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Chemical communication in spiders – a methodological review

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Abstract. Spiders use chemicals to interact with conspecifics, heterospecifics and with their environment. The focus of most past reviews on chemical communication in spiders has been on female sex pheromones (chemicals produced by females to attract or elicit courtship in males) and their biological function or chemical structure. Here, I present a methodological overview to provide suggestions for how to approach future studies on pheromone identification in spiders. This research needs more encouragement, as female sex pheromones have been described for only 11 spider species so far. Male pheromones and behavioral evidence are also presented in this work as such data have been largely overlooked in past studies, with only one male sex pheromone having been identified. Subadult females of many different families experience male cohabitation. Here it is discussed whether a subadult female pheromone or a subadult female chemical cue (unintended information understood by the receiver) may mediate this behavior. In the next section of this work, I discuss female reaction to chemical signals of conspecific females, as this interaction deserves further discourse. Chemical interactions with other species and the environment are discussed in the last section, where recent reports have extended the knowledge and pointed out types of interactions that have been overlooked in past reviews.

Keywords: Sex pheromone, chemical ecology, subadult cue, sericophily, allelochemicals

THE CHEMICAL COMMUNICATION PATHWAY

Communication generally entails a sender signaling to a receiver that then responds by changing its behavior (Wilson 1975). Spiders communicate via visual, tactile, acoustic and chemical communication channels (Huber 2005; Uhl & Elias 2011; Foelix 2015). Visual communication is insignificant in most spider taxa (Huber 2005; Foelix 2015).

Chemical communication is assumed to be the oldest channel of information conveyance (Breithaupt & Thiel 2011; Wyatt 2014). Nevertheless, the production site and emission pathway of chemical information are not known in spiders (Uhl 2013). Scattered on the legs, S-shaped hairs with a perforated tip are deemed chemoreceptors (Foelix & Chu-Wang 1973; Tichy et al. 2001; Foelix 2015; Ganske & Uhl 2018). Those hairs may be both mechano- and chemoreceptors (Foelix 2015). The transmission mode for chemical information can be either substrate-borne (contact) or air-borne (volatile) (Uhl & Elias 2011). Contact-borne chemical information requires physical contact between the emitting source and the receiver and can be, for example, on the cuticle (Prouvost et al. 1999), the silk (as silk strands (Baruffaldi & Costa 2010) or as a web (Baruffaldi & Andrade 2015)), or borne to other environmental structures such as rocks (e.g., Johnson et al. 2011). Air-borne, or volatile, chemical information does not require direct contact between the receiver and the emitter of the information. Silk or the body-cuticle of spiders may emit volatile chemical information (Schulz 2013; Fischer 2015). Interestingly, the increased surface of silk threads in webs has been argued to facilitate the evaporation (Watson 1986; Schulz & Toft 1993).

SEMIOCHEMICALS

Throughout the animal kingdom, chemical information serves functions in different contexts and can be categorized accordingly. Figure 1 presents widely used terminology (Dall et al. 2005; Wyatt 2014).

Chemical cue.—A chemical cue is defined as inadvertent information from a "sender" that elicits a behavioral response in the receiver. The response to a cue has evolved only on part of the receiver but not in the emitter (Dall et al. 2005; Wyatt 2014). For example, cues can reveal the presence of a predator and cause anti-predator behavior. The wolf spider *Pardosa milvina* (Hentz, 1844) has strongly reduced movement when exposed to chemical cues (silk and excreta) from its predator *Hogna helluo* Walckenaer, 1837 (Barnes et al. 2002). Similarly, the ant-eating spider *Habronestes bradleyi* (O. Pickard-Cambridge, 1839) (Zodariidae) uses sulcatone, an ant-alarm pheromone, to detect its prey (Clark et al. 2000). In both examples, the "emitter" of the cues did not intend to prompt the receiver's response.

Chemical signals: pheromones.—Signals, in contrast to cues, evolved on part of the sender and the receiver. Pheromones transfer information within the same species (Wyatt 2014). Pheromones, for example, can play a role in the context of foraging and orientation. Trail pheromones of ants mark and lead to profitable food sources (Hölldobler et al. 2001). Pheromones also mark territories as in lizards (Aragon et al. 2003), induce aggregation as in bark beetles (Savoie et al. 1998), or facilitate kin recognition as in mammals (Brennan & Kendrick 2006). I could not find similar pheromonal functions in spiders, as chemo-ecological research in spiders has mostly focused on mating biology (Schulz 2013). Sex pheromones of spiders that attract mating partners or elicit their courtship behavior are relatively best-studied (Uhl & Elias 2011; Schulz 2013). In general, pheromones cause a primer and/or a releaser effect. The primer effect elicits physiological changes in the receiver (Wyatt 2017). The presence of female sex pheromone which attracts adult males also accelerates maturation, instead of growth, of subadult males. Consequently, males that were exposed during their development to female pheromone are much smaller than those that were not (Kasumovic & Andrade 2006; Cory & Schneider 2017). The releaser pheromone effect, on the other hand, elicits a stereotyped behavior (Wyatt 2017). Males of many spiders show a specific

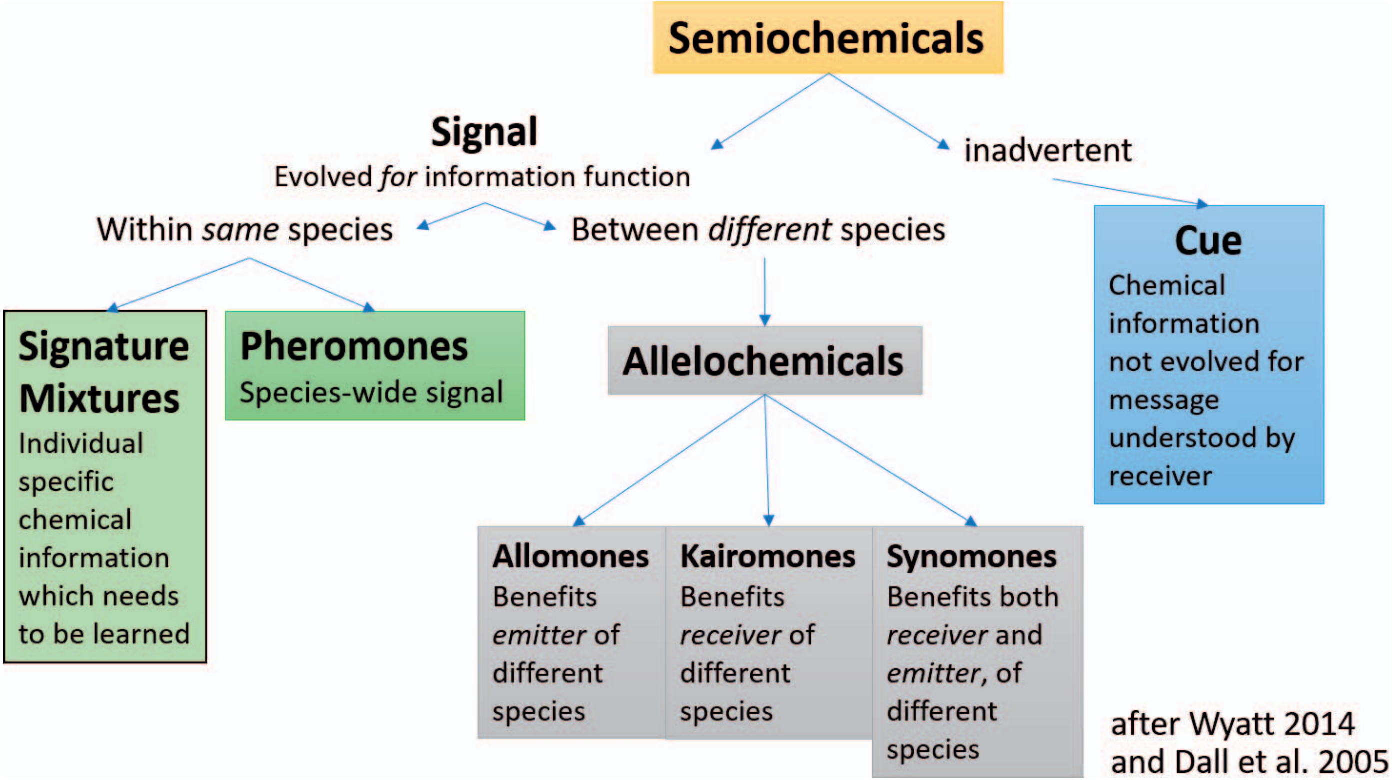

Figure 1.—Overview of terminology describing chemical communication in animals – modified after Wyatt (2014) and Dall et al. (2005).

courtship behavior when exposed to synthetic sex pheromones of conspecific females (Gaskett 2007; Uhl 2013; Wyatt 2014). In addition to pheromones, signature mixtures function as intra-specific signals. Signature mixtures are to be learned and transfer individual-specific information (Wyatt 2014). Siblings of the funnel web spider *Eratigena atrica* (C. L. Koch, 1843) (formerly *Tegenaria atrica* C. L. Koch, 1843) learn over time, based on chemical signals, to restrain from agonistic behavior (Trabalon 2013).

Allelochemicals.—Allelochemical is the umbrella term for chemicals that mediate information flow between species (Wyatt 2014). Allomones benefit the emitter species to the detriment of the receiver species. Bolas spiders (*Mastophora* sp.) attract male moths by mimicking their female sex pheromone (Eberhard 1977; Stowe et al. 1987; Gemeno et al. 2000). Kairomones benefit the receiver species to the detriment of the emitter species. The araneophagic jumping spider *Portia fimbriata* (Doleschall, 1859) preys on the salticid spider *Jacksonoides queenslandicus* Wanless, 1988, sensing its chemical signals (Jackson et al. 2002). Synomones are allelochemicals that benefit both the sender and the receiver; these are not known to occur in spiders, though more focused research may uncover such interaction. Herbivory by spider-mites triggers emission of synomones from host plants which attract phytoseiid mites that prey on spider mites. Both, the plant (sender) and the predatory mite (receiver) benefit from this communication.

Various reviews on chemical communication in spiders have been published in the last two decades (Schulz 1997, 2004, 2013; Huber 2005; Gaskett 2007; Uhl & Elias 2011;Trabalon 2013; Uhl 2013; Foelix 2015). Foelix (2015) focusses on the morphological-biological perspectives of chemical communication. Huber (2005), Uhl (2013) and Uhl & Elias (2011) focus on behavioral-biological perspectives and mostly discuss the chemicals' effect(s) on the receivers' responses. Gaskett (2007) provides a detailed overview of behavioral studies and the types of bioassays used on species with evidence for sex pheromones. Schulz (2004, 2013) focuses on the molecular structure of sex pheromones in spiders and the phylogenetic group producing them. Trabalon (2013) and Schulz (1997) discuss cuticular lipids, which function more in inter-species communication than in attraction of mates. This review is not meant to replicate past reviews. Instead, I will focus on methodological approaches of sex pheromone identification, point out pitfalls and highlight lessons to be learned from past studies. Moreover, I will present and discuss an overview of behavioral indication for the presence of male pheromones in spiders. In the third part of this review, I discuss whether subadult female spiders might have a pheromone or another chemical cue, while I argue for the latter. Reports that female spiders might interact with conspecific females based on chemical cues have not been reviewed so far; here I present an overview of this neglected chemical interaction. Allelochemicals and their function are reviewed in the last section of this work.

