



Chemical Ecology and Olfaction in Short-Horned Grasshoppers (Orthoptera: Acrididae)

Mari Nakano¹ · Mary Morgan-Richards¹ · Steven A. Trewick¹ · Andrea Clavijo-McCormick¹

Received: 16 August 2021 / Revised: 26 October 2021 / Accepted: 30 October 2021

© The Author(s), under exclusive licence to Springer Science+Business Media, LLC, part of Springer Nature 2021

Abstract

Chemoreception plays a crucial role in the reproduction and survival of insects, which often rely on their sense of smell and taste to find partners, suitable habitats, and food sources, and to avoid predators and noxious substances. There is a substantial body of work investigating the chemoreception and chemical ecology of Diptera (flies) and Lepidoptera (moths and butterflies); but less is known about the Orthoptera (grasshoppers, locusts, crickets, and wētā). Within the Orthoptera, the family Acrididae contains about 6700 species of short-horned grasshoppers. Grasshoppers are fascinating organisms to study due to their significant taxonomic and ecological divergence, however, most chemoreception and chemical ecology studies have focused on locusts because they are agricultural pests (e.g., *Schistocerca gregaria* and *Locusta migratoria*). Here we review studies of chemosensory systems and chemical ecology of all short-horned grasshoppers. Applications of genome editing tools and entomopathogenic microorganism to control locusts in association with their chemical ecology are also discussed. Finally, we identify gaps in the current knowledge and suggest topics of interest for future studies.

Keywords Chemoreception · Chemical ecology · Acrididae · Sensilla · Volatiles · Chemical-mediated behaviors

Introduction

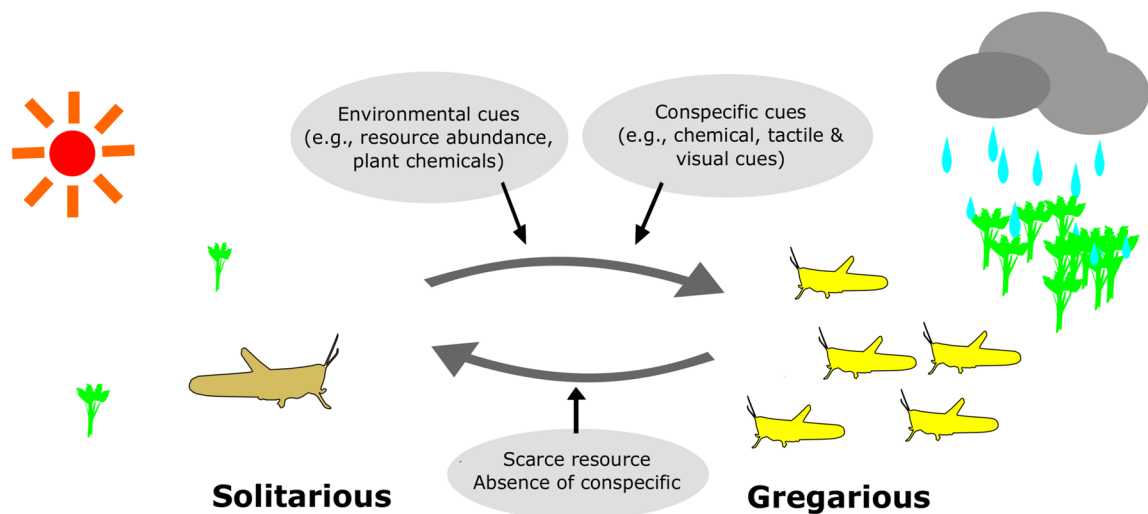
The insect order Orthoptera comprises crickets, katydids, wētā, and grasshoppers – a group that exhibits a great diversity of communication methods. Acoustic communication is well-developed in the suborder Ensifera (crickets and katydids) with about 15,500 described species using acoustic signals (Song et al. 2020). Although the majority of Caelifera (grasshoppers, locusts, and their allies) can hear, acoustic communication is less common in this group and generally less sophisticated (Song et al. 2020). However, the Caelifera do use an array of complex chemical signals for communication and foraging. Within the suborder Caelifera, the short-horned grasshoppers (Acrididae) comprise more than 6700 species described worldwide (Song et al. 2018), found in a wide range of habitats (boreal to sub-alpine zones: Ibanez et al. 2013a, 2013b; Joern 1979; Koot et al. 2020; Sergeev 2011), and displaying a wide range of diets (e.g., monophagous vs. polyphagous; forbivorous vs. graminivorous: Isely

1944; Joern 1979), and sexual communication systems (acoustic, visual and chemical: Finck et al. 2016a, 2016b; Hassanali et al. 2005; Song et al. 2020). This diversity provides an excellent opportunity to review what we know of the chemical ecology and chemoreception of short-horned grasshoppers.

To date the majority of research on grasshopper habits has been directed towards a few locust species because of their economic importance (e.g., the desert and migratory locust: *Schistocerca gregaria* and *Locusta migratoria*) despite the ecological and taxonomic diversity of the group. Locusts are notorious agricultural pests that display phase polyphenism (Pener and Simpson 2009). When resources (mates, food plants, perches, oviposition sites) are widely dispersed individual locusts are also dispersed (the solitary phase), but locusts shift to a gregarious phase when resources are clumped (Fig. 1). Outbreaks of the gregarious phase cause considerable agricultural loss as swarms of locusts damage crops. The switch between the two phases is mediated by chemical signaling with environmental and conspecific cues stimulating rapid shifts (within a few hours) in gene expression, biochemistry, and behavior, and more gradual changes (lifetime or trans-generation) of morphology and physiology (Fig. 1). Trying to understand the cues that result in switches

✉ Mari Nakano
m.nakano@massey.ac.nz

¹ Wildlife & Ecology, Massey University, Private Bag 11-222, Palmerston North 4410, New Zealand



Gene expression	Expression of genes involved in repulsive behavior ^{a,b,e,f}	Expression of genes involved in biosynthesis & perceptions of gregarious pheromones ^{a-d,g}
Hindgut microbial community	<i>Enterococcus</i> ^h	<i>Enterobacter</i> ^h
Behaviors	Avoid conspecifics ^{a,b,e,f,i} Sedentary ^{i,j}	Attracted towards conspecifics ^{a,b,e,f,i} Highly migratory ^{i,j}
Communication system	Cryptic ^{k-m} Long-range signals (smells ^{n,o} and vision ^o)	Release gregarious pheromones ^{k-m} Short-range smells ^{n,o} , touch ⁱ and taste?
Morphology	Higher sensilla abundance ^{p,q} Cryptic color, larger eyes and body ^{r,s}	Lower sensilla abundance ^{p,q} Bright color, smaller eyes and body ^{r,s}

Fig. 1 The environmental and conspecific signals that contribute to locusts switching between their solitarius and gregarious phases. References: **a** Guo et al. 2011, **b** Guo et al. 2018b, **c** Wei et al. 2019, **d** Li et al. 2016, **e** Ma et al. 2015, **f** Ma et al. 2019, **g** Chen et al. 2018, **h** Lavy et al. 2019, **i** Rogers et al. 2014, **j** Maeno et al. 2016; **k** Wei

et al. 2017, **l** Amwayi et al. 2012, **m** Njagi et al. 1996, **n** Inayatullah et al. 1994, **o** Ould Ely et al. 2006, **p** Ochieng et al. 1998, **q** Greenwood and Chapman 1984, **r** Sugahara et al. 2015, 2017, **s** Gordon et al. 2014; Rogers et al. 2010

in locust phase has therefore driven research into Acrididae chemical ecology. In addition, because insecticides used to control locusts have negative impacts on human health and the environment (Byers 1991; Zhang et al. 2019), the use of alternative control methods such as pheromone traps, genetically modified pests, and entomopathogenic fungi, that are more species-specific and environmentally safer are being investigated.

As chemical communication has a central role in triggering the switch between the two locust phases (Hassanali et al. 2005), the study of chemical ecology provides the basis for predicting when swarming is likely to happen and potentially controlling outbreaks. At sensilla, which are the sensory organs that project through the insect exoskeleton, sensory neurons and proteins respond to specific tastes or

smells. Pioneering studies identified compounds involved in gregarization (i.e., aggregation pheromones) using gas-chromatograph and mass spectrometry (GC-MS), and explored the mechanisms of perception using physiological and behavioral observations (Mahamat et al. 1993; Hansson et al. 1996; Ochieng et al. 1998; Niassy et al. 1999; Ochieng and Hansson 1999). Physiological responses to specific chemical stimuli can be investigated using electrophysiological techniques including electroantennography (EAG) (Torto et al. 1994; Njagi et al. 1996; Chen et al. 2004) and single sensillum recordings (SSRs) (Altner et al. 1981; Ochieng and Hansson 1999; Cui et al. 2011; You et al. 2016). These techniques monitor neuron response by inserting an electrode into an antenna (EAG) or a sensillum (SSRs) while the insect is exposed to a particular chemical compound.

More recently, molecular tools including transcription and genome editing have been employed to investigate chemical signaling (Guo et al. 2014, 2020; Zhang et al. 2015, 2017; Jiang et al. 2018). In these studies, genes that are potentially involved in the perception and biosynthesis of pheromones have been identified by observing expression patterns in sensory tissues and sensilla with quantitative real-time PCR (Jin et al. 2005; Zhang et al. 2015; Chen et al. 2018; Yuan et al. 2019; Li et al. 2020) and in situ hybridization (Yang et al. 2012; Jiang et al. 2017, 2018). The functional diversity of chemoreceptive proteins has been deciphered by silencing candidate genes using RNA interference (Guo et al. 2011; Wei et al. 2019) and CRISPR (Clustered Regularly Interspaced Short Palindromic Repeats) (Li et al. 2016; Chen et al. 2018; Guo et al. 2020). Together these chemical, physiological, behavioral, and molecular approaches have extended our understanding of chemical ecology and chemoreception in grasshoppers.

The detection of food, competitors, predators, and mates involves olfaction or contact-chemoreception (gustation) by discrimination of volatile or soluble stimulants (Sánchez-Gracia et al. 2009). Our review explores what is known about these mechanisms and their roles in short-horned grasshoppers (Orthoptera; Caelifera; Acrididae) with particular reference to: 1) communication systems in acridid grasshoppers, 2) the chemical signals they perceive (pheromones, cuticular hydrocarbons, and plant-derived chemicals) and their effect on grasshoppers' behaviors, 3) types and distribution of sensilla, 4) chemoreception-associated proteins, and 5) applied chemical ecology in pest control and conservation. We identify knowledge gaps and suggest useful and rewarding avenues for future research.

Communication Systems in ACRIDID Grasshoppers

Multi-Modal Communication Systems in Grasshoppers Grasshoppers communicate using visual, auditory, tactile, and chemical signals (Perdeck 1958; Ritchie 1990; Chen et al. 2004; Hassanali et al. 2005; Finck et al. 2016b; Finck and Ronacher 2017; Song et al. 2020). Acoustic mate communication is important for many species within the subfamilies Gomphocerinae and Oedipodinae (Song et al. 2018, 2020), and some of these grasshoppers are known to also use chemical signals. For example, some *Chorthippus* grasshopper species (Gomphocerinae) use acoustic signals for long-range communication and chemical signals at short-range (Perdeck 1958; Ritchie 1990; Finck et al. 2016b; Finck and Ronacher 2017). In sympatric *C. biguttulus* and *C. mollis*, acoustic signals enable long-range recognition of conspecific males and short-range chemical signals are used to detect conspecific females (Finck et al. 2016b; Finck and

Ronacher 2017). Multimodal signaling of this sort allows assortative mating and differ among even closely related lineages (Neems and Butlin 1995; Finck et al. 2016a; Finck and Ronacher 2017). For instance, *Chorthippus parallelus erythropus* females use olfaction in mate choice resulting in positive assortative mating, while females of their close relatives *C. parallelus parallelus* use male's songs to select their partners (Ritchie 1990).

Locust species use visual, tactile, acoustic, and chemical cues to locate and recognize predators, intraspecific phase, sex, and developmental stages. The use of long-range and short-range signals is phase-dependent. The gregarious phase occurs when the grasshoppers are in high density suggesting an emphasis on close range or contact signaling (Ferenz and Seidelmann 2003; Rogers et al. 2003; Hassanali et al. 2005). Touch is known to mediate behavioral phase shifts and is used as a cue for measuring rapid changes of behavior and gene expression in artificially crowded solitary and isolated gregarious locust individuals (Ould Ely et al. 2006; Guo et al. 2011; Rogers et al. 2014; Li et al. 2016). Detection of smells at short-range (up to 150 cm) in gregarious locusts has also been demonstrated (Inayatullah et al. 1994; Ould Ely et al. 2006). Conversely, for locusts at low population density (solitary phase), long-range signals like smells and sound are likely to be more important (Inayatullah et al. 1994; Ferenz and Seidelmann 2003; Hassanali et al. 2005; Ould Ely et al. 2006). Elevated sensitivity to high frequency-sound was observed in solitary *S. gregaria* which might allow detection of bat echolocation (Gordon et al. 2014). When the temperature is favorable solitary locusts are active at night (Gaten et al. 2012; Gordon et al. 2014); and this might expose them to bat predation more than day-time active gregarious locusts. Solitary locusts are repelled by conspecifics presumably to minimize competition in resource-limited conditions (Ma et al. 2015, 2019; Guo et al. 2018b), but they are attracted to each other for mating (Inayatullah et al. 1994; Ould Ely et al. 2006). Thus, long-range signals influence conspecific avoidance and mate location in solitary locusts, demonstrating that ecological circumstances shape communication systems.

Chemical Communication in Grasshoppers Chemical signals are important for the survival and reproductive success of phytophagous insects. In grasshoppers, chemical signals facilitate sexual reproduction by providing cues for the recognition of conspecifics (Neems and Butlin 1994, 1995; Tregenza et al. 2000a, 2000b; Finck et al. 2016b), their sex (Njagi and Torto 1996, 2002; Tregenza et al. 2000a; Stahr et al. 2013; Finck et al. 2016b; Stahr and Seidelmann 2016) and their quality (Stahr et al. 2013; Stahr and Seidelmann 2016). Insect-derived chemical signals are either cuticular hydrocarbons (CHCs) or volatiles. Cuticular hydrocarbons are detected either by direct contact or over short distances.

Chorthippus grasshopper males use CHCs to identify potential mates and have been observed touching the body and antennae of females with their antennae before copulation (Ritchie 1990; Finck et al. 2016b). Conversely, olfactometer studies show that detection of odour cues results in the attraction of many grasshopper species towards volatiles of conspecifics (*L. migratoria*: Guo et al. 2011; *S. gregaria*: Inayatullah et al. 1994; Ould Ely et al. 2006; *Schistocerca americana*: Stahr et al. 2013; *Dociostaurus maroccanus*: Guerrero et al. 2019) and host plants (*S. gregaria*: Njagi and Torto 1996; *Melanoplus sanguinipes*: Hopkins and Young 1990). The specific chemical compounds identified and their behavioral effect is described in the next section.

