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TASK-RELATED DIFFERENCES IN THE CUTICULAR HYDROCARBON COMPOSITION OF HARVESTER ANTS, *Pogonomyrmex barbatus*

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Abstract—Colonies of the harvester ant, *Pogonomyrmex barbatus*, perform a variety of tasks. The behavior of an individual worker appears to depend on its recent history of brief contacts with ants of the same and other task groups. The purpose of this study was to determine whether task groups differ in cuticular hydrocarbon composition. We compared the cuticular hydrocarbon composition of ants collected under natural conditions as they performed one of three tasks: patrolling (locating food sources), foraging, or nest maintenance. Task groups differed significantly in the relative proportions of classes of hydrocarbon compounds, as well as in individual compounds. Relative to nest maintenance workers, foragers and patrollers had a higher proportion of straight-chain alkanes relative to monomethylalkanes, dimethylalkanes, and

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alkenes. There was no significant difference in the chain length of *n*-alkanes among the task groups. Foragers did not differ in hydrocarbon composition from patrollers. Colonies differed significantly from one another in hydrocarbon composition, but task groups differed in consistent ways from colony to colony, suggesting that the mechanism responsible for task-related hydrocarbon composition was the same in all colonies. *P. barbatus* workers switch tasks during their lifetimes, suggesting that cuticular hydrocarbon composition changes during adulthood as well. Nest maintenance workers are probably younger than foragers and patrollers and perform very little of their work outside of the nest. Task-related hydrocarbon differences detected here may be associated with worker age, and/or the abiotic characteristics (temperature, humidity, and ultraviolet light) of the interior and exterior work environments.

Key Words—Cuticular hydrocarbons; Formicidae; *Pogonomyrmex barbatus*; task allocation; *n*-alkanes.

INTRODUCTION

Ant colonies perform a variety of tasks outside the nest. In the harvester ant *Pogonomyrmex barbatus* (F. Smith), exterior tasks include foraging, traveling up to 20 m from the nest in search of seeds and bringing them back for storage inside the nest; patrolling, the early-morning search for the day's seed sources; and nest maintenance work, carrying excavated soil out of the nest and depositing it a few centimeters from the entrance (Gordon, 1986). Nest maintenance workers inside the nest repair and maintain the chambers, plaster the walls with moist soil that dries to a hard, adobe-like surface, and pile up dry, discarded soil near the nest entrance. Unlike foragers and patrollers, most of a nest maintenance worker's task is performed inside the nest, with only brief trips outside.

Colonies adjust the number of workers engaged in each task according to colony needs and changing conditions (Gordon, 1986, 1987). When more food is available, more ants forage; when the summer rains flood the nests, more ants do nest maintenance work. Changes in the number of ants performing a task can occur because ants move between active and inactive states; for example, at times when extra nest maintenance work is being done, the numbers foraging decrease because foragers tend to remain inactive inside the nest (Gordon, 1989). Changes in the number of ants performing a task can also occur because ants switch from one task to another. When abundant food appears, nest maintenance workers and patrollers will switch tasks to forage, and once they become foragers, they will not switch back (Gordon, 1989). When new nest maintenance workers are needed they are recruited from other, probably younger, workers inside the nest (Gordon, 1989).

Task allocation, the process that results in the appropriate numbers of ants performing each task, operates without any central control or hierarchical organization (reviewed by Gordon, 1996). Individuals must use simple cues to decide which task to perform and when to perform it actively. Recent work suggests

that interaction patterns influence task decisions in harvester ants; the task a harvester ant performs depends in part on its recent history of brief antennal contacts with ants of the same and other task groups (Gordon and Mehdiabadi, unpublished data). Can one ant discern the task of another through antennal contact?

In many insect species, the identity and relative abundance of lipids on the cuticle appear to be important in social signaling. Bioassays in which insects are presented with extracts of cuticular lipids have demonstrated that at least some social insects perceive and respond to differences in lipid composition (reviewed by Howard, 1993). For example, *Reticulitermes* termites reacted more aggressively to heterospecific cuticular extracts (containing only hydrocarbons) than to conspecific extracts (Bagnères et al., 1991). Similarly, workers of the ant *Camponotus vagus* responded more aggressively toward nestmates coated with cuticular extracts from another colony than toward nestmates coated with cuticular lipids from their own colony. Although such extracts may contain a variety of compounds, hydrocarbons are the most abundant component of the cuticular lipids of many insect species (Jackson and Blomquist, 1976). Several studies have demonstrated that cuticular hydrocarbon composition differs among species and among social insect colonies, suggesting that cuticular hydrocarbons might play an important role in species and nestmate recognition (Bonavita-Cougourdan et al., 1987; Nowbahari et al., 1990; Gamboa et al., 1996; Dahbi et al., 1996).

