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The role of volatiles in aggregation and host-seeking of the haematophagous poultry red mite *Dermanyssus gallinae* (Acari: Dermanyssidae)

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Abstract Infestations with ectoparasitic poultry red mites (*Dermanyssus gallinae*) pose an increasing threat to poultry health and welfare. Because of resistance to acaricides and higher scrutiny of poultry products, alternative and environmentally safe management strategies are warranted. Therefore, we investigated how volatile cues shape the behavior of *D. gallinae* and how this knowledge may be exploited in the development of an attract-and-kill method to control mite populations. A Y-tube olfactometer bio-assay was used to evaluate choices of mites in response to cues related to conspecific mites as well as related to their chicken host. Both recently fed and starved mites showed a strong preference (84 and 85%, respectively) for volatiles from conspecific, fed mites as compared to a control stream of clean air. Mites were also significantly attracted to ‘aged feathers’ (that had remained in the litter for 3–4 days), but not to ‘fresh feathers’. Interestingly, an air stream containing 2.5% CO₂, which mimics the natural concentration in air exhaled by chickens, did attract fed mites, but inhibited the attraction of unfed mites towards volatiles from aged feathers. We conclude that both mite-related cues (aggregation pheromones) and host-related cues (kairomones) mediate the behavior of the poultry mite. We discuss the options to exploit this knowledge as the ‘attract’ component of attract-and-kill strategies for the control of *D. gallinae*.

Keywords Poultry red mite · *Dermanyssus gallinae* · Attract-and-kill method · Aggregation behavior · Host-seeking behavior · Pheromone · Kairomones · Biological control

Introduction

An infestation with the blood-feeding, ectoparasitic mite *Dermanyssus gallinae* (DeGeer) is one of the most important welfare and health problems of poultry (Chauve 1998; Emous

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et al. 2005; Hegelund and Sørensen 2007). It may lead to feather-pecking among individual chickens, to unrest and to stress. Reduced egg production, anemia, and eventually death can occur in the most severe cases (Kirkwood 1967; Kilpinen et al. 2005). Resistance to acaricides and an increased scrutiny of poultry products for human health hazards (food safety) have limited the options to control the poultry red mite (Sparagano et al. 2009). Therefore, alternative approaches are urgently needed. A little-explored avenue in this regard is the exploitation of chemical cues that mediate interactions among mites or between mites and their chicken host. For other veterinary and agricultural pests, such as ticks and herbivorous mites, the use of pheromones, whether or not in combination with a biological kill component, has shown good promise in controlling them (Sonenshine 1985, 2006).

Dermanyssus gallinae spends most of its time hidden in the numerous cracks and crevices of the poultry installation and comes out to feed during the night. Nymphal and adult stages spend approximately 30 min on their host before returning to their hiding places (Maurer et al. 1988). In general, blood feeding ectoparasites utilize a variety of cues such as body heat, CO₂ and host-specific kairomones to locate their host (Takken and Knols 1999; Guerenstein and Hildebrand 2008). Kilpinen and colleagues demonstrated that *D. gallinae* is highly sensitive to small temperature changes and that starved mites are more responsive to a heat cue than freshly fed ones (Kilpinen 2001; Kilpinen and Mullens 2004). Zeman (1988) showed that several surface skin lipids are involved in host identification and stimulation of feeding by *D. gallinae*. Under dark conditions, CO₂ does not elicit a response in terms of walking speed or turning angle, but in light conditions mites ‘freeze’ (i.e. they become motionless) in response to CO₂. The latter behavior probably reflects a defensive strategy to avoid being eaten by the host (Kilpinen 2005). After the blood meal, *D. gallinae* forms aggregations of mixed developmental stages. As is the case in the related *Dermanyssus prognepphilus*, thigmokinesis and pheromones are thought to play a role in this (Entrekin and Oliver 1982). The aim of this study was to investigate how *D. gallinae* responds to host-derived volatiles and whether CO₂ affects this response. In addition, we explored the role of volatiles in aggregation behavior and how this is affected by feeding status.