Chemical Signals Perceived and their Effect on Grasshopper Behavior

Cuticular Hydrocarbons (CHCs) Cuticular hydrocarbons are derived from the insect exoskeleton and have a primary function of preventing water loss (Blomquist et al. 2018). Cuticular hydrocarbons are relatively long carbon chains (21 to >40 carbons) with single (alkanes) or double bonds (alkenes and alkadienes) sometimes including methyl branches (Gibbs and Rajpurohit 2010; Blomquist et al. 2018). In *L. migratoria*, straight-chain 25–33 carbon alkanes are important water-proofing agents, and disruption of CHC synthesis results in high mortality due to severe water-loss (Yu et al. 2016). Cuticular hydrocarbons also provide a barrier against fungi and insecticides (Wu et al. 2020; Zhang et al. 2021).

Short-horned grasshoppers have species-specific qualitative and quantitative CHC profiles. The locusts *S. gregaria* and *L. migratoria migratiododes* each have characteristic CHCs (Lockey and Oraha 1990) with the former species dominated by straight-chain alkanes whereas the latter dominated by mono- and dimethyl-alkanes (with some compounds being specific). In the sympatric grasshoppers *C. biguttulus* and *C. mollis*, 34 carbon straight chain, and methyl-branched alkanes have been identified (Finck et al. 2016a), with the position of the methyl group in di- and tri- methyl branched alkanes differing between species and sexes (Perdeck 1958; Finck et al. 2016a; Finck and Ronacher 2017).

When CHCs are used in communication, they are usually considered to be short-range or contact-chemical signals, as opposed to volatiles that provide long-distance cues (Blomquist et al. 2018). Cuticular hydrocarbons generally have lower volatility and higher melting points than pheromones, resulting in CHC molecules remaining close to the insect while volatiles diffuse through the air (Menzel et al. 2017, 2019). However, it is unclear how the chain length or molecular weight of these molecules relates to use in

contact-chemical communication versus olfactory reception. *Chorthippus* grasshoppers use both contact and short-range (5–10 mm) olfactory reception when perceiving 25–39 carbon straight-chain and methyl-branched alkanes (Finck et al. 2016a, 2016b), suggesting that CHCs can be perceived through olfaction to some degree. The perception distance is likely to be species-specific and depend on the number of sensilla, olfactory sensory neurons (see CHEMORECEPTION) and environmental conditions (e.g., wind speed, temperature).

Cuticular hydrocarbons used for communication are subject to sexual and natural selection. Assortative mating for similar CHC profiles is seen within *C. parallelus* that comprises several subspecies in the Pyrenees mountains (Neems and Butlin 1995; Tregenza et al. 2000a, 2000b). Population-level differences in CHCs have been detected, with eastern *C. parallelus* having a higher proportion of long-chain vs. short-chain hydrocarbons than western populations (Neems and Butlin 1995). The drier eastern environment compared to the west, may explain CHC differences as long-chain hydrocarbons may provide greater waterproofing to the grasshoppers reducing desiccation. Host plant preference can also lead to CHC divergence. The north American grasshopper *Hesperotettix viridis* feeds on either *Gutierrezia* snakeweed or *Solidago* golden-rod, and assortative mating with respect to the host plant has been detected (Grace et al. 2010). This mate choice appears to derive from grasshopper CHC profiles that correlate with food plant (Grace et al. 2010), but the grasshoppers also have different body colors depending on their host plants and therefore the use of visual cues in mate selection cannot as yet be excluded.

Volatile Pheromones Volatile pheromones contribute to the detection and choice of mates (sex pheromones) but also have other roles (e.g., primer pheromones, alarm, aggregation) (Jacobson 1972; Howse et al. 1998). While some CHCs function as short-distance pheromones (especially short-chain CHCs), volatile pheromones usually function as long-distance chemical cues (Blomquist et al. 2018). The quality and quantity of the pheromones produced can communicate the quality of potential mates including mating status (Burke et al. 2015; Tabata et al. 2017), feeding condition (Barry et al. 2010), and reproductive mode (i.e., sexual or asexual: Burke et al. 2015; Tabata et al. 2017) as well as their location.

Studies of locust pheromones have revealed volatiles involved with courtship inhibition (Seidelmann and Ferenz 2002), premating behavior (Njagi and Torto 2002), oviposition (Saini et al. 1995; Rai et al. 1997), aggregation (Dillon and Charnley 2002; Dillon et al. 2002; Guo et al. 2020), maturation acceleration (Mahamat et al. 1993; Stahr et al. 2013), and sexual selection (Njagi and Torto 1996; Seidelmann and Ferenz 2002; Stahr and Seidelmann 2016; Wei et al. 2017,

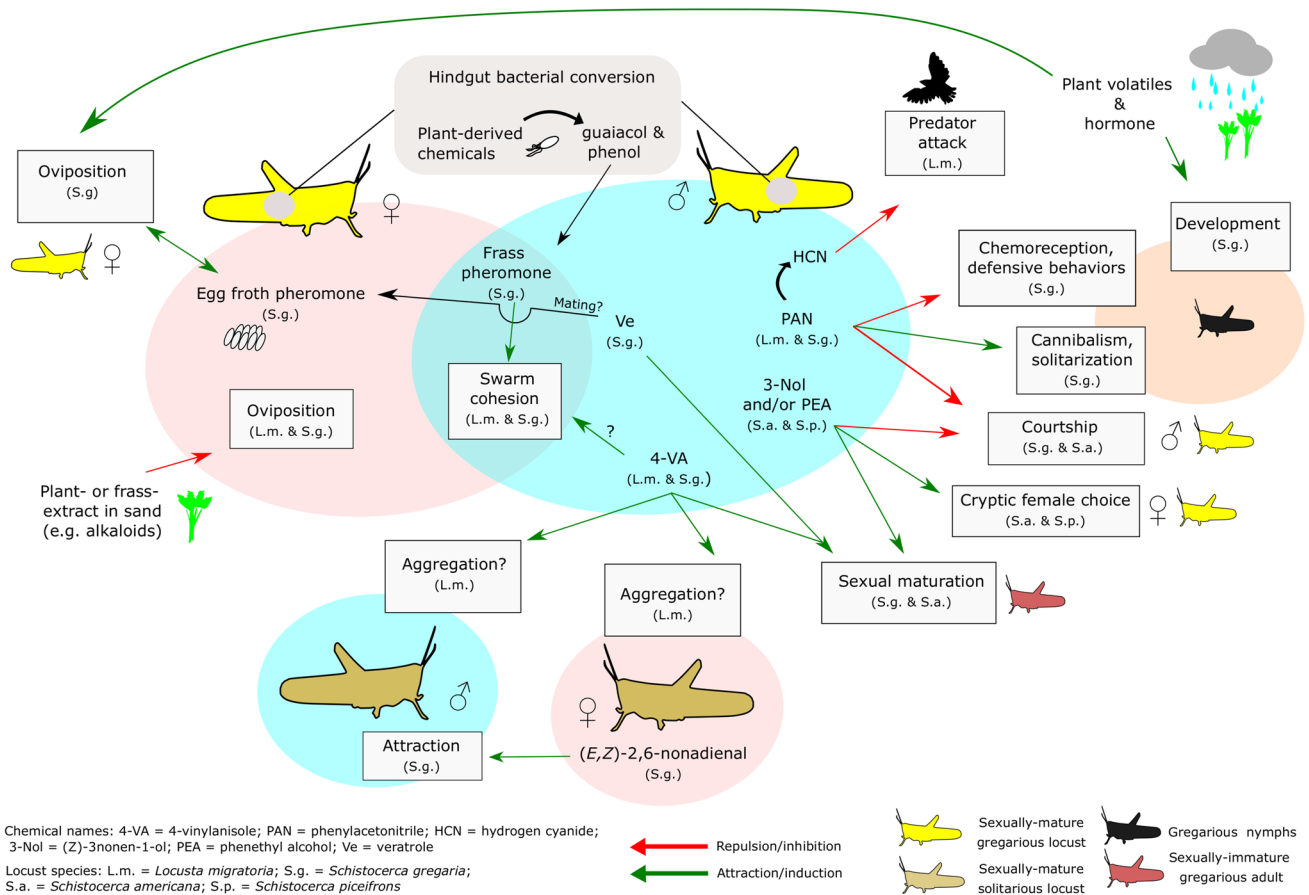


Fig. 2 Chemical ecology of phase shifts in well-studied locust species (*Locusta migratoria*, *Schistocerca gregaria*, *S. americana* and *S. piceifrons*). Compounds that are inside the blue circle are the major

component of male pheromones, in pink circles are female pheromones, and where circles overlap are compounds shared by males and females

2019; Guo et al. 2020) (Fig. 2). Although several compounds such as veratrole, guaiacol, benzaldehyde, hexanoic acid, nonanal, and (Z)-3-nonen-1-ol are found in the pheromonal blends of different locust species (e.g., *S. americana*, *S. gregaria*, *S. piceifrons*, *L. migratoria*), significant differences in emission dynamics are observed within and among them (Niassy et al. 1999; Mahamat et al. 2000; Stahr et al. 2013; Stahr and Seidelmann 2016; Wei et al. 2017). Relative concentrations in pheromone cocktails provide signals that are specific to species, sex, and developmental stages in locusts.

Most of these studies have focused on volatiles associated with the gregarious phase with the intention of improving pest control and reducing crop damage. The only pheromone documented for the solitary locust is (*E,Z*)-2,6-nonadienal released by solitary female *S. gregaria*, and is known to induce electro-physiological response and behavioral attraction by males (Ochieng and Hansson 1999; Ferenz and Seidelmann 2003).

Pheromones associated with the gregarious phase have been found in several locust species (Fig. 2). 4-vinylanisole is an aromatic compound produced by gregarious *L.*

migratoria and *S. gregaria* and higher emission is observed in adult males than in females or immature locusts in this phase (Mahamat et al. 2000; Wei et al. 2017). Although produced only by gregarious individuals 4-vinylanisole influences aggregation behavior as an attractant for both gregarious and solitary *L. migratoria* (Guo et al. 2020). In *S. piceifrons*, gregarious male-specific volatiles, phenethyl alcohol, and (Z)-3-nonen-1-ol induce neither attraction nor repulsion (Stahr and Seidelmann 2016). However, hatching success of eggs was higher after copulation with scented (either or both phenethyl alcohol and (Z)-3-nonen-1-ol) solitary males or gregarious males compared to unscented solitary males. This shows that these compounds are used in cryptic female choice in *S. piceifrons* (Stahr and Seidelmann 2016) and (Z)-3-nonen-1-ol has a similar role in *S. americana* (Stahr et al. 2013). However, in *S. americana*, it is also implicated in mate-guarding and induction of sexual maturation (Stahr et al. 2013).

Locusts have unusual group-behavior during oviposition (Saini et al. 1995; Rai et al. 1997; Tanaka and Sugahara 2017; Tanaka et al. 2019), synchronous egg-hatching

(Tanaka et al. 2018; Sakamoto et al. 2019), and development (Ellis et al. 1965; Mahamat et al. 1993; Stahr et al. 2013). These group behaviors are thought to help secure resources (e.g., food, oviposition substrate) and enhance defence against predators (Hassanali et al. 2005), and at least some are controlled by pheromone signals. In *S. americana*, the same compound that is used for cryptic female choice ((*Z*)-3-nonen-1-ol) accelerates the sexual maturity of newly moulted adults (Stahr et al. 2013). Veratrole, the major chemical component of gregarious males, also induces sexual maturation (yellowing and copulation) in *S. gregaria* (Mahamat et al. 1993, 2000; Seidelmann et al. 2003). Veratrole is also found in egg froth from female *S. gregaria* and induces gregarious females to oviposit (Saini et al. 1995; Rai et al. 1997). Locusts are selective in oviposition sites as it affects hatching rate and embryonic development (Tanaka and Sugahara 2017; Tanaka et al. 2019). Laying eggs at sites used by conspecific females may increase the chance of successful embryonic development and hatching. As veratrole is absent or only in trace amounts in the pheromonal component of female *S. gregaria* (Torto et al. 1994) it may be transferred by male contact during swarming or copulation.

The compound phenylacetone nitrile was initially considered an aggregation pheromone as it is released most by gregarious rather than solitary locusts (Njagi et al. 1996; Niassy et al. 1999), however, it is now known to repel conspecifics of *L. migratoria* and *S. gregaria* (Seidelmann and Ferenz 2002; Seidelmann et al. 2005; Wei et al. 2019). Phenylacetone nitrile is the dominant compound released by gregarious males of both *S. gregaria* (80%: Mahamat et al. 1993) and *L. migratoria* (>30%: Wei et al. 2017). Emission dynamics of phenylacetone nitrile also differ between sexes and developmental stages within each species (Mahamat et al. 1993; Niassy et al. 1999; Wei et al. 2017). In *L. migratoria*, it appears that phenylacetone nitrile can be used to deter predators as the compound is a precursor of hydrogen cyanide (toxic to vertebrates; Wei et al. 2019). Gregarious locusts may be at higher risk of predation compared to solitary locusts as they are more colorful and occur in high density (Hassanali et al. 2005). Thus, a higher emission of phenylacetone nitrile in gregarious vs. solitary locusts is considered to be an adaptation to group-living. In *S. gregaria*, phenylacetone nitrile acts as a courtship inhibitor to guard mates after copulation and to avoid homosexual attacks in a large swarm (Seidelmann and Ferenz 2002). Phenylacetone nitrile has negative effects on the nymphs of *S. gregaria*, as it disrupts chemoreception, reduces immune systems and feeding rate, and induces behavioral disorientation (Bashir and Hassanali 2010; Abdellaoui et al. 2020). In a field study, groups of marching gregarious nymphs were sprayed with phenylacetone nitrile solution (Bashir and Hassanali 2010). The marching groups started to lose coherence two days after the application (possibly due to disruption in olfaction), and enhanced

predation rate observed associated with reduced defensive behavior. Intriguingly, cannibalistic behaviors were also observed among phenylacetone nitrile-treated nymphs although the reason behind this remains unclear.

Plant-Derived Signals Phytophagous insects adapt to the chemical components of host plants in terms of recognition (e.g., green leaf volatiles) and response to plant defence (alkaloids, flavonoids) as well as nutrient composition (crude proteins, starch, and lipids). Many secondary metabolites of host plants are toxic to phytophagous insects, inhibiting their development and reproduction, and detoxification can be energy expensive and involve specialized biochemical pathways that lead to dietary specialization in insects (Ibanez et al. 2013a; Huang et al. 2017, 2020; Giron et al. 2018; Cui et al. 2019a). Short-horned grasshoppers display a wide range of feeding patterns with some species being absolute specialists (e.g., creosote bush grasshopper *Boottettix argentatus*: Chapman et al. 1988) while others are oligophagous or polyphagous (locust species). Different grasshopper species, therefore, display a range of responses to plant toxins involving recognition and avoidance, detoxification, or food mixing (polyphagy) to mitigate quantitative effects (Giron et al. 2018; Cui et al. 2019a).