FEMALE SPIDER SEX PHEROMONES – A METHODOLOGICAL REVIEW

Recent female pheromones.—So far, 14 sex pheromone blends of female spiders have been identified in 11 species (Tables 1.1-1.3 in Appendix). Since the last review (Schulz

2013), the following compounds have been described: *N*-3-methyl-butanoyl-*O*-methylpropanoyl-L-serine methyl ester is the contact sex pheromone of *Latrodectus hesperus* Chamberlin & Ivie, 1935 (Scott et al. 2015b). This structure resembles closely the sex pheromone of *L. hasselti* Thorell, 1870 (Theridiidae) (Jerhot et al. 2010). In addition to this one confirmed sex pheromone, five candidate pheromone components or pheromone blends have been described: (a) butyric acid attracts males of *L. hasselti* in lab assays but not in the field (Bryan et al. 2018); (b) 6-methyl-5-hepten-2-one is considered a volatile sex pheromone of *Araneus diadematus* Clerck, 1757 (Araneidae) (Fischer 2015); (c) a blend of 17-methylnonacosane, 11-methylnonacosane, 2-methyltriacontane, 13,17-dimethylhentriacontane and 11,15-dimethylhentriacontane may serve as the contact sex pheromone of *A. diadematus*, but behavioral bioassays are yet to be run (Fischer 2015); (d) *N*-3-methylbutyryl-*O*-propionyl-L-serine methyl ester may be a contact sex pheromone of *Latrodectus geometricus* C.L. Koch, 1841 (Baruffaldi 2016) and (e) four wax-type esters were identified in lipids of female *Argyrodes elevatus* Taczanowski, 1873: 2-methylundecyl 2,8-dimethylundecanoate, 2,8-dimethylundecyl 2,8-dimethylundecanoate, heptadecyl 4-methylheptanoate, and 14-methylheptadecyl 4-methylheptanoate (Chinta et al. 2016). Bioassays to confirm that these compounds are involved in sexual communication in *Argyrodes elevatus* have yet to be performed. The similarity of contact sex pheromones among *Latrodectus* spp., Walckenaer, 1805—varying only in a methyl branch in the *O*-ester—is striking and lets one predict similar pheromone structures in other congeners.

Elements of sex pheromone identification.—Successful sex pheromone identifications rely on the origin of the analyte(s), basis of the comparison as well as the chemical analysis method. To identify a sex pheromone, one needs to collect chemical information by sampling the headspace, extracting the body surface and/or extracting the silk with solvents. These analytes consist of a complex mixture of semiochemicals. These semiochemicals have to be separated in order to be analyzed. Chromatographic methods may be used for the separation task. Once separated, structural information of each of the semiochemicals can be obtained with spectroscopic or spectrometric methods. The separated compounds can be compared with a control analyte-group to identify candidate compounds that quantitatively or qualitatively differ to the control. Candidate compounds may then be synthesized and tested for their bioactivity. Below, I discuss sources of analytes in previous spider pheromone analyses and list them in Table 2 (Appendix). Furthermore, I discuss available methods in chemoecological analysis that may be used for spider pheromone identification. Lastly, I will discuss in this section the basis of comparison that was used in previous studies to identify candidate semiochemicals.

Origin of the analyte: body headspace.—Headspace volatiles of live female spiders provided the analyte for the identification of sex pheromones in *Agelenopsis aperta* (Gertsch, 1934) (Agelenidae) (Papke et al. 2001), *Argiope bruennichi* (Scopoli, 1772) (Araneidae) (Chinta et al. 2010) and *Araneus diadematus* (Fischer 2015). Live spiders were housed singly in a small glass chamber; air was drawn through the chamber and an adsorbent. The headspace can be collected either in a closed loop system (Papke et al. 2001), in which the same air is circled in the system, or in an open loop system, (Chinta et al. 2010; Fischer 2015) in which new air is constantly drawn from the environment. Activated charcoal was used as an adsorbent in two studies; for *Agelenopsis aperta* the adsorbent was extracted with carbon disulfide (Papke et al. 2001), whereas for *Argiope bruennichi* dichloromethane was used as the solvent (Chinta et al. 2010). A chromatoprobe system (Dötterl & Jürgens 2005) was used for *Araneus diadematus* (Fischer 2015). The chromatoprobe analyte is injected into a thermosdesorption-unit that thermally desorbs the collected compounds. This heat stress, however, might destroy heat-labile semiochemicals. The collection time was eight h for *Agelenopsis aperta* (Papke et al. 2001) and *Araneus diadematus* (Fischer 2015), but unknown for the *Argiope bruennichi* study (Chinta et al. 2010). Extraction of adsorbents may lose chemical analytes due to limits of each organic solvent or due to dilution and concentration of the analyte. Another limitation is the (in)ability of adsorbents to capture compounds of different polarity. Headspace sampling is also limited by the vapor pressure of each compound and the compatibility of the adsorbent with the analyte. Coupled gas chromatography - mass spectroscopy (GC-MS) was used to identify all airborne sex pheromones.

Origin of the analyte: cuticle.—Cuticle-extracts of female *Agelenopsis aperta* (Papke et al. 2001), *Eratigena atrica* (Prouvost et al. 1999) and *Araneus diadematus* (Fischer 2015) were analyzed via GC-MS. Whole spiders were immersed in pentane for 15 min (*E. atrica*, Prouvost et al. 1999) or in dichloromethane for 3 min (*A. diadematus*, Fischer 2015) to produce the extracts. For *Agelenopsis aperta*, a spider's abdomen was wiped with filter paper, which was then extracted with dichloromethane and pentane (Papke et al. 2001).

Origin of the analyte: silk.—Most studies used silk extracts as a substrate to identify the sex pheromone. *Latrodectus hasselti* silk was extracted in methanol for 2 weeks to identify the contact sex pheromone via GC-MS and nuclear resonance spectroscopy (NMR) (Jerhot et al. 2010). *Latrodectus hesperus* silk was extracted for >24h in methanol and analyzed via GC-MS to find the contact sex pheromone (Scott et al. 2015b). GC-MS analyses of silk extract suggested also the proposed volatile sex pheromone of *L. hasselti* (Bryan et al. 2018). Silk and the cuticle of *Eratigena atrica* were extracted for 15 min with pentane and analyzed via GC-MS to find the contact sex pheromone (Prouvost et al. 1999; Trabalon et al. 2005). Dichloromethane silk extracts that were analyzed via GC-MS lead to the sex pheromones of *Argiope bruennichi* (Chinta et al. 2010), *Pholcus beijingensis* Zhu & Song, 1999 (Pholcidae) (Xiao et al. 2009), *Linyphia triangularis* (Clerck, 1757) (Linyphiidae) (Schulz & Toft 1993) and *Araneus diadematus* (Fischer 2015). The extraction time varied from 48 h for *P. beijingensis* (Xiao et al. 2009) to up to two weeks for *A. diadematus* (Fischer 2015). The silk and cuticle extracts of adult *A. diadematus* females were found to be relatively similar in their chemical composition, especially with respect to the amount of sex pheromone information (Fischer 2015), indicating that the same pheromones are present on both substrates. Thus, cuticle extracts are not superior to silk extracts, justifying the preference in past work for silk over any other substrate. I recommend for future work to use silk and headspace analysis so that no spiders need to be sacrificed. Regarding solvents used: pentane is a very non-polar solvent, suitable, for example, for cuticular hydrocarbons (CHC) and mainly long-chained lipids and fatty acids. Dichloromethane and methanol are more polar, suitable for a broader variety of mostly polar semiochemicals. Bioassays with different solvents have to be performed for each species to clarify which solvent extracts the pheromone the best.

Separation of a mixture: gas chromatography.—Two chromatographic methods are commonly used in pheromone identification: Gas Chromatography (GC) and High-Performance-Liquid-Chromatography (HPLC) (Rouessac & Rouessac 2007). Gas chromatography separates compounds primarily by differences in volatility of the different semiochemicals, by vaporizing the mixture at around 300°C. High molecular weight and strong polarity of a compound lowers its volatility. Once vaporized, the compounds travel together with the mobile phase, an inert carrier gas (e.g., He or H_2), through a heated coiled column. Interactions of the compounds with the column (stationary phase) may lead to different retentions for the different semiochemicals. The separation can be fine-tuned by using different columns. Special chiral-columns may be used to separate enantiomers. The separated compounds may be detected at the end of the column. Various different detectors are available; however, the mass spectrometric detector can be considered the most important one for structure elucidation, and will be described below (GC is reviewed in Harris (2016), including a guide for method development). GC is relatively cheap to operate, yields a greater separation efficacy and generates much less waste than HPLC (see below). As with every method, GC has its limits. The high vaporizing temperature may deteriorate some heat-sensitive semiochemicals. Some compounds react chemically in the vapor phase with each other and alter their structure. Some other compounds may not vaporize at the given temperature and remain in the injector. Strong polar groups such as hydroxyl and amine groups strongly decrease volatility, so that even some small compounds such as sugars and amino acids cannot be easily analyzed. Polar functional groups can be derivatized to create less polar groups, enabling GC analysis. The different derivatization processes are reviewed in Millar & Haynes (1998). It is not possible to give general criteria for the suitability of compounds for GC-analysis and it has been stated that roughly 10% of all compounds are suitable for GC (Rood 2007).

Separation of a mixture: HPLC.—HPLC on the other hand, does not subject compounds to heat stress, as it separates them by polarity gradients of different solvents (mobile phase) and by the interaction of the compounds with the column (stationary phase). The solvent mixture is forced through the column with high pressure. Different separation criteria can be selected by carefully choosing the mobile and stationary phases. A decision-making guide may be found in Harris (2016). HPLC can generally separate a mixture based on the polarity, electrical charge or the molecular size of the compounds (Harris 2016). A detector, such as a mass spectrometer, may be installed at the end of the column (see below). The reduction of the number of compounds in a mixture might be helpful in some cases. Via HPLC, fractions of the crude material can be produced and each fraction may then be tested for bioactivity (Jaffe et al. 1989). The weaknesses of HPLC are high operation costs, large volumes of waste solvents and poorer separation resolution compared to GC (Harris 2016).

Structure identification: mass spectrometry (MS).—MS is the most powerful detector for GC or HPLC, allowing both quantitative and qualitative analysis. GC coupled with MS (GC-MS) can detect amounts of compounds as low as 25 femtograms to 100 picograms, while HPLC coupled with MS (HPLC-MS) may detect nanogram amounts. MS is able to distinguish between compounds that overlap in their retention time for both chromatographic methods (Harris 2016). The masses of molecules and their fragments are used to obtain structural information about a compound. MS requires a gaseous species of a compound, that becomes ionized and fragmented; the resulting fragments are then accelerated. The mass-to-charge ratio allows separation of the different fragments, which then may be detected. The masses of characteristic ions provide information about the molecular mass of the compound and its structure. As a GC operates in the gaseous phase, it can be easily coupled with MS. HPLC, however, operates in the liquid phase so that the compounds have to be volatilized and the vast amount of solvent removed. The ionization and fragmentation process of HPLC-MS differs from GC-MS, leading to reduced fragmentation in HPLC-MS. Hence, it is often difficult to derive the chemical structure via HPLC-MS. Another MS may be coupled in tandem with HPLC-MS, fractionating the molecules further to gain more characteristic ions and enhancing the structural elucidation. This method is called HPLC-MS-MS (Harris 2016). In summary, a compound may be identified in GC-MS or HPLC-MS via the characteristic fragments and the characteristic retention time of the chromatographic method. However, it is often difficult to elucidate the full chemical structure of a compound based on the mass spectra. Additionally, the heat stress during the vaporization causes similar problems as in GC with heat-labile compounds. Here, nuclear magnetic resonance spectroscopy (NMR) is often employed for support (Millar & Haynes 1998).

Structure identification: nuclear magnetic resonance (NMR) spectroscopy.—NMR is a strong tool for identification of the chemical structure of an organic compound (Bruice 2016). Once an individual compound has been isolated (e.g., via HPLC), NMR can be used to clarify its structure. Nuclei such as ^{1}H or ^{13}C, with an odd number of protons, have a magnetic moment due to their ‘spin’. The spins change when exposed to an external magnetic field, and differences between the spins can be measured with NMR. The stronger the applied magnetic field, the stronger the operating frequency of the NMR and the bigger the effect—hence the sensitivity. However the biggest weakness of the NMR is that its sensitivity is 10 orders of magnitudes worse than other analytical techniques (Spengler et al. 2017) and microgram amounts of the compound are needed (Millar & Haynes 1998). Samples often have to be pooled in order to produce enough material. NMR may provide information about the chemical surrounding of the nuclei, e.g., characteristic electron-rich groups or, in the case of ^{1}H-NMR, the presence of similar nuclei in the direct vicinity. Interpretation of these spectra allows sophisticated predictions of the chemical structure. This makes NMR the standard method for structural clarification if enough material is available (Bruice 2016).

