeed, the ornate antennae of moths were thought to act as a sieve, with the efficiency of the antennae (or probability of odorant-receptor interactions) being a function of the outline area of the antennae; the proportion of molecules that are "adsorbed" from the

airstream by the antennae; and the fraction of those molecules that actually move to the vicinity of the receptors [10]. This model broadly predicts, *ceteris paribus*, that larger, feathery (pectinate) antennae are more efficient at detecting odors. Subsequent experiments revealed that the shape of the antennae does not affect the rate of collection of the odorant, which can be better explained as a function of the concentration of the odorant and the surface area of the antennae [32]. Thus, selection has not favored the feather (pectinate) structure of the antennae because it can act as a sieve, but rather because it increases the surface area of the antennae, which can support more sensilla [32]. Indeed, sensilla are not distributed evenly across the flagellum but are typically more dense at the distal end, suggesting that other factors may also be involved in shaping antennal efficiency [8]. Similarly, Ramsey *et al*. [33] argue that the elaborate lamellate antennae of male *Rhipicera* beetles increases surface area, changes the airflow across the antennae, and thus the likelihood of odorant-receptor interactions.

Phylogenetic comparative analyses support this view [34]. Species of moths with elaborate (pectinate) antennae are typically larger, but these antennae are relatively shorter for their body size, suggesting that they cannot be supported by smaller moths. Interestingly, females of larger species are also likely to be able to produce large quantities of pheromone, contradicting the common belief that pectinate antennae evolved in order to detect the minute quantities of female sex-pheromone. Were that the case, elaborate antennae should be more common in males of species with smaller-bodied females, who produce smaller quantities of pheromone. Nevertheless, two
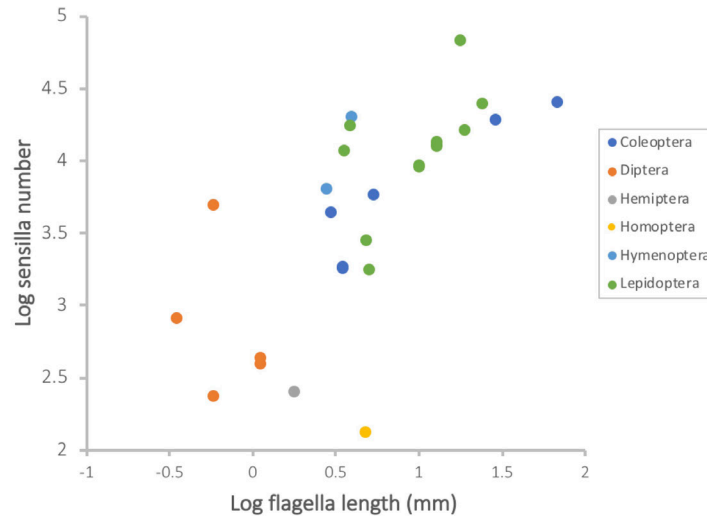
Figure 4. The number of sensilla qualitatively increases with flagella length across males and females of various insects. Data from [8].

lines of evidence suggest that the abundance and volatility of the pheromone may influence antennal size among species with pectinate antennae: antennal length was negatively correlated with both pheromone molecular weight and male abundance [34]. However, these patterns did not hold for species with simple (filiform) antennae. Interestingly, the opposite pattern may emerge in beetles: species with large, elaborate antennae use pheromones with lower volatility than species with small, simpler antennae (Figure 5), [35].

Remarkably few studies link signal perception with antennae size or sensilla number. Workers of the green tree ant *Oecophyla smaragdina*, brush their antennae across the cuticle of conspecific workers to determine their identity, responding aggressively to non-nestmate workers [27]. The level of aggression towards non-nestmates was positively correlated with the condition of the antennae of the workers: ants whose antennae had fewer sensilla were much less aggressive toward non-nestmates than workers whose antennae had greater numbers of sensilla. In this species, large numbers of sensilla are required for the workers to identify correctly whether conspecifics are from the same or different nests [27]. Similarly, the ability of bumblebees to detect volatile plant odors is influenced by antennal size. Bumblebees with longer antennae, and thus greater numbers of sensilla, could detect lower concentrations of plant odor stimulus, a pattern that was confirmed by electroantennograms [36].

Experimental studies provide additional evidence. The ability of male diamond back moths *Plutella xylostella* to detect female sex pheromone and of females to detect oviposition sites was reduced following experimental reduction of the length of the antennae [37].

Mate and oviposition search was not impaired when less than 25 percent of the antennae was ablated, but these behaviors were compromised when more than 50 percent of the length of antennae was removed. It is thought that the presence of two antennae allows insects to determine the direction of an odor source by comparing the quantity of odor detected in each antenna. For example, when one antenna is experimentally removed, the individual typically loses directionality (*Drosophila*: [38]; *Lasius*: [39]; *Bombyx*: [40]). A similar pattern occurs in cockroaches *Periplaneta americana*, but this arises through a loss of total antennal length across the two antennae, rather than antennal symmetry: individuals with one antenna could track the odor plume, but the performance of individuals with a portion of one antenna missing was similar to that of individuals with half that length removed from both antennae [41]. While these experimental studies suggest that the length of the antennae influences the ability of these insects to detect chemical signals, the result may simply reflect the damage to the integrity of the antennae.