The toxic, repellent, or feeding deterrent effects of plant synthesised compounds on grasshoppers have been tested in numerous studies. For example, the addition of certain flavonoids that are common secondary metabolites in plants (needlegrass *Stipa krylovii* and false wheatgrass *Leymus chinensis*) favored by the grasshopper *Oedaleus asiaticus* reduces its growth and survival (Cui et al. 2019a). Elevated transcription of enzymes involved in detoxification has been observed when *O. asiaticus* feed on plants with high levels of phytotoxins including flavonoids, terpenoids, alkaloids, and tannins (Huang et al. 2017, 2020). The creosote bush *Larrea tridentate* is equipped with anti-digestive resin of which a major component is a phenolic aglycone called nordihydroguaiaretic acid (NDGA). When NDGA is applied to the leaves of Jojoba *Simmondsia* under experimental conditions it increases the acceptability of this plant to the creosote-grasshopper *B. argentatus* that does not normally feed on it but deters the grasshoppers for which *Simmondsia* leaves are a preferred food (*Ligurotettix conquilletti* and *Clibolacris parviceps*; Chapman et al. 1988). Thus, although NDGA is probably a plant defense it can also be considered a plant-derived signal for grasshoppers discriminating host and non-host plants.

Similarly, plant-derived chemicals can act as signals for grasshopper biology such as molting and reproduction. During the dry season when the plants are senescent, the production of the plant hormone, gibberellic acid (a plant growth regulator) decreases. The shortage of this chemical delays ecdysis and egg-laying in *S. gregaria* two-fold

or more (Ellis et al. 1965; Carlisle et al. 1969). When gibberellic acid is added to the senescent leaves, it accelerates sexual maturation in *S. gregaria* but interestingly, delayed development was observed when the compound was added to green leaves (Ellis et al. 1965). The delayed development is possibly related to the phytotoxicity of gibberellic acid above a certain threshold. For example in *L. migratoria*, the rate of consumption, nymphal development, and oviposition of newly emerged females reduced as the concentration of this compound increased (Abdellaoui et al. 2009, 2015). These studies show that gibberellic acid signals optimal time for development and reproduction, but it also can be toxic above certain limits.

Plant-derived chemicals can influence where grasshoppers oviposit their eggs. *Schistocerca gregaria* females presented with a choice of sand containing either leaf extracts of their host plants (orchard grass, cabbage, sorghum, romaine lettuce, Japanese mustard spinach, or silver grass), frass extract from other locusts (*S. gregaria*, *L. migratoria*, and *Patanga succincta*) or water (control), laid more eggs in the control sand than in the sand containing extracts (Tanaka et al. 2019). This preference for oviposition sites is related to egg-hatching rate and embryonic development (egg size and antennal length) that were significantly reduced by the presence of frass and plant extracts. A similar inhibition effect has been observed in *L. migratoria* (Sugahara et al. 2021), the choice of oviposition sites was not influenced by phase polyphenism or bacterial activity in either species (Tanaka et al. 2019; Sugahara et al. 2021). The compounds inducing oviposition inhibition are unknown but may involve toxic compounds such as alkaloids.

Chemical Biosynthesis in Grasshoppers In insects, CHCs are synthesised from fatty acids and terpenoid lipids, in specialized cells called oenocytes present in the abdomen or fat bodies (Blomquist et al. 2018). Synthesis of different types of CHCs involves a variety of catalysts including fatty acid synthase, reductases, and elongases (Blomquist et al. 2018). In short-horned grasshoppers, biosynthetic pathways of CHC formation have only been studied in *L. migratoria* (Yu et al. 2016; Wu et al. 2020) and *S. gregaria* (Diehl 1975). Two genes from the superfamily of cytochrome P450 enzymes are expressed specifically in oenocytes and they are responsible for catalyzing the synthesis of 25–33 carbon alkanes and mono- and di-methyl branched alkanes (Yu et al. 2016; Wu et al. 2020).








In insects such as Coleoptera, Lepidoptera, and Diptera, pheromones are synthesized in a pheromone gland commonly located in the abdomen (Blomquist et al. 2018), but the production of pheromones in locusts involves specialized epidermal cells in several different body parts (abdomen, legs and/or wings; Seidelmann et al. 2003; Amwayi et al. 2012; Fürstenau et al. 2013; Stahr and Seidelmann 2016).

This has been demonstrated by injecting radio-labelled precursor compounds into the tissue of dazed specimens (Fürstenau et al. 2013) or isolated tissues (Seidelmann et al. 2003). As with CHCs, its synthesis involves specialized enzymes (Blomquist et al. 2018). An antipredator pheromone in *L. migratoria*, phenylacetoneitrile, and its derivative (hydrogen cyanide) are synthesized with an enzyme from the same gene family as enzymes involved in CHC synthesis (cytochrome P450) (Wei et al. 2019). Thus, cytochrome P450 enzymes known for their roles in the metabolism of toxic compounds (including insecticides) are also important in the production of both CHCs and pheromones. A further pathway in pheromone synthesis involves Enterobacteriaceae gut bacteria. Even when isolated and applied to sterile frass, *Pantoea* and *Klebsiella* bacteria generated guaiacol and phenol that are known to be cohesion pheromones in gregarious *S. gregaria* (Obeng-Ofori et al. 1994; Dillon et al. 2002). These compounds are also observed in other locust species (*S. americana*: Stahr et al. 2013; *S. piceifrons*: Stahr and Seidelmann 2016; *L. migratoria*: Shi et al. 2011; Wei et al. 2017) that harbor similar microbial communities (Shi et al. 2014; Lavy et al. 2020) suggesting an important role of bacterial conversion in all these locusts. However, Next Generation DNA Sequencing *S. gregaria* hindgut samples showed considerable variation in bacterial composition between different phases and generations and it is not yet clear to what extent the microbiome is under the control of the locust host, the environment, or locust density (Lavy et al. 2019).

Chemoreception

External Morphology and Types of Sensilla A sensillum is a sensory organ protruding from the exoskeleton of an insect. Different types of sensilla have been described and interpreted as being specialized for the perception of particular types of stimuli: movement, humidity, temperature, smell, and taste known as mechano-, hygro-, thermo-, olfactory- or gustatory- stimulations respectively (Nowińska and Brożek 2017). Current models assume that the external morphology of sensilla can be used to infer their function(s). In a few species the relationship between the morphology of sensilla and what they detect has been explored using information from gene expression or electrophysiological and receptor neuron response experiments (see below), but in general, function is extrapolated from size, shape (Table 1), and location. Sensilla have either no pores (aporous), an apical pore (uniporous), or wall pores (multiporous) (Fig. 3). Those without pores are typically interpreted as mechano-, hygro-, or thermo-receptors, whereas sensilla with pores are considered gustatory (uniporous) or olfactory (multiporous)

Table 1 Types of insect sensilla, their probable function, morphology, and nomenclature

Name	Function	Appearance	Pores	Socket	Length (μm)	Diameter (μm)	
Hair or trichoid sensilla ^{a,b,c}	Mechanical		Long, slender hair-like (see Fig. 3a)	Aporous	Flexible	20–400	3–10
Chaetica or long basiconic sensilla; trichoid sensilla ^{a,b,d,e}	Mechanical		Peg-like, longitudinal ridges (see Fig. 3b)	Uniporous or aporous	Inflexible	15–300	5–20
Trichoidea or short slender basiconic sensilla ^{a,b}	Olfactory		Slender hair-like (see Fig. 3e)	Wall-pored (see Fig 3d), fewer than basiconica	Inflexible	5–35	3
Basiconica or short basiconic sensilla ^{a,b,c}	Olfactory		Stout peg with wavy cuticular depression (see Fig. 3c)	Wall-pored	Inflexible	3–40, typically 10–17	4
	Olfactory		Stout peg-like (see Fig. 3d)	Wall-pored	Inflexible	3–40, typically 9–20	3–4
Coeloconica	Olfactory, thermal		A sharp-tipped peg with longitudinal ridge on the wall, contained within a pit (see Fig. 3f)	Wall-pored	Inflexible	3–10	2–25 pit diameter
	Humidity, thermal		A blunt-tipped peg without grooves, contained within a pit	Apical pore	Inflexible	4–5	2.2–5.5 pit diameter

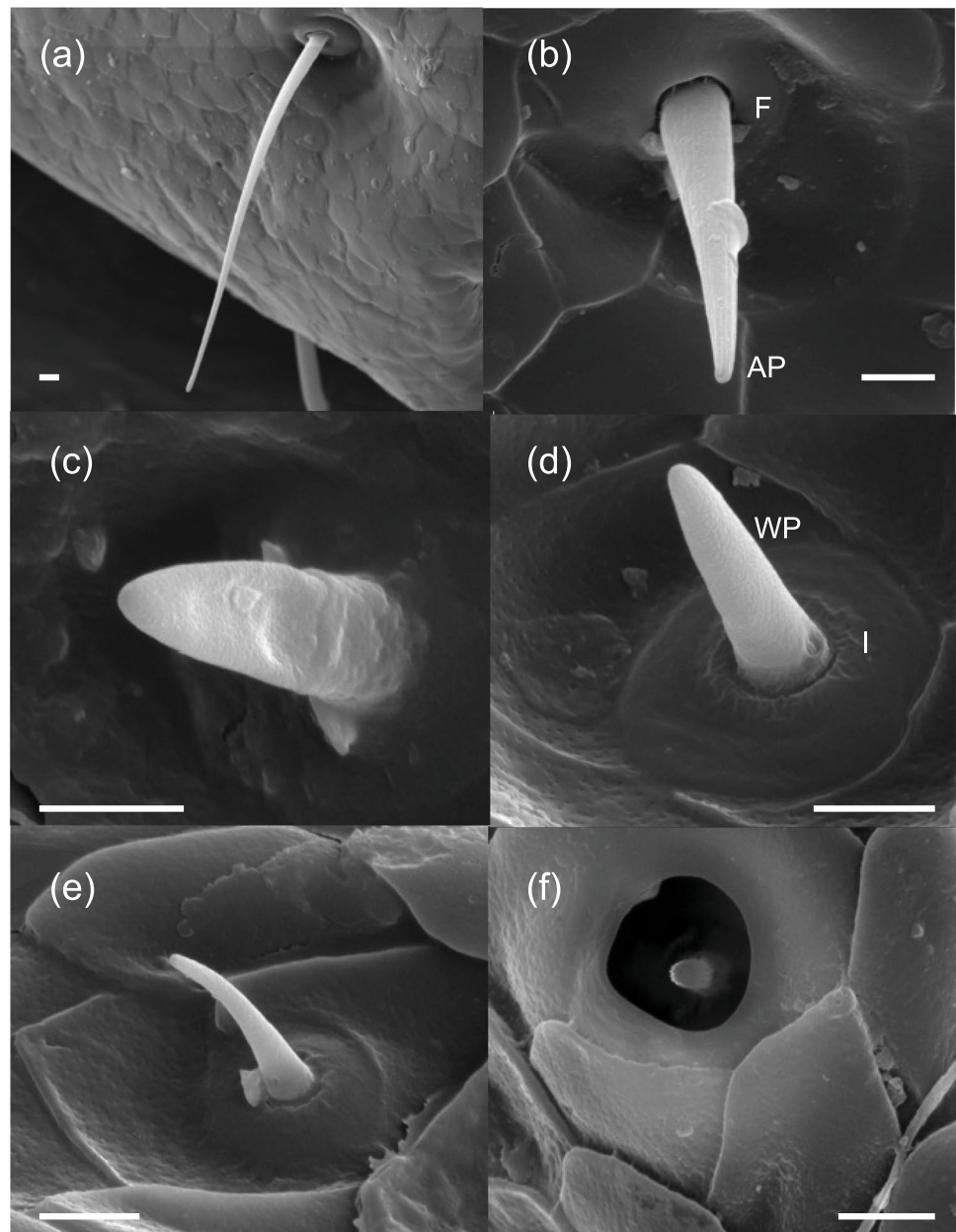
Sensilla names are based on those established for relatively well-studied short-horned grasshopper, the locust species *Locusta migratoria* and *Schistocerca gregaria* (Altner et al. 1981; Ochieng et al. 1998; Jin et al. 2005; Zhou et al. 2008), but other names used are provided with their sources: a) Bland 1989, b) Chen et al. 2003, c) Li et al. 2007, d) Greenwood and Chapman 1984, e) Chapman 1989

receptors (Nowińska and Brożek 2017). Sensilla are attached with either a flexible or inflexible base (Fig. 3). Sensilla inferred as mechano-sensitive typically have a flexible socket for movement detection, whereas sensilla with inflexible sockets probably detect humidity, temperature, smells, or taste (Nowińska and Brożek 2017). Some sensilla such as

those with a flexible socket and an apical pore may have dual functions acting as both movement and taste sensors (Ochieng et al. 1998).

The nomenclature of sensilla types varies depending on species and studies, so standardisation is a first step towards improving the understanding of grasshopper chemoreception

Fig. 3 Sensilla commonly found in Acrididae. **a** Hair sensilla in *Paprides nitidus*, **b** chaetica in *Sigaus australis*, **c** basiconica with wavy cuticular depression in *Brachaspis nivalis*, **d** basiconica in *B. nivalis*, **e** trichoidea in *B. nivalis*, **f** olfactory coeloconica in *S. australis*. F- flexible socket, I- inflexible socket, AP- apical pore, WP- wall-pored. Scale bar 5 μ m



(Table 1). Here, we use terminology derived from the study of the locusts *S. gregaria* and *L. migratoria* (Altner et al. 1981; Ochieng et al. 1998; Jin et al. 2005; Zhou et al. 2008). As arable pests, the functions of their sensilla have received the most detailed investigation with physiological (Altner et al. 1981; Ochieng and Hansson 1999) and transcriptomic (Jiang et al. 2017; Jin et al. 2005; Zhou et al. 2008) approaches providing an evidential basis for functional inference. Trichoid sensilla (Fig. 3e) that are responsible for olfaction in locusts, are slender, hair-like sensilla with pores on their walls (Ochieng et al. 1998; Ochieng and Hansson 1999). Much longer than trichoid sensilla with a flexible socket but no pores (Table 1, Fig. 3a) are the hair sensilla responsible for mechanoreception (Bland 1989; Chen

et al. 2003; Li et al. 2007; Yu et al. 2011; Zhou et al. 2008). Sensilla chaetica (Fig. 3b) associated with mechano- and gustatory-receptions are thick and peg-like with a flexible socket, ribbed wall, and an apical pore (Bland 1989; Blaney and Chapman 1969; Chen et al. 2003; Jin et al. 2006; Li et al. 2007; Ochieng et al. 1998; Yu et al. 2011; Zhou et al. 2008). Basiconic olfactory sensilla are wall-pored (Fig. 3c and d), but vary in shape among species (Bland 1989; Chapman 1989; Chen et al. 2003; Jin et al. 2006; Li et al. 2007; Ochieng et al. 1998). Sensilla coeloconica consists of a short peg in a cavity commonly considered to be temperature and humidity receptors (Nowińska and Brożek 2017; Jiang et al. 2018). Two types of coeloconica are seen in *L. migratoria*; one with wall pores and one lacking wall pores but with

a single apical pore (Table 1). These sensilla within pits are responsible for detecting smells and temperature, and humidity and temperature, respectively (Altner et al. 1981). The response of wall-pored coeloconica to olfactory stimuli has also been confirmed in *S. gregaria* (Ochieng and Hansson 1999). Wall-pored coeloconica seem to be as common on grasshopper antennae as aporous sensilla (Altner et al. 1981; Bland 1989; Chapman 1989; Chen et al. 2003; Greenwood and Chapman 1984; Li et al. 2007).