Basis for comparison.—After the analysis via GC-MS or HPLC-MS-MS, one has to identify candidate compounds out of the high number of compounds found. For insect pheromone identification, electrophysiological methods are often employed. The workhorse of pheromone identification in insects is electroantennography coupled with gas chromatography (GC-EAD) (Roelofs 1984). The compounds that have been separated by the GC are directed onto both the standard detector of the GC (e.g., MS) and over the antenna of an insect which is connected to electrodes, thus functioning as a bio-detector. By this approach the electrophysiologically active compounds are easily identified. Unfortunately, this method is not easily transferrable onto spiders, as their chemosensilla are also mechano-receptors (Foelix 2015) and hence cloak the signal in background noise. The lack of the ability to couple electrophysiological methods with GC is a major reason why only 1% of pheromone studies are related to spiders (Symonds & Elgar 2008).

The first step in pheromone identification is to know what behavioral response the pheromone elicits. *Latrodectus* males, for example, respond with web reduction behavior when exposed to virgin female silk or the synthetic pheromone (Jerhot et al. 2010; Scott et al. 2015b). In a second step, one analyzes material that does not elicit the stereotypical behavior of the sex pheromone (e.g., mated female, subadult female or subadult male silk extracts). In a third step, one compares the quantity and quality of the compounds between the bioactive and bioinactive analyte to identify candidate compounds. One exception from this pattern is the second contact sex pheromone identified in *Latrodectus*. Selective ion monitoring of a GC-MS was used by assuming that the unknown sex pheromone in *L. hesperus* had a chemical structure related to the structure of the known *L. hasselti* pheromone (Scott et al. 2015b). Another atypical approach was used in *Eratigena atrica*. Silk from receptive and non-receptive adult virgin females was used as a basis for the comparison (Prouvost et al. 1999). It remains unclear what conditions led to the non-receptivity in these adult virgin female spiders. Here I review the different basis for the comparison in past studies.

Basis for comparison: adult virgin females versus mated females.—In most studies, silk of adult virgin females was compared with silk from mated females (*Schizocosa malitiosa* Tullgren, 1905 (Baruffaldi et al. 2010); *Argiope bruennichi* (Chinta et al. 2010); *Latrodectus hasselti* (Jerhot et al. 2010); *Agelenopsis aperta* (Papke et al. 2001); *Linyphia triangularis* (Schulz & Toft 1993); *Pholcus beijingensis* (Xiao et al. 2009)), though it is not self-evident that silk from mated females lacks the sex pheromones. For example, no qualitative differences were found between extracts of silks from virgin females, mated females and adult males in *P. beijingensis* (Xiao et al. 2009).Yet, despite the qualitative presence of the candidate sex pheromone of *S. malitiosa* on silk of mated females, there is clear behavioral preference for silk of virgin females (Baruffaldi et al. 2010). As a contrasting behavioral example, mated females of *Nesticodes rufipes* (Lucas, 1846) (Theridiidae) are as attractive for males as virgin females (Molina & Christenson 2008).

Mated females are in general tentatively less attractive than adult virgin females. For males with first sperm precedence, it is a great evolutionary benefit to avoid shared paternity and discriminate among females of different mating status. Mated females of *Agelenopsis aperta* (Riechert & Singer 1995), *Pholcus phalangioides* (Fuesslin, 1775) (Schäfer & Uhl 2002), *Lycosa tarantula* (Linnaeus, 1758) (Fernández-Montraveta & Ortega 1990), *Schizocosa malitiosa* (Baruffaldi & Costa 2010; Baruffaldi et al. 2010) and *S. ocreata* (Roberts & Uetz 2005) are less attractive than virgin females. Mated *S. ocreata* females remain chemically attractive even though behaviorally monogamous (Norton & Uetz 2005). Seventy percent of *Servaea incana* (Karsch, 1878) (Salticidae) females mate only once in their lifetime, and virgin females were more frequently courted compared to mated ones (Mendez et al. 2017). Just-mated females are not attractive for males in *Latrodectus hasselti* (Stoltz et al. 2007), though they become attractive again after three months (Perampaladas et al. 2008). This information was crucial for the sex pheromone identification, to choose recently mated females as a basis for comparison with virgin females (Jerhot et al. 2010). Mated *Argiope keyserlingi* Karsch, 1878 females are not attractive to males (Gaskett et al. 2004). It remains unknown if mated *A. keyserlingi* females become attractive again as in *Latrodectus*. In order to include mated females in the differential comparison, a proper understanding of the species-specific advertisement strategies is crucial. Mated females may not differ from virgin females qualitatively, but only quantitatively in their sex pheromone titer. When samples are pooled, one needs to make sure that all the mated females are not re-advertising.

Basis for comparison: adult virgin females versus adult males.—Adult male silk was additionally compared to virgin female and mated female silk for *Agelenopsis aperta* (Papke et al. 2001) and *Pholcus beijingensis* (Xiao et al. 2009) and *Schizocosa malitiosa* (Baruffaldi et al. 2010). All three species are known for remaining attractive (at a reduced level) after mating (Riechert & Singer 1995; Schäfer & Uhl 2002; Baruffaldi & Costa 2010). For example, no candidate pheromone was found on male *S. malitiosa* silk (Baruffaldi et al. 2010). Virgin adult female silk of *Cupiennius salei* (Keyserling, 1877) (Ctenidae) was only compared with adult male silk (Papke et al. 2000). The female sex pheromone was found in reduced amounts in male *P. beijingensis* silk, though one would expect that the female sex pheromone should be qualitatively absent in male silk (Xiao et al. 2009). Virgin adult female silk, male silk, and subadult silk were compared for the contact sex pheromone of *L. geometricus*, though no further results are known (Baruffaldi 2016).

Basis for comparison: adult virgin females versus subadult females.—Subadult versus virgin adult females were solely compared for the sex pheromone of *Araneus diadematus* (Fischer 2015). Subadult female silk was additionally included to be compared with mated female silk and virgin female silk in search for the sex pheromone of *Argiope bruennichi* (Chinta et al. 2010), *Agelenopsis aperta* (Papke et al. 2001) and *Schizocosa malitiosa* (Baruffaldi et al. 2010). However, subadult females sometimes seem to be interesting for males.

Subadult females of *Schizocosa ocreata* are found to be as attractive as mated females and significantly more than a blank control (Roberts & Uetz 2005). However, subadult females of *S. malitiosa*, as well as subadult male silk are found to be unattractive (Baruffaldi & Costa 2010). Bioassays for male courtship with subadult female silk should be compared against subadult male silk, or if this is not possible against a blank control. The *S. malitiosa* study was the only one so far including subadult male silk. Whether the sex pheromone is already produced by the subadult female or it is another "subadult cue" that is received by males will be discussed in a later section. A chemical comparison of juveniles (young instars, before sex determination), just after sex determination and penultimate subadult silk should be the subject of future studies. Quantitative significant amounts of silk of younger subadults may be harder to harvest since their webs are much smaller and have thinner strands.

Effects on sex pheromones: age.—The age of the females might have a major impact on the sex pheromone concentration and needs to be considered when identifying sex pheromones. Old virgin *Argiope bruennichi* females (> 8 d after mature molt) are significantly more attractive than young ones (1 - 2 days after mature molt) (Cory & Schneider 2016). The authors argue that the sex pheromone changes quantitatively over the course of time, without testing the pheromone titer. This finding is contradicting previous reports of this species, that the sex pheromone of *A. bruennichi* peaks on day four after the female's mature molt and drops on day eight to a minimum (Chinta et al. 2010; Schulz 2013). However, the behavioral observation is consistent with other findings, as in *Schizocosa malitiosa*, where older virgin females are more attractive than recently molted or penultimate subadult females (Baruffaldi & Costa 2010, 2014; Baruffaldi et al. 2010) and *Agelenopsis aperta*, and *Latrodectus geometricus* where old virgins are more attractive than young ones (Riechert & Singer 1995; Waner et al. 2018). Chemical analysis of *S. malitiosa* silk revealed that old virgin females seem to have more of the candidate compounds than freshly molted ones (Baruffaldi et al. 2010) explaining the behavioral observation. A rise of pheromone concentration was found in *Linyphia tenuipalpis* Simon, 1884 over the course of a summer until it dropped in October (Schulz 2013). *Schizocosa ocreata* females are least attractive one week after their mature molt, after which they remain consistently highly attractive (Roberts & Uetz 2005). The silk of neither subadult females nor one week post-maturation females of *A. aperta* contains any sex pheromone (Papke et al. 2001). Females of *Neriene litigiosa* (Keyserling, 1886) do not produce any sex pheromone before seven to ten days after becoming adults (Watson 1986). The mean age after maturation for mating in *Agelena limbata* Thorell, 1897 is 8.5 days, while no mating attempt was observed within the first two days after molting (Masumoto 1991). However, higher attractiveness of the female does not necessarily lead to higher fecundity. The courtship latency decreased, and courtship intensity increased with increasing age difference between male (young) and female (old) *Pardosa pseudoannulata* (Bösenberg & Strand, 1906). The fecundity and also fitness of the offspring was not affected by the increased age of the mother (Jiang et al. 2018). In a recent study on *L. geometricus,* it was found that older females are less fecund than younger ones, though being more attractive than younger ones. No advantage for males preferring older virgins over younger ones was found. The authors argue, but did not test, that the sex pheromone titer increases with age (Waner et al. 2018). In this example it seems that the increased advertisement of older females is a dishonest signal (Johnstone & Grafen 1993) to males as males experience a higher fitness cost due to the decreased fecundity, while it seems that males gain little or no benefit. The terminal-investment hypothesis argues that, when close to death, organisms increase their investment to increase their fitness (Clutton-Brock 1984). Old virgins may emit a dishonest signal to avoid dying without offspring. Nevertheless, the tendency of increased attractiveness with age is not consistent in spiders. *Lycosa tarantula* is an example in which the attractivity decreases with age. Virgin female *L. tarantula*, which became an adult a year before the experiment, are significantly less attractive than virgin females that became adults in the same year (Fernández-Montraveta & Ortega 1990). In lepidopterans, it has been argued that in some species the pheromone titer decreases over time due to senescence and the reduction of pheromone production capability (Umbers et al. 2015). For future sex pheromone identifications, it seems practical to prefer old virgin females for the basis of comparison to increase pheromonal concentration. However, bioassays for each species have to show if an age effect is present and which age is the most attractive.

Effects on sex pheromones: diet.—The diet of a female might affect her sex pheromone production. Starved (4 weeks) *Latrodectus hesperus* females, for example, are avoided by conspecific males (Baruffaldi & Andrade 2015). However, no feeding-status discrimination was found by males of *L. hasselti*. An explanation might be that males in *L. hesperus* try to avoid pre-copulatory sexual cannibalism. In contrast, *L. hasselti* males somersault their bodies onto female fangs during mating and sexual cannibalism during and after mating is part of the sexual behavior in the species (Baruffaldi & Andrade 2015). The pheromone of *Latrodectus hesperus* females seem to act as an honest signal about their feeding status, which allows conspecific males to avoid starved females. This honest signal provides a double cost for *L. hesperus,* as they remain unmated and lose the opportunity for a meal. Based on the life history of *L. hasselti* however, it seems that males do not pay attention to the signal. Nevertheless, given that *L. hasselti* is monogynous, one would predict male choosiness and, hence, avoidance of starved females that indicate their poor state. Male *Argiope trifasciata* (Forsskål, 1775) prefer mates from a more distant population when exposed to only crickets as prey, whereas with a natural (field condition) feeding regime, mates of the same population are preferred (Henneken et al. 2015). The diet also affects the chemical composition of web-borne semiochemicals in *A. trifasciata*, and males prefer females that experienced a similar diet (Henneken et al. 2015). *Evarcha culicivora* Wesolowska & Jackson, 2003, a jumping spider preferring mosquitoes that have recently fed on blood (Jackson et al. 2005), also prefer mates that recently fed on blood-fed mosquitoes based on olfactory cues (Cross et al. 2009; Jackson & Cross 2015). Jumping spiders rely mostly on visual cues to find mating partners (Foelix 2015). However, the presence of a volatile sex pheromone in the genus *Cyrba* Simon, 1876 was shown in a recent study (Cerveira & Jackson 2013). This raises the question whether a blood-indicating cue may be a part of the sex pheromone of *E. culicivora* perceived via pharmacophagy (Henneken et al. 2017b). Nevertheless, it can be recommended to provide standardized regular food for the spiders when identifying sex pheromones of generalist feeding spiders.

