Israel Journal of Entomology
Vol. XVI (1982) pp. 87-97

PHEROMONES OF ANTS OF ISRAEL: I. THE ALARM-DEFENSE SYSTEM OF SOME LARGER FORMICINAE

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ABSTRACT

Chemical analysis of the Dufour's gland and the poison gland of 12 species belonging to the genera *Camponotus*, *Cataglyphis* and *Polyrhachis* was undertaken. Formic acid was the only component of the poison gland and was omnipresent in all species. It is the prime alarm pheromone. The Dufour's gland constituents, however, varied within each genus and the composition of the secretion seems to be species specific. The responses to the Dufour's gland constituents vary with the species and are apparently correlated to the ants' foraging behaviour.

INTRODUCTION

Aggressiveness and quick recruitment in response to an apparent enemy is a hall-mark of the social insects. The information regarding the enemy is transmitted by the insect to its nestmates by emitting an alarm pheromone from one of its various exocrine glands and the magnitude of the response depends upon the species involved (Blum and Brand 1972; Parry and Morgan 1979 and references therein).

In the Formicinae, multiple glands are implicated in this alarm defense system. While in *Acanthomyops claviger* (Roger) (Regnier and Wilson, 1968) or *Oecophyla longinoda* (Latreille) (Bradshaw *et al.*, 1975; 1979), mandibular glands, Dufour's gland and the poison gland are involved in eliciting alarm behaviour, several *Camponotus* species have reduced mandibular glands and they resort to their adnexal gland to release the same behaviour (Ayre and Blum, 1971). Quantitative measurements of the alarm reaction of *Formica rufa* (Linnaeus) revealed that there is an additive effect on the behaviour, when the ants are exposed simultaneously to formic acid and the Dufour's gland hydrocarbons (Lofqvist, 1976). Similar results had been found in *Camponotus pennsylvanicus* (Degeer) (Ayre and Blum, 1971).

Our early observations in the field indicated that species that foraged individually did not react as expected to the Dufour's gland exudate. Moreover, the alarm defense behaviour of these species was considerably different from species that exhibit mass foraging. In the present paper we have described the chemical nature and behaviour of the alarm response of some of the larger Formicinae of Israel.

METHODS AND MATERIALS

Insects

Field collected colonies of ants were reared in the laboratory in artificial nests and maintained on honey and dead insects. The different species of *Camponotus* were collected as follows: *C. sericeus* (Fabricius) from the Arava Valley near Hatzeva; *C. thoracicus fellah* (Emery) from various localities in Israel; *C. thoracicus sanctoides* (Forel) in Tel Aviv; *C. lateralis rebeccae* (Forel) on Mount Meron and *C. gestroi* (Linnaeus) on Mount Hermon (2000 m altitude).

Species of *Cataglyphis* were collected as follows: *C. nigra* (André) from various localities in Israel; *C. viaticoides* (André) and *C. livida* (André) near Tel Aviv; *C. isis** (Forel) and *C. bombycina* (Wheeler) near Eilat and *Polyrhachis simplex* (Mayr) were collected from Ein-Gedi and Hatzeva.

All ant species were kindly identified by Prof. J. Kugler, Department of Zoology, Tel Aviv University.

Chemical Analysis

Chilled living ants were dissected under cold water, their glands excised and extracted in methylene choride or alternatively in pentane. Chemical analysis was achieved using a combined Gas Chromatograph-Mass Spectrometer (LKB 9000), using a 3.7 m 10% SP 1000 column, programmed from 60°C to 220°C at 10°C/min. The components of each extract were identified by their mass spectra, which were compared with spectra of authentic samples.

Further analysis of individual glands was conducted by Gas Chromatography (Tracor 560), using a SE54 capillary column (15m x 0.25mm). Every single gland was extracted in 50 ul pentane, and 1 ul of each extract was immediately injected into the Gas Chromatograph. In several small species the amount of secretion was too small for analysis. In these cases, a pool of 10 glandular exudates extracted in 50 ul solvent was used. Whenever possible the ants used were of different colonies, otherwise they were individuals belonging to the same colony.

Before every group of analyses, a preliminary run of standards and samples were performed to verify retention times under the specified conditions. At least one coinjection of sample and standards was also done. Peak area was measured for each peak and its relative amount calculated.

