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VARIATION WITH CASTE OF THE MANDIBULAR GLAND SECRETION IN THE LEAF-CUTTING ANT *Atta sexdens rubropilosa*

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Abstract—In *Atta sexdens rubropilosa*, a strongly polyethic and polymorphic species of myrmicine ant, the contents of the mandibular gland vary with caste. Small workers of head width 0.5–1.8 mm, those generally engaged in duties inside the nest, contain chiefly 4-methyl-3-heptanone. Larger workers, those chiefly engaged in foraging, and the soldier caste contain a mixture dominated by neral and geranial, with very little of the ketone of the smaller workers. The soldiers have massive glands containing milligram amounts of neral and geranial. Virgin and mated females contain essentially only 4-methyl-3-heptanone, the amount increasing after mating, while virgin males have 4-methyl-3-heptanone and 4-methyl-3-heptanol in approximately equal proportions. Mated males have less secretion and lose the 4-methyl-3-heptanol.

Key Words—4-Methyl-3-heptanone, 4-methyl-3-heptanol, citral, neral, geranial, Hymenoptera, Formicidae, caste, *Atta sexdens rubropilosa*.

INTRODUCTION

The mandibular glands of many, perhaps most species of ant contain mixtures of volatile organic compounds. A number of these secretions have been

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analyzed, and the results of these analyses have been reviewed (Blum and Hermann, 1978; Attygalle and Morgan, 1984; Hölldobler and Wilson, 1990, p. 260). In many fewer cases have these compounds been carefully tested for behavioral effects. In general, they have been described as alarm pheromones, attracting or repelling congeners from the source of emission (cf. Cammaerts-Tricot, 1973; Morgan et al., 1978; Bradshaw et al., 1975; Hölldobler and Wilson, 1990, p. 260).

The leaf-cutting or fungus-cultivating ants of the tribe Attini provide particularly interesting problems of pheromone behavior. These ants, spread throughout the neotropics (Cherrett, 1986) are of special interest because of their unique dependence upon their fungus garden for larval food, because of their complex communication systems and well-regulated behavior, and because some of their species cause so much damage to agriculture and arboriculture. Their colonies are territorial and aggressive (Salzemann and Jaffe, 1990). The workers of *Atta* vary enormously in size (cf. Hölldobler and Wilson, 1990, p. 325). Wilson (1980) selected *A. sexdens* for particularly close study since he regards it as having one of the most complex systems of caste and polyethism found in all ants. He divided the workers into four castes according to tasks: gardener–nurses, within-nest generalists, forager–excavators, and defenders (Wilson, 1980). The divisions of labor raise further questions, such as whether they all produce the same pheromone substances and whether they all respond to pheromones in the same way. For all these reasons, the interest in their pheromonal secretions is particularly strong.

In a very early study, Butenandt et al. (1959) identified citral (an equilibrium mixture of geranial, the *trans* form, and neral, the *cis* form) in the mandibular glands of *A. sexdens rubropilosa* and described it as a warning and *schreckstoff* (perhaps best translated as a "frightening compound"). Butenandt et al. (1959) noted the large size of the mandibular glands in the soldier caste and estimated they occupied about one fifth of the volume of the head capsule. The next investigation was by Blum et al. (1968), who examined the mandibular glands of six species of *Atta*, including *Atta sexdens*. They do not state whether this is *A. sexdens nubropilosa* or *A. sexdens sexdens*, but as they were collected in the state of São Paulo, Brazil, near to where those used in our present work were collected, they were most probably *A. s. rubropilosa*. They found 4-methyl-3-heptanone and 2-heptanone in a ratio of 1:4 in *A sexdens*. They also identified citral and geraniol. In a simple bioassay of placing a ball of cotton wool impregnated with these substances near a foraging trail, they observed a confused and frantic reaction to 4-methyl-3-heptanone; 2-heptanone was mildly repellent, and neither of the monoterpenes caused any reaction. Moser et al. (1968) and Riley et al. (1974) identified 4-methyl-3-heptanone, 4-methyl-3-heptanol, 3-octanone, and traces of 3-octanol in *A. texana* and *A. cephalotes*, and in addition, 2-heptanone, 2-heptanol, and 3-heptanol in *A. texana*. In both species they found that (*S*)-(+)-4-methyl-3-heptanone was the enantiomer present, that only this enantiomer, unaffected by the inactive (*R*)-(−)-form, was active in bioassays. The other compounds mentioned were not active.