Summary.—Only very few female sex pheromones have been identified in spiders. It seems that the chemical structure does not vary greatly within one genus, as we have learned from the identified contact sex pheromone in linyphiid spiders. It is also sufficient to use only silk as the origin of the analyte. Silk is readily accessible without the sacrifice of spiders. The same contact and volatile sex pheromones can be identified from the silk as good as from cuticle extracts as one report states. Different solvents have been used in the past, particularly non-polar pentane or more polar dichloromethane or methanol. Bioassays of different solvents prior to analysis remain crucial for each test species. If possible, different analytical tools like GC-MS and HPLC-MS-MS and if necessary, NMR, should be employed to increase the likelihood of identifying the sex pheromone. For the basis of comparison, it is recommended to choose more than two comparison-sources, such as virgin female, subadult female, subadult male, and mated female silk. Bioassays must show clear differences in male response between the comparison sources. A proper understanding of the attractiveness of each female's life stage based on bioassays remains important. If supported by bioassay data, old virgin adult females should be preferred over young ones for pheromone analyses because the age of the spider seems to affect the sex pheromone. Starving may decrease the ability to produce a complete pheromone in females. Therefore, I recommend including only well-fed spiders with a standardized diet for pheromone research.

MALE PHEROMONES

Only one male sex pheromone has been identified so far, though the presence of other various male pheromones is known. Male spider pheromones are known to have different functions that are discussed here. Mating can be a time and energy consuming activity. Both can be saved by an aphrodisiac pheromone, increasing the female's acceptance. By decreasing the female's attractiveness, on the other hand, it is advantageous for males to reduce mating competition with other males, where such pheromones act as an anti-aphrodisiac on females. Inducing catalepsy in females is an advantage of males in species with a high sex cannibalism rate. The reduction of female aggression increases the fitness of a male by avoiding sex cannibalism and being able to mate again.

Male pheromones as aphrodisiacs.—The only identified male sex pheromone is (*Z*)-9-tricosene in *Pholcus beijingensis* (Xiao et al. 2010). This alkene is argued to function as an aphrodisiac for females, by initiating mating much quicker. (*Z*)-9-tricosene is also found on many other spiders and insects and hence may simply provide a cue of a living organism (Stefan Schulz pers. communication). (*Z*)-9-tricosene was identified via GC-MS. Dichloromethane-body surface extracts of adult males, subadult males, and receptive virgin females obtained by extracting for 24 h (Xiao et al. 2010) showed presence of (*Z*)-9-tricosene only in males. A form of electroantennography (EAG) was used in addition to behavioral assays to test candidate compounds (Xiao et al. 2010). The tarsus of the first leg pair was placed between two electrodes and candidate substances were air-puffed on it. Bio-detection was indicated by recorded electrophysiological responses (Xiao et al. 2010). Electrophysiology in spiders was pioneered by Tichy et al. (2001) and may enhance identification of semiochemicals in future studies in spiders, as it does in insects (Roelofs 1984).

Other, unidentified, male aphrodisiac pheromones are suggested in the literature. Females of the wolf spider, *Allocosa* sp. Banks, 1900 are attracted to male burrows by olfactory signals (Aisenberg et al. 2010). This spider is sex-role-reversed, so that females search for males (Aisenberg et al. 2010). Female *Pardosa milvina* (Lycosidae) invest in silk advertisement when exposed to the silk of courting males (Havrilak et al. 2015). The presence of a male pheromone has not been shown in this spider. Silk of courting *P. milvina* males has significantly more attachment discs than non-courting silk (Khan & Persons 2015), so the physical properties of the silk may serve as a signal instead of chemical pheromones; further investigation is required. Courting males of *Latrodectus* and linyphiid spiders cut large parts of the female's web and add their own silk (Watson 1986; Scott et al. 2012). Web reduction by courting males leads to a reduced latency until copulation in *L. hesperus*. It is argued that these males deposit pheromones onto the web along with their silk. These contact male pheromones are suggested to function as an aphrodisiac for the female (Scott et al. 2012). *Latrodectus hesperus* females show courtship behavior on vacant male webs (Ross & Smith 1979). This was not found in *L. revivensis* Shulov, 1948 (Anava & Lubin 1993).

Male pheromones as anti-aphrodisiacs.—Decreasing the attractiveness of the mating partner increases the chances for exclusive fatherhood. Web-reduction behavior has been shown to thwart the female's sex pheromone transmission in linyphiid spiders (Watson 1986). The emission of the volatile female sex pheromone is dramatically reduced by clumping the female web silk strands together. The reduction of the evaporation surface is argued to decrease emission and hence, the function of the volatile female sex pheromone (Watson 1986; Schulz & Toft 1993). However, another explanation would be the presence of a male pheromone on the male silk, which is then added to the female's reduced web (Scott et al. 2015a). The male pheromone may either mask the female sex pheromone, or directly indicate male presence to other males, which discourages them from being attracted.

Mated females are less attractive to males than virgins (Baruffaldi & Costa 2010) as reviewed in a previous section. For *Schizocosa malitiosa* (Lycosidae), it was shown that females remain highly receptive if no sperm is transferred during mating (Aisenberg & Costa 2005). Male sperm fluid might cause physiological changes in the female forcing her to lose her ability to advertise (Aisenberg & Costa 2005). An anti-aphrodisiac sperm fluid could be a primer pheromone (Wyatt 2017) of the male, which has been reviewed for other taxa (Gillott 2003; Peso et al. 2015). It remains unclear for this spider whether non-hormonal changes, which are not male- but fertilization-induced, cause the decreased advertisement.

Catalepsy-inducing pheromones.—Catalepsy-inducing pheromones are another category of male pheromones. Silk-borne male pheromones in *Schizocosa ocreata* cause decreased movement in conspecific males, and concentrated methanol extracts of such male silk cause freezing in conspecific males (Ayyagari & Tietjen 1986).

Catalepsy-inducing pheromones are not only utilized for intra-sexual mating competition, but also in inter-sexual interaction. Sexual cannibalism is a prevalent phenomenon in spiders and costly for males (Elgar 1991; Wise 2006). Reports of male-induced long-lasting female catalepsy during their courtship are rare in the literature. Females of the funnel web spider, *Agelenopsis* Giebel, 1869, fall into a catalepsy when approached by a conspecific male (Gering 1953). This male pheromone is volatile (Singer et al. 2000) and the catalepsy is induced at a distance of 3 cm (Becker et al. 2005). The male's palpal drumming is argued to direct the pheromone to the female, indicating a weak volatile character of the compounds (Becker et al. 2005). A similar report occurs for the funnel web spider, *Hololena curta* (McCook, 1894). However, here, physical contact of the male with the female induces female catalepsy (Xiao et al. 2015). Further investigation is required to test if female-catalepsy inducing pheromones are a more prevalent cannibalism-avoidance tactic.

Aggression reducing pheromones.—Female aggression reduction is another potential effect of male pheromones that decreases the risk of cannibalism for males. Web-reduction behavior is linked to decreased female aggression towards courting males in *L. hesperus* (Scott et al. 2012). There is no cause-and-effect evidence to show that it is male-released chemicals that elicit this behavior. The male's vibratory signals are an essential part of courtship (Barth 2001; Vibert et al. 2014) and may be responsible for eliciting the female response.

The "bridal veil" is another male tactic that causes decreased female aggression. Males deposit silk on the female's body, a so-called bridal veil, as part of their courtship (Bristowe 1958). This silk may function as a pheromone porter, as this behavior has been linked to inhibition of female aggression (Aisenberg et al. 2008). The bridal veil is found in various spider species: *Schizocosa malitiosa* (Aisenberg et al. 2008), *Homalonychus theologus* Chamberlin, 1924 (Domínguez & Jiménez 2005), *Cupiennius coccineus* F. O. Pickard- Cambridge, 1901 (Schmitt 1992), *Ancylometes bogotensis* (Keyserling, 1877) (Merrett 1988), *Dictyna volucripes* Keyserling, 1881 (Starr 1988), *Nephila pilipes* (Fabricius, 1793) (Zhang et al. 2011) but not in *N. clavipes* (Linnaeus, 1767) (Farr 1977), *Caerostris darwini* Kunter & Agnarsson, 2010 (Gregoric et al. 2016), *Xysticus cristatus* (Clerck, 1757) (Bristowe 1958), *Latrodectus hesperus* (Ross & Smith 1979), *L. tredecimguttatus* (Rossi, 1790) (Kullmann & Stern 1981), *L. mactans* (Fabricius, 1775) (Breene & Sweet 1985) and *L. geometricus* (Knoflach 2004). However, a problematic study attempted to untangle tactile and chemical cues of the bridal veil of *N. pilipes* (Zhang et al. 2011). To test for chemical mediation, females had their chemo-receptors destroyed with a $ZnSO_4$ solution, although the success of the treatment for destruction of the chemoreceptors was not shown. These were compared to a control group of females that received neither this treatment nor a sham-treatment. It was found that chemical cues of the bridal veil silk did not calm the female but tactile cues did.

Summary.—Many male pheromones with different functions are indicated by behavioral data. Only one male pheromone, an aphrodisiac of *Pholcus beijingensis*, has been identified (Xiao et al. 2010). Direct evidence that male chemicals cause the male and the female response is found in only two studies: silk extracts of male silk of *Schizocosa ocreata* cause the catalepsis-response in conspecific males (Ayyagari & Tietjen 1986) and volatiles emitted by living males elicit the catalepsy response in *Agelenopsis aperta* females (Becker et al. 2005). The rest of the studies presented only suggest the presence of a male pheromone. The low amount of silk produced by a male makes it hard to identify silk pheromones. I suggest to use an electrically driven reeling machine (Work & Emerson 1982; Papke et al. 2000; Tichy et al. 2001) to harvest male silk and also to provide males with female pheromone during collection. The collected silk has to be tested for bioactivity, as the forcible reeling of the silk may cause stress on the male and might effect the deposition of semiochemicals onto the silk (Schulz 2001). However, one female sex pheromone has been identified by using reeled silk (Papke et al. 2000; Tichy et al. 2001).

SUBADULT CUE

In this section, I will discuss whether subadult females are detectable by males, and if so, if this is by a cue or a pheromone. Cues can be understood by the receiver, though unintended by the emitter. A pheromone, in contrast, is intended by the emitter to transfer information to the receiver within one species. I will argue to support the hypothesis of a subadult cue rather than a subadult-pheromone and suggest further research to clarify this debate.

Males in species with first male sperm precedence increase their fitness by detecting virgin females, or subadult females that are about to molt. A few studies linked species with first male sperm precedence and male cohabitation with subadult females (Jackson 1986; Miller & Miller 1986; Watson 1990, 1991; Anava & Lubin 1993; Dodson & Beck 1993; Eberhard et al. 1993; Miyashita & Hayashi 1996; Fahey & Elgar 1997; Segev et al. 2003; Bel-Venner & Venner 2006). The cohabitation of males with subadult females is a prevalent mating tactic in spiders (Jackson 1986). There are 161 species in 74 genera and 15 families linked with this behavior, including both cursorial spiders (100 species) and web-building spiders (71 species).

Male mating tactics involving subadult females.—Cohabitation with subadult females has been observed in the wasp spider *Argiope bruennichi*, and the authors state that no sex pheromone production by subadults has been observed (Uhl et al. 2015). Males cohabit with 44% of penultimate females in the field. In a lab experiment, it has been shown that 80% of guarding males would mate while the females are molting. With this behavior, males increase their survival chances from 20% (conventional mating) to 97% (Uhl et al. 2015). No sex pheromone is found to be produced by subadult female *A. bruennichi* (Chinta et al. 2010). Whether penultimate females produce sex pheromones remains unclear, since the chemoecological study did not specify the life stage of the subadult females. A similar report on *Nephila clavata* L. Koch, 1878 shows the same male mating tactic of exploiting the female's vulnerable state after molting (Miyashita & Hayashi 1996).

