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Functional adaptation of two nitrogenous waste products in evoking attraction and aggregation of flour mites (*Acarus siro* L.)

By H. Z. LEVINSON, A. R. LEVINSON and K. MÜLLER

With 4 figures and one table

On Mites: I have observed it to be resident almost on all kinds of substances that are mouldy or putrifying, and have seen it nimbly meshing through the thickets of mould, and sometimes to lye dormant underneath them...

ROBERT HOOKE, 1665

Abstract

Populations of the flour mite *Acarus siro* L. (Acaridae, Astigmata) usually occur in biocoenotic association with a fungal microflora comprising mainly *Acremonium strictum*, *Aspergillus candidus*, *Penicillium chrysogenum* and *Saccharomyces cerevisiae* on stored cereals at high relative humidities. The flour mites excrete their nitrogenous waste mainly as guanine, while the fungi produce ammonia as one of their terminal metabolites. Both end-products of nitrogen metabolism must have acquired, early in the course of evolution, the rôle of intra- and inter-

specific signals: guanine (2-amino-6-hydroxypurine) functions as an assembly pheromone, while ammonia acts as a kairomone being attractive to both sexes of flour mites, particularly before mating. Both chemical signals communicate to flour mites the availability of a nutritious diet and the presence of conspecifics, whereby aggregation, mate finding and reproduction of this species are ensured.

1 Introduction

About half a century ago, NEEDHAM (1938) and FLORKIN (1945) reported that excretion of the poorly water-soluble uric acid (2,6,8-trihydroxypurine) is the major form of nitrogen elimination in various terrestrial arthropods. This indicates that such uricotelic species are capable of converting xanthine (2,6-dihydroxypurine) to

