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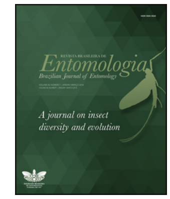

Responses of green lacewings to semiochemicals: species- and sex-specificity (Neuroptera: Chrysopidae)

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ABSTRACT

Green lacewings (Chrysopidae) are important predators in agroecosystems. Frequently there are studies which treat these beneficial insects at family level as a whole. This approach, despite its practical advantages, may, however, include many species with markedly different life history traits. As green lacewings are also rather diverse in their chemical ecology, treating several different species within one unit may lead to confusion and confounding effects of natural phenomena in research. Besides interspecific differences, sex-specificity is another important factor to consider in respect of insect chemical ecology. This is especially important for green lacewings, in particular the attraction of females, since oviposition is crucial in their application as biological control agents. The aim of our paper is to provide a brief insight into the diversity of the chemical ecology of green lacewings with a special emphasis on the species- and sex-specific differences in their responses to semiochemicals.

Introduction

Green lacewings (Chrysopidae) is a characteristic family of Neuroptera, with more than 1400 taxa described worldwide (Oswald and Machado, 2018). Chrysopid larvae are predators of many soft-bodied insects, including aphids and scale insects (Canard, 2001; Miller et al., 2004). Many Chrysopid species are present in agroecosystems, which might have a great potential for biological control of pests (Stelzl and Devetak, 1999; McEwen et al., 2001; Pappas et al., 2011). Some species are also available commercially, nevertheless, acquiring green lacewings from international sources for pest control purposes may pose the risk of introducing alien species (Henry and Wells, 2007).

Therefore, conservation biological control by the indigenous population of green lacewings may be a potential alternative (McEwen et al., 1998). For instance, attempts were made to decrease overwintering mortality of green lacewing adults (McEwen et al., 1998, 1999; Thierry et al., 2002; Weihrauch, 2008).

Another approach is application of food sprays (Tassan et al., 1979; Duelli, 1980) to the crop or sowing flower strips at field margins (Thöming and Knudsen, 2021) in order to provide food for green lacewing adults. Attraction by semiochemicals is another promising perspective; in fact, several reports are available on the attraction of green lacewings to semiochemicals (e.g. Aldrich and Zhang, 2016).

Since chrysopids are easily distinguished from other insects and due to their feeding habits all species are beneficial in respect of biological control, without any known pestiferous species, it is rather tempting to treat them at the family level as a group of beneficial insects (e.g. Lorenzetti et al., 1997; Hesler, 2016). However, despite the similarities in their life history and feeding preferences, there are considerable differences, for instance in their chemical ecology as well.

Recently a comprehensive review was published on the chemical ecology of Neuroptera (Aldrich and Zhang, 2016) and on the potentials of synthetic attractants for green lacewings (Koczor et al., 2019a). In this mini review our aim is to give an insight into the species- and sex-specific differences in the chemical ecology of Chrysopidae, with a special focus on results obtained in field experiments with semiochemical baits, where behavioral responses were recorded in comparison with respective control treatment.

Semiochemicals produced by Chrysopidae

Semiochemicals involved in intraspecific interactions are termed pheromones and those involved in interspecific interactions are termed allelochemicals (Nordlund and Lewis, 1976). Sex pheromones are the most commonly applied semiochemicals in agricultural practice

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(Witzgall et al., 2010). However, no sex pheromones have been identified in Chrysopidae so far (Aldrich and Zhang, 2016).

Zhang et al. (2004) identified (1*R*,2*S*,5*R*,8*R*)-iridodial from abdominal cuticle of male *Chrysopa oculata* Say. The compound has not been detected in females and it was only attractive to males of the species. Later on, Zhang et al. (2006a) identified the same compound from thoracic extracts of male *Chrysopa nigricornis* Burmeister, which was not found in abdominal extract of males or in extracts of females. Although the compound may be another, closely related compound instead (Jeffrey R. Aldrich, University of California, US, personal communication in Thöming et al., 2020), in field experiments male *C. nigricornis* were attracted to (1*R*,2*S*,5*R*,8*R*)-iridodial (Zhang et al., 2006a) and attraction of male *Chrysopa septempunctata* Wesmael (=*Chrysopa pallens* Rambur according to Aspöck et al. (2001)) to the compound was recorded (Zhang et al., 2006b). Although female *C. nigricornis* were not attracted to (1*R*,2*S*,5*R*,8*R*)-iridodial, Chauhan et al. (2007) reported higher abundance of females in a few meters' distance from the traps, and suggested a potential lekking behaviour during courtship of green lacewings. Since females were not attracted to the odour source, this suggests that the compound may rather have an arrestant effect for them (Dethier et al., 1960). Green lacewings are known to communicate by vibrations in the close range (Henry, 1982, 2006), nevertheless, for vibrational communication, individuals need to be on the same plant. Furthermore, to our knowledge lekking behaviour has not been reported in Chrysopidae so far, thus, other communicational mechanisms may be behind this phenomenon.

