Control of *Dermanyssus gallinae* (De Geer 1778) and other mites with volatile organic compounds, a review

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Abstract

*Dermanyssus gallinae* (De Geer 1778), commonly named the poultry red mite (PRM), is considered to be the most harmful ectoparasite in poultry farms in Europe. This species feeds on the blood of laying hens, but spends most of its time hidden in cracks and crevices around hen nests. To control PRM populations in poultry houses, chemical pesticides are currently used; however, concern is growing regarding the harmful residues found in eggs and hens, along with the increased resistance of mites against several compounds. Alternatives to synthetic compounds are now being explored, including vaccines, biological control, physical control and semiochemical control based on the chemical ecology of PRM. This review focused on the different volatile organic compounds (VOCs) identified from *D. gallinae* and other mite species that have been discovered to control them. Pheromones (aggregation pheromone, sex pheromone and alarm pheromone) and kairomones promoting attraction behaviour in *D. gallinae* and other mite species are presented, while VOCs from essential oils and plant extracts with repellent properties are also explored. Finally, devices using VOCs on PRM in the field are described, with devices that have been tested on other Acari species being mentioned as potential directions for the future control of PRM.

Introduction

The poultry red mite (PRM) *Dermanyssus gallinae* (De Geer 1778) is considered to be the most harmful ectoparasite in poultry farms in Europe (Höglund et al., 1995; Sparagano et al., 2014). Individuals mainly feed on the blood of laying hens and wild birds at night (Kirkwood, 1968), and remain hidden the rest of the time in dark places (e.g. crevices and cracks around hen nests), where they can survive for up to 9 months without feeding (Chauve, 1998; Nordenfors et al., 1999). PRM can also accidentally infest mammals, including horses, dogs and even humans (Ramsay et al., 1975; Mignon and Losson, 2008; George et al., 2015). The occurrence of *D. gallinae* negatively impacts the general health of hens and the quality of their eggs (i.e. blood marks on the shells of eggs), which leads to significant economic losses in the hen egg laying industry (Chauve, 1998; Kilpinen et al., 2005). In particular, PRM parasitism causes skin irritation, anaemia, vascular problems and, even, the death of the host (Chauve, 1998; Cosoroaba, 2001; Kilpinen et al., 2005).

At present, PRM in egg laying units is mainly controlled by using different chemical acaricides. However, the repeated use of chemical acaricides is responsible for the presence of residues in eggs and meat (with a potential impact on Public Health), and is associated with the emergence of PRM resistance to different acaricides, as reported in several European countries (Zeman and Zelezny, 1985; Beugnet et al., 1997; Marangi et al., 2009; Sparagano et al., 2009, 2014). This issue is exacerbated when chemical acaricides are used illegally (off-label), as recently demonstrated in Europe (Flochlay et al., 2017).

In addition, resistance to certain acaricides (such as carbaryl, amitraz and permethrin) has emerged in PRM populations over the last 40 years (Zeman and Zelezny, 1985; Beugnet et al., 1997; Marangi et al., 2009; Sparagano et al., 2009, 2014). Therefore, increasing awareness of the general public and changes to legislation have promoted the search for new and eco-friendly ways to control *D. gallinae*, including vaccines, entomopathogenic fungi and essential oils. Simultaneously, the chemical ecology of PRM is being increasingly studied to develop control strategies based on pheromonal communication.

Here, an overview of current information is provided, along with potential future directions, in controlling PRM. The different volatile organic compounds (VOCs) currently identified from *D. gallinae* and other mite species are presented, along with those already used to control them. Specifically, information is presented on (1) pheromones affecting mite behaviour with an attracting effect and (2) the repellent properties of VOCs on PRM. Finally, several devices using VOCs to control *D. gallinae* in field assays are described, as well as designs tested on other *Acari* species that could potentially be used on PRM.
Attractive substances

VOCs present an interesting alternative to classical acaricides for controlling acarian populations. Several types of VOCs could be used to manipulate the behaviour of Acari, potentially being integrated in « attract and kill » devices. Here, the potential of several pheromones (Table 1) and kairomones (Table 2) that have already been identified is focused on.