The authors demonstrate the presence of a volatile chemical cue elicited by any molting spider of that species, including subadult males, subadult females and adult virgin females. Adult males are attracted to this freshly-molted-cue and showed mating behavior to the immobile spider of any sex or stage. The cue is argued to derive from the molting fluid and allows males to locate mating partners with reduced risk of sexual cannibalism.

In lycosid spiders, penultimate female silk has been reported to be attractive for males of *Schizocosa ocreata* and *S. malitiosa* (Roberts & Uetz 2005; Baruffaldi & Costa 2010). However, *S. malitiosa* male response was similar when exposed to subadult male silk (Baruffaldi & Costa 2010). Chemicals were assumed to mediate this behavior, though silk extracts were not tested; physical properties of the silk may have provided information to the males. The sexual response of adult males in *S. malitiosa* and *N. clavata* towards subadult males indicate that the adult males pick up a cue rather than a signal that has evolved from their mating partner.

Another mating tactic of males avoiding sexual cannibalism associated with subadult females is found in *Latrodectus hasselti*. Adult *L. hasselti* males find final-instar subadult females, chew open the cuticle above the epigyne and mate (Biaggio et al. 2016). Males mate with 35% of penultimate *L. hasselti* in the field, or are found guarding 21% of the final-instar subadult females (Biaggio et al. 2016). Males avoid sex cannibalism when mating with subadults, compared to mating with a virgin adult female (Andrade 1996; Biaggio et al. 2016), though if a subadult female does not have developed spermatheca, the male also runs the risk of being cannibalized (Andrade 1996; Biaggio et al. 2016).

Summary.—Considering these findings, I argue in favor of a subadult cue instead of a subadult female pheromone. Males increase their fitness by detecting penultimate females. However, it seems that males of many species are not able to differentiate the sex of the subadult (Baruffaldi & Costa 2010), especially in regard to the freshly-molted-cue (Miyashita & Hayashi 1996). Females experience costs as kleptoparasitism due to cohabitating males (Watson 1990; Erez et al. 2005) or reduced chance for sexual cannibalism of their mating partner (Miyashita & Hayashi 1996; Uhl et al. 2015; Biaggio et al. 2016). Given the lack of benefit for the female of emitting information about her vulnerable state, and the benefit to the male of finding such a mating partner, I argue for a subadult cue rather than a signal from the subadult female. This argument is supported by the poor ability of the male to obtain information of the sex of the subadult individual. Identification of subadult female cues should be subject of future studies.

FEMALE-FEMALE-DETECTION IN SPIDERS

The question whether females can detect and react to sex pheromones of conspecific females has not been addressed in spiders. In insects, female-female interaction has been known for several decades and was explored in a variety of different studies (Palanaswamy & Seabrook 1978, 1985; Otter et al. 1996; Groot et al. 2005; Gökçe et al. 2007; Lim & Greenfield 2007; Lim et al. 2007; Yang et al. 2009; Harari et al. 2011; Harari & Steinitz 2013). Con-gender sex pheromone detection is suggested to induce spacing among the individuals (Otter et al. 1996), or generate intrasexual competition among females for males (Lim & Greenfield 2007), or decrease intrasexual competition by stretching the calling time window (Palanaswamy & Seabrook 1985; Gökçe et al. 2007; Yang et al. 2009). Those effects may also play a role in spiders, which has not been explored so far.

Sericophily: silk-based female-female interaction.—Female spiders can detect and react to conspecific (Dor et al. 2008), congeneric (Vetter & Rust 2010) and heterospecific (Salomon 2007) females. Spiders are often attracted to cues from the silk of conspecifics, a phenomenon known as *sericophily* (Hodge & Storfer-Isser 1997; Vetter & Rust 2008; Bell & Roberts 2017). Though there is debate whether this preference is due to (i) structural-support (Vetter & Rust 2010), or (ii) con-/hetero-specific-as-cue for environmental quality (Salomon 2009). The (i) structural-support hypothesis limits the silk cue to its physical properties and argues silk might function as an attachment for own web construction (Hodge & Storfer-Isser 1997; Pruitt et al. 2009). For example, female *Loxosceles* sp. Heineken & Lowe, 1832 prefer congeneric refugia of females over heterospecific refugia (Vetter & Rust 2008). Extracts of refugia silk with various solvents were not preferred (Vetter & Rust 2010). Washed silk was not presented to the spiders in this study. It remains open if chemically inactivated silk will still elicit the same preference. Sericophily in *Loxosceles* seem to be mediated by the physical properties of congeneric silk (Vetter & Rust 2008, 2010)

An example for the conspecific-as-cue hypothesis, female tarantulas *Brachypelma vagans* (Ausserer, 1875) prefer conspecific burrows based on chemical cues (Dor et al. 2008). Burrows with their own silk were approached significantly more quickly, though they spent more time in burrows with conspecific silk while neglecting a control burrow. Silk extracts of conspecific webs were also preferred by *B. vagans,* indicating chemical mediation (Dor et al. 2008). *Brachypelma vagans* cannibalizes conspecific females, explaining the preference for conspecific burrows (Henaut & Manchkour-M'Rabet 2005). Another example is the different life stages of females of *Coelotes terrestris* (Wider, 1834) that prefer webs and web extracts of their own life-stage (virgin females, incubating females (mated, with egg sac), parental female (mated, with spiderlings), and dispersing young) (Trabalon & Assi-Bessekon 2008). Differences in cuticular hydrocarbons between the different life stages were found and argued to mediate this behavior (Trabalon & Assi-Bessekon 2008), though physical properties of the silk also might have served as a cue for *C. terrestris*. To gain a better understanding whether sericophily is mostly mediated by chemical cues or physical cues, washed silk should be presented as an additional choice in future studies.

Sericophily and interaction of females, without testing either the structural support hypothesis or the chemical-cue hypothesis, was presented in other studies (Elgar 1994; Hodge & Uetz 1996; Hodge & Storfer-Isser 1997; Salomon 2007, 2009; Pruitt et al. 2009; McCrate & Uetz 2010; Salomon et al. 2010). Female *Latrodectus hesperus* build denser webs in presence of conspecific females and heterospecifics *Eratigena agrestis* (Walckenaer, 1802) and *E. atrica* (C. L. Koch, 1843) (Salomon 2007). Female *L. hesperus* are also more hesitant to leave a microhabitat regardless of their feeding state (Salomon 2009), and facultative group-living of two to eight females in fall/early winter is described (Salomon et al. 2010). Female *L. hesperus* share bigger webs and tolerate each other, though they forage individually. In spring and summer, these females switch to a solitary state. The identified female sex pheromone (Scott et al. 2015b) may mediate this behavior by decreased production in autumn, as is found in linyphiids (Schulz & Toft 1993), and increasing again in spring, which may induce solitary behavior; however, this hypothesis has yet to be tested. Competition for males in the summer might explain the switch from the group-living to the solitary state. That competition for prey induces this behavior is less likely, as it has been shown that group-living increases prey-capture rates compared to a solitary lifestyle (Hodge & Uetz 1996; Pruitt et al. 2009). However, virgin females of *L. revivensis* react aggressively or avoid conspecific adult and final-instar subadult female silk (Anava & Lubin 1993).

Non-silk based female-female detection.—Whether olfactory cues are involved in conspecific female-female detection was tested in three studies (Cerveira & Jackson 2013; Fischer 2015; Penfold et al. 2016). Virgin females of *Araneus diadematus* avoided olfactory cues of the body of live conspecific virgin females and preferred cues from penultimate subadults in a dual-choice-olfactometer (Fischer 2015). The relative size of the treatment spiders and the test spider did not influence the decision. Virgin females also avoided the proposed female sex pheromone sulcatone (Fischer 2015). Female spiders may react to the conspecific female sex pheromones, though sulcatone has not been verified as the female sex pheromone. Both sexes of *Cyrba* (Salticidae) were presented with olfactory cues of the body of live spiders of both sexes. Males preferred virgin female cues, while females did not prefer either sex (Cerveira & Jackson 2013). Female *Morebilus plagusius* (Walckenaer, 1837) (Trochanteriidae) significantly preferred the unscented control, avoiding conspecific chemical cues in dual choice experiments between a microhabitat with conspecific female scent (without silk) and a control habitat (Penfold et al. 2016).

The ability to detect the presence and discriminate the mating status of other conspecific females may be beneficial when competing for males. To my understanding, no studies have been conducted to approach the question of female-female interaction with the focus on mating competition.

Mother-offspring interaction.—Chemical changes of the cuticular hydrocarbons (CHC) of spiderlings seem to mediate agonistic/tolerant behavior in mothers (Trabalon et al. 1996; Trabalon & Assi-Bessekon 2008; Grinsted et al. 2012; Guimarães et al. 2016). Gregarious *Coelotes terrestris* discriminate between their own mother's web and a non-related mother's web, while dispersing spiderlings do not discriminate between the webs (Trabalon & Assi-Bessekon 2008). *Latrodectus geometricus* mothers do not discriminate between their own or conspecific egg sacs (Guimarães et al. 2016). Non-related mothers adopt gregarious spiderlings up to 20 days of age in *Eratigena atrica* (Trabalon et al. 1996) and *Chikunia* Yoshida, 2009 spiders (Grinsted et al. 2012), while up to an age of 40 days in *L. geometricus* (Guimarães et al. 2016). This may be an open door for brood parasites, though the only known brood parasites prey on unprotected eggs (Boulton & Polis 2002). All *E. atrica* spiderlings older than 40 days were killed by their mothers within four days (Trabalon et al. 1996). In *L. geometricus* the threshold for agonistic behavior is 80 days of age (Guimarães et al. 2016). The CHC-profile of the spiderlings changes with the age as GC-MS analyses showed (Trabalon et al. 1996; Guimarães et al. 2016). As the spiderlings aged, their CHC-profile became more disimilar to that of their mother (Guimarães et al. 2016), as shown in Fig. 2.

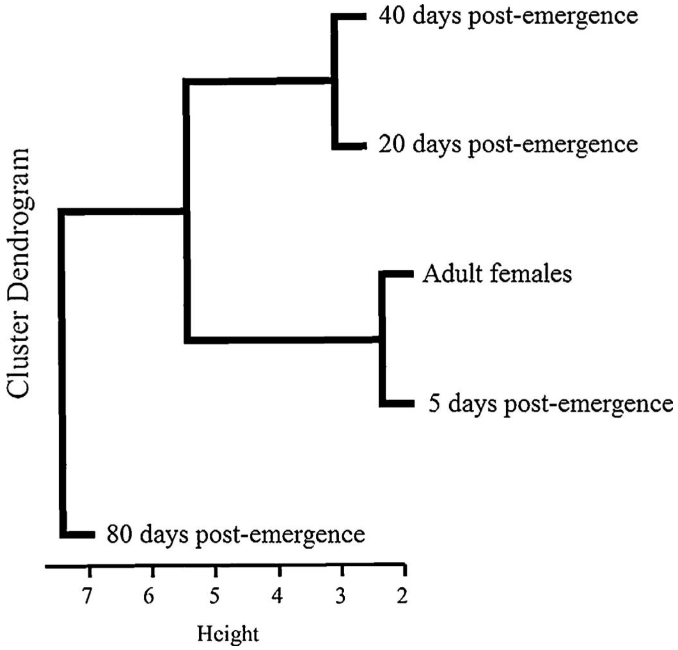

Figure 2.—Similarity Dendrogram of juveniles and adult female *Latrodectus geometricus* based on GC-MS data. Cophenetic Correlation Coefficient = 0.90 (Guimarães et al. 2016).

Summary.—Female spiders detect conspecific females; however, more studies using chemical information mediating female-female interaction need to be done to understand its role. One aspect of future studies should be whether females respond to the female sex pheromone of their species and if this mediates the observed female-female interactions. Olfactory cues emitted by live females transfer information to conspecifics in an orb-weaving spider, but not for a salticid (Cerveira & Jackson 2013; Fischer 2015). Spiderlings can discriminate their mother's web from non-related mothers, while mothers are neither able to discriminate their own egg-sac nor their own gregarious spiderlings. CHC changes may mediate the kin recognition. Besides CHC, other non-polar cuticle compounds might be involved in these interactions, as cuticular chemistry of spiders is much more diverse than of insects (Stefan Schulz pers. communication). Female reaction to their conspecific female sex pheromone is suggested to be explored in future studies, as well as whether this reaction plays a role in intra-gender mating competition.