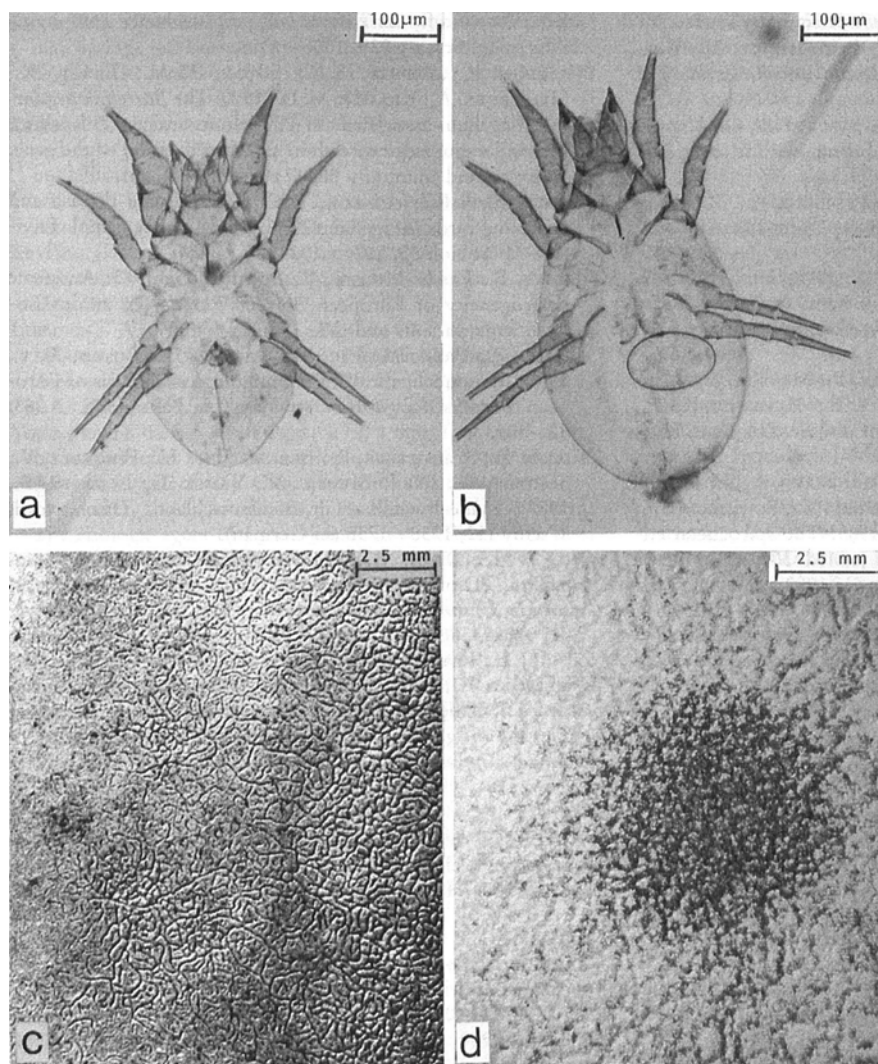


Fig. 1. Magnified view of both sexes of the flour mite, *Acarus siro* L. (mounted in Heinze's medium).

(a) Ventrum of an adult male (natural length $\sim 440\ \mu\text{m}$) which reveals the stout forelegs with a femoral spur, triangle-like genital folds between the coxae of the hindlegs as well as one adhesive sucker on either side of the anal slit.

(b) Ventrum of an adult female (natural length $\sim 570\ \mu\text{m}$) showing an egg situated somewhat below the genital folds.

(c) Grooves formed by movements of numerous flour mites in a thin layer of powdery diet ($\sim 3.7\times$ natural size).

(d) Dense aggregation of male and female flour mites in a powdery diet being infested by mould species of the genera *Acremonium*, *Aspergillus* and *Penicillium* ($\sim 5.7\times$ natural size).

uric acid which is disposed in solid form with consequent conservation of water. Hence we were surprised to discover substantial amounts of guanine (2-amino-6-hydroxypurine) in the hindgut and dry faeces of the flour mite which appears to lack the enzymes required for guanine conversion to xanthine and uric acid.

The flour mite is a minute acarid species (fig. 1 a–d, average length of idiosoma in males $\sim 390\ \mu\text{m}$, in females $\sim 500\ \mu\text{m}$) which mainly occurs in temperate zones as a common pest of stored foodstuffs (including cereal flours, damaged grain, yeast, fungus species, dried fruits and cheese). Unlike other arthropod species inhabiting food stores, *A. siro* has a conspicuous preference for high atmospheric humidity and responds to a regimen of $\sim 90\%$ relative humidity and $\sim 25^\circ\text{C}$ by a maximal rate of reproduction (SOLOMON, 1962). The above mite species, for which water conservation is obligatory, eliminates its nitrogenous waste mainly as guanine, which is about five times less water-soluble than the scarcely water-soluble uric acid. The solubility of the latter is $\sim 1:4 \times 10^4$, while that of the former is $\sim 1:2 \times 10^5$ at $18\text{--}20^\circ\text{C}$.

The moist food substrate of *A. siro* (broken and sprouted wheat with baker's yeast) is usually infested by

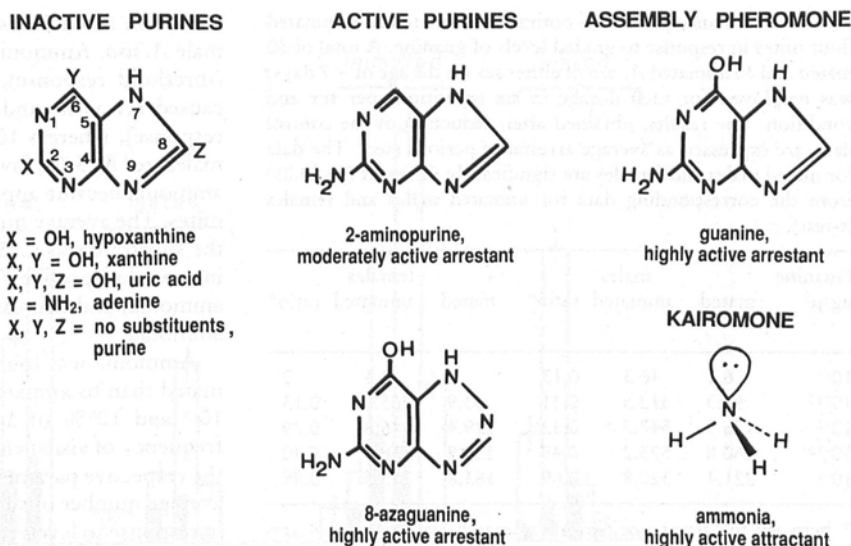
a microflora consisting mainly of *Acremonium strictum*, *Aspergillus candidus*, *Penicillium chrysogenum* (Fungi imperfecti) as well as *Saccharomyces cerevesiae* (Endomycetes). Certain amino acids and possibly some nucleotide purines originating from the food substrate of *A. siro* are usually degraded by the above microflora to yield gaseous ammonia, among other terminal metabolites.