Pheromones

Pheromones are molecules that are emitted by an individual of a species to influence the behaviour of another individual of the same species (Pageot, 2005). Several pheromones are considered to attract mites, including aggregation pheromones, immature female pheromones, female sex pheromones and, at low doses, alarm pheromones (Sonenshine, 1985; Carr and Roe, 2016). To identify the molecules present in the pheromonal mix released by a species, static headspace analyses (e.g. solid phase micro extraction or SPME) (Birkett et al., 2010; Steidle et al., 2014) and dynamic headspace analyses (e.g. thermodesorption) (Chen et al., 2019; Makarow et al., 2019) are performed. While dynamic headspace analysis has not yet been performed on mites, to our knowledge, it could prove useful, because it allows small amounts of volatile molecules to be detected and quantified (Pfannkoch and Whitecavage, 2000; Zhang and Li, 2010). The sampling technique must be coupled to gas chromatography-mass spectrometry (GC-MS) analysis to identify the different compounds (Zhang and Li, 2010). Following the identification and quantification of molecules within the pheromonal mix, behavioural tests could be performed, including Y-tube olfactometers bioassays or filter paper contact bioassays, to characterize the behaviour of mites when they are confronted with all or a part of the identified molecules (Entrekin and Oliver, 1982; Steidle et al., 2014).

Aggregation pheromones

The aggregation pheromones of mites cause non-feeding conspecific mites to aggregate in a safe environment (Carr and Roe, 2016). The aggregation behaviour in PRM was well studied before the aggregation pheromone was identified. Entrekin and Oliver (1982) studied two possible causes for this behaviour: thigmokinesis (i.e. increased locomotion in response to changes in contact with the immediate physical environment) and the release of an aggregation pheromone. Both stimuli impact the clustering of mites; however, the chemical ones form aggregates more efficiently. The aggregation phenomenon due to the perception of potential aggregation pheromones by PRM was evaluated by Koenraadt and Dicke (2010). The authors tested the attraction of two groups of conspecific mites (fed and unfed) by performing behavioural experiments. The authors showed that fed and unfed mites were attracted by volatiles emitted by fed conspecifics. This finding was consistent with a previous study showing that the aggregation of mites increases after feeding (Entrekin and Oliver, 1982). Koenraadt and Dicke (2010) proposed that unfed mites are motivated to find a host to feed, while fed ones were searching for a place to hide and reproduce after their blood meal.

Subsequently, Birkett et al. (2010) conducted SPME-GC analysis on fed adult PRM, and identified eight molecules, including seven carboxylic acids (including hexanoic acid and dodecanoic acid) and one aldehyde (an octanal) that could be components of the pheromonal mix driving aggregation-forming behaviour in PRM. Behavioural experiments confirmed the attractive effect of each compound, as well as a synergistic effect when compounds are associated. It was concluded that the eight compounds attract PRM and could be applied simultaneously, separately or sequentially to each other (Birkett et al., 2010). It is possible that the aggregation pheromone of PRM is composed of only one or several molecules, as observed in other mite species. For example, Lardolure is the only aggregation pheromone that has been identified in *Caloglyphus polyphyllyae*¹ and *Lardoglyphus konoi* mites (Kuwahara et al., 1994; Carr and Roe, 2016). In comparison, the aggregation pheromone of the European House Dust Mite (*Dermatophagoides pteronyssinus*) is mostly composed of neryl propionate, pentadecane and neryl formate (Skelton et al., 2010; Steidle et al., 2014). Finally, neryl formate might be a component of the pheromonal mix of several different species, as it was identified as a major compound of the aggregation pheromone in the American House Dust Mite, *Dermatophagoides fariniae* and EHDM (Skelton et al., 2010).