ANTENNAL STRUCTURES, ODORANT-RECEPTOR INTERACTIONS, AND COMPUTATIONAL MODELLING

Our understanding of the mechanism by which antennae can "capture" odorants from the air flow and thus increase the likelihood of odorant-receptor interactions is likely to be best informed by simulation models. Computational models in particular provide exciting opportunities to investigate the fluid, structural, and particle physics at the scales of structures of insect antennae — something that is near impossible to achieve through
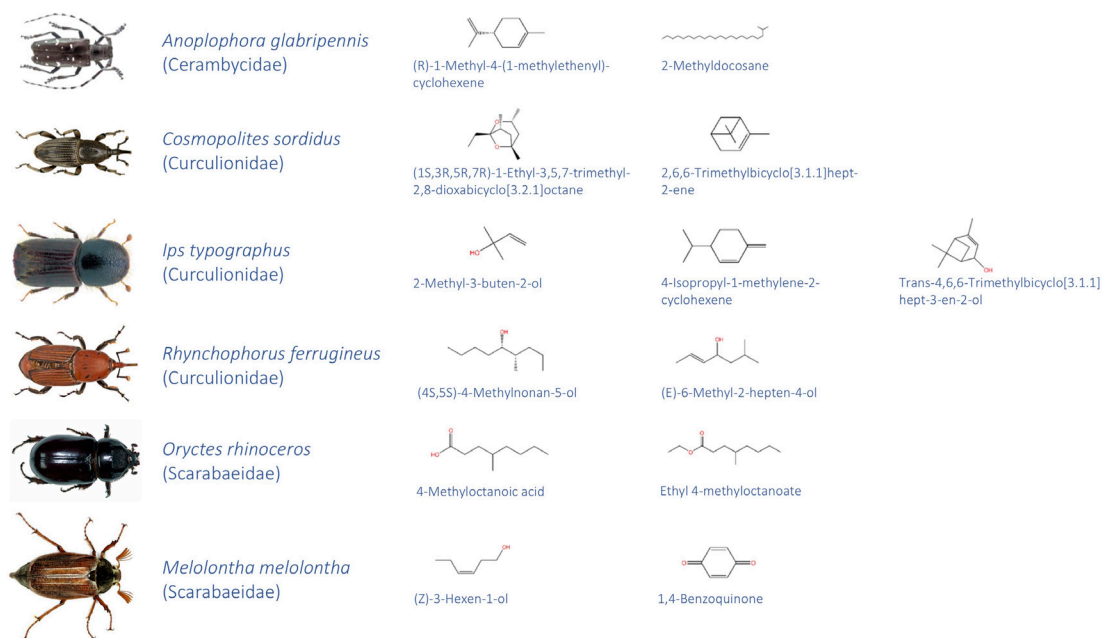
Figure 5. Beetles with different antennal morphology and their representative pheromones. Beetles with relatively larger and more elaborate antennae (bottom three species) use pheromones with lower volatility, while species with relatively more simple, smaller antennae (top three species) use more volatile pheromones. (Data from [35]). (Image credits: *A. glabripennis*, Dutch Government; *C. sordidus*, Joachim Rheinheimer; *I. typographus*, Udo Scmidt; *R. ferrugineus*, Didier Descouens; *O. agamemnon*, source unknown, http://www.enature.qa/specie/rhinoceros-beetle/; *M. melolontha*, Josef Dvorak).

experimental methods because of the size and invasive nature of measurement devices. The level of detail and quantitative data from modelling and simulation provides visualizations that can reveal flow behavior influencing pheromone transport in the air and its deposition onto odorant receptors. Fluid-Structure-Interaction (FSI) simulation studies can reveal how macro and micro-morphological features of insect antennae influence the airflow patterns [42].

The pectinate antennae of many species of moths may increase the perception of sex pheromone, but most moths have simple, filamentous antennae [31,32], which begs the question how can males of smaller species improve the likelihood of detecting sex pheromones? One possibility is that the abundant scales, which cover the surface of the antennae, alter the airflow that carries the pheromone molecules, thereby increasing the chance of interacting with sensilla. Qike Wang and colleagues [42] investigated this idea by comparing the efficiency of moth antennae that vary in size and arrangement of scales: in some species, the scales run parallel to the length of the antennae, while in others they are slightly raised and form regular rings.

Certain arrangements of scales concentrate the nano-sized particles (the size of pheromone molecules) around the antennae, while diverting micron-sized parti-