ALLELOCHEMICALS AND ENVIRONMENTAL CUES

Allelochemicals are semiochemicals that are not used in intra-species communication (Wyatt 2014) (see Fig. 1). Kairomones, allomones and environmental cues that are used in chemical communication in spiders are reviewed in this section. Table 3 (Appendix) shows the overview of allelochemicals used by spiders.

Kairomones in spiders: predator cues.—Kairomones are chemical information that benefits the receiver, who is of another species than the emitter. The wolf spider *Pardosa milvina* (prey) is preyed upon by the larger wolf spider *Hogna helluo* (predator) (Persons & Rypstra 2001). Female *P. milvina* (prey) detect their predator by chemical cues from silk, excreta (Barnes et al. 2002) and the olfactory cues from the body of *H. helluo* (Schonewolf et al. 2006). The age of these cue residuals, as well as the hunger state and relative size of the predator is understood by the prey species *P. milvina* (Barnes et al. 2002; Bell et al. 2006). Predator-avoidance behavior may also change maternal chemical information (Persons & Lynam 2004; Li & Jackson 2005). *Pardosa milvina* spiderlings stay longer on the back of their mother when exposed to cues of early instar *H. helluo* (Persons & Lynam 2004). In a similar system, courting *Rabidosa punctulata* (Hentz, 1844) males experience a higher predation pressure due to *Rabidosa rabida* (Walckenaer, 1837) compared to non-courting ones (Wilgers et al. 2014). In the presence of *R. rabida* (predator) silk, male *R. punctulata* skipped the courtship altogether and tried to mount females directly (Wilgers et al. 2014). *Scytodes pallida* Doleschall, 1859 reduce the incubation time when cues of their salticid predator *Portia labiata* (Thorell, 1887) are present (Li & Jackson 2005), particularly, when *P. labiata* (predator) was recently fed with *Scytodes* (prey) rather than with house flies (Li & Jackson 2005).

A cuticle-contact mediated kairomonal interaction is found between the kleptoparasitic and araneophagic *Neospintharus trigonum* (Hentz, 1850) and its host *Frontinella* F. O. Pickard-Cambridge, 1902, as the prey retreats on contact with its predator (Suter et al. 1989).

More general predator avoidance is found in the ant-spider interaction. *Phylloneta impressa* (L. Koch, 1881) (Theridiidae) has an 80% increase in web-based dispersal when exposed to *Lasius niger* Linnaeus, 1758 (Formicidae) cues, and *Xysticus* C. L. Koch, 1835 (Thomisidae) doubles its dispersal rate and increases walking activity when exposed to *Formica clara* Forel, 1886 (Formicidae) cues (Mestre et al. 2014). The flat rock spiders *Morebilus plagusius* avoid chemical cues of the ant *Polyrachis sokolova* Forel, 1902 when choosing a new habitat (Penfold et al. 2016). This ant avoidance response in various spider taxa is potentially mediated by general ant cues informing the spiders of the presence of potential danger.

Kairomones in spiders: prey cues.—Kairomones are used not only to avoid predation, but also to find prey (Schulz 2004; Uhl 2013). *Evarcha culicivora* (Salticidae) is specialized on mosquito prey (Jackson & Cross 2015); it detects *Anopheles* Meigen, 1818 (Culicidae) based on olfactory cues, and prefers recently blood-fed mosquitoes (Jackson et al. 2005). The ability to smell its prey's feeding status helps to identify the prey quality. Surprisingly, increased attractiveness to mating partners is experienced by *E. culicivora* that fed recently on blood-fed mosquitoes (Cross et al. 2009). This prey-detection is learned, as primed *E. culicivora* use selective olfactory attention to find their prey (Jackson & Cross 2015). *Lantana camara* (Verbenaceae) is a preferred host plant for *Anopheles* (Cross et al. 2009). Mosquito-primed spiders have more difficulty in discriminating prey cues in a *Lantana*-odor-masked environment (Cross & Jackson 2010). However, *E. culicivora* is also attracted to the *Lantana* volatiles (*E*)-β-caryophyllene, α-humulene and 1,8-cineole (Nelson et al. 2012). Olfactory prey detection also mediates venom usage in the wandering spider *Cupiennius salei* (Hostettler & Nentwig 2006). Male *Xysticus ferox* (Hentz, 1847) crab spiders and scavenging flies (Diptera: Milichiidae and Chloropidae) are attracted to (*E*)-2-decenal and (*E*)-2-octenal, the defensive chemicals of true bugs (Heteroptera) (Aldrich & Barros 1995). It remains undetermined if males are attracted to find prey, or if these aldehydes are part of the female sex pheromone of *X. ferox*. The microhabitat choice of *Latrodectus hesperus* (Theridiidae) is directed by chemical prey cues from crickets (Johnson et al. 2011). *Agelenopsis aperta* detect olfactory cues of freshly killed flies (Riechert 1985).

Highly specialized predators also use kairomones to find their prey (Allan et al. 1996; Clark et al. 2000; Jackson et al. 2002; Henaut & Manchkour-M'Rabet 2005; Cárdenas et al. 2012). The cannibalistic tarantula *Brachypelma vagans* is known to feed on conspecifics (Henaut & Manchkour-M'Rabet 2005) by finding their burrows via chemical cues (Dor et al. 2008). The araneophagic jumping spider *Portia fimbriata* uses chemical cues to identify its prey *Jacksonoides queenslandicus* (Jackson et al. 2002). *Habronestes bradleyi* uses the ant-alarm pheromone sulcatone to detect its ant prey (Allan et al. 1996). The same alarm-pheromone is also exploited by the salticid *Naphrys pulex* (Hentz, 1846) to find their ant-prey (Clark et al. 2000). *Zodarion rubidum* Simon, 1914 (Zodariidae) is attracted by decyl acetate and undecane, compounds extracted from the gaster and Dufour's gland of three different formicine ants (Cárdenas et al. 2012). These compounds may function as an ant pheromone, hence it reduces the movement of the ant (Cárdenas et al. 2012).

Allomones in spiders: prey attraction.—Allomones are chemical signals beneficial to the sender and disadvantageous to the receiver (Wyatt 2014). *Mastophora* (Araneidae) hunt by chemically attracting their insect prey (reviewed in Uhl (2013)). Wing vibrations of prey cause female *Mastophora* to produce a droplet on a silk strand (bolas) and hit their prey with it (Haynes et al. 2001). It is not the bolas that attracts the prey (Stowe et al. 1987). Males and young females do not hunt with bolas, but sit and wait with lifted front legs, ready to attack (Yeargan 1994). Juvenile *Mastophora* attract psychodid flies as their prey (Yeargan & Quate 1996), while older females hunt for moths (Eberhard 1977). This co-evolution of two completely different kairomone systems in different life stages of the spider is poorly understood. It is known, however, that *Mastophora* attract their diverse prey by emitting only common components of the sex pheromone of their prey (Stowe et al. 1995). *Mastophora cornigera* (Hentz, 1850) e.g., attracts up to 19 different moth species, and up to nine moth species were found in one individual spider's diet (Stowe et al. 1995). Different prey species are attracted in their activity time window, providing the spider with different species throughout their activity time (Haynes et al. 2002). Furthermore *M. hutchinsoni* Gertsch, 1955 consistently produces two different blends of allomones to attract two different moth species. It seems that the compounds of each blend do not interfere with the other blend and hence increase the effectiveness of the chemical mimicry (Haynes et al. 1996). Lepidopteran pheromones are categorized according to their structure into Type I, which makes up 75% and Type II that makes up 15% of lepidopteran pheromones (Ando et al. 2004). The two blends found in *M. hutchinsoni* consist respectively of the common Type I and rare Type II.

Allomones in spiders: predator avoidance.—The silk-borne ant deterrent 2-pyrrolidinone was found on webs of *Nephila antipodiana* (Walckenaer, 1841) (Zhang et al. 2012). Younger instars did not produce this compound, but larger instars, with webs that can support a potential ant invasion, did contain this alkaloid in increased amounts (Zhang et al. 2012). 2-pyrrolidinone is reported to be found on silk of *Araneus diadematus* (Schildknecht et al. 1972), where it is thought to function as a hygroscopic compound in glue droplets of orb-weaving spiders (Sahni et al. 2011). I found this compound on webs of adult theridiid *Steatoda grossa* C.L. Koch 1838 (unpublished data). It is likely that 2-pyrrolidinone is a widespread silk-borne compound and hence a general spider cue for ants, rather than a specialized deterring signal of spiders.

Allomones in spiders: unknown compounds.—Besides these examples, a few literature indications for allomones are known. The strongly reduced webs of *Phoroncidia studo* Levi, 1964 (Theridiidae) exclusively attract male *Bradysia* (Sciaridae, Diptera) (Eberhard 1981). The orb-weaver genus *Kaira* O. Pickard-Cambridge, 1889 is said to attract male moths into a basket formed by their legs (Levi 1993). Putrescine, a silk-borne semiochemical, may function as a prey-attracting allomone in the orb-weaver *Argiope keyserlingi,* as webs with artificially increased amount of putrescine attract more dipteran prey than control webs (Henneken et al. 2017a). Putrescine is regarded as a protein cue, thus an attractant and oviposition cue for various Diptera (Kendra et al. 1989; Easton & Feir 1991). Interestingly, pest management traps for fruit flies are baited with putrescine (Heath et al. 2004).

(*Z*)-9-octadecenyl is reported on linyphiid webs (Schulz 2013) and is an aggregation pheromone for *Drosophila tesacae* (Jaenike et al. 1992). (*Z*)-9-octadecenyl is also part of the male marker pheromone of *Bombus* (Apidae) that attracts females to mating sites (Appelgren et al. 1991).

Allomones in spiders: sex pheromones.—Sex pheromones of spiders are suggested to have a prey-attracting function (Schulz 2013). The volatile female sex pheromone (8-methyl-2-nonanone) of *Agelenopsis aperta* (Papke et al. 2001) is found to be an efficient attractant for the mosquito *Culex pipiens* Linnaeus, 1758 (Ikeshoji & Mulla 1974). The major component of the female sex pheromone of *P. beijingensis*, farnesyl acetate (Xiao et al. 2009) is also part of the female sex pheromone of the coleopteran *Agriotes ustuatus, A. proximus* and *Synaptus filiformis* (Yatsynin et al. 1996). Sulcatone, the proposed volatile female sex pheromone of *Araneus diadematus* (Fischer 2015) is described as attracting different taxa such as the Diptera *Anopheles gambiae* (Meijerink et al. 2000), the cattle flies *Musca autumnalis*, *Haematobia irritans*, *Hydrotaea irritans*, *Stomoxys calcitrans*, *Wohlfahrtia magnifica* (Birkett et al. 2004) and *Atherigona soccata* (Padmaja et al. 2010). Sulcatone is a primary terpene-degradation product, thus widespread in nature. The mere presence of potential prey attracting compounds is nevertheless only a suggestion for a potential allomone function. Insect attraction tests with synthetic semiochemicals in the web-borne concentrations are suggested for future studies.

Allomones in spiders: web-decorations.—Web-decorations of decaying matter are also associated with prey-attracting allomones (Henneken et al. 2017a). Prey is attracted by odors produced by a yeast that grows on previously fed-upon flies in the webs of *Mallos gregalis* (Simon, 1909) (Dictynidae) (Tietjen et al. 1987). Fresh decaying plant and food decorations in the web of the golden orb-weavers *Nephila edulis* (Labillardière, 1799) are found to attract sheep blow flies (Bjorkman-Chiswell et al. 2004). Web decorations of the closely related *N. clavipes* attract saprophagous insects (Hénaut et al. 2010). Whether decaying web decorations always function as allomone-producers remains undetermined, as well as whether certain yeast genera always produce these allomones.