Alarm pheromones

Alarm pheromones are emitted by an individual that has been stressed by an unsafe environment or that has been injured through direct contact (Carr and Roe, 2016). Detection of low concentrations of alarm pheromones causes attraction and clustering behaviour in mites, as part of group survival strategies (i.e. formation of a ‘safety net’). Above a given concentration, the pheromone becomes repulsive, which causes the strategies of individuals changing (i.e. scattering and hiding) (Carr and Roe, 2016). To date, the alarm behaviour or the possible emission of this pheromone has not been studied in PRM; however, several compounds of this pheromone have been identified in other species of Astigmatid mites, including neryl formate and neral (Kuwahara, 2010, 2011; Carr and Roe, 2016). When neral is applied in low doses (1 and 3 ng) on filter paper, mites (*Schwiebea elongata*) are attracted to this compound; however, at higher doses (30 ng), they exhibited repulsive behaviour (Nishimura et al., 2003; Carr and Roe, 2016). Neryl formate was identified as an alarm pheromone for several species, including *Tetranychus putrescentiae* (Schrank 1781), leading to alarm behaviour (Kuwahara, 2010); however, it attracts also other species, such as *D. fariniae* and *D. pteronyssinus* at high doses (10 and 100 ng), and is considered to be an aggregation pheromone (Skelton et al., 2010). Therefore, it is essential to clearly differentiate alarm pheromones that attract mites at low doses from aggregation pheromone that attract mites at all doses. Studies on the PRM alarm behaviour or the potential alarm pheromone emission have yet to be conducted, which could represent an interesting future direction for research.

Sex pheromones

Two types of sex pheromones have been detected in mites: (1) immature female pheromones, also known as arrenat sex pheromones and (2) female sex pheromones (Sonenshine, 1985; Carr and Roe, 2016). There is a competition between male mites to reproduce with conspecific females. Consequently, males might detect differences between a deutonymph (i.e. second nymphal stage) from a protonymph (i.e. first nymphal stage) by using the immature pheromone signature emitted by deutonymph females, which is composed of citronellol, farnesol and nerolidol in *Tetranychus urticae* females (Reges and Cone, 1975, 1976, 1980). Following the discovery of a deutonymph female, males exhibit guarding behaviour (i.e. association of a male with a deutonymph female) in some acarian species [e.g. *Hercia* sp. (Canestrini 1888) or *Tetranychus kanzawai* (Kishida 1927)], until the deutonymph becomes an adult female (Sonenshine, 1985; Witaliński et al., 1992; Yasui, 1992; Fashing, 2003; Oku, 2009; Carr and Roe, 2016), Colloff (2009), cited by Carr and

¹All complete species names could be found in Table 1.
Roe (2016), highlighted that only deutonymphs are able to emit the immature female pheromone. Nevertheless, this pheromone has not been identified in *D. gallinae* so far.

The female sex pheromone is normally released by fed mature females to attract preferably fed males, as the two sexes have a high reproductive success status (Sonenshine, 1985; Carr and Roe, 2016). The female sex pheromone might also be released by males, explaining the mounting behaviour between males that is sometimes observed (Mori and Kuwahara, 2000; Mizoguchi et al., 2005; Carr and Roe, 2016). Again, the female sex pheromone was not studied in *D. gallinae*, but different compounds have been identified as female sex pheromones in mites (Table 1).

PRM is part of the Acari. The molecules identified in closely related species could be potential candidates for characterizing the sex pheromones of PRM, especially as some compounds are