cles (the size of debris) away from the antennal surface, thereby reducing contamination (Figure 6). Interestingly, these scales retain nano-sized particles within a trajectory that corresponds with the height of the trichoid sensilla, whereas the larger, potentially contaminating micro-sized particles are dispersed away from the sensilla. Increasing the angle of the scale with respect to the surface of the antennae improved signal detection for smaller, but not larger, antennae. If pheromone perception is determined by the frequency of interactions between the odorant molecules and receptors located in the antennal sensilla, then species that typically detect low concentrations of pheromone are expected to have larger numbers of sensilla [1,43]. Greater investment in sensilla may be accompanied by other aerodynamic mechanisms that improve pheromone detection, such as antennal scales, and this prediction was corroborated with data from heliozelid moths (Figure 6). Clearly, this approach has great potential for explaining the functions of antennal structures more generally, and investigating how the different antennal structures vary in detection efficiency in different environmental circumstances.
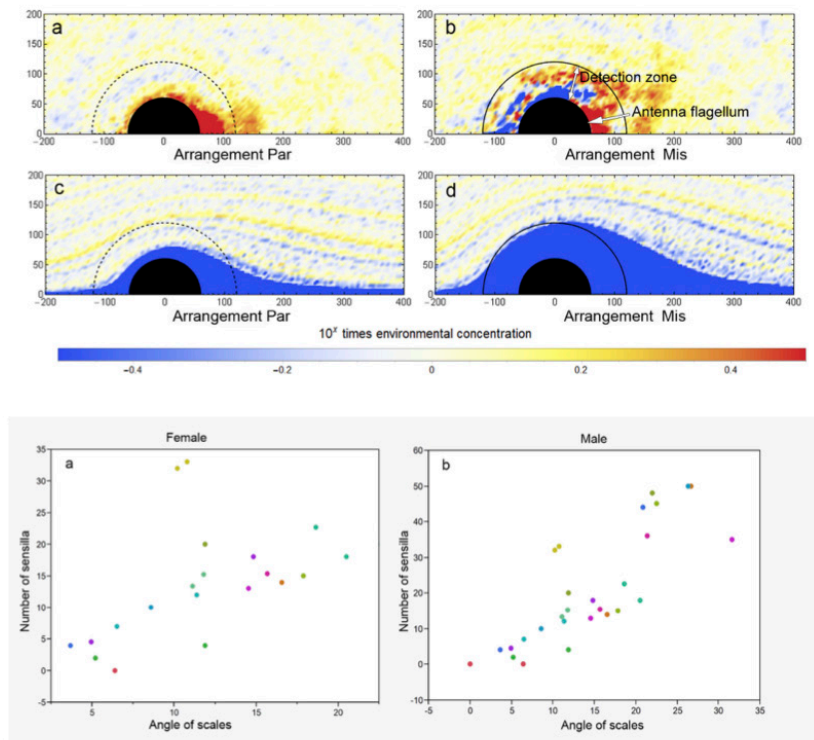
Figure 6. Predicted concentration (red is high) around the surface of the antennae of nano-particles (pheromone molecules) in the (**a**) parallel and (**b**) ringed arrangement of antennal scales, and of micro-particles in the (**c**) parallel and (**d**) ringed arrangement of antennal scales. Sensilla number increases with the angle of the scales across genera (indicated by different colors) of heliozelid moths (Reproduced from [42]).

EVIDENCE OF SELECTION ON ANTENNAL MORPHOLOGY

Several lines of evidence indicate that insect antennal morphology is under selection to increase the efficiency of detecting signals and odors. The role of selection may arise in several contexts because adult insects rely on odors to locate food resources, oviposition sites and reproductive partners [2]. Additionally, social insects rely on odors as a form of communication necessary for organizing colony activities. The following section documents how each of these processes influence variation in antennal morphology.

Mate Location and Sexual Selection

There is striking sexual dimorphism in the shape and size of insect antennae. The males of many species of moths and beetles have elaborate, feathery antennae, whereas their conspecific females have simple, filiform antennae. Males of longhorn beetles (Cerambycidae) have antennae that clearly exceed their body length, while conspecific female antennae are much shorter. Such extremes of sexual dimorphism are not uncom-

mon in animals [44,45] and Darwin [46] proposed that sexual selection is responsible for those characters that determine the competition over mating opportunities: the armaments used by males in physical contests with other males [47], or the extravagant displays of males that females use to select their mates [44,48]. There is also an emerging interest in the role of odor signals in conveying information about mate quality [49,50].

Less well appreciated is Darwin's [46] suggestion that sexual selection may act on "organs of sense," such as insect antennae [51]. He argued that males with more "highly developed" organs of sense would be better equipped to find the signaling female and thus be at a competitive advantage over other males. Indeed, this may provide females with a mechanism to ensure they encounter high quality males. Females that reduce their output of sex-attracting pheromone might attract only males whose antennae are more sensitive to these low concentrations of pheromone, perhaps because the antennae are larger or more elaborate. If the cost of these "extravagant," sensitive antennae is not trivial, then only "high quality" males would be able to support them [51]. Indirect support for Darwin's key prediction comes from field studies re-

vealing that mated males of the long-horned borers *Phoracantha semipunctata* (Cerambycidae) were larger and had longer antennae than unmated males [52]; the ability of female pollen katydids *Kawanaphila nartee* to detect male calls was influenced by the size of their thoracic auditory spiracles [53]; and that male false garden mantids *Pseudomantis albofimbriata* arrived at calling females more quickly if the density of their antennal trichoid sensilla was greater [54]. Johnson *et al.* [55] manipulated the quantity of sex-attracting pheromone released by female gum leaf skeletoniser moths *Uraba lugens* by placing either one or two restrained females in delta traps and measuring the size of the antennae of captured males. The mean antennal length of males caught in traps with a single female was longer than that of males caught in traps with two females that emitted more pheromone.

Anticipatory Investment in Antennal Morphology

Developmental phenotypic plasticity, in which an individual's developmental trajectory is advantageously modified to match the environment it is likely to encounter at maturity, has been documented for diverse taxa [56,57]. These adaptive, "plastic" responses require physical and social environmental cues that reliably indicate the expected adult environment [58]. Numerous behaviorally, physiologically, and morphologically plastic characters have been documented, including insect antennae.

A key feature of locusts is that they respond to local density by shifting between a cryptic solitarious phenotype and a high density, gregarious phenotype. Among the differences between these two phenotypes is the density of olfactory sensilla on their antennae, presumably reflecting different sensory requirements. For example, solitarious adults of the locust *Locusta migratoria* have more olfactory sensilla on their antennae than gregarious adults [59], a pattern observed in other species of acridids [60]. In the desert locust *Schistocerca gregaria*, the gregarious phenotype emerges if nymphs either see, smell or are touched by other locusts [61], while touching the antennae triggers the gregarious phenotype in the Australian plague locust *Chortoicetes terminifer* [62].