The scope of the investigation described below was to elucidate the eco-physiological significance of guanine and ammonia in the behaviour of flour mite populations being maintained at a constant microclimate. Fig. 2 reveals the molecular configuration of guanine, several other purines and ammonia in correlation with the biological activity of those catabolic end-products.

2 Material and Methods

The laboratory culture of *A. siro*, originally derived from a strain of Prof. Dr. W. KNÜLLE (Institute of Applied Zoology, University of Berlin), was maintained since 1988 on a diet of 82.0% broken wheat, 14.4% sprouted wheat, 3.6% baker's yeast (Gist-Brocades, Delft) and the above fungal microflora at $22 \pm 0.2^\circ\text{C}$, $85\text{--}90\%$ relative humidity and complete darkness.

Fig. 2. Molecular configuration of some purines and ammonia which are either active or inactive for male and female flour mites. Guanine (2-amino-6-hydroxypurine) is a metabolic waste product of *A. siro* and ammonia is a dietary decomposition product of certain *Ascomycetes* occurring in biocenotic association with flour mites.



Unmated flour mites of either sex were collected by retaining single resting tritonymphs in gypsum-lined chambers (volume ~ 500 µl) until the emerged adults were 7 days old (LEVINSON et al., 1989). Groups comprising 5 male and 5 female flour mites were kept together from emergence until the age of 7 days (allowing 6–12 matings), whereupon they were employed as mated.

The chemosensory responses of unmated and mated *A. siro* were investigated in a glass-covered, circular arena (diam. ~ 15 mm, rim height ~ 8 mm) consisting of a sheet of porous tissue paper adjusted above a horizontal sheet of filter paper. Graded amounts (from 10⁻³ to 10⁻¹ µg per µ²) of a purine base or derivative were placed in a central, circular region (diam. ~ 2 mm) between the above filter and tissue paper, whereby the test substance was compressed in the space between the two layers. In an additional set of experiments, an open glass vial (diam. ~ 15 mm, height ~ 3 mm) comprising 1.0 µl of aqueous ammonia solutions (ranging from 10⁻⁴ to 10⁰% of NH₃) was centrally deposited below the horizontal arena of porous tissue paper. Under experimental conditions (22 ± 0.1 °C, 60–65% r.h. and ~ 450 Lux), gaseous ammonia was released within 30 min from the above test solutions.

Number and duration of visits made by female and male *A. siro* in the central region of the arena (delivering the test compounds) as well as the frequency of mite penetration through the centre of the arena were recorded for periods of 30 min. Observations were carried out under a binocular microscope at a magnification of ~ 10×.

Faecal guanine was estimated by the reaction between the former and p-diazobenzenesulfonic acid (SHAPIRO, 1968) as well as by guanine conversion by guanase and xanthine-oxidase (VAN BRONSWIJK et al., 1989) to yield uric acid. Nessler's reagent was employed for the determination of ammonia.

3 Results

3.1 Guanine as an assembly pheromone

Our results showed that batches of 25 female and 25 male flour mites discharge 20–100 µg of guanine per batch to their food substrate within two weeks following emergence, while guanine excretion of females exceeds that of males ~ 1.4–2.0 times. Guanine was found to induce arrestance in unmated female and male *A. siro* and to a lesser extent in mated flour mites of both sexes. Moreover, female and male *A. siro* perform intense dig-

ging movements by both forelegs (fig. 1 a, b) in presence of guanine levels ranging from 10^{-2.3} to 10⁻¹ µg/µ².