Males of *Chrysotropia ciliata* (Wesmael) were found to emit p-anisaldehyde, which also showed sex-specific activity attracting only conspecific males in field experiments (Thöming et al., 2020). The compound was only found in air entrainment samples, but not in body extracts, which only contained p-methoxybenzoic acid and methyl p-anisate, presumed precursors of p-anisaldehyde (Thöming et al., 2020).

Green lacewings are known to use defensive secretions, for instance *Chrysopa* spp. can be recognized by the strong, penetrant odour emitted when disturbed or caught (Güsten and Dettner, 1991). Defensive secretions have been found to affect potential predators (Blum et al., 1973). From the secretion of *C. oculata* skatole and 1-tridecene were identified (Blum et al., 1973), however, later on Aldrich et al. (2009) suggested that instead of 1-tridecene, (*Z*)-4-tridecene is the actual compound. Both skatole and (*Z*)-4-tridecene have been identified in several green lacewing species from different geographic regions, including *Ceraeochrysa cubana*, *Chrysopa* spp. and *Plesiochrysa ramburi* (Aldrich and Zhang, 2016; Koczor et al., 2018). On the other hand, only (*Z*)-4-tridecene has been identified from *Chrysoperla* spp. so far (Zhu et al., 2000, Aldrich and Zhang, 2016) (Table 1).

Despite the identification of skatole and (*Z*)-4-tridecene from multiple green lacewing species, reports on behavioural responses of green lacewings to these compounds are scarce. Skatole is presumed to have importance in defence against mammalian predators (Güsten and Dettner, 1991) and this compound is responsible for the characteristic, strong odour emitted upon disturbance of *Chrysopa* spp. (Blum et al., 1973; Aldrich and Zhang, 2016). Nevertheless, skatole did not elicit behavioural responses in field experiments from neither *Chrysopa formosa* Brauer, nor from *Chrysoperla carnea* species complex (Koczor et al., 2015a).

On the other hand, (*Z*)-4-tridecene strongly decreased attraction of a nearctic *Chrysoperla* species referred to as *C.* '*carnea*' (Zhu et al., 2000, possibly *C. plorabunda* (Fitch) according to Henry et al., 2001; Henry and Wells, 2007), *C. carnea* species complex and *C. formosa* (Koczor et al., 2018) to otherwise highly attractive stimuli. Bearing in mind the emission of this compound upon disturbance, these observations suggest an alarm function. Since the compound has also been identified from other chrysopids, it may possibly elicit similar behavioural responses in other species as well, serving as a rather general warning signal. Taking into account the still relatively few green lacewing species studied with respect to their chemical ecology (Aldrich and Zhang, 2016), this compound could possibly be produced by several other species. Furthermore, other similar, yet undiscovered warning semiochemicals might occur in Chrysopidae as well.

Aphid-related semiochemicals

Aphid sex pheromones are produced by sexual forms of aphids, and in many species these are combinations of enantiomers of nepetalactol and nepetalactone (Pickett et al., 2013). These compounds have been found to attract green lacewing species including *Chrysopa cognata* McLachlan (= *Chrysopa pallens* Rambur according to Aspöck et al., 2001), *Chrysopa formosa* Brauer, *C. nigricornis*, *C. oculata*, *C. pallens*, *Chrysopa septempunctata* Wesmael (= *C. pallens* according to Aspöck et al., 2001), *Nineta vittata* (Wesmael) and *Peyerimhoffina gracilis* (Schneider) (Boo et al., 1998, 1999; Hooper et al., 2002; Zhang et al., 2004, 2006a, 2006b; Weihrauch, 2005; Zhu et al., 2005; Koczor et al., 2010). Interestingly, attraction was found to be strongly sex biased as almost exclusively males were caught of the respective species. For the nearctic *C. oculata* it was suggested that these compounds might serve as exogenous precursors for iridodial production of green lacewings obtained through pharmacophagy (Aldrich et al., 2016). Nevertheless, although *Chrysopa* spp. are predatory as adults (Canard, 2001) these compounds are not produced by asexual forms of aphids (Fernández-Grandon et al., 2013) which are available as food source for adult green lacewings, therefore in that case other natural sources of these precursors might be exploited by male chrysopids.