The larvae of the gum leaf skeletoniser moth *U. lugens* are gregarious as young instars but tend to disperse in later instars. Adult males have bipectinate antennae, and males with larger antennae are more capable of detecting lower concentrations of female pheromone [55]. Thus, males should benefit by a greater investment in mate location strategies when population densities are low, and in mating effort strategies when population densities are high. Experiments confirmed this prediction: adults of larvae reared in low density conditions had larger antennae than those reared in high density conditions, who had larger testes [63]. This capacity for anticipatory flexibility in sensory investment may explain why long-term selection through population density failed to generate changes in antennal morphology in the Indian meal moth *Plodia interpunctella* [64].

Social Environment

Communication is crucial for maintaining social organization — at the very least, it allows individuals to recognize cooperating individuals and respond appropriately. Increasing complexity in social organization is likely to be accompanied by a greater diversity of signals that coordinate social activities. In social insects, this information is typically conveyed through chemical signals and thus may require an increasing number of receptors to detect the greater diversity of signals. As a result, we would expect larger antennae and/or greater density of antennal sensilla in social than solitary species. Similarly, within social species, we expect greater investment in sensory structures in individuals typically responding to a greater range of signals.

Arguably the earliest documented experimental evidence of the social communication function of antennae is provided by Auguste Forel, who ablated, on the 12th August, 1886 the antennae of many workers of *Formica sanguinea*, *F. pratensis*, *Camponotus ligniperdus,* and *Lasius niger*, and placed these workers together in a single container. He noted that "Little by little, my various ants huddled piously together, one on top of another, despite the diversity of species and formicaries" [65]. As Forel [65] explains, had their antennae remained intact, the workers would have been able to detect the identity of the other ants, and responded appropriately: workers of social insects are typically aggressive to individuals that are not conspecific nestmates [66].

Differences in the diversity and abundance of sensilla between castes have been reported in several species of social insects [67-69], which may reflect their different tasks. For example, Grüter *et al.* [70] found that guards of the social stingless bee *Tetragonisca angustula* were larger and so had greater antennal surface area. Larger guards were more effective at detecting conspecific non-nestmates [70]. There are two kinds of workers of the green tree ant *Oecophylla smaragdina*: major workers that leave the nest, and minor workers that typically remain inside or on the surface of the nest. Major workers have greater numbers of antennal sensilla than minor workers [67], and also react more aggressively to conspecific non-nestmates [71]. Workers of the social stingless bee *Tetragonula carbonaria* may be guards, who remain close to the nest entrance, or foragers, who leave the nest in search of food. While workers engaged in these two activities are morphologically indistinguishable to the naked eye, they differ in the density of antennal sensilla, with density greater for guards than foragers [72]. Presumably the greater density of sensilla in guards equips

them with greater perception of unwanted intruders. It would be interesting to discover whether these "cryptic castes" [72], defined by differences in the micro-morphological features of the antennae, are more widespread among social insects.

The full range of social organization, from solitary to eusocial, are found within the halictid bees, and while there have been several gains of eusociality within this group, there have been many more reversions to a solitary lifestyle [73]. Phylogenetic comparative analyses reveal that an evolutionary loss of social behavior is associated with a *loss* in antennal sensilla density [74]. Interestingly, the same pattern emerges when comparing social and solitary populations of the socially polymorphic bee, *Lasioglossum albipes* [74]. These data highlight the significance of costly sensory systems for social behavior, and also suggest that the evolution of social behavior requires a pre-existing high investment in sensory morphology. However, the suggestion that the link between behavioral lateralization and an asymmetric distribution of antennal sensilla in social, but not solitary bees, provides greater efficiency for social organization [75] finds little broader phylogenetic support [76].

Searching for Food

Odors provide insects with a significant source of information about the location and nature of food sources. Some insects are polyphagous, feeding on a range of different species, while oligophagous species confine their food plants to one or two species. These differences in foraging strategies may translate into differences in antennal morphology. Drawing on data for European orthopterans, Chapman [1] suggested that insects with a generalist diet require a greater number of sensilla than species with a more specialized diet. More recent studies provide mixed support for this view. Species of *Dendroctonus* bark beetles have club-shaped antennae, and two morphologically similar species – *D. rhizophagus* and *D. valens* – have different host plant ranges. The average number of long basiconica sensilla, typically associated with chemoreception, was qualitatively greater in the strongly polyphagous secondary beetle *D. valens* than in the primary beetle *D. rhizophagus*, which has a quarter of the number of hosts [77].

However, the opposite pattern emerges among populations of the aphid *Uroleucon ambrosiae*, whose host range varies with geography in North America: aphids on the eastern seaboard specialize on the giant ragweed, *Ambrosia trifida*, while those from the southwest have a more catholic diet. These differences in diet breadth are thought to derive from their capacity to make oviposition decisions — the generalist aphids may be less deterred by chemicals found on plants other than ragweed. While larger aphids generally have more rhinaria (olfactory

plate organs) on their antennae, the number of rhinaria was greater on specialist than generalist aphids [78], contradicting the predicted [1] pattern.

Other studies are unable to support or refute Chapman's [1] prediction. There is no difference among non-parasitic halictid bees in the density of sensilla between pollen-specialist and other species [79], and no consistent differences in the density of various antennal sensilla between a polyphagous and several species of oligophagous *Delia* root flies [80], or in the number of antennal sensilla across species of grasshoppers with different feeding ecologies [81,82].