Grasshoppers have sensilla on the antennae (Altner et al. 1981; Bland 1989; Chapman 1989; Chen et al. 2003; Greenwood and Chapman 1984; Li et al. 2007; Ochieng et al. 1998), mouthparts (Blaney and Chapman 1969; Chapman 1989; Jin et al. 2006), cerci (Yu et al. 2011), wings (Zhou et al. 2008), and tarsi (Blaney and Chapman 1969; Chapman 1989; Zhou et al. 2009). The relative abundance of particular types of sensilla indicates their function. Sensilla chaetica are abundant on mouthparts (labial and maxillary palps) so they appear to detect gustatory stimuli (Blaney and Chapman 1969; Chapman 1989; Jin et al. 2006), whereas olfactory sensilla including basiconica, trichoidea, and wall-pored coeloconica are more abundant on antennae (Bland 1989; Chen et al. 2003; Li et al. 2007; Ochieng et al. 1998). The proximal end of the antenna (scape and pedicel) is responsible for antennal movements and here mechano-sensilla are abundant (Bland 1989; Chen et al. 2003; Li et al. 2007).

The function of sensilla cannot be inferred purely from morphological examination because many sensilla types vary in shapes and sizes within a type (Bland 1989; Chen et al. 2003; Li et al. 2007; Yu et al. 2011; Zhou et al. 2008, 2009) and the degree to which morphological diversity relates to functional diversity is not known. For example, basiconic sensilla are commonly stout peg-like (either with or without a cuticular depression: Table 1), but other forms have been recorded such as egg-shaped (Chen et al. 2003) or having a peg with an expanded base (Bland 1989; Chen et al. 2003). Subtypes of chaetica are also described in *L. migratoria* according to their size (Yu et al. 2011; Zhou et al. 2009) and the number of neurons connected to them (Jin et al. 2006; Zhou et al. 2009). Incorporating physiological studies such as single sensillum recordings or transcriptomic studies of the expression of receptor protein genes (discussed more in detail later) will help us elucidate the functional diversity of sensilla (Cui et al. 2011; Li et al. 2018; Ochieng and Hansson 1999; Yang et al. 2012).

Sensilla Functional Diversity A variety of pheromones are emitted by insects in various situations (see *Pheromones*) and single sensillum recordings can be used to identify sensillum-specific sensitivity to particular compounds. In the locust *S. gregaria* antennal sensilla were discovered to respond to a variety of odors: basiconica to aggregation pheromones, oviposition attractant, and (*E,Z*)-2,6-nonadienal

which is emitted by a preferred host plant (*Tribulus terrestris*) and is potentially a sex pheromone in *S. gregaria*; trichoidea also respond to (*E,Z*)-2,6-nonadienal; and coeloconica to nymph and oviposition pheromones (Ochieng and Hansson 1999). The reason basiconica are capable of detecting multiple olfactory stimuli is likely because they contain as many as 50 olfactory neurons (one to three in trichoidea and coeloconica: Ochieng et al. 1998). Each neuron is potentially responsive to a different odor.

In *L. migratoria*, seven functional subtypes of trichoid sensilla on the antenna have been identified, each housing two to three olfactory neurons (Cui et al. 2011). These neurons responded in several different combinations (i.e., inhibitory vs. excitatory) and intensities to nine different compounds found in frass pheromones (Cui et al. 2011). Some of the compounds found in *L. migratoria* frass pheromones also occur in nymphal (e.g., octanal, hexanal) and aggregation (e.g., guaiacol) pheromones of *S. gregaria* (Ochieng and Hansson 1999) but are detected by basiconica and coeloconica in *S. gregaria* (as mentioned above). Furthermore, trichoid sensilla in *L. migratoria* were discovered to respond to 18 chemicals that were commonly found in their host plants (You et al. 2016) suggesting that trichoid sensilla may be tuned to detect a wider range of compounds in *L. migratoria* than in *S. gregaria*. Together, these studies suggest grasshoppers have a complex pheromone-based communication system that will benefit from further investigation.

Grasshopper Ecology and Sensilla Abundance The number of each type of sensilla on an insect's exoskeleton is linked to the species' ecology. It is thought that high antennal sensitivity results from having a high density of sensilla (Greenwood and Chapman 1984; Bland 1989; Chen et al. 2003). In locusts *S. gregaria* and *L. migratoria*, solitary individuals have more olfactory sensilla on their antennae than gregarious ones (Greenwood and Chapman 1984; Ochieng et al. 1998). Single sensillum recordings indicate that solitary *S. gregaria* have a stronger electrophysiological response to some pheromone compounds (e.g., benzaldehyde, acetophenone, and solitary sex pheromone) than gregarious locusts (Ochieng and Hansson 1999). As the solitary phase occurs at low population density (Hasanali et al. 2005), higher sensilla abundance in solitary locusts may reflect a benefit for elevated sensitivity to long-range chemical signals for locating distant conspecifics (Bland 1989; Chen et al. 2003). The number of sensilla may also reflect feeding range (monophagous, oligophagous, or polyphagous) and the heterogeneity of vegetation in the grasshopper's habitat. For example, in Moroccan grasshoppers, polyphagous species (e.g., *S. gregaria* and *Calliptamus barbarus*) have more sensilla on their labrum (about 400-700) than monophagous or oligophagous species (e.g., *Sphingonotus coerulans*, *Oedipoda miniata*; about 200-300

sensilla; Zaim et al. 2013). In another study, desert species *B. argentatus*, *L. coquilletti*, and *C. parviceps* have fewer sensilla (800 – 2000) on their antennae than species living in more equitable habitats such as *Chorthippus curtipennis* and *Metaleptea brevicornis* (4000 – 8500 sensilla; Bland 1989). Species with a limited diet range or desert grasshoppers may be exposed to fewer chemical compounds than species that are polyphagous or living in more complex environments.

Male grasshoppers have more olfactory sensilla on their antennae than females in most grasshopper species studied (80%, $n = 75$; Chen et al. 2003; Bland 1989; Li et al. 2007). Higher electrophysiological responses to chemical signals in males have also been observed in some of the studies using single sensillum recordings or electroantennography (Ochieng and Hansson 1999; Chen and Kang 2000; Chen et al. 2004). This suggests that males are subject to sexual selection for locating (and possibly discriminating) females (Ritchie 1990). Chinese *Anagaracris barabensis* grasshoppers rely on acoustic and visual cues to find mates and there is no sexual difference in sensilla abundance (Chen and Kang 2000). No clear pattern of the sensilla was found among subfamilies or tribes (Bland 1989; Chen et al. 2003; Li et al. 2007; Zaim et al. 2013); and therefore, specific ecological aspects including habitat, feeding patterns and sex roles may influence sensilla abundance and distribution.

Types and Functions of Chemoreceptive Proteins Chemoreceptive proteins are conserved in insects, each type identified by specific amino acid sequences and three-dimensional structures (Sánchez-Gracia et al. 2009). Proteins involved in insect chemoreception are of two distinct types: odorant-binding proteins and chemosensory proteins. These binding proteins are produced in several places in an insect including within sensilla that have chemosensory neurons, where they are secreted in the sensilla lymph (Fig. 4) and transduce chemical signals (e.g., semiochemicals, hormones, nutrients, and toxic compounds) by binding to molecules and moving them to the receptors on the sensory neuron surface (Sánchez-Gracia et al. 2009; Wicher and Miazzi 2021).

Olfactory sensory neurons are nerve cells specialized for transmitting information about smells (Fig. 4). They are equipped with a variety of protein receptors (odorant, ionotropic or sensory neuron membrane) on their dendritic membranes (Sánchez-Gracia et al. 2009) that mediate peripheral neural processing and trigger signals that are transmitted to the brain via ganglia. Odorant receptors are solely responsible for detecting volatiles whereas ionotropic receptors have multiple roles including detection of smells, tastes, humidity, and temperature (Wicher and Miazzi 2021). These receptors have co-receptor(s) for their proper function (Sánchez-Gracia et al. 2009; Cassau and Krieger 2021). Although the exact role of the co-receptors is a mystery, odorant and ionotropic receptors form a complex with their respective

co-receptor(s) to function as ligand-gated ion channels (Knecht et al. 2017; Cassau and Krieger 2021). Sensory neuron membrane proteins (SNMPs) are another important membrane protein involved in insect olfaction. There are two main types of SNMPs: co-receptors of pheromone sensitive odorant receptor complex (SNMP1); and proteins expressed in support cells of olfactory sensory neurons (SNMP2) (Cassau and Krieger 2021). The presence of SNMP1 in an olfactory-sensitive neuron and co-expression with odorant receptors show these proteins are involved in the detection of pheromones. Depending on the insect species, there are three (Table 2) or more types (16 in dung beetles) of SNMPs described, although their functions are unknown (Cassau and Krieger 2021).

Functions of Chemoreceptive Proteins Identifying the diversity and function of chemoreceptive proteins involves large-scale genome sequencing, transcription, proteomics, and experimental molecular evolution. Among short-horned grasshoppers these detailed and time-consuming steps have as yet been completed only for *L. migratoria* (Guo et al. 2011, 2020; Wang et al. 2015; Li et al. 2016, 2020; Yu et al. 2016; Chen et al. 2018; Wei et al. 2019). However, the diversity of chemoreceptive proteins has been explored in seven locust species where more olfactory receptor genes are found than ionotropic receptor genes (Table 2). The expansion of olfactory receptors could mean that locusts rely heavily on olfactory cues rather than taste when assessing mates or host plants, whereas in model insect species such as *Drosophila melanogaster*, olfactory receptors, and ionotropic receptors occur in equal numbers (Sánchez-Gracia et al. 2009; Croset et al. 2010).

The potential functions of specific proteins are explored using quantitative real-time PCR and *in situ* hybridization to identify expression in specific tissues, sex, phase, and sensilla. Protein functions can be further inferred by exposing tissues and sensilla to specific chemical stimuli (using electroantennogram or single sensillum recordings) or genome editing tools (Maleszka et al. 2007; Guo et al. 2011; Zhang et al. 2017; Jiang et al. 2021). The genome editing tools RNA interference (RNAi) and Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR) have been used on locust species. These techniques allow silencing of the genes that are contributing to discrimination of host and nonhost plants and perception and biosynthesis pheromones and CHCs (Jurado-Rivera et al. 2009; Perkin et al. 2016) by introducing double-stranded RNA (RNAi) or restriction enzymes (CRISPR).

In locusts, olfactory binding proteins and odorant receptors show exclusive or biased expression patterns in antennae and mouthparts suggesting a chemosensory role, whereas chemosensory proteins and ionotropic receptors show broader expression including antennae, abdomen,

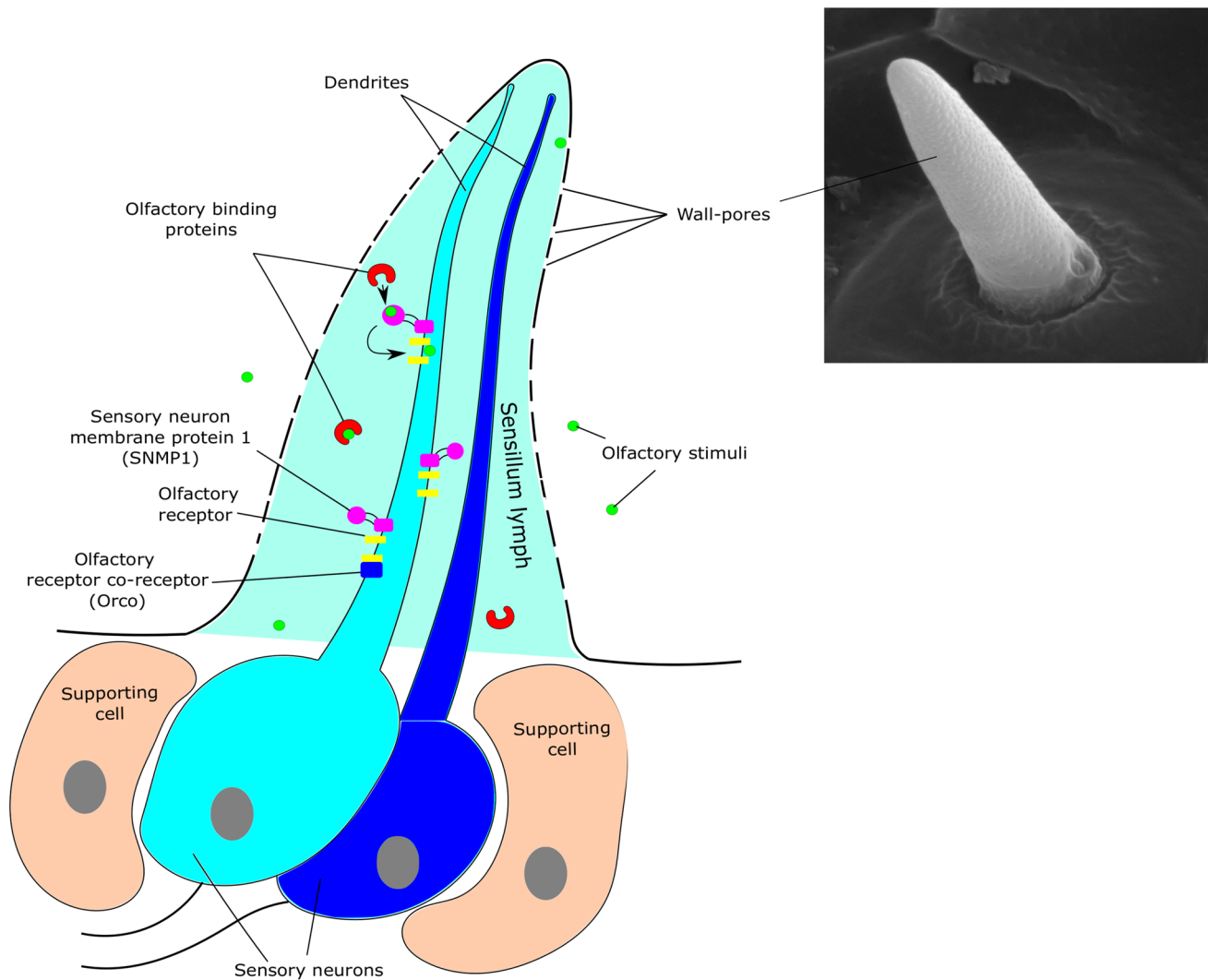


Fig. 4 Simplified scheme of the internal structure of an olfactory sensillum and associated proteins