Histological Studies

For histological observation, glands were dissected in Levy physiological saline (9.00 g NaCl; 0.708 g KCl and 0.458 g $CaCl_2$ in 1 litre distilled water), and placed in cold (4°C) Bouin's solution overnight. The tissue was washed in 70% ethanol and dehydrated in graded ethanol. Glands were embedded in Butanol and Paraplast. Serial sections of 8 um were stained with Ehrlich hematoxylin eosin.

For electron microscope observations, the glands were fixed in 3.5% glutaral-

*The identification of this species as *C. isis* is not certain as yet.

dehyde, buffered at pH 7.4 with 0.1 M sodium cacodylate. The glands were fixed for 24 hr at 4°C and then rinsed thoroughly in sodium cacodylate buffer. Post-fixation was performed for 1 hr in the same buffer to which 1% osmium tetroxide was added. The glands were rinsed as before and then stained with saturated uranyl acetate for 20 min. After fixation and total staining the glands were dehydrated in graded ethanol and embedded in Epon 812. They were sectioned with a LKB Ultramicrotome and then double-stained in uranyl acetate, followed by lead citrate and studied under a Jeol 100B electron microscope.

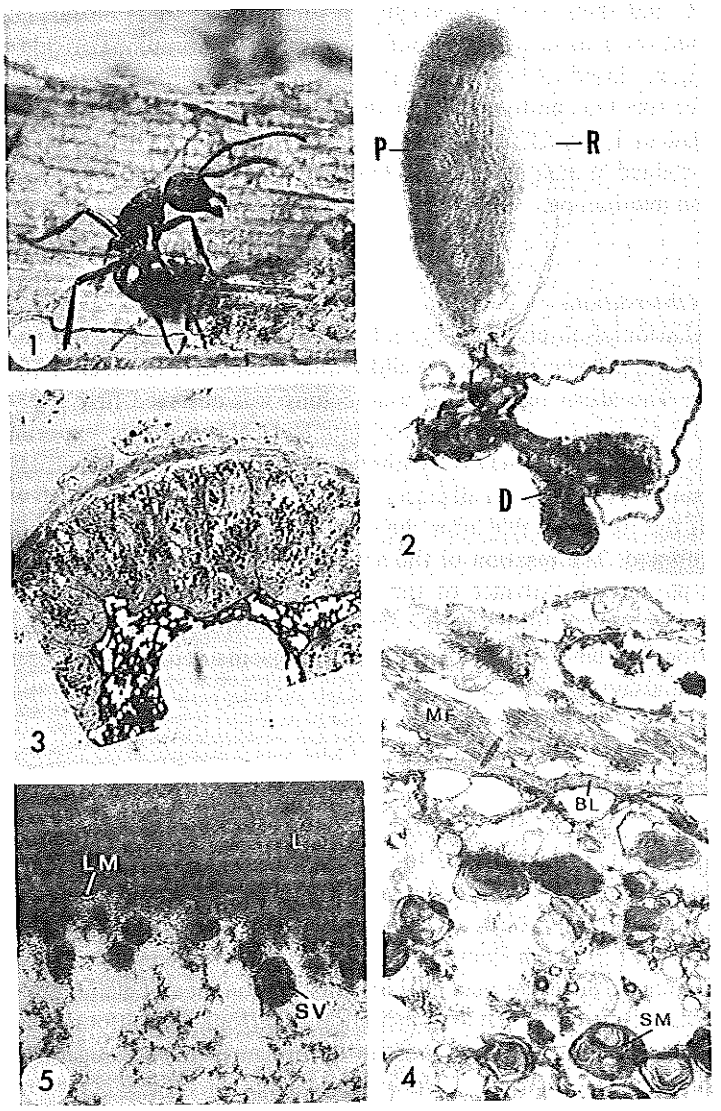
Behavioural Observations

For behavioural observation, the ant colonies were transferred to a special foraging arena (0.6 x 2 m) where they were allowed to acclimatize for at least 10 days prior to any assay. The alarm response of each colony was observed first after physically disturbing the arena and then, after the ants had calmed down, exposing them to glandular exudate or alternatively to synthetic compounds. The chemicals assayed were applied in a suitable solvent to small pieces of cardboard (5 x 5 mm), which were placed randomly on the foraging table after the solvant had evaporated, along with a control piece of cardboard. The reaction of the ants was recorded and compared to that obtained after physical disturbance of the arena. Attraction of the ants to the assayed cardboard was compared to that of the control cardboard and expressed as per cent of total attraction. All laboratory bioassays were supplemented by field observations as well as field bioassays.