Fig. 3 reveals that a level of 10⁻³ µg guanine/µ² causes an arrestance period of ~ 46 sec in unmated males but fails to induce arrestance in unmated females of *A. siro*, while 10^{-2.3} µg guanine/µ² elicits respective arrestance periods of ~ 312 sec in unmated males and ~ 265 sec in unmated females, at average. A guanine level of 10⁻² µg/µ² induces maximal arrestance periods, i.e. ~ 547 sec in unmated males and ~ 446 sec in unmated females, whereas guanine levels exceeding 10⁻² µg/µ² elicit definitely shorter arrestance periods in both sexes of unmated flour mites. Levels of 10^{-1.3} and 10^{-1.0} µg of guanine/µ² cause respective arrestance periods of ~ 523 and ~ 320 sec in unmated males

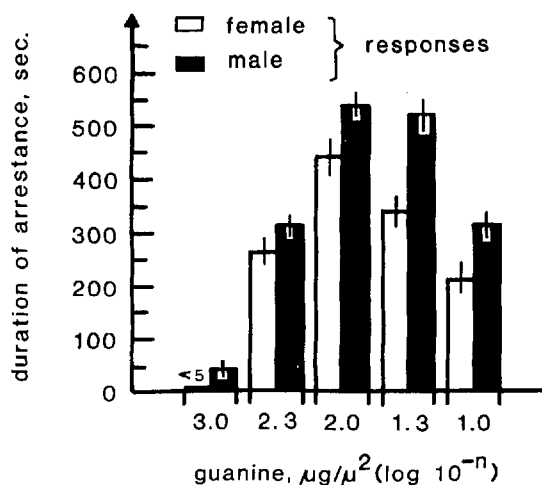


Fig. 3. Assembly pheromone action of graded levels of guanine (ranging from 10⁻³ to 10⁻¹ µg per µ²) on unmated male and female *A. siro*, at an age of ~ 7 days. Each column represents the average arrestance period of 5 flour mites in 6 repetitions (after subtraction of the control data) as well as the corresponding standard error (vertical line). The results concerning unmated males and females are significantly different (0.05 > p > 0.01) except for the data concerning 10^{-2.3} µg guanine/µ² (t-test).

Table 1. Arrestance periods of both sexes of mated and unmated flour mites in response to graded levels of guanine. A total of 30 mated and 30 unmated *A. siro* of either sex (at the age of ~ 7 days) was employed for each dosage in six repetitions per sex and condition. The results, obtained after deduction of the control data, are expressed as average arrestance periods (sec). The data for mated males and females are significantly different ($p < 0.01$) from the corresponding data for unmated males and females (*t*-test).

Guanine $\mu\text{g}/\mu^2$	males			females		
	mated	unmated	ratio*	mated	unmated	ratio*
10^{-3}	6.1	46.3	0.13	0	2.4	0
$10^{-2.3}$	97.3	312.5	0.31	33.9	265.6	0.13
10^{-2}	176.5	547.7	0.32	129.4	446.8	0.29
$10^{-1.3}$	260.8	523.2	0.49	136.2	338.5	0.40
10^{-1}	221.4	320.8	0.69	183.8	215.3	0.85

* between the arrestance periods of mated and unmated *A. siro*

as well as ~ 338 and ~ 215 sec in unmated females. It follows that the responses of unmated males to guanine are about 1.2–1.5 times stronger than the corresponding responses of unmated females of *A. siro* (fig. 3). Interestingly enough, guanine levels ranging from $10^{-2.3}$ to $10^{-1} \mu\text{g}/\mu^2$ induce arrestance periods which are ~ 69–30 % shorter in mated than in unmated males and ~ 87–15 % shorter in mated than in unmated females. The gap between the arrestance periods of mated and unmated flour mites decreased upon increasing the guanine level per surface unit (table 1).