Schildknecht (1976), by extraction of 20,000 freshly prepared worker heads, identified 16 further constituents in the mandibular glands and gave quantitative figures for 10 of these in micrograms per head. By far the major compounds were geranial and neral (together making 40 μg/head).

All these studies were made on mass extracts and did not distinguish between the different castes. As a preliminary to behavioral tests we have therefore reexamined the mandibular gland contents of all the castes of *A. sexdens rubropilosa* using the technique of analyzing individual glands or insect parts by combined gas chromatography–mass spectrometry, to discover whether there are any differences with caste and in order to be able to provide the appropriate substances and in the correct amounts for behavioral studies. We have indeed found that the mandibular pheromone varies with caste and sex.

METHODS AND MATERIALS

Mandibular glands from a complete range of worker sizes of *Atta sexdens rubropilosa* Forel, with head width varying from 0.6 to 4.8 mm were taken from a single nest in the laboratory at Leuven. In some cases the individual mandibular glands were dissected under water using a binocular microscope, lightly dried, and sealed in soft glass capillaries (Morgan, 1990). In other cases the whole head capsule (if it was small enough) was sealed in the capillary. Large heads were sealed in larger glass capillaries and stored until analyzed. The capillary and head was then crushed in a small tissue grinder with 100 μl of hexane and 1 μl of the solution taken for analysis.

Samples of mandibular glands of virgin and mated males and females of *A. s. rubropilosa* were collected in the mating season near Vicosa (Minas Gerais, Brazil) dissected, sealed, and sent to Keele. All these materials were chemically analyzed as described below.

Gas chromatography–mass spectrometry (GC-MS) was performed on a Hewlett-Packard 5890 gas chromatography coupled to a 5970B Mass Selective Detector as described elsewhere (cf. Bagnères et al., 1991) and using the same immobilized polydimethylsiloxane stationary phase in a 12-m fused silica capillary column (Bagnères et al., 1991). For this work, the sealed capillary was heated in the injection port, which was maintained at 150°C, for 4 min before crushing the capillary (Morgan and Wadhams, 1972). The oven was programmed from 30°C at 8°C/min to 150°C. The split vent was closed before crushing the sample and reopened 30 sec later. The chemical substances separated were identified from their mass spectra and confirmed by comparison of retention time and mass spectrum with synthetic standards, either purchased or synthesized. In a few cases confirmation was by published mass spectrum. In particular, 4-methyl-3-heptanol and citral were purchased (Aldrich, Gillingham, Dorset, UK), and 4-methyl-3-heptanone was prepared from the corresponding alcohol by chromic acid oxidation. These compounds were used as external standards for quantification of the components.

RESULTS

Some of the mandibular glands were carefully dissected out of the head capsules (for number, see Tables 1 and 2), and the chromatograms obtained from these samples were compared with chromatograms obtained from whole head capsules of approximately the same size of worker. There were no additional peaks in the same range of volatilities from the head capsules, so that results from them could be safely combined with those of the isolated glands. A total of 64 glands or heads of individual workers were analyzed by GC-MS, and the identified compounds and the percentage composition for each worker were entered on a large table. It was evident that for this sample, there was a clear division of type of secretion at a head width of 1.8–2.0 mm. The similar results for workers of head width 0.5–1.8 mm were therefore combined to give the mean values in Table 1. The glands were relatively small (mean of 60 ng secretion) and contained a small number of compounds, heavily dominated by 4-methyl-3-heptanone; there were a few other alcohols, aldehydes, and ketones

TABLE 1. PERCENTAGE COMPOSITION OF MANDIBULAR GLAND SECRETION OF SMALL WORKERS OF *Atta sexdens rubropilosa* (HEAD WIDTH 0.5–1.8 mm) WITH SAMPLE STANDARD DEVIATION, INCLUDING WORKERS FROM WITHIN THE NEST AND FORAGING AREA[a]