Materials and methods

Mites

Poultry red mites (*Dermanyssus gallinae*) were obtained from an in vivo rearing with eight chickens held in a cage (2 by 3 m) located at experimental station De Haar, Department of Animal Sciences, Wageningen University, The Netherlands. Average temperature in this facility was 20 ± 2°C. Because poultry red mites are nocturnal feeders (Maurer et al. 1988), they were held in the experimental room with a reversed light–dark period (14L:10D).

Bio-assay

Olfactory preferences of the mites were tested in a closed-system Y-tube olfactometer (Takabayashi and Dicke 1992). Briefly, pressurized air was filtered through activated charcoal, humidified and split in two streams with a flow rate of 2 l/min each. Air was then led through 2.5 l glass jars for experiments that tested the response to host cues or 50 ml plastic tubes for experiments that tested the response to volatiles from conspecific mites. An extra inlet was available to add 100% CO₂ from a cylinder to the air stream. By using

flow meters (Brooks Instruments, Ede, The Netherlands), CO₂ was mixed with the air stream to a concentration of 2.5% v/v. During the experiments, average temperature was $25.3 \pm 0.9^\circ\text{C}$ and relative humidity $70 \pm 9\%$ inside the Y-tube. Mites were released individually at the down-wind end of the stem of the Y-tube. They were given the opportunity to walk upwind and choose for one of the odor sources for a maximum of 5 min. ‘First choice’ was recorded as soon as the mite entered either the left or right arm. If a mite remained in one arm for a consecutive period of 1 min, this choice was recorded as ‘final choice’ and the mite was then discarded. All other situations were recorded as ‘no choice’. To observe the mites’ behavior under darkness conditions, a red light was installed ~ 50 cm above the Y-tube.

Experiments

The experiments tested the response of mites to host volatiles as well as to volatiles from conspecific mites. Both experiments were carried out with mites that had obtained a blood meal recently (within 0–1 days; indicated as ‘fed’ mites) as well as with mites that had been starved for 4–5 days by keeping them in 50-ml tubes in the experimental room at $24 \pm 0.4^\circ\text{C}$ and $67 \pm 6\%$ RH (indicated as ‘unfed’ mites). In each experiment the response of 60 mites was assessed. Stimuli were alternated between left and right arms after every batch of ten mites. Experiments with host odor cues were spread over 3–6 days, while experiments with conspecific mites were spread over 2–4 days. New odor sources were used on each experimental day.

Response to host odor cues

We investigated the response towards freshly cut feathers (FF) versus clean air, aged feathers (AF) versus clean air and fresh feathers versus aged feathers. Fresh feathers were obtained by cutting feathers located in the neck area of one of the eight experimental chickens. Ten of these feathers were placed in the 2.5 l glass jar and served as a stimulus. Aged feathers were obtained by collecting naturally shed feathers from the litter of the cage and that were not visibly contaminated with fecal matter. Because all shed feathers were collected at regular intervals, the time that feathers remained in the litter was 3–4 days. Ten of these feathers were placed in a glass jar and served as a stimulus. A final experiment compared the response of mites towards fresh feathers versus feathers that had been incubated at 37°C for 7 days. For this purpose, a sample of fresh feathers was split into two equal portions and either placed in sealed Petri dishes in the freezer at -20°C or in an incubator at 37°C .

In the next series of tests, we investigated the effects of CO₂ on the host-seeking response. CO₂ was provided in a concentration of 2.5% that mimics the concentration naturally exhaled by a chicken (Gleeson et al. 1985). The following combinations were tested: 2.5% CO₂ versus clean air, fresh feathers + 2.5% CO₂ versus clean air and aged feathers + 2.5% CO₂ versus clean air.

Response to volatiles cues from conspecific mites

Two hundred adult mites, either fed or unfed, were placed in a 50-ml tube. Air was led through this tube and introduced into the Y-tube olfactometer set-up described above. We investigated the response of mites to the volatiles from 200 fed mites versus clean air, the

volatiles from 200 unfed mites versus clean air and to the volatiles from 200 fed mites versus those from 200 unfed mites.