Results

Formicine ants react typically to any disturbance in their foraging area by quick running towards its source with extended mandibles and protruding antennae. Upon arrival near the disturbing object, they attain a typical defensive posture and emit a stream of defensive secretion from the tip of their abdomen (Fig. 1).

The source of the secretions in these ants is a complex of glands associated with the vestigial sting apparatus, including the poison gland and the Dufour's gland (Fig. 2). The appearance of these glands was similar in all formicine ants investigated. The poison gland is composed of a secretory part, which is long, narrow and convoluted, and lies adanate to the rather transparent poison reservoir. The secretion of the formicine poison gland is comprised of a single component, formic acid. Dufour's gland, on the other hand, is much smaller and bilobed, but at times, when the gland is partially full, it appears as having one lobe only. Both Dufour's and the poison glands empty via separate ducts into the acidopore, which is situated at the tip of the abdomen. Histology of the Dufour's gland revealed that it is built of a single layer of elongated cells which are filled with droplets of oily secretion (Fig. 3). This secretion, as seen in the electron micrograph (Fig. 4), forms micelles due to its hydrophobic nature. As the micelles migrate towards the lumen of the gland, they turn into secretory vesicles that finally pass through the lumen wall and accumulate in the glandular lumen wall and accumulate in the glandular lumen as oily secretions (Fig. 5).



Figs. 1-5. Behaviour and glands of ants. 1. *Polyrhachis simplex* in a typical alarm-defensive posture. 2. The adnexal glands of *Cataglyphis bicolor.* P – the convoluted poison gland. R – Poison reservoir. D – Dufour's gland. The glands were dissected from emerging ants and mounted in Hoyer's mounting medium. 3. Cross section of the Dufour's gland of *P. simplex*, emphasizing the epithelial monolayer and the granules of secretion. 4. Electron micrograph of the Dufour's gland of *P. simplex* (x 36000). SM – Secretory micelles, M – Mitochondrion, C.M. – Cell membrane, B.L. – Basement lamina, MF – Microfibriles. 5. Electron micrograph of the Dufour's gland of *P. simplex* (x 72000). SV – Secretory Vesicles. LM – Luminar Membrane. L – Glandular Lumen.

The Dufour's glands belonging to the formicine ants investigated, appear to synthesize exclusively hydrocarbons. The secretion, however, is not uniform, but seems to be species specific. Figure 6 represents typical gas chromatograms of the glandular constituents in five species of *Camponotus*. The secretion produced by *C. thoracicus fellah* is dominated by undecane, which constitutes over 90% of the total amount (Table 1). Undecane is also the prevalent compound in the glandular secretion.

TABLE 1. DUFOUR'S GLAND'S CONSTITUENTS OF 5 SPECIES OF *CAMPONOTUS*.
Numbers are expressed as percent of total peaks area.

Peak No.	Compound	Camponotus sericeus[1]	Camponotus gestroi[1]	Camponotus lateralis rebeccae[2]	Camponotus thoracicus fellah[1]	Camponotus thoracicus sanctoides[1]
1	Decane	–	–	–	2.5 ± 0.5	t
2	Undecane	3.4 ± 0.9	11.6 ± 1.6	2.0	92.0 ± 2.6	75.5
3	Dodecane	1.8 ± 0.2	t	2.0	1.0 ± 0.5	t
4	Tridecene	–	–	2.0	1.5 ± 0.3	–
5	Tridecane	70.7 ± 6.3	21.0 ± 1.7	93.4	4.5 ± 1.6	11.0
6	7-methyltridecane	9.0 ± 2.0	–	–	–	–
7	5-methyltridecane	9.0 ± 2.0	–	–	–	–
8	Tetradecane	0.8 ± 0.4	–	–	–	t
9	Pentadecene	t	t	–	–	4.0
10	Pentadecane	10.0 ± 2.8	15.2 ± 2.2	0.6	0.5 ± 0.2	t
11	5-methylpentadecane	–	30.3 ± 2.5	–	–	–
12	Hexadecane	1.5 ± 1.1	8.9 ± 2.5	–	–	–
13	Unknown	–	–	–	–	9.5
14	Heptadecene	3.1 ± 0.5	–	–	–	–
15	Heptadecane	2.8 ± 0.6	12.6 ± 3.4	–	1.0 ± 0.3	t

1. Relative amounts are calculated from averages of 10 individually analysed glands.
2. Relative amounts were calculated from one sample of pooled glands.