Compound	Number in Figure 1A	Composition (% ± SD)
Pentanal		0.02 ± 0.10
4-Methyl-3-heptanone	1	89.5 ± 14.5
4-Methyl-3-heptanol		5.7 ± 9.6
6-Methyl-3-heptanone		0.2 ± 1.1
3-Octanone		0.7 ± 1.6
Geranial		1.6 ± 7.7
2-Decanone		1.6 ± 4.2
Decanal		0.4 ± 2.1

[a] Mean values from 22 dissected glands and 15 whole head capsules. Mean total amount: 0.6 μg ± 2.5.

TABLE 2. PERCENTAGE COMPOSITION OF MANDIBULAR GLAND SECRETION OF LARGER WORKERS AND SOLDIERS OF *A. sexdens rubropilosa* (HEAD WIDTH 2.0–4.8 mm, TOGETHER WITH SAMPLE STANDARD DEVIATION[a]

Compound	Number in Figure 1B	Composition (% ± SD)
4-Methyl-3-heptanone	1	6.8 ± 8.2
4-Methyl-3-heptanol		0.8 + 2.9
6-Methyl-5-hepten-2-one	2	3.3 ± 3.7
6-Methyl-5-hepten-2-ol		0.1 ± 0.5
Octanal		2.6 ± 5.0
6-Methyl-3-heptanone		0.02 ± 0.1
1-Nonanol		0.3 ± 1.8
Citral-like isomer-1	3	1.0 ± 1.0
Citral-like isomer-2	3	2.4 ± 2.3
Citral-like isomer-3	3	2.9 ± 3.2
Decanal	4	3.1 ± 3.0
Neral	5	28.6 ± 9.6
Isogeraniol	6	3.9 ± 9.8
Geranial	7	40.6 ± 11.5
2-Decanone		0.3 ± 1.3
Methyl decanoate		0.1 ± 0.3
Dodecanal	8	0.7 ± 0.9
γ-Decalactone	9	1.0 ± 1.6
Neric acid		0.4 ± 2.0
Geranic acid		0.5 ± 2.4
Geranylacetone	10	1.8 ± 1.7
Unknown ketone		0.4 ± 1.3
Verbenone		0.2 ± 0.9
Farnesol		0.4 ± 1.9

[a]Mean values from 16 dissected glands and 11 whole head capsules.
Mean total amount: head width 2.0–2.8 mm, 34.8 μg; head width 3.0–3.9 mm, 170 μg; and head width 4.0–4.8 mm, 1.43 mg.

in trace amounts, but no citral (Figure 1A). The variability in amount of these minor components is indicated by the large sample standard deviations in Table 1.

The first group of 26 samples of these small workers were taken from outside the fungus compartment of the nest. Recognizing that the duties of the small workers are essentially within the nest (Wilson, 1980), we took a further 11 samples from inside the fungus garden and compared the two sets of results, to be sure there was nothing anomolous about those taken outside. No difference was evident in the two groups, so they were combined in Table 1.