Characteristics of the prey of predatory insects may also influence antennal micro-morphology. A comparison among species of wasp predators suggests differences in sensilla types and density between bee-hunting and beetle-hunting species [83], although this would require confirmation from a larger data set and using phylogenetic comparative analyses. Mosquitoes are not typically regarded as predators, but McIver [84] found some evidence that sensilla numbers and types varied across species of mosquitoes according to their preferred hosts.

Searching for Hosts

The larval stages of insect parasitoids rely on their hosts for nutrition, and adult parasitoids use host-derived signals and cues to locate their victims [85]. Some parasitoids are host specific, laying eggs on a single host species, while others may attack a range of hosts. Following Chapman [1], host generalist parasitoids are predicted to have greater numbers of sensilla than specialist parasitoids, in order to accommodate the additional olfactory cues [86]. However, the opposite pattern emerged in a comparison of the density of sensilla associated with chemoreception (basiconica and placoidea) of braconid parasitoid wasps: sensilla density of the host specialist *Microplitis croceipes* was greater than that of the generalist *Cotesia marginiventris* [87]. Comparisons between two species are inevitably inconclusive, but a phylogenetic comparative analysis of chalcid wasps did not reveal consistent covariation between host specialization and antennal length, although chalcids that parasitize Hemipteran hosts tend to have larger antennae [86].

The antennal morphology of parasites and parasitoids may also be influenced by the nature of particular chemical cues that reveal specific oviposition sites. For example, horse stomach bot flies (*Gasterophilus* Leach) are obligate intestinal parasites of their equid hosts that include horses, donkeys, and zebras [88,89]. These flies have similar life cycles, and while different species are often found in the same hosts, they differ in their oviposition site, with each species ovipositing on different body parts or on the food of their hosts [90]. The diversity of antennal morphology, including the types and arrange-

ments of antennal sensilla, among the eight species of this genus [91] may be associated with chemical cues that are specific to the different oviposition sites. Clearly, the relationship between host specialization and antennal morphology requires further investigation, especially where host diet influences the odors used as cues [see 50].

Background Noise and Abiotic Modifiers

The diversity of odors produced by plants and other insects means that background olfactory noise can generate a significant challenge to signal transmission and perception [92-95]. While a "cacophony" of odors can have an impact on detecting specific chemical compounds, it may also be used as long-range habitat cues, providing initial generalized information for plant and other host-seeking insects that can subsequently focus on specific signals or cues in the correct habitat [96]. We do not know whether the intensity of background olfactory noise acts as a selection pressure on antennal morphology.

Humidity, temperature, and air pollution can affect the ability of receivers to detect pheromones and odor cues, because high humidity and air pollution can reduce the life-span of the odor, effectively attenuating the signal or cue [97-100]. For example, wind tunnel experiments showed that fewer males of the European corn borer *Ostrinia nubilalis* took flight in response to female sex pheromones in trials with higher levels of humidity [98]. This may explain the increase in pheromone titre with an increase in relative humidity in this species [100]. However, humidity did not affect the response of bark beetles *Ips grandicollis* to synthetic aggregation pheromone [101]. Clearly, this is an effect that requires investigation with a range of taxa, including whether there are changes in antennal morphology with humidity gradients.

CONCLUSIONS

There is emerging experimental and observational evidence that antennal morphology is subject to both natural and sexual selection, and yet surprisingly few studies have addressed the ways in which antennal morphology influences odorant-receptor interactions. While we know a great deal about the chemistry and transmission of odors, and the neurobiology of odorant perception, we know relatively little about how insects optimize their perception of odors and cues. Thus, there is a rich seam of potential research questions that address how the size and structure of insect antennae have been shaped by natural and sexual selection. In particular, fluid dynamic modelling coupled with phylogenetic comparative analyses offer exciting opportunities to understand precisely how micro-morphological features of the antennae can influence odorant-receptor interactions.

REFERENCES

1. Chapman RF. Chemoreception: the significance of receptor numbers. Adv Insect Physiol. 1982;16:247–356.
2. Wyatt TD. Pheromones and animal behavior. Cambridge, UK: Cambridge University Press; 2014.
3. Symonds MR, Elgar MA. The evolution of pheromone diversity. Trends Ecol Evol. 2008;23:220–8.
4. Mohamedsaid MS, Furth DG. Secondary sexual characteristics in the Galerucinae (*sensu stricto*) (Coleoptera: chrysomelidae). ISRN Zool. 2011;2011:328670.
5. Wang Q, Goodger JQ, Woodrow IE, Elgar MA. Location-specific cuticular hydrocarbon signals. Proc Biol Sci. 2016;283:20160310.
6. Greenfield MD. Signalers and Receivers. Oxford, UK: Oxford University Press; 2002.
7. Maynard Smith J. Optimization theory in evolution. Annu Rev Ecol Syst. 1978;9:31–56.
8. Zacharuk RY. Antennae and sensilla. Comp Insect Physiol Biochem Pharmacol. 1985;6:1–69.
9. Schneider D. Insect antennae. Annu Rev Entomol. 1964;9:103–22.
10. Kaissling KE. Insect olfaction. In: Beidler LM, editor. Handbook of Sensory Physiology. Volume IV. Heidelberg, Germany: Springer; 1971. pp. 351–431.
11. Liu XH, Zhang M, Shi JN, Li K, Zhang D. Ultrastructure of antennal sensilla of a parasitoid fly, *Pales pavida* Meigen (Diptera: tachinidae). Micron. 2013;54:36–42.
12. Ryan MF. Insect Chemoreception: Fundamental and Applied. Kluwer Academic Publishers; 2002.
13. Schulz S, editor. The Chemistry of Pheromones and other Semiochemicals, vols I and II. Springer; 2004,2005.
14. Murlis J, Elkington JS, Caré RT. Odor plumes and how insects use them. Annu Rev Entomol. 1992;37:505–32.
15. Bau J, Cardé RT. Modeling optimal strategies for finding a resource-linked, windborne odor plume: theories, robotics, and biomimetic lessons from flying insects. Integr Comp Biol. 2015;55:461–77.
16. Missbach C, Dweck HK, Vogel H, Vilcinskas A, Stensmyr MC, Hansson BS, et al. Evolution of insect olfactory receptors. eLife. 2014;3:e02115.
17. Fleischer J, Pregitzer P, Breer H, Krieger J. Access to the odor world: olfactory receptors and their role for signal transduction in insects. Cell Mol Life Sci. 2018;75:485–508.
18. Malnic B, Hirono J, Sato T, Buck LB. Combinatorial receptor codes for odors. Cell. 1999;96:713–23.
19. Hallem EA, Dahanukar A, Carlson JR. Insect odor and taste receptors. Annu Rev Entomol. 2006;51:113–35.
20. Maynard Smith J, Harper DG. Animal Signals. Oxford, UK: Oxford University Press; 2003.
21. Stevens M. Sensory Ecology, Behaviour, and Evolution. Oxford, UK: Oxford University Press; 2013.