<table>
<thead>
<tr>
<th>Species</th>
<th>Tested substances</th>
<th>Experiments</th>
<th>Effect</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acarus immobilis</em> (Griffith 1964)</td>
<td>2-Hydroxy-6-methylbenzaldehyde</td>
<td>Filter paper bioassays Petri dishes experiments</td>
<td>Attraction</td>
<td>Sato et al. (1993)</td>
</tr>
<tr>
<td><em>Aenneuroglyphus ovatus</em> (Troupeau 1879)</td>
<td>2-Hydroxy-6-methylbenzaldehyde</td>
<td>Filter paper bioassays Petri dishes experiments</td>
<td>Attraction</td>
<td>Kuwahara et al. (1991)</td>
</tr>
<tr>
<td><em>Cologlyphus sp.</em></td>
<td>(2R,3R)-Epoxyneral Rosefuran</td>
<td>Petri dishes experiments</td>
<td>Attraction</td>
<td>Mori et al. (1996); Mori et al. (1996)</td>
</tr>
<tr>
<td><em>Cologlyphus polyphyllae</em> (Zakhvatkin 1941)</td>
<td>β-Acaridial</td>
<td>Petri dishes experiments</td>
<td>Attraction</td>
<td>Shimizu et al. (2001)</td>
</tr>
<tr>
<td><em>Carpoglyphus lactis</em> (Linneaeus 1767)</td>
<td>Lardolure</td>
<td>Not described</td>
<td>Attraction</td>
<td>Kuwahara et al. (1994)</td>
</tr>
<tr>
<td><em>Cosmaglyphus hughesis</em> (Samsinak 1966)</td>
<td>2-Hydroxy-6-methylbenzaldehyde</td>
<td>Filter paper bioassays Petri dishes experiments</td>
<td>Attraction</td>
<td>Ryono et al. (2001)</td>
</tr>
<tr>
<td><em>Delemonyssus gallinae</em> (De Geer 1778)</td>
<td>Aggregation pheromone</td>
<td>Petri dishes experiments Y-tube olfactometers 4 arms-olfactometers</td>
<td>Attraction</td>
<td>Entrekin and Oliver (1982); Birkett et al. (2010); Koenraadt and Dicke (2010)</td>
</tr>
<tr>
<td><em>Dermatophagoides farinae</em> (Hughes 1961)</td>
<td>2-Hydroxy-6-methylbenzaldehyde</td>
<td>Filter paper bioassays Petri dishes experiments</td>
<td>Attraction</td>
<td>Tatami et al. (2001); Skelton et al. (2010)</td>
</tr>
<tr>
<td><em>Dermatophagoides pteronyssinus</em> (Trouessart 1897)</td>
<td>2-Hydroxy-6-methylbenzaldehyde</td>
<td>Filter paper bioassays Petri dishes experiments</td>
<td>Attraction</td>
<td>Skelton et al. (2010); Steidle et al. (2014)</td>
</tr>
<tr>
<td><em>Lardoglyphus konoi</em> (Sasa and Asanuma 1951)</td>
<td>Lardolure</td>
<td>Not described</td>
<td>Attraction</td>
<td>Kuwahara et al. (1994)</td>
</tr>
<tr>
<td><em>Rhizoglyphus robinii</em> (Claparède 1869)</td>
<td>α-Acaridial</td>
<td>Petri dishes experiments</td>
<td>Attraction</td>
<td>Mizoguchi et al. (2003)</td>
</tr>
<tr>
<td><em>Rhizoglyphus setosus</em> (Manson 1972)</td>
<td>S-Isorobinal</td>
<td>Petri dishes experiments</td>
<td>Attraction</td>
<td>Mizoguchi et al. (2005)</td>
</tr>
<tr>
<td><em>Schwibeeoa elongata</em> (Banks 1906)</td>
<td>Neral</td>
<td>Petri dishes experiments</td>
<td>Attraction</td>
<td>Nishimura et al. (2003)</td>
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<tr>
<td></td>
<td>Neral (low dose) Pentadecane</td>
<td>Pasteur pipet experiments</td>
<td>Repulsion</td>
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<tr>
<td></td>
<td>Neral (high dose) (Z)-8-heptadecene</td>
<td>Petri dishes experiments</td>
<td></td>
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<tr>
<td><em>Tetranychus urticae</em> (Koch 1836)</td>
<td>Citronellol Farnesol Nerolidol</td>
<td>Petri dishes experiments</td>
<td>Attraction</td>
<td>Regev and Cone (1975), (1976), (1980)</td>
</tr>
</tbody>
</table>
already shared by different species, including 2-hydroxy-6-methylbenzaldehyde in *Acarus immobilis*, *Aleuroglyphus ovatus*, *Cosmoglyphus hughesi* and *D. farinae* (Kuwahara et al., 1991; Sato et al., 1993; Ryono et al., 2001; Tatami et al., 2001).