In the latter case, however, tridecane appears in larger amounts (11%) than in *C. thoracicus fellah* (2.0%). *C. thoracicus sanctoides*, in addition, has another component eluting at 169°C, whose identity is yet unknown, and comprises 9.5% of the total amount. In two other species, *C. lateralis rebeccae* and *C. sericeus*, tridecane is the major compound while undecane appears only in minor quantities. In all other respects, however, the secretion of these two species differs. The secretion of *C. sericeus* is rather diverse and exhibits two methyl branched alkanes, 7-methyltridecane (0.7%) and 5-methyltridecane (9.0%), that are totally lacking in *C. lateralis rebeccae*, the latter having little besides tridecane.

The secretion of *C. gestroi* is dissimilar from all other *Camponotus* species investigated. Rather than having a dominant component, there are 6 components, each of which is in appreciable amounts. The secretion is also unique in having 5-methylpentadecane and large amounts of pentadecane and heptadecane.

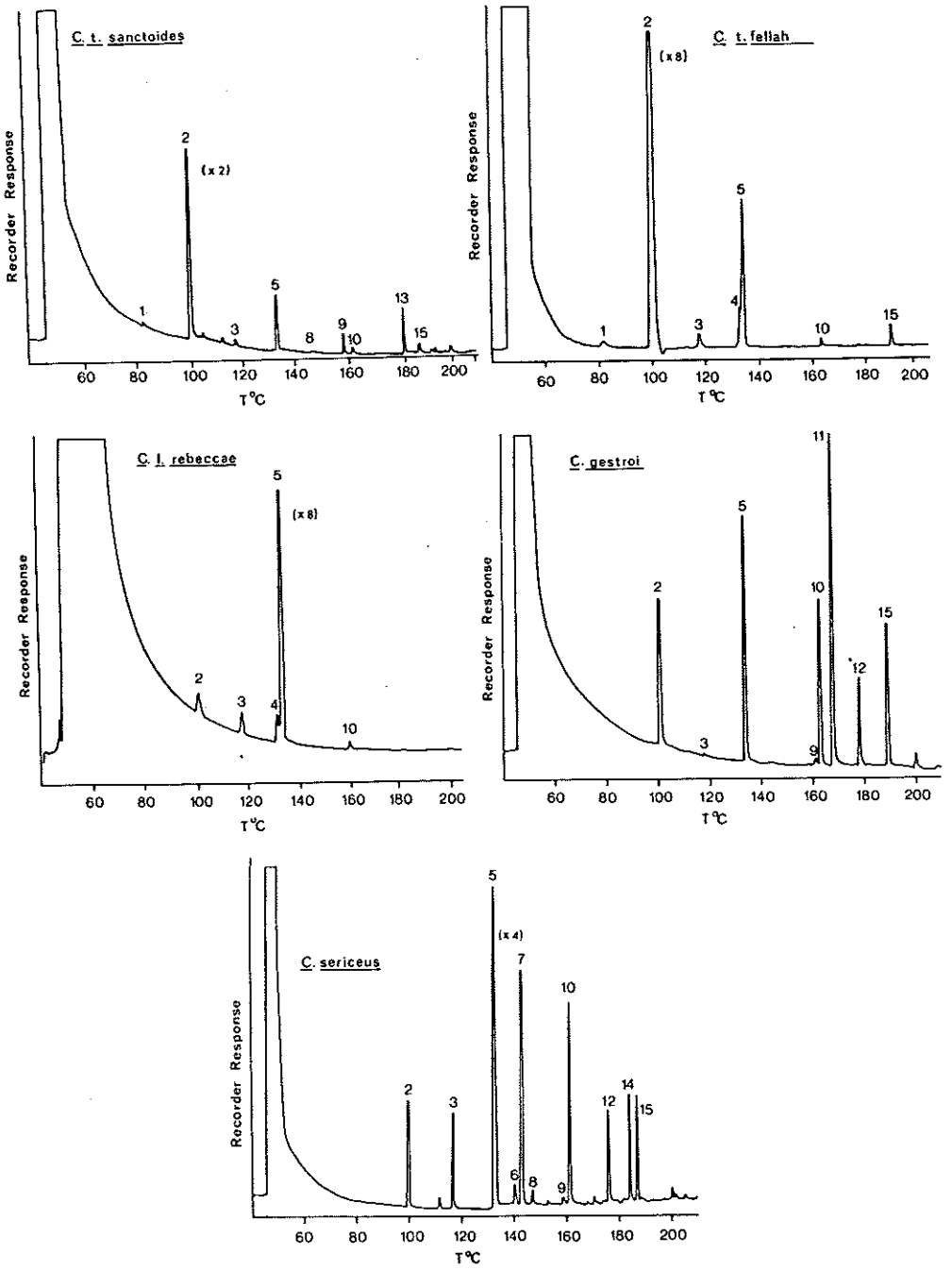


Fig. 6. Typical chromatogram of the Dufour's gland exudate of 5 species of *Canponotus*. Samples were run on an SE 54 capillary column from 60°C to 200°C at 10°C/min.

The Dufour's glands of *Cataglyphis* species are also characterized by the production of hydrocarbons exclusively. Like in *Camponotus*, the different components accumulate in the gland in different amounts, resulting in a species specific secretion (Table 2). It is interesting to compare the secretions of two closely related species, *C. livida* and *C. viaticoides*. In both, tridecane is the major component, comprising about half of the total secretion, but the rest of the components appear to give each of the species a unique blend. *C. viaticoides* exhibits hexadecane in its secretion, which is totally lacking in *C. livida*. The latter, on the other hand, has 3 times as much undecane as has *C. viaticoides*. A third species having tridecane as its major glandular product is *C. nigra*, where it is accompanied mostly by undecane and pentadecane. In *C. nodus* the major component of the Dufour's gland secretion is pentadecane (68%), as compared to 11% in *C. nigra*, while tridecane appears in relatively low amounts. *C. nodus* is also distinguished by the production of heptadecane, a compound totally lacking in *C. nigra*. Pentadecane is also the major hydrocarbon in the Dufour's gland of *C. bombycina* and, like in *C. nodus*, it is accompanied mainly by tridecane and heptadecane. Unique in all formicine analyzed, is the secretion of *C. isis*, which has hexadecane as its major component, accompanied by tridecane and small amounts of octadecane.

TABLE 2. DUFOURS' GLAND CONSTITUENTS OF 6 SPECIES OF *CATAGLYPHIS*.
Numbers are expressed as percent of total peaks area.

Peak No.	Compound	Cataglyphis nigra[1]	Cataglyphis nodus[1]	Cataglyphis viaticoides[2]	Cataglyphis livida[3]	Cataglyphis isis[1]	Cataglyphis bombycina[1]
1	Undecane	25.0 ± 3.7	5.5 ± 3.7	6.5	19.6 ± 2.8	3.3 ± 0.9	0.2 ± 0.3
2	Dodecane	2.6 ± 0.5	t	2.0	0.6 ± 0.2	–	t
3	Tridecene	–	t	–	–	–	–
4	Tridecane	58.6 ± 4.9	14.5 ± 4.3	53.5	51.0 ± 3.5	30.2 ± 3.7	24.5 ± 3.1
5	Tetradecane	2.0 ± 0.3	2.3 ± 1.3	t	1.3 ± 0.3	–	1.3 ± 0.8
6	Pentadecene	–	t	t	t	–	t
7	Pentadecane	11.7 ± 3.5	68.3 ± 8.5	18.0	27.5 ± 2.3	5.4 ± 0.7	70.8 ± 4.1
8	Hexadecane	t	–	20.0	–	57.6 ± 3.7	t
9	Heptadecane	–	7.2 ± 1.8	–	t	–	4.3 ± 0.7
10	Octadecane	–	–	t	–	3.9 ± 1.4	t

1. Relative amounts are calculated from averages of 10 individually analysed glands.
2. Relative amounts were calculated from one sample of pooled glands.
3. Relative amounts were calculated from 10 samples, each containing 5 pooled glands.

Another large formicine ant occurring in Israel is the weaver ant, *Polyrhachis simplex*. Similar to all other formicine investigated, its Dufour's gland content is comprised of hydrocarbons, of which tridecane is the major component (81%), undecane is the second largest peak (12.5%), while dodecane comprises 5% of the total secretion. The additional hydrocarbons that occur in the glandular secretion, 5-methyltridecane, tetradecane, pentadecene and pentadecane, are all minor or trace components.