Allomones in spiders: camouflage.—Many social parasites are chemically camouflaged by mimicking the cuticular hydrocarbons (CHC) of their host; a few spider species have evolved to parasitize ants (Cushing 1997). *Sicariomorpha maschwitzi* (Oonopidae) behaviorally and chemically (CHC mediated) mimic their host, *Leptogenys distinguenda* (Formicidae) (Witte et al. 2009). The ant larvae-eating salticid *Cosmophasis bitaeniata* (Keyserling, 1882) is chemically disguised as a major worker of their host, the weaver ant *Oecophylla smaragdina* (Formicidae) (Allan et al. 2002). The CHC profile of *C. bitaeniata* mimics that of a minor worker of *O. smaragdina* on a colony specific level which allows the spider to have access to the ant larvae (Elgar & Allan 2006).

Environmental cues.—A chemical cue is defined as inadvertent information from a "sender" that elicits a behavioral response in the receiver (Wyatt 2014). Chemical cues that help spiders to gain information on their environment are discussed here. The nursery web spider *Pisaura mirabilis* (Clerck, 1757) hunts on plants and is found to be attracted to leaves and leaf extracts but repelled by common floral scents as β-caryophyllene and nerolidol (Junker et al. 2011). The crab spider *Thomisus spectabilis* Doleschall, 1859 prefers olfactory cues from host plants of their prey *Apis mellifera* (Heiling et al. 2004). Various *Thomisus* sp. Walckenaer, 1805 are attracted by eugenol (Krell & Krämer 1998). However, another crab spider, *Misumena vatia* (Clerck, 1757), does not discriminate chemical cues from potential host plants (Junker et al. 2011). General phytochemicals, such as eugenol, limonene, isoamyl acetate and heptanol, are not found to influence recluse spiders *Loxosceles laeta* (Nicolet, 1849) (Calbiague et al. 2017). Nicotine, a phytochemical of *Nicotiana* plants, is found to repel wolf spiders (Kumar et al. 2014). Hornworm larvae fed on *Nicotania* are approached by wolf spiders—though abandoned after near field contact—while non-*Nicotania* fed larvae are preyed on by the wolf spiders (Kumar et al. 2014). Folklore reports chestnuts as a generalist repellent for spiders (Kishore & Chaudhary 2014). Chestnuts and mint oil repel *Latrodectus geometricus* (Theridiidae) and *Araneus diadematus* (Araneidae). *Steatoda grossa* (Theridiidae) did not respond to mint oil but seem to avoid chestnuts. Lemon oil was not preferred over a control by *L. geometricus, S. grossa* and *A. diadematus* (Fischer et al. 2018).

Summary.—Spiders react to chemicals from their environment. Predator indication and avoidance are a common application of kairomones and allomones (Uhl 2013). The chemical structure of these semiochemicals is only occasionally known. How commonly prey-pheromones are used to identify potential prey or predators is understudied. Spider sex pheromones have been suggested to have an allelochemical function, though no direct evidence has been shown. Decaying matter as web decoration produces allomones, and one study indicated a yeast-spider symbiosis responsible for this effect (Tietjen et al. 1987). Spiders also detect and react to phytochemicals as environmental cues, which may result in pest-control management applications. A stronger chemo-ecological focus in future studies will help to understand such complex interactions better and help to estimate the ecological impact and role of spiders.

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APPENDICES

Table 1.1.—Chemical structures of identified female spider sex pheromones of the species *Linyphia triangularis, L. tenuipalpis, L. montana, Argiope bruennichi*, *A. blenda*, *A. argentata, Agelenopsis aperta*, *Cupiennius salei* and *Pholcus beijingensis*.

Table 1.2.—Chemical structures of identified female spider sex pheromones of *Latrodectus hasselti*, *L. geometricus* and *L. hesperus*. Boxes indicate structural differences among the contact sex pheromones.

Table 1.3.—Chemical structures of identified female spider sex pheromones of *Eratigena atrica* and the proposed sex pheromone of *Araneus diadematus*.

Table 2.—Overview of the methodological approach for identification of female sex pheromones.

Table 3.—Overview of allelochemicals in spiders.

Table 1.1.—Chemical structures of identified female spider sex pheromones of the species *Linyphia triangularis, L. tenuipalpis, L. montana, Argiope bruennichi*, *A. blenda*, *A. argentata, Agelenopsis aperta*, *Cupiennius salei* and *Pholcus beijingensis*.

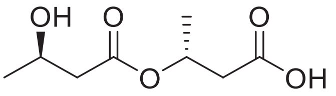
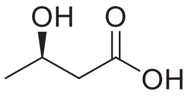
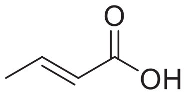
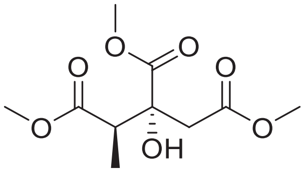
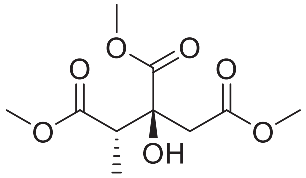
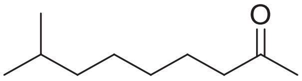
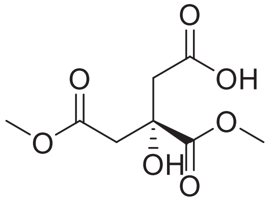
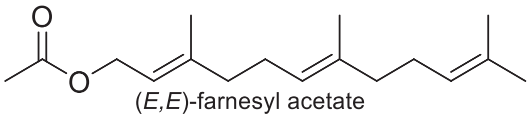
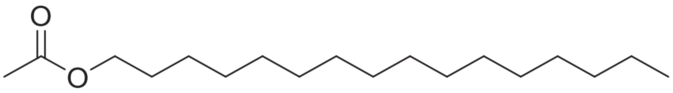
Species and pheromone type	Structure	Reference
Linyphia triangularis, *L. tenuipalpis,* *L. montana,* Contact and volatile sex pheromone	 (*R*)-3-[(*R*)-3-hydroxybutyryloxy]-butyric acid contact breaks down to:  2x (*R*)-3-hydroxybutyric acid contact + volatile  Crotonic acid	Schulz & Toft 1993 Schulz 2013
Argiope bruennichi, *A. blenda, A. argentata* Contact and volatile sex pheromone	 2*R*,3*R* trimethyl methyl citrate 1:6  2*S*,3*S* trimethyl methyl citrate	Chinta et al. 2010 Schulz 2013
Agelenopsis aperta volatile and contact sex pheromone	 8-methyl-2-nonanone	Papke et al. 2001
Cupiennius salei contact sex pheromone	 *S*-dimethyl citrate	Papke et al. 2000
Pholcus beijingensis volatile sex pheromone	 (*E,E*)-farnesyl acetate 2:1  hexadeyl acetate	Xiao et al. 2009

Table 1.2.—Chemical structures of identified female spider sex pheromones of *Latrodectus hasselti*, *L. geometricus* and *L. hesperus*. Boxes indicate structural differences among the contact sex pheromones.

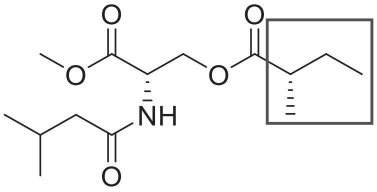
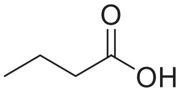
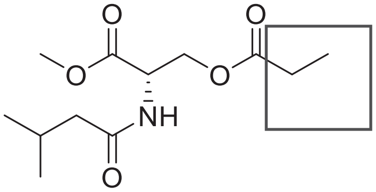
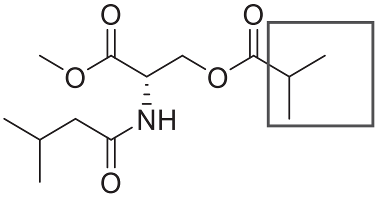
Species and pheromone type	Structure	Reference
Latrodectus hasselti Australian redback Contact sex pheromone	 *N*-3-methylbutyryl-*O*-(*S*)-2-methylbutyryl-L-serine	Jerhot et al. 2010
Latrodectus hasselti Proposed volatile sex pheromone	 Butyric acid	Bryan et al. 2018
Latrodectus geometricus Brown Widow contact sex pheromone	 *N*-3-methylbutyryl-*O*-propionyl-L-serine-methyl ester	Baruffaldi 2016, PhD Thesis
Latrodectus hesperus Western Black Widow contact sex pheromone	 *N*-3-Methyl-butanoyl-*O*-methylpropanoyl-L-serine-methyl ester	Scott et al. 2015

Table 1.3.—Chemical structures of identified female spider sex pheromones of *Eratigena atrica* and the proposed sex pheromone of *Araneus diadematus*.

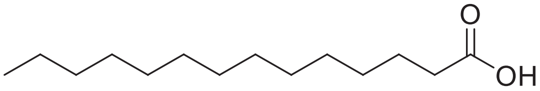
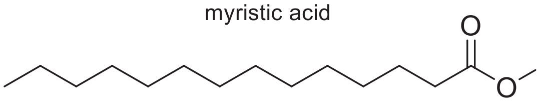
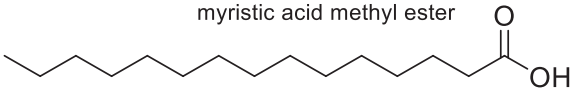
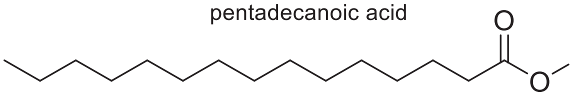
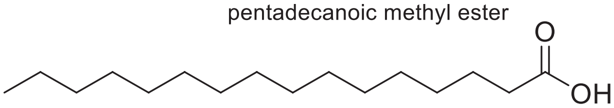
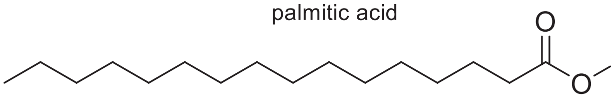
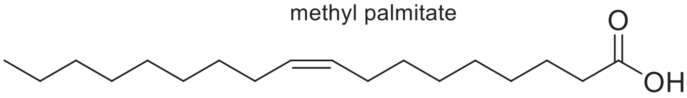
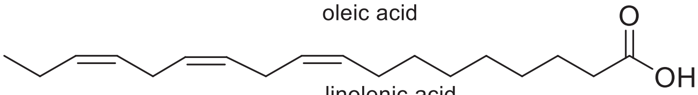
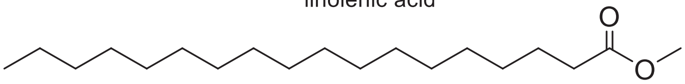
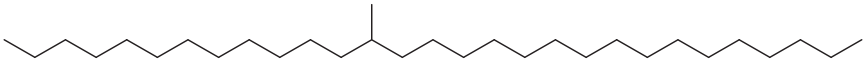
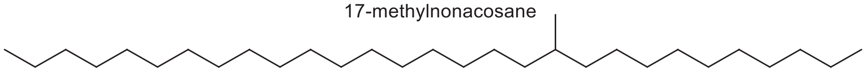
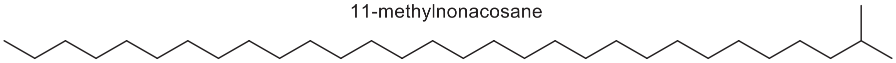
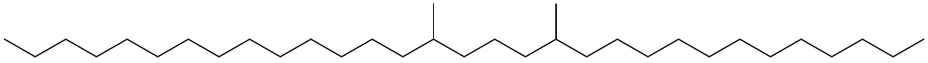
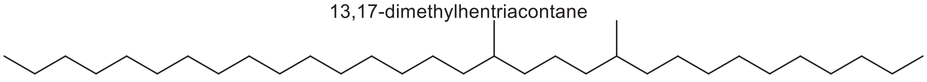
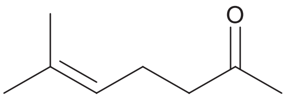
Species and pheromone	Structure	Reference
Eratigena atrica Contact sex pheromone	 myristic acid  myristic acid methyl ester  pentadecanoic acid  pentadecanoic methyl ester  palmitic acid  methyl palmitate  oleic acid  linolenic acid  methyl stearate	Prouvost et al. 1999 Trabalon et al. 2005
Araneus diadematus Proposed contact and volatile sex pheromone	 17-methylnonacosane  11-methylnonacosane  2-methyl-triacontane  13,17-dimethylhentriacontane  11,15-dimethylhentriacontane  Sulcatone	Fischer 2015

Table 2.—Overview of the methodological approach for identification of female sex pheromones.