Sexual chemical communication between mites has been extensively investigated in several species, but not in PRM. Thus, it would be interesting to fill this knowledge gap on chemical communication in PRM. The potential synergic effects between the sex pheromone and aggregation pheromone could potentially be identified, which could be used to control PRM.

### Host kairomones

Kairomones are molecules emitted by individuals mediating interspecific interactions that are generally harmful to the emitters (Pageat, 2005). This section addresses kairomones that are attractive to some mites, including *D. gallinae* (Table 2). PRM aim to localize potential hosts to feed. The uropygial gland products of chicken might have potential kairomones in the host location process (Pageat, 2005; Koenraadt and Dicke, 2010). Several experiments confirmed with tube olfactometer experiments. A synergic effect of four molecules characterizing gallinaceous bird scent [(E)-non-2-enal, nonanoic acid, octanal and oct-1-en-3-ol] was highlighted by olfactometry (Roy et al., 2018). More generally, the attracting capacity of VOCs from the skin and feather extracts of hens (composition not available in the paper) was identified in a study where it was necessary to attract PRM to feed on synthetic skin extracts or whether they serve as contact cues for skin recognition. Several studies have investigated kairomones produced by hens; however, knowledge remains limited about the potential attracting role of VOCs in PRM than fresh feathers (feathers cut from live hens). Mites responded to small numbers of feathers (10 feathers in a 2.5 L glass jar), indicating that they can detect very low amounts of these kairomones; however, no precise measurement was made (Koenraadt and Dicke, 2010). Carbon dioxide (CO2) can also be considered as a kairomone for PRM. A gradual increase to CO2 levels induces host-seeking behaviour in mites, whereas a quick increase induces mites to freeze. This attitude is probably linked to the potential presence of predators (Kilpinen, 2005). Finally, temperature is a powerful stimulus that activates mites and, coupled with vibrations, might contribute to host detection and localization (Kilpinen, 2001, 2005).

Following host localization, PRM are attracted by several kairomones produced by the host (Roy et al., 2018). Several compounds were identified from living hens by SPME, followed by GC/MS analyses. Their attracting effect to PRM was confirmed with tube olfactometer experiments. A synergic effect of four molecules characterizing gallinaceous bird scent [(E)-non-2-enal, nonanoic acid, octanal and oct-1-en-3-ol] was highlighted by olfactometry (Roy et al., 2018). More generally, the attracting capacity of VOCs from the skin and feather extracts of hens (composition not available in the paper) was identified in a study where it was necessary to attract PRM to feed on synthetic membranes (Harrington et al., 2010). However, it is not clear whether these molecules are involved in attracting *D. gallinae* to the host (*i.e.* detection of skin VOCs) or whether they serve as contact cues for skin recognition. Several studies have investigated kairomones produced by hens; however, knowledge remains limited about the potential attracting role of VOCs in

### Table 2. Chemical compounds of host kairomones with an attractive effect on mites

<table>
<thead>
<tr>
<th>Species</th>
<th>Tested substances</th>
<th>Experiments</th>
<th>Effect</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dermanyssus gallinae</em> (De Geer 1778)</td>
<td>1-Heptadecane 9-Octadecene-ol 1 (oleyl alcohol) Carbone dioxide Chicken skin extracts (E)-non-2-enal Ethyl acetate Feathers (Aged and Fresh) Heptadecane Nonanal Nonanoic acid Oct-1-en-3-ol Octadecane Octanal</td>
<td>Feeding experiments Field experiments Y-tube olfactometers</td>
<td>Attraction</td>
<td>Pageat (2005); Harrington et al. (2010); Koenraadt and Dicke (2010); Roy et al. (2018)</td>
</tr>
<tr>
<td><em>Macrocheles muscaædomesticæ</em> (Scopoli 1772)</td>
<td>N-Phenyl-N-glucoside N-Phenyl-N-mannoside</td>
<td>No details available</td>
<td>Attraction</td>
<td>Carr and Roe (2016)</td>
</tr>
<tr>
<td><em>Phytoseiulus macropilis</em> (Banks 1904)</td>
<td>VOC from <em>Tetranychus urticae</em></td>
<td>Y-Tube olfactometers</td>
<td>Attraction</td>
<td>Amin et al. (2010)</td>
</tr>
<tr>
<td><em>Varroa destructor</em> (Anderson and Trueman 2000)</td>
<td>Ethyl palmitate Methyl linolenate Methyl palmitate</td>
<td>Mite wind tunnel experiments</td>
<td>Attraction</td>
<td>Calderone and Lin (2001)</td>
</tr>
<tr>
<td><em>Varroa jacobsoni</em> (Oudemans 1904)</td>
<td>Ethyl palmitate Methyl linolenate Methyl palmitate</td>
<td>4 arms-olfactometers</td>
<td>Attraction</td>
<td>Le Conte et al. (1989)</td>
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</table>
the environment of hens, with future studies being required on this subject.