3.2 Structural requirements for pheromone activity

The function of guanine (2-amino-6-hydroxypurine) as an assembly pheromone for flour mites appears to be highly specific, since both sexes neither respond to purine (imidazo[4,5-d]-pyrimidine), hypoxanthine (6-hydroxypurine), xanthine (2,6-dihydroxypurine), uric acid (2,6,8-trihydroxypurine) nor to adenine (6-aminopurine) when offered in levels ranging from 10^{-3} to $10^{-1} \mu\text{g}/\mu^2$ (fig. 2). However, 2-aminopurine exerts a clearcut arrestant activity in both sexes of *A. siro*, indicating the particular importance of an amino group on carbon 2 of the purine moiety. 8-Azaguanine (2-amino-6-hydroxy-8-azapurine) is the only compound, among ten purines tested, which shows an arrestant activity like that of guanine. The molecular structure of 8-azaguanine closely resembles that of guanine except for having a trivalent nitrogen instead of the methyne group in position 8 (fig. 2). It follows that the structural requirements for assembly pheromone activity include the purine ring system, an amino group on carbon 2, a hydroxyl group (or oxygen) on carbon 6 as well as a carbon or nitrogen atom in position 8.

3.3 Ammonia as an attractant

Gaseous ammonia, a microbial degradation product of certain amino acids and nucleotide proteins, was found to be highly attractive for male and moderately attractive for female flour mites. Fig. 4 reveals a marked dependence between the ammonia dosage and the degree of

attraction as well as substrate penetration of female and male *A. siro*. Ammonia levels of 10^{-4} % evoked 0.75 visits (threshold response), 10^{-3} % induced 1.5 visits, 10^{-2} % caused 6.1 visits and 10^{-1} % elicited 8.5 visits (optimal response), whereas 10^0 % subdued the visits of unmated males to 3.25, at average. At dosages beyond 10^0 %, ammonia became appreciably toxic to both sexes of flour mites. The average number of unmated males penetrating the substrate was 0.75 in presence of 10^{-3} % ammonia; it increased respectively to 2.3 and 2.0 at 10^{-2} and 10^{-1} % of ammonia, and decreased to 0.25 in presence of 10^0 % of ammonia.

Ammonia was found to be definitely less attractive to mated than to unmated males of *A. siro* (fig. 4). Levels of 10^{-1} and 10^0 % of ammonia evoked in mated males a frequency of visits which was ~ 86 and ~ 88 % lower than the respective parameters recorded in unmated males. The average number of substrate penetrations by mated males in response to levels ranging from 10^{-3} to 10^{-1} % ammonia was 68–50 % lower than those observed in unmated males.

The average number of visits performed by unmated females was 2.0 in response to 10^{-2} %, 4.25 due to 10^{-1} % and 5.75 in response to 10^0 % of ammonia. The average number of substrate penetrations by unmated females was 1.0 in response to 10^{-2} %, 1.5 due to 10^{-1} % and 1.75 in response to 10^0 % of ammonia. Moreover, ammonia was found to be distinctly less attractive to mated than to unmated females of *A. siro*. At a level of 10^0 %, ammonia elicited in mated females a frequency of visits and penetrations being ~ 70 and ~ 86 % lower than the respective parameters observed in unmated females (fig. 4).

It is noteworthy that mated males of *A. siro* avoided an ammonia level of 10^0 %, while unmated males responded to this dosage by performing 3.25 visits, at average. Moreover, mated females responded to 10^0 % of ammonia by 1.25 visits, whereas unmated females displayed 5.75 visits (maximal response) in presence of the same dosage. Comparison between the threshold levels of ammonia inducing attraction of flour mites revealed that the males are at least 10^2 times more responsive to ammonia than the females being either unmated or mated (fig. 4).

4 Discussion

4.1 Functional adaptation of terminal products of protein and purine metabolism as attractants and arrestants

The above results permit the conclusion that two terminal products of nitrogen metabolism have attained the rôle of chemical signals promoting attraction and arrestance in *A. siro*. Guanine, a nonvolatile excretory metabolite of *A. siro*, functions as an assembly pheromone particularly for unmated flour mites of both sexes, while gaseous ammonia, a microbial degradation product of certain amino acids and purines, acts as an efficient attractant for male and female *A. siro*, particularly before mating (fig. 2). Our results recall the assumptions of MOORE (1967) and THIESSEN (1977) indicating that end-products of metabolic processes rather than compounds produced by *de novo* biosynthesis are employed as food and sex attractants. The above hypothesis is supported