22. Searcy WA, Nowicki S. Evolution of animal communication: reliability and deception in signaling systems. Princeton, USA: Princeton University Press; 2005.

23. Endler JA. A predator's view of animal color patterns. Evol Biol. 1978;11:319–64.

24. Schaefer HM, Ruxton GD. Signal diversity, sexual selection and speciation. Annu Rev Ecol Evol Syst. 2015;46:573–92.

25. Hebets EA, Barron AB, Balakrishnan CN, Hauber ME, Mason PH, Hoke KL. A systems approach to animal communication. Proc Biol Sci. 2016;283:20152889.

26. Caves EM, Brandley NC, Johnsen S. Visual acuity and the evolution of signals. Trends Ecol Evol. 2018;33:358–72.

27. Gill KP, van Wilgenburg E, Macmillan D, Elgar MA. Density of sensilla influences efficacy of communication. Am Nat. 2013;182:834–40.

28. Hedrick TL, Combes SA, Miller LA. Recent developments in the study of insect flight. Can J Zool. 2015;93:925–43.

29. Niven JE, Laughlin SB. Energy limitation as a selective pressure on the evolution of sensory systems. J Exp Biol. 2008;211:1792–804.

30. Stöckl A, Heinze S, Charalabidis A, el Jundi B, Warrant E, Kelbe A. Differential investment in visual and olfactory brain areas reflects behavioral choices in hawk moths. Sci Rep. 2016;6:26041.

31. Phelan PL. Evolution of mate signaling in moths. In: Choe JC, Crespi BJ, editors. Evolution of mating systems in insects and arachnids. Cambridge, UK: Cambridge University Press; 1997. pp. 240–56.

32. Mankin RW, Mayer MS. The insect antenna is not a molecular sieve. Experientia. 1984;40:1251–2.

33. Ramsey A, Houston TF, Ball AD, Goral T, Barclay MV, Cox JP. Towards an understanding of molecule capture by the antennae of male beetles belonging to the Genus *Rhipicera* (Coleoptera, Rhipiceridae). Anat Rec (Hoboken). 2015;298:1519–34.

34. Symonds MR, Johnson TL, Elgar MA. Pheromone production, male abundance, body size, and the evolution of elaborate antennae in moths. Ecol Evol. 2011;2:227–46.

35. El-Sayed AM. The Pherobase: Database of Pheromones and Semiochemicals. http://www.pherobase.com; 2018.

36. Spaethe J, Brockmann A, Halbig C, Tautz J. Size determines antennal sensitivity and behavioral threshold to odors in bumblebee workers. Naturwissenschaften. 2007;94:733–9.

37. Yan X-z, Deng C-P, Sun X-J, Hao C. Effects of various degrees of antennal ablation on mating and oviposition preferences of the diamondback moth, *Plutella xylostella* L. J Integ Agricult. 2014;13:131-1319.

38. Duistermars BJ, Chow DM, Frye MA. Flies require bilateral sensory input to track odor gradients in flight. Curr Biol. 2009;19:1301–7.

39. Hangartner W. Spezifitä t und inaktivierung des spurpheromons von *Lasius fuliginosus* Latr. und orientierung der arbeiterinnen im duftfeld. Z Vgl Physiol. 1967;57:103–36.

40. Takasaki T, Namiki S, Kanzaki R. Use of bilateral information to determine the walking direction during orientation to a pheromone source in the silkmoth *Bombyx mori*. J Comp Physiol A Neuroethol Sens Neural Behav Physiol. 2012;198:295–307.

41. Lockey JK, Willis MA. One antenna, two antennae, big antennae, small: total antennae length, not bilateral symmetry, predicts odor-tracking performance in the American cockroach *Periplaneta americana*. J Exp Biol. 2018;218:2156–65.

42. Wang Q, Shang Y, Hilton DS, Inthavong K, Zhang D, Elgar MA. Antennal scales improve signal detection efficiency for moth communication. Proc Biol Sci. 2018;285:20172832.