Field experiments on stimuli with potentially different ecological roles might bring interesting results on species-specificity of behavioural responses. For instance, aphid sex pheromone components were found to be attractive to *Chrysopa* spp. such as *C. oculata* (Zhu et al., 2005) and

Table 1
Green lacewings from which skatole or (*Z*)-4-tridecene have been identified (+ present, - absent).* according to Aspöck et al. 2001, ** the species is possibly *Chrysoperla plorabunda* (Fitch) according to Henry et al. 2001; Henry and Wells, 2007.

species	(*Z*)-4-tridecene	response	skatole	response	reference
Ceraeochrysa cubana (Hagen)	+	no data	+	no data	Aldrich and Zhang (2016)
Chrysopa formosa Brauer	+	repellency	+	no response	Koczor et al. (2015a, 2018)
Chrysopa incompleta Banks	+	no data	+	no data	Aldrich and Zhang (2016)
Chrysopa nigricornis Burmeister	+	no data	+	no data	Aldrich and Zhang (2016)
Chrysopa oculata Say	+	no data	+	no data	Aldrich and Zhang (2016)
Chrysopa quadripunctata Burmeister	+	no data	+	no data	Aldrich and Zhang (2016)
Chrysopa septempunctata (=*pallens* Rambur*)	+	no data	+	no data	Aldrich and Zhang (2016)
Chrysoperla 'carnea' (=*plorabunda*? (Fitch)**)	+	repellency	-	-	Zhu et al. (2000)
Chrysoperla rufilabris (Burmeister)	+	no data	-	-	Aldrich and Zhang (2016)
Plesiochrysa ramburi (Schneider)	+	no data	+	no data	Aldrich and Zhang (2016)

C. formosa (Koczor et al., 2010, 2015a), whereas in the same experiments no attraction was found for a nearctic *Chrysoperla* '*carnea*' (Zhu et al., 2005, possibly *C. plorabunda* according to Henry et al., 2001; Henry and Wells, 2007) and for *C. carnea* complex (Koczor et al., 2010, 2015a), whereas these species were attracted to floral attractants, which did not attract the respective *Chrysopa* spp.

Surprisingly, when aphid sex pheromones were combined with a ternary floral bait, catches of *C. formosa* and *C. pallens* were unaffected, whereas, catches of *C. carnea* complex were decreased markedly (Koczor et al., 2010). Further studies confirmed that the effect on *C. carnea* complex was due to the aphid sex pheromone components (Koczor et al., 2015a).

Plant related semiochemicals

A large portion of green lacewing species are flower visitors, feeding on pollen and nectar as adults (Canard, 2001). This is also the case for *Chrysoperla* spp. which are of crucial importance in respect of biological control in agrecosystems (Pappas et al., 2011). In accordance with the feeding habits of *Chrysoperla* spp. adults, floral volatiles were suggested as attractants, such as caryophyllene (Flint et al., 1979), 2-phenylethanol (Zhu et al., 1999, 2005) and phenylacetaldehyde (Tóth et al., 2006). Furthermore, both males and females were found to be attracted (e.g. Zhu et al., 1999; Tóth et al., 2006).

Herbivore-induced plant volatiles (HIPV) are produced by plants upon feeding of herbivorous insects (Paré and Tumlinson, 1999). Among these, the compound eliciting the highest scientific interest in Chrysopid chemical ecology is methyl salicylate. The reports on responses of Chrysopidae to this compound are rather controversial; some studies report significant attraction (e.g. James, 2003; James and Price, 2004 for *C. nigricornis*), however, other studies do not confirm these findings unambiguously (e.g. Jones et al., 2011). When compared with other attractants, the compound in general elicited moderate, or no attraction, for instance in *C. plorabunda*, *C. rufilabris* (Burmeister), *C. oculata*, *C. nigricornis* (Jones et al., 2011; Salamanca et al., 2017) or in *C. carnea* complex (Tóth et al., 2009). Nevertheless, methyl salicylate showed a synergistic effect in combination with other attractive stimuli, such as phenylacetaldehyde for *C. carnea* complex (Tóth et al., 2009), 2-phenylethanol for nearctic *Chrysoperla* spp. (Jones et al., 2016) or iridodial for *C. oculata* and *C. nigricornis* (e.g. Zhang et al., 2004; Jones et al., 2011).