Statistical analyses

Two-sided binomial tests were carried out to evaluate whether choices of the mites in the Y-tube olfactometer differed from a 50:50 distribution. Binary logistic regression models were used to test for the effect of feeding status on both response rate, i.e. the proportion of mites making a choice for either arm of the olfactometer out of the total number of mites exposed ($n = 60$), and relative attractiveness, i.e. the proportion of mites making a choice for one of the stimulus arms, excluding non-responding mites. All analyses were carried out in SPSS v15.0 (Chicago, IL, USA).

Results

Response towards host odor cues

When fed and unfed mites were exposed to two streams of clean air ('control'), no preference was shown for either arm (Fig. 1). Aged feathers were significantly attractive for both fed and unfed mites (binomial test, $P = 0.012$ and $P < 0.001$, respectively), whereas fresh feathers were not attractive (binomial test, $P = 0.32$ and $P = 1.00$, respectively). When mites were exposed to both types of feather simultaneously, unfed mites preferred aged feathers (binomial test, $P = 0.016$) whereas fed mites did not show a

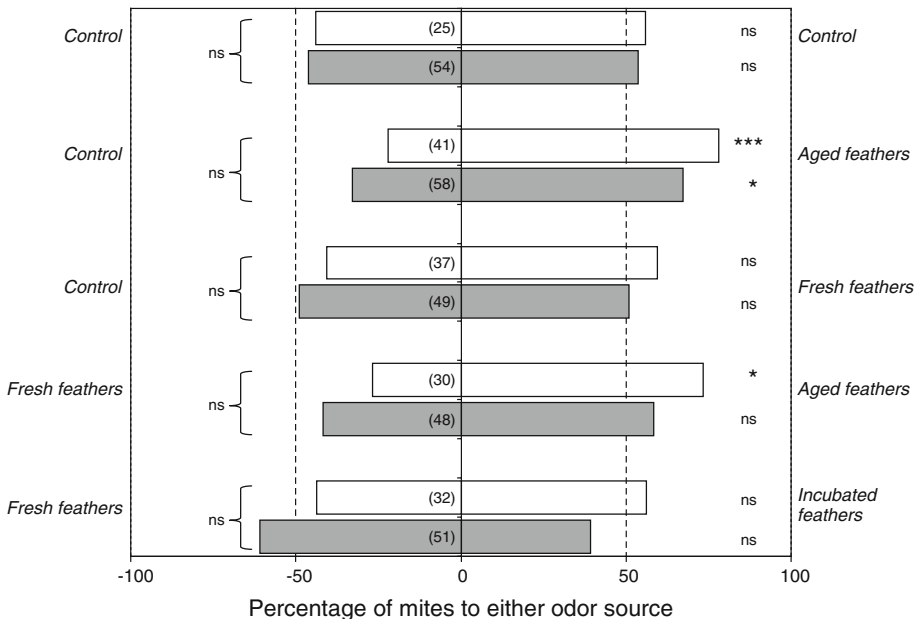


Fig. 1 Response of unfed (white bars) and fed (grey bars) *Dermanyssus gallinae* to various host-related sources. Tests were performed in a Y-tube olfactometer; ns not significant, * $P < 0.05$, *** $P < 0.001$. The total number of mites (out of 60 tested) choosing one of the two ports is given in parentheses