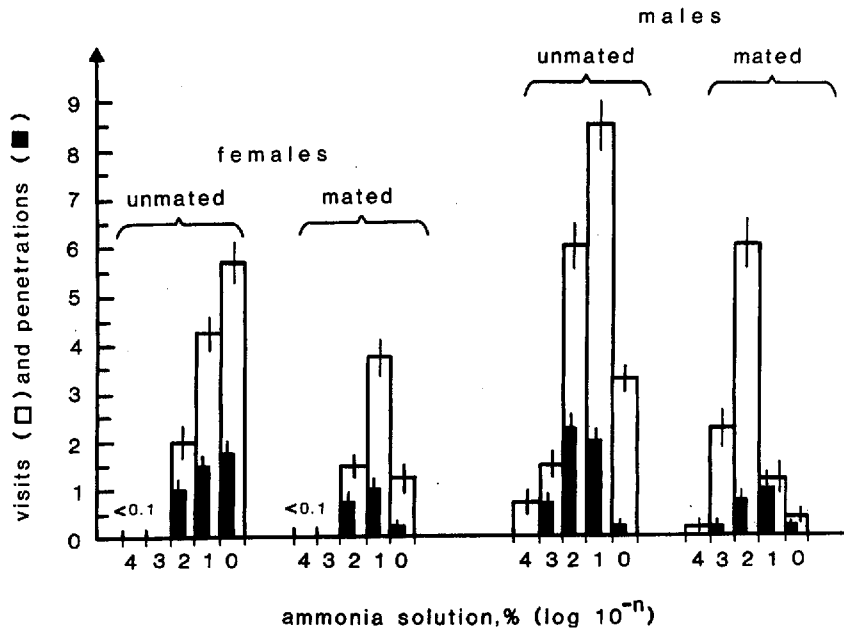


Fig. 4. Kairomone action of graded levels of ammonia (ranging from 10^{-4} to $10^0\%$) on unmated and mated flour mites of both sexes, at an age of ~ 7 days. Each column represents the average number of visits (white rectangles) and substrate penetrations (black rectangles) performed by 5 flour mites in 8 repetitions per sex, condition and dosage (after deduction of the control data) as well as the relevant standard error (vertical line). The frequency of visits and substrate penetrations by unmated females and

males is significantly different ($0.05 > p > 0.01$) at levels extending from 10^{-4} to $10^0\%$. The frequency of visits and penetrations differs significantly ($p < 0.01$) at $10^0\%$ between unmated and mated females. The number of visits differs significantly ($p < 0.01$) at 10^{-1} and $10^0\%$ between unmated and mated males, while the number of substrate penetrations differs significantly ($p < 0.01$) at levels ranging from 10^{-3} to $10^{-1}\%$ between unmated and mated males (t-test).

by the functional adaptation of ammonia and guanine, being the end-products of metabolic pathways which prevailed in ancestral organisms of aquatic and terrestrial habitats.

Faecal guanine deposited by *A. siro* in their biotope is exceedingly insoluble in water, while it will be readily dissolved in aqueous ammonia and become adsorbed on the food substrate of the mites. While walking at random, flour mites are likely to perceive such guanine residues by their tarsal contact chemoreceptors (on both forelegs), become arrested thereby and eventually assemble near the faecal deposits of their conspecifics (fig. 1 d). The respective threshold levels of guanine as an assembly pheromone for unmated male and female *A. siro* are $\sim 10^{-3}$ and $\sim 10^{-2.3} \mu\text{g}/\mu^2$, whereas the sex pheromones emitted by unmated flour mites act at different threshold levels than the assembly pheromone: attraction and mating of males are induced by $\sim 10^{-4}$ equivalent of the female's sex pheromone, while attraction and arrestance of females are evoked by $\sim 10^{-1}$ equivalent of the male's sex pheromone (LEVINSON et al., 1989).

The mode of nitrogen excretion in certain species of soft ticks (Argasidae) as well as hard ticks (Ixodidae) (HAMDY, 1972, 1973, 1977; OTIENO et al., 1985) resembles the respective process in the humidity-dependent flour mite. Moreover, guanine was found to induce aggregation, e.g. in larvae of *Amblyomma cohaerens*, in nymphs of *Ornithodoros porcinus porcinus*, in adults of *Rhipicephalus appendiculatus* (OTIENO et al., 1985; HASSANALI, 1989) as well as in young nymphs and adults

of *Argas walkerae* (GOTHE, 1987). However, the pheromone activity of guanine has a lower specificity in nymphs of *Argas persicus* (OTIENO et al., 1985) than in adult *Acarus siro* which tolerate only minor changes in the structural configuration of 2-amino-6-hydroxy-purine (fig. 2).