The larger workers and soldiers (head width 2.0–4.8 mm), although varying

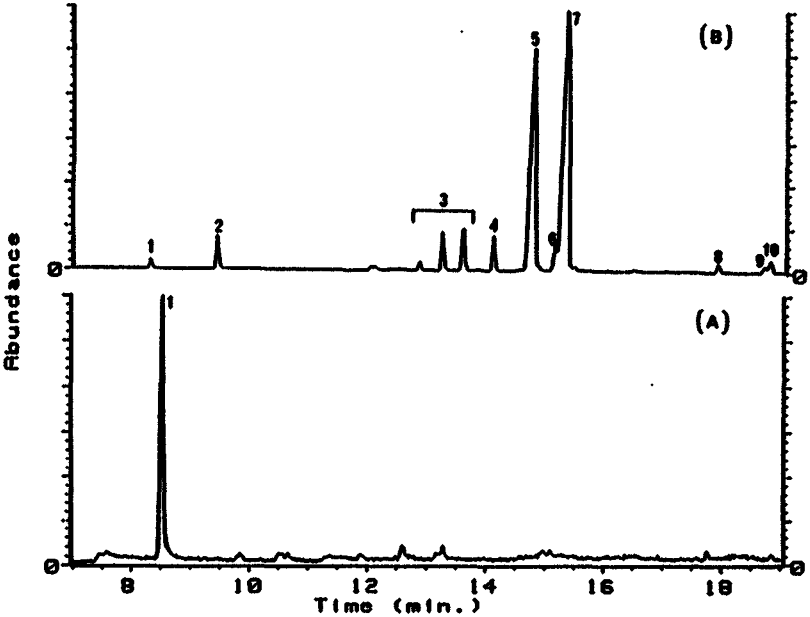

FIG. 1. Gas chromatograms illustrating (A) a single worker mandibular gland from *Atta sexdens rubropilosa*, with head width less than 1.8 mm, and (B) a single worker with head width greater than 2.0 mm. For identification of numbered peaks, see Table 2.

greatly in the size of their mandibular glands, showed a constancy of composition in the secretion, with very little 4-methyl-3-heptanone and having citral (the isomers neral and geranial in their natural ratio) as the major compound pair (Figure 1B). There were a larger number of minor components, many of them terpene-derived (Table 2). Not all the minor components matched those identified by Schildknecht (1976), e.g., β-pinene and 2-phenylethanol were not found here, but γ-decanolactone and farnesol, identified by Schildkneckt were also found in our samples. The 2-heptanone recorded by Blum et al. (1968) was not found. Three minor compounds, eluting before neral and having mass spectra similar to neral and geranial, were found in both the gland and commercial citral. They are isomeric monoterpenes, probably close in structure to citral, but they were not fully identified. The total amount of secretion in the glands varied widely. The mean amount for three groups are given in Table 2.

Mated females collected in Brazil and dissected and sealed there showed a constancy of composition similar to the smaller workers (Table 3) and 4-methyl-3-heptanone comprising about 90% of the secretion (Figure 2A). Unmated females also contained 4-methyl-3-heptanone (Fig. 2B), but there was less secretion (Table 3).

TABLE 3. PERCENTAGE COMPOSITION OF MANDIBULAR GLAND SECRETION OF FOUR SAMPLES OF UNMATED AND 12 SAMPLES OF MATED FEMALE *Atta sexdens rubropilosa*

Compound	Number in Figure 2	Composition (% ± SD)	
		Unmated	Mated
4-Methyl-3-hexanone	1	1.7 ± 1.5	
4-Methyl-3-hexanol	2	t[a]	
3-Heptanone	3	0.2 ± 0.3	0.2 ± 0.6
2-Heptanone	4	t	
4-Methyl-3-heptanone	5	94.8 ± 3.4	91.7 ± 6.7
4-Methyl-3-heptanol	6	0.8 ± 1.7	6.0 ± 3.4
3-Octanone	7	1.1 ± 1.2	0.5 ± 1.5
3-Octanol			t
4,5-Dimethyl-4-hexen-2-one	8	0.2 ± 0.3	t
6-Methyl-3-octanone	9	0.2 ± 0.2	t
4-Methyl-3-octanone		0.5 ± 0.9	
3-Nonanol			t
5-Ethyl-4-methyl-3-heptanone	10	0.4 ± 0.5	t
2-Decanone			0.4 ± 1.4
Decanal		0.3 ± 0.6	
p-Cymen-α-ol		0.1 ± 0.1	t
α-Terpineol			t
Neral			t
Geranial			t
Geraniol			t
Geranylacetone			0.1 ± 0.2
2-Tridecanone			0.2 ± 0.7
3-Undecene			0.1 ± 0.4
Mean total amount (μg)		4.9	8.8 ± 5.6

[a]t = trace, less than 0.1%.

The mated males had a glandular composition similar to that of the mated females, but rather less of the secretion (Figure 3A, Table 4). The unmated males contained a much higher proportion of 4-methyl-3-heptanol than was found in any other group, and more secretion in the gland than in those analyzed after mating.