Table 2 Diversity of proteins involved in chemoreception that bind particles and move them to the receptors in the insect sensilla are shown as numbers of putative functional genes characterized in seven grasshopper species

Name	OBP	CSP	OR	IR	SNMP	References
<i>Ceracris kiangsu</i> Bamboo locust	13	6	91	13	2	Li et al. 2020
<i>Ceracris nigricornis</i>	20	10	71	8	3	Yuan et al. 2019
<i>Locusta migratoria</i> Migratory locust	17	58	142	32	N/A	Wang et al. 2015; Martín-Blázquez et al. 2017; Guo et al. 2018a, 2018b
<i>Oedaleus asiaticus</i> Band-winged grasshopper	15	17	60	6	3	Zhang et al. 2015; Zhou et al. 2019
<i>Oedaleus infernalis</i>	18	N/A	N/A	N/A	N/A	Zhang et al. 2018
<i>Oxya chinensis</i> Rice grasshopper	18	13	94	12	2	Cui et al. 2019b
<i>Schistocerca gregaria</i> Desert locust	14	42	119	>2	2	Guo et al. 2014; Martín-Blázquez et al. 2017; Pregitzer et al. 2017

OBP odorant-binding protein, CSP chemosensory protein, OR odorant receptor, IR ionotropic receptor, SNMP sensory neuron membrane protein. The diversity of OR and IR includes its coreceptor(s)

thorax, legs, and wings (Jin et al. 2005; Guo et al. 2011; Wang et al. 2015; Zhang et al. 2018; Cui et al. 2019b; Yuan et al. 2019; Zhou et al. 2019; Li et al. 2020) implying broader functions. Some odorant receptors might be tuned to perceive pheromones, and in insects, odorant receptors are co-expressed with the protein SNMP1 only in pheromone-sensitive neurons (Cassau and Krieger 2021). Co-expression of odorant receptors and SNMP1 in sensilla basiconica and trichoidea of *S. gregaria* (Pregitzer et al. 2017) are responsible for detecting an aggregation pheromone and a putative sex pheromone respectively (Ochieng and Hansson 1999). In *L. migratoria*, specific odorant receptors expressed in sensilla basiconica are responsible for detecting aggregation pheromone (Guo et al. 2020). The co-receptor of an odorant receptor plays a crucial role in insect olfaction, and laboratory silencing of this protein in *L. migratoria*, using both RNAi (Wang et al. 2015) and CRISPR/Cas9 (Li et al. 2016), resulted in the loss of sensitivity to pheromones and food plant odors. Wang et al. (2015) also found that two co-receptors of ionotropic receptors were silenced but this did not affect the sensitivity of the grasshopper to the pheromone, suggesting reception may be specific to odorant receptors. Furthermore, odorant receptors are also expressed in trichoidea, which are responsible for perceiving plant-derived chemicals (ketones and esters) (You et al. 2016) and frass pheromones (Cui et al. 2011). These studies show odorant-receptor families respond to both insect- and plant-derived olfactory stimuli. Ionotropic receptors also respond to some chemical stimuli. In *S. gregaria*, some ionotropic receptors are expressed in sensilla chaetica and coeloconica (Guo et al. 2014). Coeloconica are tuned to detect odors of food plants (Ochieng and Hansson 1999) and chaetica are considered to be taste receptors (Ochieng et al. 1998). Thus, it is possible that these ionotropic receptors are responsible for detecting a range of chemical cues from food plants. Whether or not ionotropic receptors are involved in other roles (e.g., temperature and humidity perceptions) is not known for locusts.

Sex-biased (Wang et al. 2015; Zhang et al. 2015, 2018; Cui et al. 2019b; Yuan et al. 2019; Zhou et al. 2019; Li et al. 2020) or phase-biased (Guo et al. 2011) variation in the amount produced of some proteins indicates they are used to mediate chemosensory processing that is specific to sex (e.g, males to perceive female pheromone; females to locate oviposition site) or phase. In *L. migratoria*, one of the chemosensory proteins showed significantly higher expression in gregarious nymphs compared to solitary ones, and RNAi-mediated silencing showed this chemosensory protein was involved in an attraction response to an aggregation pheromone (Guo et al. 2011). Sex-biased or -specific expression of some odorant-binding proteins, chemosensory proteins, odorant receptors, and ionotropic receptors has been observed in several locust species (Table 2), suggesting they

mediate sex-specific chemosensory processing (e.g., males to perceive female pheromone; females to locate oviposition sites).

Applied Chemical Ecology in Pest Control and Conservation

Knowledge of the chemical ecology of insect species presents an opportunity to reduce reliance on insecticides, which present major concerns for environmental resilience, biodiversity, human health, and the development of insect resistance to insecticides (Giron et al. 2018). The application of genome editing tools has recently provided new opportunities for pest control and may be important for reducing the devastation that results from locust plagues. The shift to the swarming phase of locusts is controlled by pheromone signaling and is accompanied by rapid change in their olfactory pathways (Hassanali et al. 2005). Thus, identification and knockdown of the genes involved in the pheromone synthesis or pheromone-reception of the gregarious phase have been the primary interest of chemical ecology studies of locust species. So far, only the genome of *L. migratoria* has been edited in this way. Genes involved in the perception (Guo et al. 2011, 2020; Ma et al. 2015, 2019; Li et al. 2016; Zhang et al. 2021) and biosynthesis of aggregation pheromones (Wei et al. 2019) and CHCs (Wu et al. 2020; Zhang et al. 2021) have been successfully silenced using RNAi and CRISPR/Cas9. RNAi interferes with existing gene expression but CRISPR results in permanent genetic modification; thus, higher stability and the potential to pass genetic changes to their offspring. Moreover, CRISPR along with gene-drive has the potential to help spread the manipulated alleles in the field more rapidly than via normal Mendelian processes (Giron et al. 2018; Courtier-Orgogozo et al. 2020). The stability of transformed genes in natural populations is not known and could be affected by the presence/absence of resistant strains (Sugahara et al. 2017) and natural selection may reduce its effectiveness. There are unknown but potentially serious implications of the spread of modified genetics to non-target species through hybridization and/or horizontal transfer via vectors such as mites, parasitoids, viruses, or microsporidia (Sugahara et al. 2017; Giron et al. 2018; Courtier-Orgogozo et al. 2020). Risk assessment of the genetic spill-over using mathematical models is a current focus of gene editing and gene drive (Courtier-Orgogozo et al. 2020; Greenbaum et al. 2021). Studies using experimental evolution under controlled and semi-controlled conditions are also required before applying this method in the field.

Although the application of genome editing tools in pest control is increasing, the efficacy of artificially modified

SUBFAMILY	Studied species	CHC	Pheromone	Sensilla	Chemo-protein	RNAi or CRISPR	Phase-switch	Flight	Diet range	Diet type	Habitat type	Example species		
Marellinae										aqua.	aquatic	<i>Marellia remipes</i>		
Pauliniinae										aqua.	aquatic	<i>Paulinia acuminata</i>		
Ommatolampidinae								X			rainforest	<i>Psiloscirtus aptera</i>		
Leptysmiinae								F		aqua.	aquatic	<i>Cormops aquaticum</i>		
Ommatolampidinae								X	poly	mix forb	rainforest	<i>Locheuma brunneri</i>		
Rhytidochrotinae								X	mono	fern	rainforest	<i>Gallidacris variabilis</i>		
Ommatolampidinae								F			rainforest	<i>Hylopedetes nigrithorax</i>		
Ommatolampidinae								F			tropics	<i>Coryphosima stenoptera</i>		
Hemiacridinae								P			tropics	<i>Leptacris filiformis</i>		
Tropidopodinae								F				<i>Petamella prostermalis</i>		
Coptacrinae														
Catantopinae														
Gomphocerinae										grass	prairie	<i>Dichromorpha viridis</i>		
Acridinae										grass	prairie	<i>Mermiria intertexta</i>		
Gomphocerinae														
Acridinae														
Gomphocerinae	<i>Chorthippus</i> spp.	o	o					X	F	poly	grass	arid		
Gomphocerinae	<i>Docostaurus maroccanus</i>	o	o					P	F	poly	grass	arid		
Gomphocerinae	<i>Boettettix argentatus</i>	o	o					X	F	mono	forb	desert		
Gomphocerinae	<i>Ligurotettix coquilletti</i>	o	o					X	F	oligo	forb	desert		
Gomphocerinae	<i>Gbolacris parviceps</i>	o	o					X	F	poly	forb	desert		
Acridinae														
Oedipodinae														
Gomphocerinae														
Acridinae	<i>Metaleptea brevicornis</i>		o							grass	wetland			
Gomphocerinae														
Acridinae														
Oedipodinae	<i>Locusta migratoria</i>	o	o	o	o			P	F	poly	grass			
Oedipodinae	<i>Oedaleus asiaticus</i>	o	o	o	o			?	F	poly	grass			
Oedipodinae	<i>Oedaleus infernalis</i>	o	o	o	o			X	F	poly	grass			
Oedipodinae	<i>Angaracris barbensis</i>	o	o	o	o			?	F	poly	forb			
Oedipodinae	<i>Ceracris kigansu</i>	o	o	o	o			P	F	poly	grass			
Oedipodinae	<i>Ceracris nigricornis</i>	o	o	o	o			P	F	poly	grass	marsh		
Gomphocerinae												<i>Stethophyma grossum</i>		
Oedipodinae											coast	<i>Psinidia fenestralis</i>		
Hemiacridinae								X			arid	<i>Euloryma larsenororum</i>		
Oxyinae								X			arid	<i>Euloryma lapollai</i>		
Hemiacridinae								X			alpine	<i>Kosciuscola tristis</i>		
Spathosterninae														
Oxyinae	<i>Oxya chinensis</i>		o	o	o			X	F	oligo	grass	tropics	<i>Spathosternum nigrotaeniatum</i>	
Copiocerinae											palm	tropics	<i>Copiocera austera</i>	
Proctolabinae														
Melanoplinae	<i>Melanoplus bivittatus</i>		o	o	o			P	F	poly	mix forb	alpine		
Melanoplinae	<i>Melanoplus sanguinipes</i>		o	o	o			P	F	oligo	mix forb	prairie		
Melanoplinae	<i>Hesperotettix viridis</i>		o	o	o			X	F	poly	mix forb			
Melanoplinae	<i>Leptysma marginicollis</i>		o	o	o			?	oligo	forb				
Melanoplinae	<i>Hypochlora alba</i>		o	o	o			F	oligo	grass	aquatic			
Melanoplinae			o	o	o			X	oligo	forb				
Eyreprocnemidinae												arid	<i>Eyreprocnemis plorans</i>	
Calliptaminae	<i>Calliptamus barbarus</i>		o							poly	mix forb			
Euryphyminae												arid	<i>Euryphymus eremobioides</i>	
Euryphyminae												arid	<i>Euryphymus exemptus</i>	
Catantopinae														
Cyrtacanthacridinae	<i>Schistocerca gregaria</i>	o	o	o	o			X	F	poly	mix			
Cyrtacanthacridinae	<i>Schistocerca americana</i>	o	o	o	o			P	F	poly	mix forb			
Cyrtacanthacridinae	<i>Schistocerca piceifrons</i>	o	o	o	o									
Catantopinae												mix forb	arid	<i>Buforania crassa</i>
Catantopinae								X	poly	mix forb	alpine	<i>Sigaus australis</i>		
Catantopinae								X	poly	mix forb	alpine	<i>Brachaspis nivalis</i>		
Catantopinae								X	poly	mix forb	alpine	<i>Paprides nitidus</i>		

Fig. 5 Our current knowledge of Acrididae chemical ecology is patchy, as revealed by examination of its extent in a phylogenetic context (derived from Song et al. 2018). Grasshopper biological traits (phase switch, flight/flightless, diet range, diet type, and habitat) of best studied species are indicated. Availability of information on cuticular hydrocarbon (CHC), pheromone, sensilla, chemo-protein and/or genome editing tools (RNAi or CRISPR) is indicated (o indicates the species has been studied). Exemplars of the broader, unstudied, ecological diversity of the Acrididae is indicated on the right. P- capable of phase-switching, F- capable of flying, X- incapable of phase-switching or flying, poly- polyphagous, oligo- oligophagous, mono- monophagous, mix forb- feeding on both grasses and forbs but prefer forbs more

individuals may be reduced if plant-insect and insect-insect interactions are altered in natural populations of locusts by factors associated with climate change. Changes in irradiation intensity, temperature, CO₂ concentration, and humidity are known to affect the chemical composition (nutrients and secondary metabolites) of plants by altering biosynthetic pathways, and emission quantity and frequency by modifying stomatal opening/closing (where volatiles are predominantly emitted) (Giron et al. 2018; Effah et al. 2020). As feeding, oviposition, and development of locusts (and likely other short-horned grasshoppers) respond to plant-derived chemical signals (discussed in *Plant-derived Signals*), alteration of plant chemical signals could influence plant-insect interactions. Changes in host plant-derived chemicals may also alter symbiotic microbiome composition since certain bacteria contribute to locust pheromone signals (e.g., guaiacol and phenol: see *Chemical Biosynthesis in Grasshoppers*), and play an important role in resistance against pathogens and parasites (Lavy et al. 2020). Moreover, an increase in ambient temperature can increase body temperature in insects, which in turn, affects biosynthetic pathways in insects (Giron et al. 2018). This can alter locust chemical communication as some aggregation pheromones (i.e., guaiacol and phenol) are reliant on bacterial conversion. Humidity levels probably exert strong selection pressure on the chemical composition of their cuticular hydrocarbons (as discussed in *Cuticular Hydrocarbons (CHCs)*).