Ammonia is a highly diffusible and water-soluble gas which can be produced by enzymic degradation of proteins (deamination of amino acids) and nucleic acids (oxidative catabolism of guanine and adenine) in various aquatic and semi-aquatic organisms. The ammonotelic larvae of several muscid species (e.g. *Calliphora vicina*, *Hylemyia antiqua* and *Lucilia cuprina*) were shown to aggregate in response to ammonia being released by the former to their biotope (ZVEREVA, 1989), while females of the uricotelic muscid adults were also found to be attracted by ammonia to suitable oviposition sites (BARTON BROWN, 1965). The threshold level of ammonia for the aggregation of third instar larvae of *Musca domestica* is $\sim 10^{-1}\%$ (ZVEREVA, 1989), while the corresponding ammonia level for the attraction of adult *M. domestica* is $\sim 10^{-6}\%$ (WIETING and HOSKINS, 1939).

As evident from fig. 4, unmated male and female flour mites are capable of perceiving relatively low ammonia concentrations by their olfactory sensilla which thus enable them to approach an ammonia source by oriented movements. The threshold responsiveness of *A. siro* to ammonia ranges from $\sim 10^{-4}\%$ in unmated males to $\sim 10^{-2}\%$ in unmated females. The susceptibility to ammonia in unmated flour mites is thus $\sim 10^1$ to 10^3 fold

higher than the respective parameter of housefly larvae and $\sim 10^2$ to 10^4 fold lower than that of adult houseflies.

4.2 Ecological considerations

It became evident that populations of *A. siro* coexist in a biocoenotic relationship with a microflora of *Acremonium strictum*, *Aspergillus candidus*, *Penicillium chrysogenum*, *Saccharomyces cerevisiae* and some less conspicuous species. The joint action of the kairomone ammonia and the pheromone guanine results in attraction and aggregation of flour mites (fig. 1d) on a substrate which provides an adequate diet for *A. siro* as well as the above fungal species. It is worth recalling that *A. siro* rarely consumes wheat endosperm unless it is mouldy (SOLOMON, 1962) and that this species has a marked dietary preference for certain seed-borne fungi (GRIFFITHS, 1959) which may fulfil the nutritional requirements of *A. siro* for growth and reproduction (SINHA, 1966, 1968). Hence it is conceivable that flour mites also contribute to the regional dispersal of fungal conidia and ascospores. The combined supply of ammonia and guanine signals to flour mites the availability of a nutritious diet with a fungal microflora and the presence of their conspecifics. This will encourage further aggregation, mate finding and reproduction, particularly of unmated male and female *A. siro* as well as propagation of the above fungal microflora.

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Zusammenfassung

Funktionsanpassung zweier Endprodukte des Stickstoff-Stoffwechsels als lockwirksames Kairomon und Aggregationspheromon für Mehlmilben

Mehlmilben (*Acarus siro*) leben in Gemeinschaft mit Schlauchpilzen der Gattungen *Acremonium*, *Aspergillus*, *Penicillium* und *Saccharomyces* an Nahrungsvorräten zu wechselseitigem Vorteil (Biocoenose), wobei die Mehlmilben wasserunlösliches Guanin (2-Amino-6-Hydroxypurin) ausscheiden und die genannten Pilzarten gasförmiges Ammoniak abgeben. Die Verwendung beider terminalen Stickstoffmetabolite als Botenstoffe dürfte in einem relativ frühen Stadium der Phylogenese stattgefunden haben: Bei Mehlmilben übernahm Ammoniak die Rolle eines anlockenden Kairomons und Guanin die Aufgabe eines aggregationsfördernden sowie strukturspezifischen Pheromons. Im Endeffekt tragen die genannten Schlauchpilze zum Populationsaufbau noch ungepaarter Mehlmilben bei, während diese für Verbreitung der Schlauchpilze an gespeicherten Nahrungsmitteln sorgen.

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