DISCUSSION

Wilson (1980), by observing the tasks they performed, divided the workers of *A. s. rubropilosa* into four groups. The minims, described as gardener–nurses with mean head width 1.0 mm, and the medians or within-nest generalists of

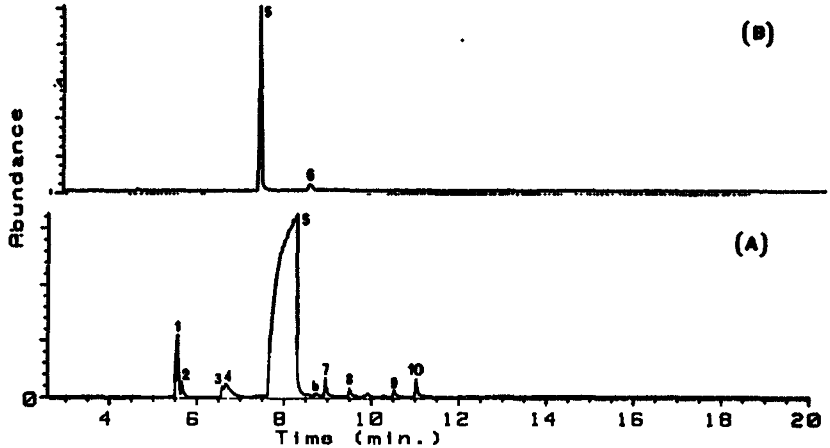

FIG. 2. Gas chromatograms of the mandibular secretion of (A) unmated and (B) mated females of *A. sexdens rubropilosa*. Numbered peaks are identified in Table 3. Retention times are not exactly comparable because of a change of column between two sets of data. One whole head of a female was used for (A); for (B) a solution in hexane containing 1% of the total secretion from one female was used.

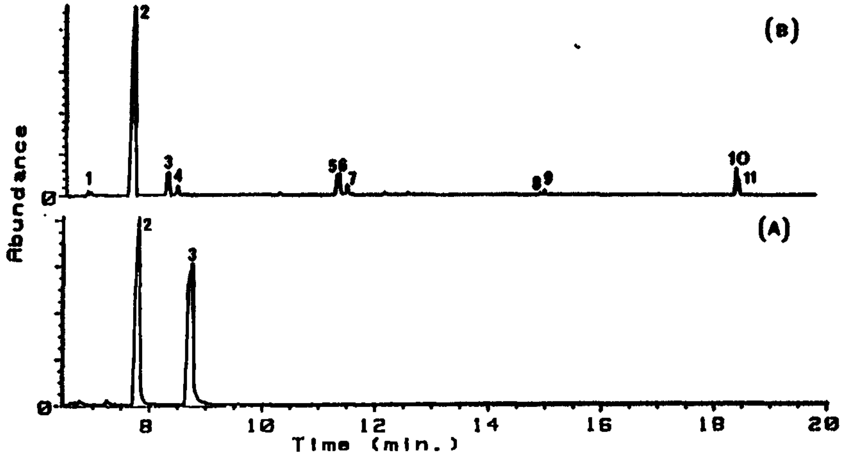

FIG. 3. Gas chromatograms of the mandibular section of (A) unmated and (B) mated males of *A. sexdens rubropilosa*. Numbered peaks are identified in Table 4. Retention times were altered by a change of column between determinations.

TABLE 4. PERCENTAGE COMPOSITION OF MANDIBULAR GLAND SECRETION OF SIX SAMPLES OF UNMATED AND 17 SAMPLES OF MATED MALE *A. sexdens rubropilosa*