The alarm behaviour of the ants varies considerably with the species and seems to correlate with their foraging behaviour, the size of the colony assayed and the size of the ants involved. The general response is an aggressive alarm expressed in the form of increased motility, recruitment towards the emitting source, biting and spraying into it and finally carrying it out of the foraging arena. The intensity of the alarm response depends also on the glandular source. In general, all the ant species assayed reacted similarly and strongly to crushed poison glands or, alternatively, to synthetic formic acid, provided it was diluted before application. The reaction to one whole gland was movement towards the source, but as the ants reached about 1 cm from the source, they were strongly deterred by it. If, on the other hand, only 1/10 of a gland was applied, the ants moved directly towards the source, biting at any object around and finally removed the piece of cardboard containing the pheromone.

The reaction of the ants to the Dufour's gland exudate was much more complex and the species differed considerably in their responses. Two of the three *Camponotus* species assayed, *C. fellah* and *C. gestroi*, responded to the exudates in the typical aggressive alarm behaviour: excitations and quick recruitment towards the source with open mandibles. The third species, *C. sericeus*, on the other hand, reacted very mildly and showed little gathering around the emitting source. The response of *C. sericeus* to tridecane or any of the straight chain alkanes present in the gland, was comparable to their reaction to the whole gland. It is worthwhile noting that this species, in contrast to the former two, does not forage in masses, but in small groups of 2-5 ants. In *C. fellah* the response to undecane was the strongest, but a strong response was also demonstrated after exposure to tridecane. The response of *C. gestroi* to the single components was the strongest when tridecane was used, but any of the other alkanes gave a remarkable reaction as well. In all the *Camponotus* species investigated, there was no particular alteration in behaviour in response to excised mandibular glands. In these species, with the exception of *C. gestroi*, the mandibular glands are rather small and probably do not play a role in the alarm-defense system.

Cataglyphis is a genus in which the ants forage individually and do not exhibit mass recruitment. The genus, as a whole, behaves similarly in its alarm whereat only few ants gather around the disturbing source. This is especially true for *C. nigra*, *C. nodus* and *C. isis*, where only 5-10 ants were out on the foraging table, as compared to several dozens in *C. fellah* for example. The smaller species, *C. livida*, having more foraging individuals at one time in the arena, showed a slightly stronger response than the bigger species of this genus. The response to the Dufour's gland exudate or, alternatively, the authentic compounds, is very weak. The ants, only when very close to the source, show slight interest which fades out rapidly. *Cataglyphis* species also emit a lemongrass odour from their mandibular glands, suggesting the existence of terpene like compound. While all the species investigated reacted with an alarm to crushed heads, the response of *C. bombycina* and *C. livida* was the strongest. In these two species, the odour emitted is also the strongest and preliminary gas-chromatographic analysis revealed that their secretion is the richest. The chemistry of these secretions, however, has not been elucidated yet.

The response of *P. simplex* to formic acid was a strong alarm and excitement, while that to tridecane was similar to that of the *Cataglyphis* species. *P. simplex* is also characterized by the production of ketones in its mandibular glands (Hefetz & Lloyd,

1982). In contrast to *Cataglyphis*, the response of *P. simplex* to this glandular exudate or to the reconstituted synthetic pheromone is freezing *in situ*, while attaining a defensive posture (Fig. 1, for detailed behaviour see Hefetz & Lloyd, 1982).

In order to see if the Dufour's gland secretion synergises the response to the poison gland compound, we have assayed them together. The initial response was similar as that to formic acid alone, but lasted longer. In all cases where the piece of cardboard was not removed from the arena, the ants recruited to the spot remained there and investigated the emitting source long after the acid had evaporated.

DISCUSSION

Formicine ants are notable for their developed abdominal exocrine glands, including the poison and Dufour's gland. While formic acid is a ubiquitous product of the poison gland, the Dufour's gland produces a variety of branched and unbranched hydrocarbons that seem to be species specific.

In an extensive study utilizing several species in the genera *Formica* and *Camponotus*, Bergström and Lofqvist (1971, 1972) have found that in addition to the hydrocarbons the Dufour's gland secretion is characterized by oxygenated compounds. These compounds occurred in the glands in very little amounts compared to the hydrocarbons present there. In the species investigated by us when analyzing pooled samples, several compounds could be detected by gas-chromatography in the high boiling range, but their mass spectra were too weak to enable proper interpretation. In all cases these compounds were in minute quantities and could not be detected when individual glands were used for analysis.