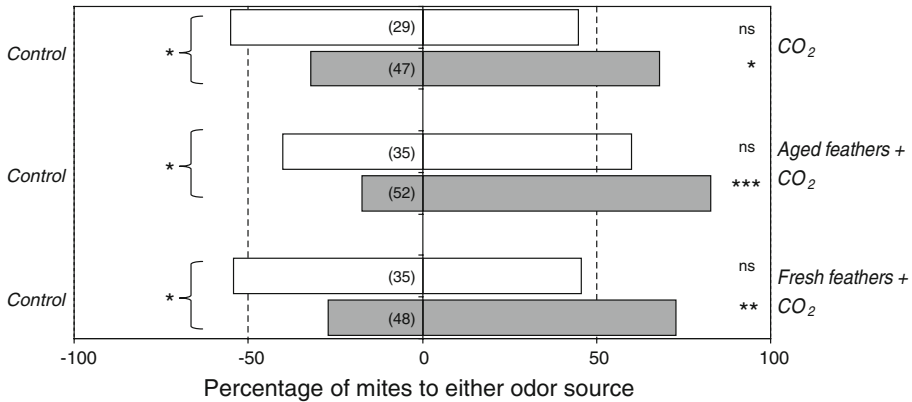


Fig. 2 Response of unfed (white bars) and fed (grey bars) *Dermanyssus gallinae* to CO₂ alone or in combination with host-related sources. Tests were performed in a Y-tube olfactometer; ns not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The total number of mites (out of 60 tested) choosing one of the two ports is given in parentheses

preference (binomial test, $P = 0.31$). When mites were exposed to fresh and incubated feathers, both fed and unfed mites did not show a preference for either type (binomial test, $P = 0.16$ and $P = 0.60$, respectively), although there was significant day-to-day variation in the response of fed mites (50, 36, 63 and 0% towards incubated feathers over the four experimental days). For all experiments, the response rates, i.e. the number of mites making a choice for either of the two arms (provided in brackets in the horizontal bars of Fig. 1), were significantly lower for unfed than for fed mites (logistic regression, $P < 0.05$). There were no effects of feeding status on attractiveness (Fig. 1): choices of fed and unfed mites were not significantly different (logistic regression, $P > 0.05$).

When fed mites were exposed to 2.5% CO₂, they were significantly attracted to this stimulus (binomial test, $P = 0.019$; Fig. 2). However, this response varied significantly over the five experimental days (44, 75, 63, 83 and 100% towards CO₂, respectively). Unfed mites were not attracted towards CO₂ (binomial test, $P = 0.71$). Also when combinations of fresh or aged feathers plus CO₂ were tested versus clean air, only fed mites were significantly attracted (binomial test, $P < 0.001$ and $P = 0.002$ for AF + CO₂ and FF + CO₂, respectively) whereas unfed mites were not (binomial test, $P = 0.31$ and $P = 0.74$ for AF + CO₂ and FF + CO₂, respectively). As was the case in the first series of experiments, response rates (provided in brackets in the horizontal bars of Fig. 2), were significantly lower for unfed than for fed mites (logistic regression, $P < 0.05$). In addition, feeding status affected attractiveness (Fig. 2): choices made by unfed mites towards a stimulus were significantly weaker for all three tests when compared with the choices made by fed mites.

Response towards conspecific mites

Both fed and unfed mites were significantly attracted towards volatiles derived from 200 conspecific fed mites: 84 and 85% of the mites, respectively, chose for the volatiles from fed mites (Fig. 3; binomial test, $P < 0.001$ and $P = 0.003$, respectively). Fed mites were also attracted towards unfed mites (binomial test, $P = 0.005$), but this response varied significantly over the three experimental days (89, 50 and 100%, respectively). Unfed