43. Greenfield MD. Moth sex pheromones: an evolutionary perspective. Fla Entomol. 1981;64:4–17.

44. Andersson M. Sexual selection. Princeton, USA: Princeton University Press; 1994.

45. Fairbairn DJ. Odd Couples: extraordinary differences between males and females in the animal kingdom. Princeton, USA: Princeton University Press; 2013.

46. Darwin C. The descent of man and selection in relation to sex. London, UK: John Murray; 1871.

47. Emlen DJ, Marangelo JJ, Ball B, Cunningham CW. Diversity in the weapons of sexual selection: horn evolution in the beetle genus *Onthophagus* (Coleoptera: Scarabaeidae). Evolution. 2005;59:1060–84.

48. Hopkins J, Baudry G, Candolin U, Kaitala A. I'm sexy and I glow it: female ornamentation in a nocturnal capital breeder. Biol Lett. 2015;11:20150599.

49. Johansson BG, Jones TM. The role of chemical communication in mate choice. Biol Rev Camb Philos Soc. 2007;82:265–89.

50. Henneken J, Jones TM, Elgar MA. Diet-mediated pheromones and signature mixtures can enforce signal reliability. Front Ecol Evol. 2017;4:145.

51. Elgar MA, Johnson TL, Symonds MR. Sexual selection and organs of sense: darwin's neglected insight. Anim Biol Leiden Neth. Forthcoming 2019.

52. Hanks LM, Millar JG, Paine TD. Body size influences mating success of the Eucalyptus longhorned borer (Coleoptera: cerambycidae). J Insect Behav. 1996;9:369–82.

53. Gwynne DT, Bailey WJ. Female-female competition in katydids: sexual selection for increased sensitivity to a male signal? Evolution. 1999;53:546–51.

54. Jayaweera A, Barry KL. Male antenna morphology and its effect on scramble competition in false garden mantids. Sci Nat. 2017;104:75.

55. Johnson TL, Symonds MR, Elgar MA. Sexual selection on receptor organ traits: younger females attract males with longer antennae. Sci Nat. 2017;104:44.

56. Pigliucci M. Phenotypic Plasticity: Beyond Nature and Nurture. Baltimore, USA: John Hopkins University Press; 2001.

57. West-Eberhard MJ. Developmental Plasticity and Evolution. Oxford, UK: Oxford University Press; 2003.

58. Kasumovic MM, Brooks RC. It's all who you know: the evolution of socially cued anticipatory plasticity as a mating strategy. Q Rev Biol. 2011;86:181–97.

59. Greenwood M, Chapman RF. Differences in numbers of sensilla on the antennae of solitarious and gregarious *Locusta migratoria* L (Orthoptera: acrididae). Int J Insect Morphol Embryol. 1984;13:295–301.

60. Simpson SJ, Sword GA, Lo N. Polyphenism in insects. Curr Biol. 2011;21:R738–49.

61. Simpson SJ, Despland E, Hägele BF, Dodgson T. Gregarious behavior in desert locusts is evoked by touching their back legs. Proc Natl Acad Sci USA. 2001;98:3895–7.

62. Cullen D, Sword GA, Dodgson T, Simpson SJ. Behavioural phase change in the Australian plague locust, *Chortoicetes terminifera*, is triggered by tactile stimulation of the antennae. J Insect Physiol. 2010;56:937–42.

63. Johnson TL, Symonds MR, Elgar MA. Anticipatory flexibility: larval population density in moths determines male investment in antennae, wings and testes. Proc Biol Sci. 2017;284:20172087.

64. Ashman KR, McNamara KB, Symonds MR. Experimental evolution reveals that population density does not affect moth signaling behavior and antennal morphology. Evol Ecol. 2016;30:1009–21.

65. Forel A (Ogden CK, translator). The social world of ants compared with that of man. Volume 1 and 2. London, UK: GP Putnam's sons; 1928.

66. van Wilgenburg E, Elgar MA. Confirmation bias in studies of nestmate recognition: a cautionary note for research into the behavior of animals. PLoS One. 2013;8:e53548.

67. Babu MJ, Ankolekar SM, Rajashekhar KP. Castes of the weaver ant *Oecophylla smaragdina* (Fabricius) differ in the organization of sensilla on their antennae and mouthparts. Curr Sci. 2011;101:755–64.

68. Renthal R, Velasquez D, Olmos D, Hampton J, Wergin WP. Structure and distribution of antennal sensilla of the red imported fire ant. Micron. 2003;34:405–13.

69. Ravaiano SV, Ferreira Rde P, Campos LA, Martins GF. The antennal sensilla of *Melipona quadrifasciata* (Hymenoptera: Apidae: Meliponini): A study of different sexes and castes. Naturwissenschaften. 2014;101:603–11.

70. Grüter C, Segers FH, Santos LL, Hammel B, Zimmermann U, Nascimento FS. Enemy recognition is linked to soldier size in a polymorphic stingless bee. Biol Lett. 2017;13:20170511.

71. Kamhi JF, Nunn K, Robson SK, Traniello JF. Polymorphism and division of labour in a socially complex ant: neuromodulation of aggression in the Australian weaver ant, *Oecophylla smaragdina*. Proc Biol Sci. 2015;282:20150704.

72. Wittwer B, Elgar MA. Cryptic castes, social context and colony defence in a social bee, *Tetragonula carbonaria*. Ethology. 2018;124:617–22.

73. Kocher SD, Paxton RJ. Comparative methods offer powerful insights into social evolution in bees. Apidologie (Celle). 2014;45:289–305.