In addition to genome-editing tools, entomopathogenic microorganisms have also been considered for insect pest management. Entomopathogenic microorganisms are biopesticides, impairing chemical signaling, reproduction, and mobility of their hosts. Some are acridid-specific (e.g., *Metarhizium anisopliae* var. *acridum*: Atheimine et al. 2014; Abdellaoui et al. 2020; *Paranosema locustae*: Shi and Njagi 2004; Shi et al. 2014), which suggests a limited effect on non-target organisms. The gut microsporidian parasite, *P. locustae* has been observed in *L. migratoria* (Shi and Njagi 2004; Shi et al. 2014) and found to disrupt chemical communication in the locusts by reducing olfactory sensitivity (Shi and Njagi 2004), preventing biosynthesis of bacterial mediated pheromones, and lowering activities

of neurotransmitters (serotonin and dopamine) that are required for initiation and maintenance of gregarious behavior (Shi et al. 2014). Furthermore, the effectiveness of dry coinidia (fungal spores) of the entomopathogenic fungus *M. anisopliae* var. *acridum* on 4th instar *S. gregaria* was apparent at varying vegetation composition, temperatures (23–48 °C), and relative humidity (4–52%) (Atheimine et al. 2014), suggesting potential to remain useful in a changing climate. In comparison to chemical pesticides, both genome editing and entomopathogenic techniques are relatively new and their use in pest control is still developing. Studies relating to these tools are accumulating and considered to be promising alternatives to insecticides. A better understanding of chemical ecology and chemoreception of insects as well as chemical changes in plants associated with climate change can aid our development of both pest control tools and species conservation strategies.

Future Directions

Short-horned grasshoppers are fascinating subjects for the study of chemoreception and chemical ecology by virtue of their taxonomic and ecological diversity (Fig. 5). The use of chemical signals has been inferred for a variety of short-horned grasshopper species but, not surprisingly, most chemical ecology studies are focused on the economically important locust pest species (Fig. 5). Locust species exhibit similar ecology and structures including strong flight, phase-switching, chemical signaling (e.g., aggregation pheromones), and diversity of chemoreceptive proteins (i.e., greater diversity of odorant receptors compared to ionotropic receptors), yet they do not form a monophyletic group. A locust is therefore a converged strategy that has independently evolved in four subfamilies; Gomophocerinae, Oedipodinae, Melanoplinae, and Cyrcanthacridinae (Fig. 5). As such, our understanding of the convergence of signaling traits will be enhanced by studies of their phylogenetic relatives. Mechanisms of chemoreception (sensilla), chemical-mediated behaviors, diversity of expression patterns, and specific functions of chemoreceptive proteins in locusts have provided an invaluable framework for the study of the Acrididae more widely. Future research involving species that represent the taxonomic breadth of the family and the range of biological traits that they display (e.g., flightless, monophagous, alpine, aquatic, rainforest) could reveal evolutionary constraints on chemoreception and chemical ecology. Several strands of research would be illuminating: 1) The morphological diversity of sensilla in a variety of species can be explored using SEM, and the functional diversity of specific sensilla types could be further investigated using single sensillum recordings or chemoreceptor-deorphaning approaches. It would be extremely valuable to know whether

the function of a sensillum can be accurately inferred from its external characters. 2) The genetic and functional diversity and expression patterns of chemoreceptive proteins of acridids other than locusts require further research using genome sequencing, transcriptomics, and molecular evolution approaches. 3) The use of short- (CHCs) vs. long- (volatile) distance chemical signals could be elucidated using a combination of analytical tools, behavioral assays, and electrophysiology. The potential for using pheromones to control grasshopper species that damage crops is likely to be an economically important line of research. 4) Exploring the biosynthetic pathways and the role of catalysts and gut bacteria in the synthesis of pheromones would be valuable. Determining the host-specificity of gut microbes in grasshoppers, their method of transmission, and potential for host switching and transferring chemical signaling phenotypes between species is an exciting area of current research. Manipulating insect physiology by feeding them bacteria is one avenue of pest management likely to reduce insecticide use. The interactions of microbes and their grasshoppers can be revealed using a range of experimental tools, biochemical and -omics approaches (metagenomics, transcriptomics, and metabolomics). Integrated research involving these tools could enhance our understanding of the evolution of chemoreception and chemical ecology in the Acrididae, with implications for species interactions, speciation, conservation, pest management and resilience to environmental change (e.g., Dyer et al. 2018; Mori and Noge 2021; Wang et al. 2021).

Acknowledgments The work was supported by funding from the Miss E. L. Hellaby Indigenous Grassland Research Trust. We thank Kambiz Esfandi, Kyaw Min Tun, Evans Effah, and Shogo Yarita for their critical comments on this review. We are grateful to Dr. Matthew Savoian, Raoul Solomon, and Yanyu He at the Manawatu Microscopy and Imaging Centre, Massey University, for technical assistance and advice with a scanning electron microscope (SEM).

Code Availability (Software Application or Custom Code) Inkscape 1.0.

Authors' Contributions All authors contributed to the writing and funding acquisition.

Funding Miss E. L. Hellaby Indigenous Grassland Research Trust.

Data Availability Not applicable.

Declarations

Conflict of Interest Not applicable.

References

Abdellaoui K, Ben M, Habib HM, Hamouda B (2009) Insecticidal activity of gibberellic acid against *Spodoptera littoralis*

- (Lepidoptera, Noctuidae) and *Locusta migratoria migratoria* (Orthoptera, Acrididae). *Pest Technol* 3:28–33
- Abdellaoui K, Ben Halima-Kamel M, Fatma A et al (2015) Effects of gibberellic acid on ovarian biochemical composition and ecdysteroid amounts in the migratory locust *Locusta migratoria* (Orthoptera, Acrididae). *Int J Pest Manag* 61:68–72. <https://doi.org/10.1080/09670874.2014.995746>
- Abdellaoui K, Miladi M, Mkhinini M et al (2020) The aggregation pheromone phenylacetone nitrile: joint action with the entomopathogenic fungus *Metarhizium anisopliae* var. *acridum* and physiological and transcriptomic effects on *Schistocerca gregaria* nymphs. *Pestic Biochem Physiol* 167:1–14. <https://doi.org/10.1016/j.pestbp.2020.104594>
- Altner H, Routil C, Loftus R (1981) The structure of bimodal chemo-, thermo-, and hygroreceptive sensilla on the antenna of *Locusta migratoria*. *Cell Tissue Res* 215:289–308. <https://doi.org/10.1007/BF00239116>
- Amwayi PW, Masiga DK, Govender P et al (2012) Mass spectral determination of phenylacetone nitrile (PAN) levels in body tissues of adult desert locust, *Schistocerca gregaria*. *J Insect Physiol* 58:1037–1041. <https://doi.org/10.1016/j.jinsphys.2012.03.012>
- Atheimine MO, Bashir MO, Ely SO et al (2014) Efficacy and persistence of *Metarhizium acridum* (Hypocreales: Clavicipitaceae) used against desert locust larvae, *Schistocerca gregaria* (Orthoptera: Acrididae), under different vegetation cover types. *Int J Trop Insect Sci* 34:106–114. <https://doi.org/10.1017/S1742758414000228>
- Barry KL, Holwell GI, Herberstein ME (2010) Multimodal mate assessment by male praying mantids in a sexually cannibalistic mating system. *Anim Behav* 79:1165–1172. <https://doi.org/10.1016/j.anbehav.2010.02.025>
- Bashir MO, Hassanali A (2010) Novel cross-stage solitarising effect of gregarious-phase adult desert locust (*Schistocerca gregaria* (Forskål)) pheromone on hoppers. *J Insect Physiol* 56:640–645. <https://doi.org/10.1016/j.jinsphys.2010.01.012>
- Bland RG (1989) Antennal sensilla of Acrididae (Orthoptera) in relation to subfamily and food preference. *Ann Entomol Soc Am* 82:368–384. <https://doi.org/10.1093/aesa/82.3.368>
- Blaney WM, Chapman RF (1969) The fine structure of the terminal sensilla on the maxillary palps of *Schistocerca gregaria* (Forskål) (Orthoptera, Acrididae). *Z Zellforsch Mikrosk Anat* 99:74–97. <https://doi.org/10.1007/BF00338799>
- Blomquist GJ, Tittiger C, Jurenka R (2018) Cuticular hydrocarbons and pheromones of arthropods. In: Wilkes H (ed) *Hydrocarbons, oils and lipids: diversity, origin, chemistry and fate*. Springer Nature Living Reference, Basel, pp 1–32
- Burke NW, Crean AJ, Bonduriansky R (2015) The role of sexual conflict in the evolution of facultative parthenogenesis: a study on the spiny leaf stick insect. *Anim Behav* 101:117–127. <https://doi.org/10.1016/j.anbehav.2014.12.017>
- Byers JA (1991) Pheromones and chemical ecology of locusts. *Biol Rev Camb Philos Soc* 66:347–378. <https://doi.org/10.1111/j.1469-185x.1991.tb01146.x>
- Carlisle DB, Ellis PE, Osborne DJ (1969) Effects of plant growth regulators on locusts and cotton stainer bugs. *J Sci Food Agric* 20:391–393. <https://doi.org/10.1002/jsfa.2740200703>
- Cassau S, Krieger J (2021) The role of SNMPs in insect olfaction. *Cell Tissue Res* 383:21–33. <https://doi.org/10.1007/s00441-020-03336-0>
- Chapman RF (1989) The chemosensory system of the monophagous grasshopper, *Boettettia argentatus* Bruner (Orthoptera: Acrididae). *Int J Insect Morphol Embryol* 18:111–118
- Chapman RF, Bernays EA, Wyatt T (1988) Chemical aspects of host-plant specificity in three *Larrea*-feeding grasshoppers. *J Chem Ecol* 14:561–579. <https://doi.org/10.1007/BF01013907>

- Chen H, Kang L (2000) Olfactory responses of two species of grasshoppers to plant odours. *Entomol Exp Appl* 95:129–134. <https://doi.org/10.1046/j.1570-7458.2000.00650.x>
- Chen H, Zhao YX, Kang L (2003) Antennal sensilla of grasshoppers (Orthoptera: Acrididae) in relation to food preferences and habits. *J Biosci* 28:743–752. <https://doi.org/10.1007/BF02708435>
- Chen H, Zhao Y, Kang L (2004) Comparison of the olfactory sensitivity of two sympatric steppe grasshopper species (Orthoptera: Acrididae) to plant volatile compounds. *Sci China Ser C Life Sci* 47:115–123. <https://doi.org/10.1360/02yc0258>
- Chen D, Tang JX, Li B et al (2018) CRISPR/Cas9-mediated genome editing induces exon skipping by complete or stochastic altering splicing in the migratory locust. *BMC Biotechnol* 18:1–10. <https://doi.org/10.1186/s12896-018-0465-7>
- Courtier-Orgozozo V, Danchin A, Gouyon PH, Boëte C (2020) Evaluating the probability of CRISPR-based gene drive contaminating another species. *Evol Appl* 13:1888–1905. <https://doi.org/10.1111/eva.12939>
- Croset V, Rytz R, Cummins SF et al (2010) Ancient protostome origin of chemosensory ionotropic glutamate receptors and the evolution of insect taste and olfaction. *PLoS Genet* 6. <https://doi.org/10.1371/journal.pgen.1001064>
- Cui X, Wu C, Zhang L (2011) Electrophysiological response patterns of 16 olfactory neurons from the trichoid sensilla to odorant from fecal volatiles in the locust, *Locusta migratoria manilensis*. *Arch Insect Biochem Physiol* 77:45–57. <https://doi.org/10.1002/arch.20420>
- Cui B, Huang X, Li S et al (2019a) Quercetin affects the growth and development of the grasshopper *Oedaleus asiaticus* (Orthoptera: Acrididae). *J Econ Entomol* 112:1175–1182. <https://doi.org/10.1093/jee/toz050>
- Cui Y, Kang C, Wu Z, Lin J (2019b) Identification and expression analyses of olfactory gene families in the rice grasshopper, *Oxya chinensis*, from antennal transcriptomes. *Front Physiol* 10:1–13. <https://doi.org/10.3389/fphys.2019.01223>
- Diehl PA (1975) Synthesis and release of hydrocarbons by the oenocytes of the desert locust, *Schistocerca gregaria*. *J Insect Physiol* 21:1237–1246. [https://doi.org/10.1016/0022-1910\(75\)90093-1](https://doi.org/10.1016/0022-1910(75)90093-1)
- Dillon RJ, Charnley KA (2002) Mutualism between the desert locust *Schistocerca gregaria* and its gut microbiota. *Res Microbiol* 153:503–509. [https://doi.org/10.1016/S0923-2508\(02\)01361-X](https://doi.org/10.1016/S0923-2508(02)01361-X)
- Dillon RJ, Vennard CT, Charnley AK (2002) A note: gut bacteria produce components of a locust cohesion pheromone. *J Appl Microbiol* 92:759–763. <https://doi.org/10.1046/j.1365-2672.2002.01581.x>
- Dyer LA, Philbin CS, Ochsenrider KM et al (2018) Modern approaches to study plant–insect interactions in chemical ecology. *Nat Rev Chem* 2:50–64. <https://doi.org/10.1038/s41570-018-0009-7>
- Effah E, Barrett DP, Peterson PG et al (2020) Herbivory and attenuated uv radiation affect volatile emissions of the invasive weed *Calluna vulgaris*. *Molecules* 25. <https://doi.org/10.3390/molecules25143200>
- Ellis PE, Carlisle DB, Osborne DJ (1965) Desert locusts : sexual maturation delayed by feeding on senescent vegetation. *Science* 149:546–547
- Ferenz HJ, Seidelmann K (2003) Pheromones in relation to aggregation and reproduction in desert locusts. *Physiol Entomol* 28:11–18. <https://doi.org/10.1046/j.1365-3032.2003.00318.x>
- Finck J, Ronacher B (2017) Components of reproductive isolation between the closely related grasshopper species *Chorthippus biguttulus* and *C. mollis*. *Behav Ecol Sociobiol* 71:1–13. <https://doi.org/10.1007/s00265-017-2295-3>
- Finck J, Berdan EL, Mayer F et al (2016a) Divergence of cuticular hydrocarbons in two sympatric grasshopper species and the evolution of fatty acid synthases and elongases across insects. *Sci Rep* 6:1–13. <https://doi.org/10.1038/srep33695>
- Finck J, Kuntze J, Ronacher B (2016b) Chemical cues from females trigger male courtship behaviour in grasshoppers. *J Comp Physiol A Neuroethol Sensory, Neural, Behav Physiol* 202:337–345. <https://doi.org/10.1007/s00359-016-1081-4>
- Fürstenau B, Muñoz L, Coca-Abia M et al (2013) Phytal: a candidate sex pheromone component of the moroccan locust *Docicostaurus maroccanus*. *ChemBioChem* 14:1450–1459. <https://doi.org/10.1002/cbic.201300247>
- Gaten E, Huston SJ, Dowse HB, Matheson T (2012) Solitary and gregarious locusts differ in circadian rhythmicity of a visual output neuron. *J Biol Rhythm* 27:196–205. <https://doi.org/10.1177/0748730412440860>
- Gibbs AG, Rajpurohit S (2010) Cuticular lipids and water balance. In: Blomquist GJ (ed) *Insect hydrocarbons biology, biochemistry, and chemical ecology*. Cambridge University Press, Reno, pp 100–120
- Giron D, Dubreuil G, Bennett A et al (2018) Promises and challenges in insect–plant interactions. *Entomol Exp Appl* 166:319–343. <https://doi.org/10.1111/eea.12679>
- Gordon SD, Jackson JC, Rogers SM, Windmill JFC (2014) Listening to the environment: hearing differences from an epigenetic effect in solitary and gregarious locusts. *Proc R Soc B Biol Sci* 281. <https://doi.org/10.1098/rspb.2014.1693>
- Grace T, Wisely SM, Brown SJ et al (2010) Divergent host plant adaptation drives the evolution of sexual isolation in the grasshopper *Hesperotettix viridis* (Orthoptera: Acrididae) in the absence of reinforcement. *Biol J Linn Soc* 100:866–878. <https://doi.org/10.1111/j.1095-8312.2010.01458.x>
- Greenbaum G, Feldman MW, Rosenberg NA, Kim J (2021) Designing gene drives to limit spillover to non-target populations. *PLoS Genet* 17:1–25. <https://doi.org/10.1371/journal.pgen.1009278>
- Greenwood M, Chapman RF (1984) Differences in numbers of sensilla on the antennae of solitary and gregarious *Locusta migratoria* L. (Orthoptera: Acrididae). *Int J Insect Morphol Embryol* 13:295–301. [https://doi.org/10.1016/0020-7322\(84\)90004-7](https://doi.org/10.1016/0020-7322(84)90004-7)
- Guerrero A, Ramos VE, López S et al (2019) Enantioselective synthesis and activity of all diastereoisomers of (*E*)-phytal, a pheromone component of the Moroccan locust, *Docicostaurus maroccanus*. *J Agric Food Chem* 67:72–80. <https://doi.org/10.1021/acs.jafc.8b06346>
- Guo W, Wang X, Ma Z et al (2011) CSP and takeout genes modulate the switch between attraction and repulsion during behavioral phase change in the migratory locust. *PLoS Genet* 7:1–14. <https://doi.org/10.1371/journal.pgen.1001291>
- Guo M, Krieger J, Große-Wilde E et al (2014) Variant ionotropic receptors are expressed in olfactory sensory neurons of coeloconic sensilla on the antenna of the desert locust (*Schistocerca gregaria*). *Int J Biol Sci* 10:1–14. <https://doi.org/10.7150/ijbs.7624>
- Guo W, Ren D, Zhao L et al (2018a) Identification of odorant-binding proteins (OBPs) and functional analysis of phase-related OBPs in the migratory locust. *Front Physiol* 9:1–12. <https://doi.org/10.3389/fphys.2018.00984>
- Guo X, Ma Z, Du B et al (2018b) Dop1 enhances conspecific olfactory attraction by inhibiting MIR-9a maturation in locusts. *Nat Commun* 9:1–17. <https://doi.org/10.1038/s41467-018-03437-z>
- Guo X, Yu Q, Chen D et al (2020) 4-Vinylanisole is an aggregation pheromone in locusts. *Nature* 584:584–588. <https://doi.org/10.1038/s41586-020-2610-4>
- Hansson BS, Ochieng SA, Grosmaître S, Anton X, Njagi PGN (1996) Physiological responses and central nervous projections of antennal olfactory receptor neurons in the adult desert locust, *Schistocerca gregaria* (Orthoptera: Acrididae). *J Comp Physiol - A Sensory, Neural, Behav Physiol* 179:157–167. <https://doi.org/10.1007/BF00222783>