Low boiling hydrocarbons are also the major constituents of the Dufour's gland of *Polyrhachis simplex*, tridecane being the major compound. These results are comparable with those of *Polyrhachis* sp. (Brophy *et al.*, 1982) using whole gaster extracts. The latter species differ from *P. simplex* in having pentadecane as the second major compound and undecane third, while in *P. simplex* undecane is the second largest compound. The two species differ considerably, however, in their mandibular gland content. The head extracts of the *Polyrhachis* sp. contained only high molecular weight hydrocarbons as compared with 4-heptanone, 6-methyl-5-heptane-2-one and 6-methyl-5-heptane-2-ol produced by the mandibular glands of *P. simplex*.

It is evident that the poison gland has a major role in the alarm defense system of the ants, but the role of the Dufour's gland in this behaviour is ambiguous. All ant colonies reacted similarly to an alarming object in their vicinity: the ants rushed to it, bending the tip of their abdomen and emitting their pungent secretion onto any moving object. At this time the sharp odour of formic acid could be detected. Formic acid is undoubtedly the prime alarm pheromone of all these species, eliciting an aggressive behaviour similar to that induced by actual disturbance of the ants' foraging area. The Dufour's gland contents, on the other hand, do not elicit a commensurate response in all species. In four species of *Camponotus* it is a strong alarm releaser in the magnitude of formic acid, while in *C. sericeus* it evokes only slight interest and mild attraction of the ants in the area. In contrast, the reaction of *C. sericeus* to formic acid is swift and comparable to the other *Camponotus* species.

In view of these results it is worthwhile to separate the alarm behaviour exhibited in response to pheromonal cues into two components; aggressiveness, which is elicited by formic acid, and attraction or recruitment induced by the Dufour's gland hydrocarbons. In species that use mass foraging, the recruiting component is rather developed, while in species that forage in small numbers, it is undeveloped. For example, *C. sericeus* uses mostly tandem running (Holldobler *et al.*, 1974) possibly explaining its very mild response to the Dufour's gland hydrocarbons. This assumption is corroborated by the alarm behaviour exhibited by species of *Cataglyphis*. Species in that genus forage individually (Harkness and Wehner, 1977; Hefetz, unpublished observations) and locate their nest by visual cues. Like in *Camponotus sericeus*, their response to Dufour's gland hydrocarbons is very weak, except for the smaller species, *C. livida*. Ants in this latter species, when observed in the laboratory, exhibited more mass recruitment than did the others, a fact that may be correlated to their relatively small size. In *Cataglyphis*, as in *Acanthomyops claviger* (Regnier and Wilson, 1968), alarm behaviour is also evoked by the mandibular gland exudate superimposing on the reaction to the adnexal gland's exudate. A somewhat different response is demonstrated by *Polyrhachis simplex* to the different glandular secretions (Hefetz and Lloyd, 1982). Here we apparently have one more behavioural component which is: attaining a prealarm defensive posture in response to the mandibular gland's exudate, and only after formic acid has been released, the ants enter into a frenzy alarm. *P. simplex*, like *C. sericeus*, is effected only slightly by the Dufour's gland secretion.

In addition to their role in alarm, the hydrocarbons of the Dufour's gland serve as wetting agents for formic acid (Regnier and Wilson, 1968). This fact, by itself, however, hardly explains the diversity of compounds exhibited by this gland in the Formicinae (Blum and Hermann, 1978). In the 12 species investigated by us, species specificity can be demonstrated, but only in 4 of them the exudates function as an alarm releaser. It is possible, thus, that these secretions function in species recognition as was postulated for other formicine ants (Bergstrom and Lofqvist, 1971). Lately, it was found that virgin queens of *Formica polyctena* have a different blend of compounds in their Dufour's gland than do workers, implicating a sex pheromone role (Lofqvist and Bergstrom, 1980) and demonstrating again the pheromonal parsimony in ants.

ACKNOWLEDGEMENT

We would like to thank Prof. J. Kugler of the Department of Zoology, Tel Aviv University, for identifying the ants and for his valuable comments on their taxonomy. To Dr. H.H. Fales and Dr. H.A. Lloyd, Laboratory of Chemistry, NHLBI, National Institute of Health, Bethesda, MD, for their hospitality and the opportunity to use their mass-spectrometer, and to A. Shoob and his staff, Department of Zoology, Tel Aviv University, for photographic assistance. This research was supported by The Israel Academy of Sciences and Humanities: Basic Research Foundation (Grant No. 7392).

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