74. Wittwer B, Hefetz A, Elgar MA, Pierce NE, Kocher SD. Solitary bees reduce investment in communication compared with their social relatives. Proc Natl Acad Sci USA. 2017;114:6569–74.

75. Frasnelli E, Vallortigara G. Distribution of antennal olfactory and non-olfactory sensilla in different species of bees. Symmetry (Basel). 2017;9:135.

76. Freelance CB, Majoe M, Tierney SM, Elgar MA. Antennal asymmetry is not associated with social behavior in Australian Hymenoptera. Austral Entomol. Forthcoming 2018.

77. López MF, Armendáriz-Toledano F, Sámano JE, Shibayama-Salas M, Zúñiga G. Comparative study of the antennae of *Dendroctonus rhizophagus* and *Dendroctonus valens*

78. Bernays EA, Funk DJ, Moran NA. Intraspecific differences in olfactory sensilla in relation to diet breadth in *Uroleucon ambrosiae* (Homoptera: aphididae). J Morphol. 2000;245:99–109.

79. Wicslo WT. Sensilla numbers and antennal morphology of parasitic and non-parasitic bees (Hymenoptera: apoidea). Int J Insect Morphol Embryol. 1995;24:63–81.

80. Ross KT. Comparative study of the antennal sensilla of five species of root maggots: *Della radicum* L., *D. floralis* F., *D. antiqua* MG., *D. platura* MG. (Diptera: Anthomyiidae) and *Psila rosae* F. (Diptera: Psilidae). Int J Insect Morphol Embryol. 1992;21:175–97.

81. Chen HH, Zhao YX, Kang L. Antennal sensilla of grasshoppers (Orthoptera: Acrididae) in relation to food preferences and habits. J Biosci. 2003;28:743–52.

82. Dumas P, Tetreau G, Petit D. Why certain male grasshoppers have clubbed antennae? C R Biol. 2010;333:429–37.

83. Polidori C, Garcia AJ, Nieves-Aldrey JL. Antennal sensillar equipment in closely related predatory wasp species (Hymenoptera: Philanthinae) hunting for different prey types. C R Biol. 2012;335:279–91.

84. McIver SB. Comparative study of antennal sense organs of female culicine mosquitoes. Can Entomol. 1970;102:1258–67.

85. Zuk M, Kolluru GA. Exploitation of sexual signals by predators and parasitoids. Q Rev Biol. 1999;73:415–38.

86. Symonds MR, Elgar MA. The evolution of body size, antennal size and host use in parasitoid wasps. PLoS One. 2013;8:e78297.

87. Das P, Chen L, Sharma KR, Fadamiro HY. Abundance of antennal chemosensilla in two parasitoid wasps with different degree of host specificity may explain sexual and species differences in their response to host-related volatiles. Microsc Res Tech. 2011;74:900–9.

88. Zumpt F. Myiasis in Man and Animals of the Old World. London, UK: Butterworths; 1985.

89. Colwell DD, Hall MJ, Scholl PJ. The Oestrid Flies: Biology, Host-Parasite Relationships, Impact and Management. Wallingford, UK: CABI Publishing; 2006.

90. Bezdekova B, Jahn P, Vyskocil M. Pathomorphological study on gastroduodenal ulceration in horses: localization of lesions. Acta Vet Hung. 2007;55:241–9.

91. Zhang D, Li X, Liu X, Wang Q, Pape T. The antenna of horse stomach bot flies: morphology and phylogenetic implications (Oestridae, Gasterophilinae: *Gasterophilus* Leach). Sci Rep. 2016;6:34409.

92. Lürling M, Scheffer M. Info-disruption: pollution and the transfer of chemical information between organisms. Trends Ecol Evol. 2007;22:374–9.

93. Schroder R, Hilker M. The relevance of background odor in resource location by insects: a behavioral approach. Bioscience. 2008;58:308–16.

94. Deisig N, Dupuy F, Anton S, Renou M. Responses to pheromones in a complex odor world: sensory processing and behavior. Insects. 2014;5:399–422.

95. Conversano J, Tan EJ, van Wilgenburg E, Elgar MA. Background odor may reduce efficacy of chemical signals for social recognition. Austral Entomol. 2014;53:432–5.

96. Webster B, Cardé RT. Use of habitat odor by host-seeking insects. Biol Rev Camb Philos Soc. 2017;92:1241–9.

97. McFrederick QS, Fuentes JD, Roulston T, Kathilankal JC, Lerdau M. Effects of air pollution on biogenic volatiles and ecological interactions. Oecologia. 2009;160:411–20.

98. Royer L, McNeil JN. Effect of relative humidity conditions on responsiveness of European corn borer (*Ostrinia nubilalis*) males to female sex pheromone in a wind tunnel. J Chem Ecol. 1993;19:61–9.

99. Fuentes JD, Chamecki M, Roulston T, Chen B, Pratt KR. Air pollutants degrade floral scents and increase insect foraging times. Atmos Environ. 2016;141:361–74.

100. Camerini G, Groppali R, Rama F, Maini S. Semiochemicals of *Ostrinia nubilalis*: diel response to sex pheromone and phenylacetaldehyde in open field. Bull Insectol. 2015;68:45–50.

101. Bassett MA, Baumgartner JB, Hallett ML, Hassan Y, Symonds MR. Effects of humidity on the response of the bark beetle *Ips grandicollis* (Eichhoff) (Coleoptera: Curculionidae: Scolytinae) to synthetic aggregation pheromone. Aust J Entomol. 2011;50:48–51.