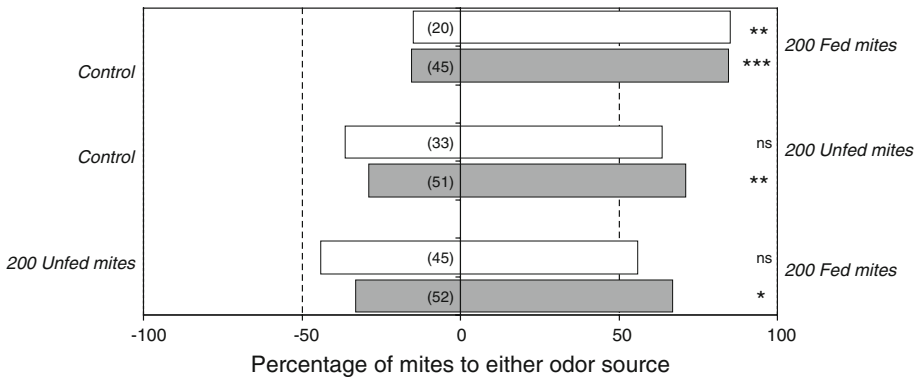


Fig. 3 Response of unfed (white bars) and fed (grey bars) *Dermanyssus gallinae* to 200 conspecific mites. Tests were performed in a Y-tube olfactometer; ns not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The total number of mites (out of 60 tested) choosing one of the two ports is given in parentheses

mites were not attracted to unfed conspecifics (binomial test, $P = 0.16$). When mites were offered the choice between fed and unfed mites, fed mites significantly preferred fed mites (binomial test, $P = 0.018$), whereas unfed mites had no preference for either odor source (binomial test, $P = 0.55$). Response rates were significantly lower for unfed than for fed mites (logistic regression, $P < 0.05$), except for the test where both odors of fed and unfed mites were offered (logistic regression, $P = 0.104$).

Discussion

Our results indicate that volatile cues from conspecific mites and from host-related sources play an important role in the behavioral ecology of *D. gallinae* mites. Because of the fact that these volatile cues mediate interactions between individuals from the same species (mite) or between species (mite and chicken), they can be classified as ‘pheromones’ and ‘kairomones’, respectively (Dicke and Sabelis 1988). In line with our expectations, fed mites, which are probably searching for a place to hide and aggregate with conspecifics after a blood meal, responded strongly to volatile cues from conspecific mites. Interestingly, fed mites were also motivated when host-related cues, including CO_2 , were offered. We expected that unfed (starved) mites would be more responsive than fed mites to the combination of feathers and CO_2 , because both signal the presence of a chicken host from which a blood meal can be taken, but this was not the case. The role of CO_2 in mediating behavioral responses of *D. gallinae* towards host-related volatiles will be discussed below.

A variety of chemical compounds may be responsible for the attraction of *D. gallinae* towards feathers. Lipids from the uropygial (preen) gland waterproof the plumage and inhibit microbial growth, but these compounds are generally not very volatile (Haahti and Fales 1967; Bernier et al. 2008). Therefore, microbial breakdown products of uropygial gland secretions are more likely to serve as kairomones in the host location process. The fact that unfed mites were more attracted to aged than to fresh feathers supports this suggestion, but when we artificially stimulated microbial growth by incubating fresh feathers at 37°C for 7 days, mites did not distinguish between fresh and incubated feathers. Because aged feathers had been in contact with the litter for 3–4 days, it is well possible that other factors, such as litter-associated microbes and chemical components from

manure, play a role in the attraction of the mites towards aged feathers. The diversity and amount of compounds on chicken skin is enormous, and includes alcohols, ketones, diones and aldehydes (Bernier et al. 2008). The fact that the attraction in our study occurred with only a small number of feathers suggests that mites are able to detect low levels of kairomones.