Few studies have investigated the kairomones of other mite species. The methodology exploited with other species is similar to that used with PRM. After analysing the body extracts of male and female adult houseflies Musca domestica and after feeding experiments, N-phenyl-N-glucoside and N-phenyl-N-mannoside were identified as two kairomones that attracted the phoretic mite, Macrocheles musaeasciunctalis (Wicht et al., 1971; Achiano and Giliomee, 2006 cited in ref of the review of Carr and Roe, 2015). In addition, female predator mites Phytoseiulus macropilis were attracted by unidentified kairomones from T. urticata in Y-tube olfactometer experiments (Amin et al., 2010). However, three kairomones (methyl palmitate, ethyl palmitate and methyl linolenate) were identified in Varroa jacobsoni and Varroa destructor, which are two species of honey bees parasites, following behavioural experiments with four-armed olfactometers and mite wind tunnels (Le Conte et al., 1989; Calderone and Lin, 2001). The use of a wind tunnel allows the long-range effect of different compounds to be tested. The use of this methodology on PRM could extend current knowledge on the potential attracting properties of pheromones and kairomones.

**Repulsive substances**

Olfactive repellents can be divided into two categories: (1) true repellents (also called expellents) or spatial repellents, and (2) odour masking compounds (or attraction inhibitors) (Deletre et al., 2016). A true repellent induces a shift in orientation from an odour source without direct contact. In comparison, odour masking compounds induce the attractiveness of the host to decline, or difficulties to localize the host using odour cues (Deletre et al., 2016).

Several experiments were conducted to test the repellent properties of substances studied on PRM, including contact experiments (i.e. Petri dishes with filter paper saturated with the compound) and olfactive experiments using olfactometers (Nechita et al., 2015; Masoumi et al., 2016). Globally, it is interesting to evaluate the repellent effect of a substance to: (1) test a potential negative repellent effect of a toxic substance (e.g. acaricide) (Lundh et al., 2005) and (2) confirm the repulsive effect of a substance that could be used as a pure repellent (Nechita et al., 2015). The different compounds tested on PRM are summarized in Table 3, showing the level of repellent effect.

**Essential oils**

The repulsive and/or acaricidal efficiency of essential oils has been extensively studied. For instance, Lundh et al. (2005) showed that neem oil, Azadirachta indica (Jussieu) (concentrations of 15 to 20%), has a good acaricide effect associated with a low repellent effect under laboratory conditions. In another study, Camarda et al. (2018) tested the effectiveness of this oil under field conditions. The authors showed that a 20% neem oil formulation (RP03T™) caused the mite population in poultry farms to decline by 95.65% to 99.80% after three nebulizations of the product over one week (Camarda et al., 2018). Other essential oils are also effective, particularly essential oils from the family of Lamioaceae (Martinov) such as Origanum (L.), Satureja (L.), Thymbra (L.) and Thymus (L.) species. These species are characterized by a major compound, carvacrol, which is a good acaricide candidate with a toxic effect on D. gallinae. It has no repellent effect at 1% concentration; however, above this concentration, repellence occurs (Kirim et al., 1995; Barimani et al., 2016).