Compound	Number in Fig. 3	Composition (% ± SD)	
		Unmated	Mated
4-Methyl-3-hexanone	1	1.0 ± 0.7	2.5 ± 10.2
4-Methyl-3-hexanol		0.2 ± 0.2	
3-Heptanone		0.4 ± 0.9	
3-Heptanol		0.1 ± 0.2	0.2 ± 0.6
2-Heptanone		0.5 ± 0.6	
2-Heptanol		0.4 ± 0.5	
4-Methyl-3-heptanone	2	49.1 ± 7.4	81.8 ± 27.0
4-Methyl-3-heptanol	3	48.0 ± 7.7	8.1 ± 12.2
3-Octanone	4		t
3-Octanol			0.1 ± 0.4
Octanal			0.1 ± 0.2
Decanal			t
Terpinen-4-ol	5	t[a]	0.3 ± 0.6
α-Terpineol	6	0.1 ± 0.1	0.3 ± 0.9
p-Cymen-α-ol	7	t	0.3 ± 0.6
Neral			t
Isogeraniol			t
Geranial			t
Methyl decanoate			t
γ-Decalactone	8		t
Geranylacetone	9		t
9-Heptadecanone	10	0.1 ± 0.1	5.9 ± 22.8
9-Heptadecanol	11	t	t
Mean total amount (μg)		11	2.3 ± 5.1

[a] t = trace, less than 0.1%.

mean head width 1.4 mm both worked within the nest. Those working outside the nest were the major workers or foragers and excavators, centered on head width 2.2 mm, and the defenders, those workers over 3.0 mm in head width.

Rather than use his behavioral divisions of workers, we inspected the complete range of chemical analyses of worker mandibular glands and came to the conclusion that between 1.8 and 2.0 mm there is a sharp chemical division between smaller and larger workers. There is, therefore, chemical support for the divisions proposed by Wilson (1980). Those workers with duties inside the nest have a mandibular gland containing very largely 4-methyl-3-heptanone. Those workers engaged outside the nest, whether foragers or defenders, have a mandibular pheromone based on citral. The clear division in composition between these two mandibular secretions means that different messages in different contexts are conveyed by these substances. It is difficult to reconcile our findings with the behavioral tests described by Blum et al. (1968). The behavioral responses to these substances of the different castes of workers inside and outside the nest need to be reexamined. The lack of distinction in place and caste in earlier behavioral experiments makes them now of reduced value. The value of the massive quantities of citral stored in the heads of the soldier caste is puzzling if this isomeric pair of compounds causes no reaction in the species as stated by Blum et al. (1968).

In some unpublished work by Morgan and Inwood, we drew air continually over a quietly organized colony of *Myrmica scabrinodis* in an artificial glass nest. We were surprised to find the air contained readily detectable amounts of 3-octanol and 3-octanone, the mandibular gland secretion of this species, yet the ants did not appear disturbed. These observations allow the possibility that the volatile mandibular substances provide short-range nondirectional communication between the workers.

There have been few studies on the mandibular glands of sexuals in ants. Pasteels et al. (1980) have described the mandibular pheromones of *Tetramorium impurum* [wrongly described there as *T. caespitum*, see Pasteels et al. (1981)]. 4-Methyl-3-hexanol and 4-methyl-3-hexanone were found in quantity in males, and in lesser amount in females, whereas only the alcohol was found in workers. Nevertheless, finding such similarity between males and females here was surprising. In view of the short life of about two days of the males once they leave the nest, one wonders what purpose is served. The presence of larger amounts of 4-methyl-3-heptanol in the males would give them a different odor, and this suggests behavioral tests as a sexual attractant. It is noteworthy that among the sexuals, the unmated males have the largest amount of secretion (Table 4). After mating, it drops considerably, and the 4-methyl-3-heptanol is lost. In females, the amount of secretion increases after mating. To complete this study, the chirality of the 4-methyl-3-heptanone must be determined. It is noteworthy that in a marine worm, *Platynereis dumerilli*, 5-methyl-3-heptanone is used as a sexual pheromone, males responding to the *R*-(−) enantiomer and females to the *S*-(+) enantiomer (Zeeck et al., 1992).

Wilson (1980) introduced the hypothesis of a primitive caste and concluded for *A. s. rubropilosa* that the small workers represent the primitive caste. It is perhaps worth noting that it is the mandibular secretion of the small workers that is close to that of the females, and the large workers have developed different substances.

The present work illustrates the value of analyzing insects individually. The mandibular pheromones of *A. sexdens rubropilosa* are more complex than previously recognized. We now propose to produce the blends of substances appropriate to the various castes for behavioral testing.

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