Cuticular hydrocarbon composition can vary among workers within a social insect colony as well. Studies of *Camponotus* ants (Bonavita-Courgourdan et al., 1993; Lavine et al., 1990) and of termites (Howard et al., 1982; Haverty et al., 1996) showed that workers in different task groups also differed in cuticular hydrocarbon composition. Task-related differences in the cuticular hydrocarbon profiles of *P. barbatus* workers might allow ants to distinguish, in the course of brief antennal contacts, the task of the ants they meet. Here we investigate whether *P. barbatus* workers in distinct task groups differ in cuticular hydrocarbon composition.

METHODS AND MATERIALS

Ant Collections. Ants were collected from three *P. barbatus* colonies in October 1996 near Rodeo, New Mexico, USA. Colonies were estimated to be at least five years old, based on the width of the pebble-covered mound surrounding the nest entrance. Ants were collected while they performed one of three tasks: foraging, patrolling, or nest maintenance work (Gordon, 1986). Foragers were collected as they returned to the nest carrying seeds. Patrollers were identified by their characteristic zig-zag path of movement with the abdomen tucked under the thorax. Nest maintenance workers were collected after they exited the nest carrying dirt. Ants were placed directly onto Dry Ice and

shipped overnight to Stanford University, where they were stored at −70°C until chemical analyses were performed.

Chemical Analysis. Cuticular components were extracted from each ant separately by immersing the ant in 1 ml of pentane (Sigma, St. Louis, Missouri) for 10 min. Suspensions were gently shaken during the first and last minute of the soak period. Ants were then removed from vials and the extracts were dried under a stream of N_2. The residue was redissolved in 50 μl of chloroform. Chloroform is less volatile than pentane, and we used it as the final solvent in order to reduce variability in sample concentration prior to analysis. Samples were analyzed by using combined gas chromatography–mass spectrometry (HP5990 series II/5971). Aliquots of 1 μl were introduced by spitless injection onto a capillary column (SPB-1 fused silica, 30 m, 0.25 mm ID, 0.25-μm film thickness; Supelco, Bellefonte, Pennsylvania); samples were purged after 1 min. Helium was the carrier gas, flowing at 1 ml/min. The injector temperature was kept at 300°C. The oven was kept at 100°C during injection, and then the temperature was increased rapidly from 100 to 220°C at 25°C/min, then more slowly from 220 to 310°C at 3°C/min (Provost et al., 1993). To confirm consistency of retention times among runs, samples of a standardized mixture of alkanes were interspersed among ant samples in each run.

To assist in identifying the compounds found on individual ants, a concentrated extraction was prepared by soaking a sample of 42 ants from five colonies in 3 ml of hexane for 1 hr at 50°C with occasional mixing. One milliliter of extract was dried under a stream of N_2 and the residue resuspended in 50 μl chloroform. Samples were analyzed with an HP 5890/5971A gas chromatograph–mass selective detector. Aliquots of 1–5 μl were introduced by 2-min splitless injection onto a DB-1 fused silica capillary column (30 m × 0.32 mm, 0.25-mm film thickness, J&W Scientific, Folsom, California), with helium as the carrier gas. The injector temperature was 350°C. The temperature was 170°C during injection, and was then increased to 260°C at 30°C/min, 260–295°C at 2.5°C/min, 295–350°C at 15°C/min, followed by a constant 350°C for 3 min. A standard mixture containing various straight-chain hydrocarbons (boiling point calibration sample #1, Hewlett Packard, Palo Alto, California) was also analyzed as above, with the exception that 1 μl of sample (~10 mg/ml in chloroform) was injected in split mode with a split ratio of 50:1.

Mass spectra were analyzed and compounds identified according to Nelson et al. (1980). Peaks that appeared in individual ants were matched to peaks in the more concentrated sample on the basis of relative elution time and mass spectra. Identification of compounds from the concentrated sample was used to confirm the identity of compounds found in individual ants.

Data Analysis. The relative abundance of each compound was estimated as the proportional peak area from total ion chromatograms. All compounds that

constituted at least 1% of the total hydrocarbon abundance on at least one ant were included in the analyses. We used linear discriminant analysis to determine whether ants of different task groups or different colonies had different relative abundances of cuticular hydrocarbons. Data were transformed by taking the arcsine of the square root of the proportion under each peak. We included only the five most abundant hydrocarbon compounds in the discriminant analysis of single compounds, for two reasons: (1) Large numbers of independent variables relative to the sample size can lead to significant discrimination where no actual grouping exists (Panel on Discriminant Analysis and Clustering, 1989). (2) Scarce compounds had poorer signal-to-noise ratios than abundant compounds and therefore were likely to bring little information to the discriminant analysis. We tested for differences in the relative abundance of classes of hydrocarbon compounds (alkanes, monomethylalkanes, dimethylalkanes and alkenes), as well as single compounds.