Out of several essential oils tested for their pure repellent properties in vitro contact bioassays, thyme and lavender oils had the highest repellent activity with, respectively, 80 and 40% of the oil-treated surface area being avoided by PRM (Nechita et al., 2015; Pritchard et al., 2016). Nevertheless, in this type of experiment, it is not possible to distinguish whether mites are repelled by olfactory or contact cues, with complementary studies in olfactometers being required (Deletre et al., 2016). The association of thymol (i.e. the major compound of thyme essential oil) and carvacrol was evaluated in olfactometer bioassays for potential synergic repellent effects (Masoumi et al., 2016). The study, unfortunately, revealed that the addition of thymol to carvacrol decreased the repellent effect of carvacrol. Other studies analysed the different compounds present in a given essential oil by GC-MS experiments, and tested the repellent effect of the oil on PRM by Y-tube olfactometer experiments (Tabari et al., 2017; Santana et al., 2018). The essential oil of Artemisia sieberi (Besser) [rich in α-thujone (31.5%), β-thujone (11.92%), camphor (12.3%) and 1,8-cineole (10.09%)] and the essential oil of Myrica oblongata (DC) [rich in carophyllene oxide (22.03%) and trans-verbenol (11.94%)] showed a significative repellent effect to D. gallinae. Nevertheless, the effect of each of their constituent compounds was not evaluated (Tabari et al., 2017; Santana et al., 2018). Finally, a study by Lee et al. (2019) obtained interesting results, in which two essential oils (cinnamon bark and clove bud oils) and some of their constitutive compounds were tested for their repellent abilities. The two oils and their compounds were repellent to PRM, except for cinnamyl acetate from cinnamon bark oil, and for two compounds from clove bud oil (eugenol and eugenol acetate), which even showed an attractant effect, following 120 min of application. The concentration of the active compound over time might be an issue, as many essential oils exhibit high repellent activity against D. gallinae over the short-term due to their high volatility (George et al., 2008, 2009). A dose effect exists for several molecules, including thyme oil, which could be used as a repellent or as an acaricide, depending on the concentration. When used as an acaricide, essential oils have a short-term effect; however, it is possible to couple them with other biological control methods, such as entomopathogenic fungus. When these two methods are coupled, the short-term acaricide effect of essential oils is complemented with the delayed, but long-term effect, of the fungus. For example, an entomopathogenic fungus [Beauveria bassiana (Balsamo-Crivelli Vuillemin)] in combination with essential oils [Eucalyptus globulus (La Billardiére), Eucalyptus citriodora (Hook), Thymus vulgaris (Linné), and Eugenia caryophyllata (Thunb.)] was tested to create a new way to control D. gallinae (Immediato et al., 2016).

Following toxicity tests, it was found that the combination of B. bassiana and E. globulus at 0.2% might be the best combination for an acaricide effect against D. gallinae.

**Plant extracts**

Most studies on plant extracts have focused on the acaricide properties of the extracts, and are not evaluated in this review, because repellent properties are not discussed. Only two studies evaluated the repellent properties of two plant extracts. Rajabpour et al. (2018) showed that aquatic and ethanolic extracts of Conocarpus erectus are repellent for PRM using contact experiments. Nevertheless, the repellent effect described here was unclear, as it was not possible to distinguish the contact and olfac- tive repellent effects. In another study, the acaridal and repellent activities of a methanolic extract and fractions from the rhizome of Cnidium officinale were tested to control D. gallinae (Kim et al., 2018). Kim et al. (2018) showed that the methanolic extract of C. officinale has a 91.3% repellent activity on PRM, while (Z)-lignustilide, which is an isolated compound from C. officinale
roots, showed a repellent response rate equal to 100% using a T-tube olfactometer.

**Application of VOCs in field assays**

Here, current applications of VOCs to control PRM are described along with potential other strategies from other Acari species relevant for PRM control. The introduction of repulsive substances to hen feed could make the emission of repellent VOCs against the PRM possible (El Adouzi et al., 2019). For instance, Nor-Mite® (mostly composed of >2% eugenol) was added to hen feed, and the VOCs emitted by hens were analysed. GC-MS analysis showed that Nor-Mite® fed hens released several VOCs, including eugenol. Following olfactometer experiments, the repellent effect of eugenol and other VOCs from Nor-Mite® fed hens was confirmed. In addition, the authors suggested that other molecules present in Nor-Mite®, such as trans-caryophyllene and geraniol, might contribute to this repellent effect, with possible additive/synergic effects (not tested in this paper) (El Adouzi et al., 2019).