- Hassanali A, Njagi PGN, Bashir MO (2005) Chemical ecology of locusts and related acridids. *Annu Rev Entomol* 50:223–245. <https://doi.org/10.1146/annurev.ento.50.071803.130345>
- Hopkins TL, Young H (1990) Attraction of the grasshopper, *Melanoplus sanguinipes*, to host plant odors and volatile components. *Entomol Exp Appl* 56:249–258
- Howse PE, Stevens IDR, Jones OT et al (1998) Insect pheromones and their use in pest management, 1st edn. Springer, Dordrecht
- Huang X, Ma J, Qin X et al (2017) Biology, physiology and gene expression of grasshopper *Oedaleus asiaticus* exposed to diet stress from plant secondary compounds. *Sci Rep* 7:1–9. <https://doi.org/10.1038/s41598-017-09277-z>
- Huang X, Lv S, Zhang Z, Chang BH (2020) Phenotypic and transcriptomic response of the grasshopper *Oedaleus asiaticus* (Orthoptera: Acrididae) to toxic rutin. *Front Physiol* 11. <https://doi.org/10.3389/fphys.2020.00052>
- Ibanez S, Lavorel S, Puijalon S, Moretti M (2013a) Herbivory mediated by coupling between biomechanical traits of plants and grasshoppers. *Funct Ecol* 27:479–489. <https://doi.org/10.1111/1365-2435.12058>
- Ibanez S, Manneville O, Miquel C et al (2013b) Plant functional traits reveal the relative contribution of habitat and food preferences to the diet of grasshoppers. *Oecologia* 173:1459–1470. <https://doi.org/10.1007/s00442-013-2738-0>
- Inayatullah C, El Bashir S, Hassanali A (1994) Sexual behavior and communication in the desert locust, *Schistocerca gregaria* (Orthoptera: Acrididae): sex pheromone in solitaria. *Environ Entomol* 23:1544–1551. <https://doi.org/10.1093/ee/23.6.1544>
- Isely FB (1944) Correlation between mandibular morphology and food specificity in grasshoppers. *Ann Entomol Soc Am* 37:47–67. <https://doi.org/10.1093/aesa/37.1.47>
- Jacobson M (1972) Insect sex pheromone. Elsevier, New York
- Jiang X, Krieger J, Breer H, Pregitzer P (2017) Distinct subfamilies of odorant binding proteins in locust (Orthoptera, Acrididae): molecular evolution, structural variation, and sensilla-specific expression. *Front Physiol* 8:1–15. <https://doi.org/10.3389/fphys.2017.00734>
- Jiang X, Ryl M, Krieger J et al (2018) Odorant binding proteins of the desert locust *Schistocerca gregaria* (Orthoptera, Acrididae): topographic expression patterns in the antennae. *Front Physiol* 9:1–12. <https://doi.org/10.3389/fphys.2018.00417>
- Jiang X, Xu H, Zheng N et al (2021) A chemosensory protein detects antifeedant in locust (*Locusta migratoria*). *Insects* 11:1–15. <https://doi.org/10.3390/insects12010001>
- Jin X, Brandazza A, Navarrini A et al (2005) Expression and immunolocalisation of odorant-binding and chemosensory proteins in locusts. *Cell Mol Life Sci* 62:1156–1166. <https://doi.org/10.1007/s00018-005-5014-6>
- Jin X, Zhang SG, Zhang L (2006) Expression of odorant-binding and chemosensory proteins and spatial map of chemosensilla on labial palps of *Locusta migratoria* (Orthoptera: Acrididae). *Arthropod Struct Dev* 35:47–56. <https://doi.org/10.1016/j.asd.2005.11.001>
- Joern A (1979) Feeding patterns in grasshoppers (Orthoptera: Acrididae): factors influencing diet specialization. *Oecologia* 38:325–347. <https://doi.org/10.1007/BF00345192>
- Jurado-Rivera JA, Vogler AP, Reid CAM et al (2009) DNA barcoding insect-host plant associations. *Proc R Soc B Biol Sci* 276:639–648. <https://doi.org/10.1098/rspb.2008.1264>
- Knecht ZA, Silbering AF, Cruz J et al (2017) Ionotropic receptor-dependent moist and dry cells control hygrosensation in *Drosophila*. *Elife* 6:1–11. <https://doi.org/10.7554/eLife.26654>
- Koot EM, Morgan-Richards M, Treweek SA (2020) An alpine grasshopper radiation older than the mountains, on Kā Tiritiri o te Moana (southern Alps) of Aotearoa (New Zealand). *Mol Phylogenet Evol* 147:106783. <https://doi.org/10.1016/j.ympev.2020.106783>
- Lavy O, Gophna U, Gefen E, Ayali A (2019) The effect of density-dependent phase on the locust gut bacterial composition. *Front Microbiol* 10:1–8. <https://doi.org/10.3389/fmicb.2018.03020>
- Lavy O, Gophna U, Gefen E, Ayali A (2020) Locust bacterial symbionts: an update. *Insects* 11:1–10. <https://doi.org/10.3390/insects11100655>
- Li N, Ren BZ, Liu M (2007) The study on antennal sensilla of eight Acrididae species (Orthoptera: Acridoidea) in Northeast China. *Zootaxa*:59–68. <https://doi.org/10.11646/zootaxa.1544.1.3>
- Li Y, Zhang J, Chen D et al (2016) CRISPR/Cas9 in locusts: successful establishment of an olfactory deficiency line by targeting the mutagenesis of an odorant receptor co-receptor (Orco). *Insect Biochem Mol Biol* 79:27–35. <https://doi.org/10.1016/j.ibmb.2016.10.003>
- Li H, Wang P, Zhang L et al (2018) Expressions of olfactory proteins in locust olfactory organs and a palp odorant receptor involved in plant aldehydes detection. *Front Physiol* 9:1–12. <https://doi.org/10.3389/fphys.2018.00663>
- Li R, Jiang GF, Shu XH et al (2020) Identification and expression profile analysis of chemosensory genes from the antennal transcriptome of bamboo locust (*Ceracris kiangsu*). *Front Physiol* 11:1–18. <https://doi.org/10.3389/fphys.2020.00889>
- Lockey KH, Orahá VS (1990) Cuticular lipids of adult *Locusta migratoria migratoriodes* (R and F), *Schistocerca gregaria* (Forskål) (Acrididae) and other orthopteran species—II. Hydrocarbons. *Comp Biochem Physiol Part B Comp Biochem* 95:721–744
- Ma Z, Guo X, Lei H et al (2015) Octopamine and tyramine respectively regulate attractive and repulsive behavior in locust phase changes. *Sci Rep* 5:1–11. <https://doi.org/10.1038/srep08036>
- Ma Z, Liu J, Guo X (2019) A retinal-binding protein mediates olfactory attraction in the migratory locusts. *Insect Biochem Mol Biol* 114:103214. <https://doi.org/10.1016/j.ibmb.2019.103214>
- Maeno KO, Ould Ely S, Nakamura S et al (2016) Daily microhabitat shifting of solitary-phase desert locust adults: implications for meaningful population monitoring. *Springerplus* 5:1–10. <https://doi.org/10.1186/s40064-016-1741-4>
- Mahamat H, Hassanali A, Odongo H et al (1993) Studies on the maturation-accelerating pheromone of the desert locust *Schistocerca gregaria* (Orthoptera: Acrididae). *Chemoecology* 4:159–164. <https://doi.org/10.1007/BF01256551>
- Mahamat H, Hassanali A, Odongo H (2000) The role of different components of the pheromone emission of mature males of the desert locust, *Schistocerca gregaria* (Forskål) (Orthoptera: Acrididae) in accelerating maturation of immature adults. *Int J Trop Insect Sci* 20:1–5
- Maleszka J, Forêt S, Saint R, Maleszka R (2007) RNAi-induced phenotypes suggest a novel role for a chemosensory protein CSP5 in the development of embryonic integument in the honeybee (*Apis mellifera*). *Dev Genes Evol* 217:189–196. <https://doi.org/10.1007/s00427-006-0127-y>
- Martín-Blázquez R, Chen B, Kang L, Bakkali M (2017) Evolution, expression and association of the chemosensory protein genes with the outbreak phase of the two main pest locusts. *Sci Rep* 7:1–16. <https://doi.org/10.1038/s41598-017-07068-0>
- Menzel F, Blaimer BB, Schmitt T (2017) How do cuticular hydrocarbons evolve? Physiological constraints and climatic and biotic selection pressures act on a complex functional trait. *Proc R Soc B Biol Sci* 284. <https://doi.org/10.1098/rspb.2016.1727>
- Menzel F, Morsbach S, Martens JH et al (2019) Communication versus waterproofing: the physics of insect cuticular hydrocarbons. *J Exp Biol* 22. <https://doi.org/10.1242/jeb.210807>
- Mori N, Noge K (2021) Recent advances in chemical ecology: complex interactions mediated by molecules. *Biosci Biotechnol Biochem* 85:33–41. <https://doi.org/10.1093/bbb/zbba034>