In general, CO₂ is used as a cue by insects and mites for a variety of behaviors such as finding suitable host plants for oviposition (mainly in Lepidoptera), locating living or dead plant material as a food source and detecting suitable hosts for a blood meal by hematophagous insects (Guerenstein and Hildebrand 2008). For example, the blood-feeding mosquito *Aedes aegypti* is capable of detecting small changes in background levels of CO₂: an increase from 0.035 to 0.05% activates these mosquitoes and sensitizes them to human skin odors (Dekker et al. 2005). Similarly, CO₂ may act in synergism with host-specific odors, as is the case in ornithophilic black flies (Fallis and Smith 1964). We found that unfed (starved) mites were not attracted to levels of CO₂ comparable to the amount exhaled by chickens (~2.5%, (Gleeson et al. 1985)). In contrast, recently fed mites were attracted to this concentration of CO₂. Carbon dioxide even appeared to be capable of masking attractive compounds, because the attractiveness of aged feathers to unfed mites was lost in the presence of CO₂. This was contrary to our expectations, because we hypothesized that mites in need of a blood meal are more motivated to respond to CO₂ as a host cue. Kilpinen (2005) found that CO₂ induced a different type of behavior: in response to brief pulses of 5 and 100% CO₂, *D. gallinae* becomes motionless ('freezes') until further stimulated. This behavior was observed in light conditions, but not in the dark. This was interpreted as a defense against being eaten by a potential host. The mites in our experiments were continuously exposed to the airstream with CO₂ and did not show a freezing response within the Y-tube set-up. Mites may thus be able to differentiate between a sudden puff of CO₂, indicating the presence of a potential predator at very close range, and more continuously elevated levels of CO₂ that may make mites responsive to other host related odors, similar to what has been observed with mosquitoes (Dekker et al. 2005). It remains to be elucidated why recently fed mites were attracted to CO₂. After blood feeding, *D. gallinae* searches for a suitable hiding place and aggregates with conspecific mites. Aggregations of mites can also emit small, but detectable levels of CO₂ (C.J.M. Koenraadt, unpublished data). It remains to be investigated whether these CO₂ levels act synergistically with other volatile cues emitted by mites such as aggregation pheromones. Responses of mites towards CO₂ are thus likely to be dose and context dependent.

We hypothesized that unfed mites would not respond strongly to conspecific mites, because they would be more motivated to locate a blood meal than a hiding place with conspecifics. This was indeed the case when unfed mites were exposed to 200 unfed conspecifics. When looking at the response towards fed conspecifics, only few unfed mites made a choice, but those that did choose, strongly preferred the odor of fed conspecifics. We hypothesize that, in contrast to unfed mites, fed mites are more motivated to locate aggregations of conspecific mites. They indeed strongly preferred air led over both fed and unfed conspecifics. This is consistent with earlier findings that demonstrated that aggregations were more quickly formed with fed than with unfed mites (Entrekin and Oliver 1982), but visual and tactile stimuli were not excluded in the experiments of the latter study. The composition of the pheromone that triggers aggregation remains to be elucidated. As is the case with other ectoparasitic arthropods, it probably consists of a blend of various compounds (Sonenshine 1985; Siljander et al. 2008).

For all experiments, the number of unfed mites actually choosing one of the stimuli (response rate) was lower than of fed mites. We think this may be related to the speed with

which mites walked through the Y-tube set-up. Unfed mites were generally walking faster than fed mites (personal observation) and may thus be less likely to remain in one of the ports for 1 min. Another experimental study with medically and economically important mites did not find an effect of starvation on behavioral responses in a Y-tube olfactometer (Skelton et al. 2007). In our study, the only instance where the response rates of fed and unfed mites were similar was when they were offered the choice between both fed and unfed mites. This may be related to the overall stronger stimulus that these mites were exposed to (odors from 400 mites instead of 200 mites).

For poultry farmers, *D. gallinae* poses an increasing challenge in their daily management of the farm. One option as an alternative to conventional spraying of synthetic acaricides is the development of an attract-and-kill strategy. This has shown promising results with other agricultural pests, such as codling moths, fruit flies and banana weevils (Charmillot et al. 2000; Stetter and Lieb 2000; Vargas et al. 2003; Tinzaara et al. 2007). A major advantage of this strategy is that smaller amounts of the killing agent are needed and that this agent can be administered at specific locations. This results in lower exposure and hazard to chickens. It will also slow down the development of resistance to chemical components. Ideally, biological kill components that are more environmentally friendly, such as essential plant oils and entomopathogenic fungi (Kim et al. 2004; Tinzaara et al. 2007; Tavassoli et al. 2008) are incorporated in this strategy. The concealed lifestyle of the mite during the day makes it hard for a pesticide to actually hit the mite. Therefore, an attract-and-kill strategy that ‘brings the pest to the pesticide’ is likely to be more effective. The present study provides stimulating data to address setting up an attract-and-kill-strategy in future studies.

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