Several devices have been tested to control other Acari species. For example, one design using attracting VOCs is an ‘attract and kill’ trap has been applied to others species of Acari. A system based on the encapsulation of an attracting pheromone coupled to an acaricide was developed for the brown dog tick *Rhipicephalus sanguineus* (Latreille 1806) by Dhivya et al. (2014). The capsule was made of a natural polymer (i.e. chitosan). The species assembly pheromone was chosen as an attractant, and was coupled with deltamethrin as acaricide. Laboratory and field tests showed a reduction of infestation, as the ticks were discovered dead around the traps. Another study using aggregation-attachment pheromone together with deltamethrin to attract and kill *Amblyomma variegatum* (Fabricius 1794) (the tropical bont tick) demonstrated an overall tick control efficiency of 92% (Kelly et al., 2014). Similar studies could be conducted for *D. gallinae* by coupling the aggregation pheromone with a natural acaricide (e.g. an essential oil) or entomopathogenic fungi.

**Conclusions**

PRM is a world economic problem for the poultry industry, and the development of solutions with low risk on human health should be promoted to control their populations, especially in hen egg laying farms. The development of sustainable pest control based on an understanding of chemical ecology is being increasingly implemented, and should be applied to PRM. New insights on pheromonal communication of PRM are fundamental to create efficient control strategies.
Knowledge remains more limited about chemical communica-
tion in mites including PRM compared to ticks, mainly due to
their smaller size and, consequently, the lower emission of
VOCs. In the last decade, the identification of attractants in
mites has increased, along with more information on their asso-
ciated effects on mite behaviour. Nevertheless, a large knowledge
gap exists on VOCs that attract PRM that should be addressed in
the future.

The lack of knowledge, especially on PRM pheromones, could be
explained by the difficulties encountered to maintain an artifi-
cial breeding of PRM (Kirkwood, 1971; Zeman, 1988; Bruneau
et al., 2001; Harrington et al., 2010). This hurdle prevents the
availability of fed mites reducing the implementation of phero-
mones studies. For the development of further PRM pheromone
studies, an efficient artificial or semi-artificial breeding system
must be developed to facilitate the supply of fed individual as
well as to allow a control of several parameters (e.g. time since
the last meal, female fertilization or not etc.). Among the current
possible alternative, the use of a semi-artificial laboratory breeding
on alive chicken (i.e. a plastic bag filled with PRM in contact with
the chicken) seems to be a promising solution as it provides a high
number of individuals in a short period of time (Nunn et al.,
2019).

Concerning PRM’s kairomones, several studies are currently
available with no assays of these molecules in field conditions
(Pageat, 2005; Koenraadt and Dicke, 2010; Roy et al., 2018).
Different implementations are still to be needed to consider
these molecules as an efficient field attractant such as the emission
source apposition or the concentration of the synthetic molecule.
Moreover, the interference of kairomones from hosts when
synthesized kairomones are applied in layer farms would be diffi-
cult to avoid and should decrease the efficacy of the product.

In contrast to the limited number of studies on attracting
VOCs, many studies exist on repulsive VOCs to PRM. This phe-
nomenon might be explained by the fact that repelling PRM out-
side poultry farms is the first solution that comes to mind in
terms of control strategies. Essential oils and plant extracts seem
to represent promising repellents, despite their short-term effi-
ciency. Several designs using VOCs on PRM have been elaborated
and tested under field conditions. Further studies are needed to
optimize these strategies, or to create new ones based on ‘attract
and kill’ or ‘push-pull’ principles.

Finally, although mites and ticks are two separated groups in
the Acari taxon, similarities exist in how they communicate.
Therefore, researchers investigating the chemical communication
of mites should refer to studies on chemical communication in
ticks, for which there is extensive published literature.

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