Species and pheromone type	Analyzing method	Solvent extraction time	Origin of analyte	Basis for comparison	Reference
Linyphia triangularis *L. triangularis* (*L. montana*) Contact and volatile sex pheromone	GC-MS + enantiomere selective GC	Dichloromethane ? time	Silk extract	virgin ♀ mated ♀	Schulz & Toft 1993
Argiope bruennichi contact and volatile sex pheromone	GC-MS enantiomere selective GC	Dichloromethane ? time	Body headspace Silk extract	virgin ♀ subadult ♀ mated ♀	Chinta et al. 2010
Agelenopsis aperta volatile and contact sex pheromone	GC-MS	Headspace adsorbent: charcoal closed loop for 8h headspace: CS2 Body wipe solvent: DCM/pentane	Body headspace closed loop body wipe	subadult ♀ young virgin ♀ old virgin ♀ mated ♀ adult ♂	Papke et al. 2001
Cupiennius salei contact sex pheromone	NMR	Methanol ? time	Silk extract	virgin ♀ ♂	Papke et al. 2000
Pholcus beijingensis volatile sex pheromone	GC-MS	Dichloromethane 48h	Silk extract	virgin ♀ mated ♀ adult ♂	Xiao et al. 2009
Latrodectus hasselti contact sex pheromone	GC-MS + MSTFA derivatisation NMR	Methanol 2 weeks	silk	virgin ♀ mated ♀	Jerhot et al. 2010
Latrodectus hasselti volatile sex pheromone	GC-MS	Methanol ? time	silk	?	Bryan et al. 2018
Latrodectus geometricus contact sex pheromone	GC-MS NMR	Methanol ? time	silk	virgin ♀ subadult ♀ adult ♂	Baruffaldi 2016
Latrodectus hesperus contact sex pheromone	GC-MS	Methanol > 24h	silk	virgin (selective ion monitoring)	Scott et al. 2015
Eratigena atrica Contact sex pheromone	GC-MS + silica catridges	Pentane 15min	Silk extract Cuticle extract	virgin ♀ virgin ♀	Prouvost et al. 1999 Trabalon et al. 2005
Araneus diadematus proposed volatile and contact sex pheromone	GC-MS	chromatoprobe Dichloromethane 3 min	Headspace Cuticle extract Silk extract	virgin ♀ vs. subadult ♀	Fischer 2015

Table 3.—Overview of allelochemicals in spiders.

Spider species	Allelomone	Cue function	Semiochemical
Brachypelma vagans (Theraphosidae)	Kairomone	prey localization	unknown
Cupiennius salei (Ctenidae)	Kairomone	prey localization; venom adjustment	unknown
Pardosa milvina (Lycosidae)	Kairomone	predator avoidance; increased brood care	unknown
Scytodes pallida (Scytodidae)	Kairomone	predator avoidance; reduced incubation	unknown
Portia fimbriata (Salticidae)	Kairomone	prey localization	unknown
Naphrys pulex (Salticidae)	Kairomone	prey localization	Sulcatone
Evarcha culicivora (Salticidae)	Kairomone	prey localization	unknown
		habitat choice	(*E*)-β-caryophyllene, α-humulene and 1,8-cineole
Xysticus sp. (Thomisidae)	Kairomone	predator avoidance	unknown
Xysticus ferox (Thomisidae)	Kairomone	prey localization	(*E*)-2-decenal (*E*)-2-octenal
Thomisus spectabilis (Thomisidae)	Kairomone	habitat choice	unknown
Thomisus sp. (Thomisidae)	Kairomone	habitat choice	Eugenol
Zodarion rubidium (Zodariidae)	Kairomone	prey localization	Decyl acetate Undecane
Habronestes bradleyi (Zodariidae)	Kairomone	prey localization	Sulcatone
Latrodectus hesperus (Theridiidae)	Kairomone	microhabitat choice	unknown
Phylloneta impressa (Theridiidae)	Kairomone	predator avoidance	unknown
Phoroncidia studo (Theridiidae)	Allomone	*?prey attraction?*	unknown
Agelenopsis aperta (Agelenidae)	Kairomone	Prey localization	unknown
	?*Allomone*?	?*prey attraction*?	8-methyl-2-nonanone
Argiope keyserlingi (Araneidae)	Allomone	*?prey attraction?*	Putrescine
Mastophora hutchinsoni (Araneidae)	Allomone	prey attraction	(*Z*)9-tetradecenyl acetate (*Z,E*)-9,12-tetradecenyl- acetate 6*S*,7*R*-epoxy-3*Z*,9*Z*-heneicosene 3*Z*,6*Z*,9*Z*-heineicosene unknown
Mastophora phrynosoma (Araneidae)	Allomone	prey attraction	unknown
Mastophora bisaccata (Araneidae)	Allomone	prey attraction	unknown
Mastophora cornigera (Araneidae)	Allomone	prey attraction	(*Z*)-9 tetradecenyl acetate (*Z*)-9-tetradecanal (*Z*)-11-hexadecanal
Kaira sp. (Araneidae)	*?Allomone?*	?*prey attraction*?	unknown
Araneus diadematus (Araneidae)	?*Allomone*?	?*prey attraction*?	Sulcatone
Nephila edulis (Araneidae)	?*Allomone*?	?*prey attraction*?	unknown
Nephila clavipes (Araneidae)	?*Allomone*?	?*prey attraction*?	unknown
Nephila antipodiana (Araneidae)	Allomone	Predator deterrent	2-pyrrolidinone
Mallos gregalis (Dictynidae)	?*Allomone*?	?*prey attraction*?	unknown

Table 3.—Extended.

Cue source	Disadvantaged species	Reference
silk (extract)	*Brachypelma vagans* (Araneae:Theraphosidae)	(Dor et al. 2008 ; Henaut & Manchkour-M'Rabet 2005)
volatile body cue	*Nauphoeta* cinereal (Blattodae:Blaberidae) *Acheta domesticus* (Orthoptera:Gryllidae)	(Hostettler & Nentwig 2006)
excreta, silk, volatile body cues	*Hogna helluo* (Araneae:Lycosidae)	(Barnes et al. 2002 ; Bell et al. 2006 ; Persons & Rypstra 2001 ; Persons & Lynam 2004 ; Schonewolf et al. 2006)
volatile body cues	*Portia labiata* (Araneae:Salticidae)	(Li & Jackson 2005)
volatile body cue	*Jacksonoides queenslandicus* (Araneae:Salticidae)	(Jackson et al. 2002)
alarm pheromone	*Monomorium antarctium* (Hymenoptera:Formicidae)	(Clark et al. 2000)
		Cited as *Habrocestum pulex*
volatile body cue	*Anopheles gambiae* (Diptera:Culicidae)	(Jackson et al. 2005; Cross & Jackson 2010)
plant volatiles	*Lantana camara* (Lamiales:Verbenaceae)	(Nelson et al. 2012)
volatile body cue	*Formica clara* (Hymenoptera:Formicidae)	(Mestre et al. 2014)
defensive cues of true bugs	Hemiptera and Diptera: Milichiidae and Chloropidae	(Aldrich & Barros 1995)
volatile plant cue	*Chryanthemum frutescens* (Asterales:Asteraceae)	(Heiling et al. 2004)
volatile plant cue	unspecified	(Krell & Krämer 1998)
Dafour's gland gaster extract	*Formica rufibarbis,* (Hymenoptera:Formicidae)	(Cárdenas et al. 2012)
alarm pheromone	*Iridomyrmes purpureus* (Hymenoptera:Formicidae)	(Allan et al. 1996)
undescribed cues	*Acheta domesticus* (Orthoptera:Gryllidae)	(Johnson et al. 2011)
volatile body cues	*Lasius niger* (Hymenoptera:Formicidae)	(Mestre et al. 2014)
volatile web cue	♂ Bradysia (Diptera:Sciaridae)	(Eberhard 1981)
volatile body cue (dead prey)	"Flies" (Diptera)	(Riechert 1985)
web cue	*Culex pipiens* (Diptera:Culicidae)	(Ikeshoji & Mulla 1974; Papke et al. 2001)
volatile web cue	Diptera (general) (Diptera:Tephritidae)	(Henneken et al. 2017b)
volatile body and web	♂ *Lacinipolia renigera* (Lepidoptera:Noctuidae)	(Gemeno et al. 2000)
		Type I pheromone
Volatile body and web	♂ *Tetanolita mynesalis* (Lepidoptera:Noctuidae)	(Haynes et al. 1996)
		Type II pheromone
volatile body (juvenile)	*Psychoda trinodulosa* (Diptera:Psychodidae)	(Yeargan & Quate 1996)
volatile body (juvenile)	*Psychoda phalaenoides* (Diptera:Psychodidae)	
volatile body (juvenile)	*Psychoda satchelli, P. phalaenoides* (Diptera:Psychodidae)	
volatile body	♂ *Peridroma saucia* ♂ *Pseudaletia unipuncta* ♂ *Leucania phragmatidicola* ♂ *Scotogramma trifolii* ♂ *Heliothis phloxiphaga* ♂ *Euxoa messoria* ♂ *Euxoa olivia* (Lepidoptera:Noctuidae) ♂ *Plutella xylostella* (Lepidoptera:Plutellidae)	(Stowe et al. 1987)
volatile web cue	"moths" (Lepidoptera)	(Levi 1993)
volatile web cue	*Anopheles gambiae* (Diptera:Culicidae) *Musca autumnalis, Haematobia irritans, Hydrotaea irritans, Stomoxys calcitrans, Wohlfahrtia magnifica* *Atherigona soccata* (Diptera:Muscidae) *Platypus mutatus* (Coleoptera:Platypodidae) *Aphis fabae* (Hemiptera:Aphidoidae) *Mastrus ridibundus* *Aphidus ervi* (Hymenoptera:Ichneumonidae)	(Fischer 2015) (Meijerink et al. 2000) (Birkett et al. 2004) (Padmaja et al. 2010) (Audino et al. 2005) (Webster et al. 2008) (Jumean et al. 2005) (Du et al. 1998)
decaying web decoration	*Lucilia cuprina* (Diptera:Calliphoridae)	(Bjorkman-Chiswell et al. 2004)
decaying web decoration	Diptera:Phoridae, Sciaridae Coleoptera:Staphylinidae, Elateridae	(Hénaut et al. 2010)
web	*Monomorium pharaonic* (Hymenoptera:Formicidae)	(Zhang et al. 2012)
yeast in decaying web decoration	Diptera:Muscoidea	(Tietjen et al. 1987)

Table 3.—Continued.

Spider species	Allelomone	Cue function	Semiochemical
Linyphia sp. (Linyphiidae)	*?Allomone?*	?*prey attraction*?	(*Z*)-9-octadecenyl acetate
Frontinella pyramitela (Linyphiidae)	Kairomone	predator avoidance	unknown
Pholcus beijingensis (Pholcidae)	?*Allomone*?	?*prey attraction*?	(*E*,*E*)-farnesyl acetate

Table 3.—Continued, Extended.

Cue source	Disadvantaged species	Reference
web cue	*Cerconota anonella* (Lepidoptera:Oecophoridae)	(Schulz 2013)
	Drosophila testacea (Diptera: Drosophilidae)	(Pires et al. 2016)
	Bombus veteranus, B. muscorum (Hymenoptera:Apidae)	(Jaenike et al. 1992)
		(Appelgren et al. 1991)
contact	*Argyrodes trigonum* (Araneae:Theridiidae)	(Suter et al. 1989)
web cue	*Agriotes ustuatus, A. proximus, Synaptus filiformis* (Coleoptera:Elateridae)	(Xiao et al. 2009)
		(Yatsynin et al. 1996)