The combination of floral volatiles and methyl salicylate resulted in powerful attractants for males and females of *C. carnea* complex. Furthermore, these also affected oviposition site choice of females (Tóth et al., 2009; Jaastad et al., 2010; Koczor et al., 2015b). Within the *C. carnea* complex no difference was found in attraction of *C. carnea* s.str. (Stephens), *C. lucasina* (Lacroix) and *C. pallida* Henry, Brooks, Duelli & Johnson to the phenylacetaldehyde-based ternary floral bait (Koczor et al., 2015b). This combination was also found attractive to *Chrysoperla sinica* Tjeder in Asia (Deng et al., 2013).

Other semiochemicals

Acid-hydrolised tryptophan was applied on crop as food spray for green lacewings in several experiments and attraction of *Chrysoperla* spp. was also reported (e.g. Hagen et al., 1976). Nevertheless, later studies suggested that the attraction was due to bacterial breakdown products or to plant volatiles emitted in response to damage caused by the acidic spray (Harrison and McEwen, 1998).

Attraction of *C. nigricornis* males to squalene was found in field experiments conducted in Washington state (USA); however, neither *C. oculata* nor *Chrysoperla plorabunda* showed attraction to the compound, suggesting a rather species-specific response (Jones et al., 2011). The ecological background of sex-specific attraction to this compound is currently not understood. Squalene also attracted *C. formosa* males in field experiments in Hungary (Koczor et al., 2019b). Similarly to the North American results, this compound did not attract *C. carnea* complex. Addition of squalene to ternary floral baits did not affect attraction of *C. carnea* complex considerably; however, the bait combination also attracted males of *C. formosa* (Koczor et al., 2019b).

Conclusions

Despite the relatively low number of species studied, green lacewings show rather marked diversity in their chemical ecology. Sex pheromones have not been identified from chrysopids so far, however, (1*R*,2*S*,5*R*,8*R*)-iridodial and p-anisaldehyde may act as a special aggregation pheromone that is produced by males and is attractive to males. Attraction of some green lacewing species (e.g. *Chrysopa* spp.) to aphid sex pheromone components was reported; however, this attraction was also found to be highly sex-specific as these compounds were found to attract males only.

Pollen- and nectar feeding adults of *Chrysoperla* spp. were found to be attracted to floral volatiles and these semiochemicals attracted both males and females. Furthermore, combinations of these floral volatiles with other plant-related semiochemicals resulted in increased attraction. No difference was found in attraction within the *C. carnea* complex, suggesting similarities in the chemical ecology of these species.

As adults of *Chrysoperla* spp. are not predatory, multi-species lures attracting predatory *Chrysopa* adults could be advantageous from the aspect of biological control. Surprisingly, addition of aphid sex-pheromone compounds to the ternary floral bait strongly decreased the number of attracted *C. carnea* complex lacewings, which indicates a remarkable difference in chemical ecology of these chrysopids underlining the potential risks of treating Chrysopidae as one unit in research.

On the other hand, some semiochemicals might have rather universal effects. For instance (*Z*)-4-tridecene strongly decreased attraction of *Chrysoperla* spp. and *C. formosa*. Since the compound has been identified from some other species, it is possible that these would show similar behavioural responses, thus the compound could serve as a rather universal warning signal among Chrysopidae.

From the practical aspect, attraction of females may have a special benefit through manipulation of oviposition site choice, as predatory larvae would hunt for prey in the vicinity, therefore their activity could be concentrated as well. Attractants for female green lacewings are key to the development of effective oviposition attractants; however, for many species only male attractants are known. Discovery of female attractants for these species (e.g. *Chrysopa* spp.) could bring novel and important details to the chemical ecology of Chrysopidae, which could provide further important prospects to practical applications as well.

As information on the chemical ecology of at most only a few percents of green lacewing species are available, it is rather safe to assume that there is a lot to discover in the chemical ecology of Chrysopidae. Undoubtedly, these future discoveries will not only provide important contributions to our knowledge on chemical ecology of insects, but also could benefit practical applications.

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Conflicts of interest

The authors declare no conflict of interest.

Author contribution statement

All authors have contributed to and approved the manuscript.

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