- Neems RM, Butlin RK (1994) Variation in cuticular hydrocarbons across a hybrid zone in the grasshopper *Chorthippus parallelus*. *Proc R Soc B Biol Sci* 257:135–140. <https://doi.org/10.1098/rspb.1994.0106>
- Neems RM, Butlin RK (1995) Divergence in cuticular hydrocarbons between parapatric subspecies of the meadow grasshopper, *Chorthippus parallelus* (Orthoptera, Acrididae). *Biol J Linn Soc* 54:139–149. <https://doi.org/10.1111/j.1095-8312.1995.tb01028.x>
- Niassy A, Torto B, Njagi PGN et al (1999) Intra- and interspecific aggregation responses of *Locusta migratoria migratorioides* and *Schistocerca gregaria* and a comparison of their pheromone emissions. *J Chem Ecol* 25:1029–1042. <https://doi.org/10.1023/A:1020873623852>
- Njagi PGN, Torto B (1996) Responses of nymphs of desert locust, *Schistocerca gregaria* to volatiles of plants used as rearing diet. *Chemoecology* 7:172–178. <https://doi.org/10.1007/BF01266309>
- Njagi PGN, Torto B (2002) Evidence for a compound in Comstock-Kellogg glands modulating premating behavior in male desert locust, *Schistocerca gregaria*. *J Chem Ecol* 28:1065–1074. <https://doi.org/10.1023/A:1015222120556>
- Njagi PGN, Torto B, Obeng-Ofori D, Hassanali A (1996) Phase-independent responses to phase-specific aggregation pheromone in adult desert locusts, *Schistocerca gregaria* (Orthoptera: Acrididae). *Physiol Entomol* 21:131–137. <https://doi.org/10.1111/j.1365-3032.1996.tb00845.x>
- Nowińska A, Brożek J (2017) Morphological study of the antennal sensilla in *Gerromorpha* (Insecta: Hemiptera: Heteroptera). *Zoomorphology* 136:327–347. <https://doi.org/10.1007/s00435-017-0354-y>
- Obeng-Ofori D, Torto B, Njagi PGN et al (1994) Fecal volatiles as part of the aggregation pheromone complex of the desert locust, *Schistocerca gregaria* (Forsk.) (Orthoptera: Acrididae). *J Chem Ecol* 20:2077–2087. <https://doi.org/10.1007/BF02066244>
- Ochieng SA, Hansson BS (1999) Responses of olfactory receptor neurones to behaviourally important odours in gregarious and solitary desert locust, *Schistocerca gregaria*. *Physiol Entomol* 24:28–36. <https://doi.org/10.1046/j.1365-3032.1999.00107.x>
- Ochieng SA, Hallberg E, Hansson BS (1998) Fine structure and distribution of antennal sensilla of the desert locust, *Schistocerca gregaria* (Orthoptera: Acrididae). *Cell Tissue Res* 291:525–536. <https://doi.org/10.1007/s004410051022>
- Ould Ely S, Mahamat H, Njagi PGN et al (2006) Mate location mechanism and phase-related mate preferences in solitary desert locust, *Schistocerca gregaria*. *J Chem Ecol* 32:1057–1069. <https://doi.org/10.1007/s10886-006-9045-8>
- Pener MP, Simpson SJ (2009) Locust phase polyphenism: an update. *Adv Insect Phys* 36:1–272
- Perdeck AC (1958) The isolating value of specific song patterns in two sibling species of grasshoppers (*Chorthippus brunneus* Thunb. and *C. biguttulus* L.). *Behaviour* 12:1–75
- Perkin LC, Adrianos SL, Oppert B (2016) Gene disruption technologies have the potential to transform stored product insect pest control. *Insects* 7. <https://doi.org/10.3390/insects7030046>
- Pregitzer P, Jiang X, Grosse-Wilde E et al (2017) In search for pheromone receptors: certain members of the odorant receptor family in the desert locust *Schistocerca gregaria* (Orthoptera: Acrididae) are co-expressed with SNMP1. *Int J Biol Sci* 13:911–922. <https://doi.org/10.7150/ijbs.18402>
- Rai MM, Hassanali A, Saini RK et al (1997) Identification of components of the oviposition aggregation pheromone of the gregarious desert locust, *Schistocerca gregaria* (Forsk.). *J Insect Physiol* 43:83–87. [https://doi.org/10.1016/S0022-1910\(96\)00051-0](https://doi.org/10.1016/S0022-1910(96)00051-0)
- Ritchie MG (1990) Are differences in song responsible for assortative mating between subspecies of the grasshopper *Chorthippus parallelus* (Orthoptera: Acrididae)? *Anim Behav* 39:685–691. [https://doi.org/10.1016/S0003-3472\(05\)80379-3](https://doi.org/10.1016/S0003-3472(05)80379-3)
- Rogers SM, Cullen DA, Anstey ML et al (2014) Rapid behavioural gregarization in the desert locust, *Schistocerca gregaria* entails synchronous changes in both activity and attraction to conspecifics. *J Insect Physiol* 65:9–26. <https://doi.org/10.1016/j.jinsphys.2014.04.004>
- Rogers SM, Harston GWJ, Kilburn-Toppin F, et al (2010) Spatiotemporal receptive field properties of a looming-sensitive neuron in solitary and gregarious phases of the desert locust. *J Neurophysiol* 103(2):779–792. <https://doi.org/10.1152/jn.00855.2009>
- Rogers SM, Matheson T, Despland E et al (2003) Mechanosensory-induced behavioural gregarization in the desert locust *Schistocerca gregaria*. *J Exp Biol* 206:3991–4002. <https://doi.org/10.1242/jeb.00648>
- Saini RK, Rai MM, Hassanali A et al (1995) Semiochemicals from froth of egg pods attract ovipositing female *Schistocerca gregaria*. *J Insect Physiol* 41:711–716. [https://doi.org/10.1016/0022-1910\(95\)00016-N](https://doi.org/10.1016/0022-1910(95)00016-N)
- Sakamoto H, Tanaka S, Hata T (2019) Identification of vibrational signals emitted by embryos of the migratory locust *Locusta migratoria* (Orthoptera: Acrididae) that induce synchronous hatching. *Eur. J Entomol* 116:258–268. <https://doi.org/10.14411/eje.2019.030>
- Sánchez-Gracia A, Vieira FG, Rozas J (2009) Molecular evolution of the major chemosensory gene families in insects. *Heredity* (Edinb) 103:208–216. <https://doi.org/10.1038/hdy.2009.55>
- Seidemann K, Ferenz HJ (2002) Courtship inhibition pheromone in desert locusts, *Schistocerca gregaria*. *J Insect Physiol* 48:991–996. [https://doi.org/10.1016/S0022-1910\(02\)00178-6](https://doi.org/10.1016/S0022-1910(02)00178-6)
- Seidemann K, Weinert H, Ferenz HJ (2003) Wings and legs are production sites for the desert locust courtship-inhibition pheromone, phenylacetone nitrile. *J Insect Physiol* 49:1125–1133. <https://doi.org/10.1016/j.jinsphys.2003.08.005>
- Seidemann K, Warnstorff K, Ferenz HJ (2005) Phenylacetone nitrile is a male specific repellent in gregarious desert locusts, *Schistocerca gregaria*. *Chemoecology* 15:37–43. <https://doi.org/10.1007/s00049-005-0290-z>
- Sergeev MG (2011) Distribution patterns of grasshoppers and their kin in the boreal zone. *Psyche A J Entomol* 2011:1–9. <https://doi.org/10.1155/2011/324130>
- Shi WP, Njagi PGN (2004) Disruption of aggregation behaviour of oriental migratory locusts (*Locusta migratoria manilensis*) infected with *Nosema locustae*. *J Appl Entomol* 128:414–418. <https://doi.org/10.1111/j.1439-0418.2004.00865.x>
- Shi WP, Sun HL, Edward N, Yan YH (2011) Fecal volatile components elicit aggregation in the oriental migratory locust, *Locusta migratoria manilensis* (Orthoptera: Acrididae). *Insect Sci* 18:166–174. <https://doi.org/10.1111/j.1744-7917.2010.01341.x>
- Shi W, Guo Y, Xu C et al (2014) Unveiling the mechanism by which microsporidian parasites prevent locust swarm behavior. *Proc Natl Acad Sci U S A* 111:1343–1348. <https://doi.org/10.1073/pnas.1314009111>
- Song H, Mariño-Pérez R, Woller DA, Cigliano MM (2018) Evolution, diversification, and biogeography of grasshoppers (Orthoptera: Acrididae). *Insect Syst Divers* 2:1–25. <https://doi.org/10.1093/isd/ixy008>
- Song H, Béthoux O, Shin S et al (2020) Phylogenomic analysis sheds light on the evolutionary pathways towards acoustic communication in Orthoptera. *Nat Commun* 11:1–17. <https://doi.org/10.1038/s41467-020-18739-4>
- Stahr C, Seidemann K (2016) Individual pheromone signature in males: prerequisite for pheromone-mediated mate assessment in the central American locust, *Schistocerca piceifrons*. *J Chem Ecol* 42:1304–1313. <https://doi.org/10.1007/s10886-016-0793-9>
- Stahr C, Svatoš A, Seidemann K (2013) Chemical identification, emission pattern and function of male-specific pheromones released

- by a rarely swarming locust, *Schistocerca americana*. J Chem Ecol 39:15–27. <https://doi.org/10.1007/s10886-012-0233-4>
- Sugahara R, Tanaka S, Jouraku A, Shiotsuki T (2015) Functional characterization of the corazonin-encoding gene in phase polyphenism of the migratory locust, *Locusta migratoria* (Orthoptera: Acrididae). Appl Entomol Zool 51:225–232. <https://doi.org/10.1007/s13355-015-0391-2>
- Sugahara R, Tanaka S, Jouraku A, Shiotsuki T (2017) Geographic variation in RNAi sensitivity in the migratory locust. Gene 605:5–11. <https://doi.org/10.1016/j.gene.2016.12.028>
- Sugahara R, Hirota K, Sakakibara S (2021) Ovipositional inhibition effect of locust fecal extracts in the migratory locust, *Locusta migratoria* (Orthoptera: Acrididae). Appl Entomol Zool 56:199–205. <https://doi.org/10.1007/s13355-021-00725-x>
- Tabata J, Ichiki RT, Moromizato C, Mori K (2017) Sex pheromone of a coccoid insect with sexual and asexual lineages: fate of an ancestrally essential sexual signal in parthenogenetic females. J R Soc Interface 14:1–11. <https://doi.org/10.1098/rsif.2017.0027>
- Tanaka S, Sugahara R (2017) Desert locusts *Schistocerca gregaria* (Acrididae: Orthoptera) do not lay eggs in old sand: why? Appl Entomol Zool 52:635–642. <https://doi.org/10.1007/s13355-017-0518-8>
- Tanaka S, Sakamoto H, Hata T, Sugahara R (2018) Hatching synchrony is controlled by a two-step mechanism in the migratory locust *Locusta migratoria* (Acrididae: Orthoptera): roles of vibrational stimuli. J Insect Physiol 107:125–135. <https://doi.org/10.1016/j.jinsphys.2018.03.010>
- Tanaka S, Kotaki T, Nishide Y et al (2019) Effects of water extracts of frass from three locust species and various plants on oviposition and embryonic development in the desert locust, *Schistocerca gregaria*. J Orthop Res 28:195–204. <https://doi.org/10.3897/jor.28.34665>
- Torto B, Njagi PGN, Hassanali A, Amiani H (1994) Aggregation pheromone system of nymphal gregarious desert locust, *Schistocerca gregaria* (Forskål). J Chem Ecol 20:1749–1762. <https://doi.org/10.1007/BF02029546>
- Tregenza T, Buckley SH, Pritchard VL, Butlin RK (2000a) Inter- and intrapopulation effects of sex and age on epicuticular composition of meadow grasshopper, *Chorthippus parallelus*. J Chem Ecol 26:257–278. <https://doi.org/10.1023/A:1005457931869>
- Tregenza T, Pritchard VL, Butlin RK (2000b) Patterns of trait divergence between populations of the meadow grasshopper, *Chorthippus parallelus*. Evolution (NY) 54:574–585. <https://doi.org/10.1111/j.0014-3820.2000.tb00060.x>
- Wang Z, Yang P, Chen D et al (2015) Identification and functional analysis of olfactory receptor family reveal unusual characteristics of the olfactory system in the migratory locust. Cell Mol Life Sci 72:4429–4443. <https://doi.org/10.1007/s00018-015-2009-9>
- Wang X, Verschut TA, Billeter JC, Maan ME (2021) Seven questions on the chemical ecology and neurogenetics of resource-mediated speciation. Front Ecol Evol 9:1–13. <https://doi.org/10.3389/fevo.2021.640486>
- Wei J, Shao W, Wang X et al (2017) Composition and emission dynamics of migratory locust volatiles in response to changes in developmental stages and population density. Insect Sci 24:60–72. <https://doi.org/10.1111/1744-7917.12396>
- Wei J, Shao W, Cao M et al (2019) Phenylacetonitrile in locusts facilitates an antipredator defense by acting as an olfactory aposematic signal and cyanide precursor. Sci Adv 5:1–14. <https://doi.org/10.1126/sciadv.aav5495>
- Wicher D, Miazzi F (2021) Functional properties of insect olfactory receptors: ionotropic receptors and odorant receptors. Cell Tissue Res 383:7–19. <https://doi.org/10.1007/s00441-020-03363-x>
- Wu L, Yu Z, Jia Q et al (2020) Knockdown of LmCYP303A1 alters cuticular hydrocarbon profiles and increases the susceptibility to desiccation and insecticides in *Locusta migratoria*. Pestic Biochem Physiol 168:1–10. <https://doi.org/10.1016/j.pestbp.2020.104637>
- Yang Y, Krieger J, Zhang L, Breer H (2012) The olfactory co-receptor Orco from the migratory locust (*Locusta migratoria*) and the desert locust (*Schistocerca gregaria*): identification and expression pattern. Int J Biol Sci 8:159–170. <https://doi.org/10.7150/ijbs.8.159>
- You Y, Smith DP, Lv M, Zhang L (2016) A broadly tuned odorant receptor in neurons of trichoid sensilla in locust, *Locusta migratoria*. Insect Biochem Mol Biol 79:66–72. <https://doi.org/10.1016/j.ibmb.2016.10.008>
- Yu Y, Zhou S, Zhang S, Zhang L (2011) Fine structure of the sensilla and immunolocalisation of odorant binding proteins in the cerci of the migratory locust, *Locusta migratoria*. J Insect Sci 11:1–10. <https://doi.org/10.1673/031.011.5001>
- Yu Z, Zhang X, Wang Y et al (2016) LmCYP4G102: an oenocyte-specific cytochrome P450 gene required for cuticular waterproofing in the migratory locust, *Locusta migratoria*. Sci Rep 6:1–11. <https://doi.org/10.1038/srep29980>
- Yuan H, Chang H, Zhao L et al (2019) Sex- and tissue-specific transcriptome analyses and expression profiling of olfactory-related genes in *Ceracris nigricornis* Walker (Orthoptera: Acrididae). BMC Genomics 20:1–20. <https://doi.org/10.1186/s12864-019-6208-x>
- Zaim A, Petit D, Elghadraoui L (2013) Dietary diversification and variations in the number of labrum sensilla in grasshoppers: which came first? J Biosci 38:339–349. <https://doi.org/10.1007/s12038-013-9325-8>
- Zhang S, Pang B, Zhang L (2015) Novel odorant-binding proteins and their expression patterns in grasshopper, *Oedaleus asiaticus*. Biochem Biophys Res Commun 460:274–280. <https://doi.org/10.1016/j.bbrc.2015.03.024>
- Zhang XY, Zhu XQ, Gu SH et al (2017) Silencing of odorant binding protein gene AlinOBP4 by RNAi induces declining electrophysiological responses of *Adelphocoris lineolatus* to six semiochemicals. Insect Sci 24:789–797. <https://doi.org/10.1111/1744-7917.12365>
- Zhang Y, Tan Y, Zhou XR, Pang BP (2018) A whole-body transcriptome analysis and expression profiling of odorant binding protein genes in *Oedaleus infernalis*. Comp Biochem Physiol - Part D Genomics Proteomics 28:134–141. <https://doi.org/10.1016/j.cbd.2018.08.003>
- Zhou SH, Zhang J, Zhang SG, Zhang L (2008) Expression of chemosensory proteins in hairs on wings of *Locusta migratoria* (Orthoptera: Acrididae). J Appl Entomol 132:439–450. <https://doi.org/10.1111/j.1439-0418.2007.01255.x>
- Zhang L, Lecoq M, Latchinsky A, Hunter D (2019) Locust and grasshopper management. Annu Rev Entomol 64:15–34. <https://doi.org/10.1146/annurev-ento-011118-112500>
- Zhang T, Ma P, Zhou J et al (2021) Group I CDAs are responsible for a selective CHC-independent cuticular barrier in *Locusta migratoria*. Pestic Biochem Physiol 175:1–8. <https://doi.org/10.1016/j.pestbp.2021.104854>
- Zhou SH, Zhang SG, Zhang L (2009) The chemosensilla on tarsi of *Locusta migratoria* (Orthoptera: Acrididae): distribution, ultrastructure, expression of chemosensory proteins. J Morphol 270:1356–1363. <https://doi.org/10.1002/jmor.10763>
- Zhou YT, Li L, Zhou XR et al (2019) Identification and expression profiling of candidate chemosensory membrane proteins in the band-winged grasshopper, *Oedaleus asiaticus*. Comp Biochem Physiol - Part D Genomics Proteomics 30:33–44. <https://doi.org/10.1016/j.cbd.2019.02.002>