Linear discriminant analyses were performed by using SPSS Professional Statistics (Norusis/SPSS, Inc. 1994). Discriminant scores were calculated for each ant as the position of that data point along a new axis, the linear combination of variables that provided the best discrimination among groups. When there were only two groups in the analysis, discriminant scores of ants in different groups were compared with analysis of variance with k and $n_1 + n_2 - (k + 1)$ degrees of freedom, where k is the number of variables and n_i is the number of ants per group (Selvin, 1995). When discriminant analysis was applied to more than two groups, analysis of variance could no longer be used. In this case we applied an approximate test of the overall effectiveness of the discriminant function by using Wilks' lambda (λ), transformed to approximate a chi-square distribution as follows: $\chi^2 = -m \log(\lambda)$; where $m = [N - 0.5(k + g) - 1]$, where N is the number of ants, and g is the number of groups (Selvin, 1995). Discriminant scores were then used to predict group membership (Norusis/SPSS, Inc. 1994), by using a technique based on Bayes' rule (Hand, 1981; Norusis/SPPS, Inc., 1994).

We also compared the relative abundance of long- versus short-chain n-alkanes among the task groups. We calculated the proportion of the total n-alkane ion abundance contributed by n-alkanes greater than, or equal to, 28 carbons, the median chain length, and analyzed the data with one-way ANOVA.

RESULTS

Thirty-four cuticular hydrocarbons were detected on *P. barbatus* workers (Table 1). Hydrocarbon compounds were of four classes, n-alkanes, monomethylalkanes, dimethylalkanes, and alkenes. Several long-chain fatty acids (hexadecanoic acid, 9,12-octadecadienoic acid, and undecyesterdodecanoic acid)

TABLE 1. AVERAGE PERCENT COMPOSITION OF CUTICULAR HYDROCARBONS RECOVERED FROM *P. barbatus* ANTS FROM 3 COLONIES[a]

Component	TIC peak no.[b]	Colony B F (9)	Colony B P (10)	Colony B N (5)	Colony C F (10)	Colony C P (9)	Colony C N (10)	Colony E F (9)	Colony E P (10)	Colony E N (8)
Alkanes										
n-Tricosane	1	3.6	3.5	3.3	2.8	2.6	2.2	2.0	2.1	2.5
n-Tetracaosane	2	1.0	1.3	1.6	0.5	0.4	0.3	0.0	0.0	0.6
n-Pentacosane[c]	3	19.8	22.9	13.5	25.2	23.0	17.2	20.6	20.4	15.5
n-Hexacosane	6	2.0	2.3	2.0	2.2	1.8	2.1	2.1	2.1	2.3
n-Heptacosane[c]	8	5.6	7.6	4.4	7.8	6.4	5.9	8.0	9.5	6.6
n-Octacosane	13	0.0	0.1	0.6	0.7	0.3	0.4	0.5	0.4	0.2
n-Nonacosane[c]	15	4.2	4.5	3.8	4.5	4.6	5.1	4.5	4.9	4.0
n-Triacontane	20	1.1	0.9	0.7	0.5	0.6	0.7	0.5	0.6	1.0
n-Hentriacontane	23	4.0	3.5	3.0	3.9	4.1	4.4	4.5	4.8	4.4
n-Tritriacontane	29	0.7	0.3	0.3	0.7	0.3	0.7	0.4	0.4	0.3
Total *n*-alkanes		42.1	46.8	33.3	48.7	44.1	39.1	43.2	45.1	36.6
Monomethylalkanes										
13-Methylpentacosane	4	2.2	2.3	3.1	2.3	2.6	3.0	2.4	2.6	3.0
7-Methylpentacosane	5	0.8	0.2	0.7	0.3	0.0	0.1	0.0	0.0	0.0
13-Methylheptacosane[c]	9	5.2	5.5	5.4	6.3	6.3	7.3	6.6	6.8	7.4
7-Methylheptacosane[c]	10	4.1	4.1	3.6	4.0	4.1	4.4	4.2	4.4	4.7
5-Methylheptacosane	11	0.6	0.1	1.4	0.3	0.5	1.2	0.4	0.4	1.1
15-Methylnonacosane	16	7.6	6.8	7.7	6.4	7.4	8.0	7.4	7.5	8.1
9-Methylnonacosane	17	2.7	2.5	2.6	2.8	2.6	2.7	2.6	3.3	2.8
7-Methylnonacosane	18	3.9	3.8	3.8	2.9	3.1	2.9	2.8	3.0	2.8

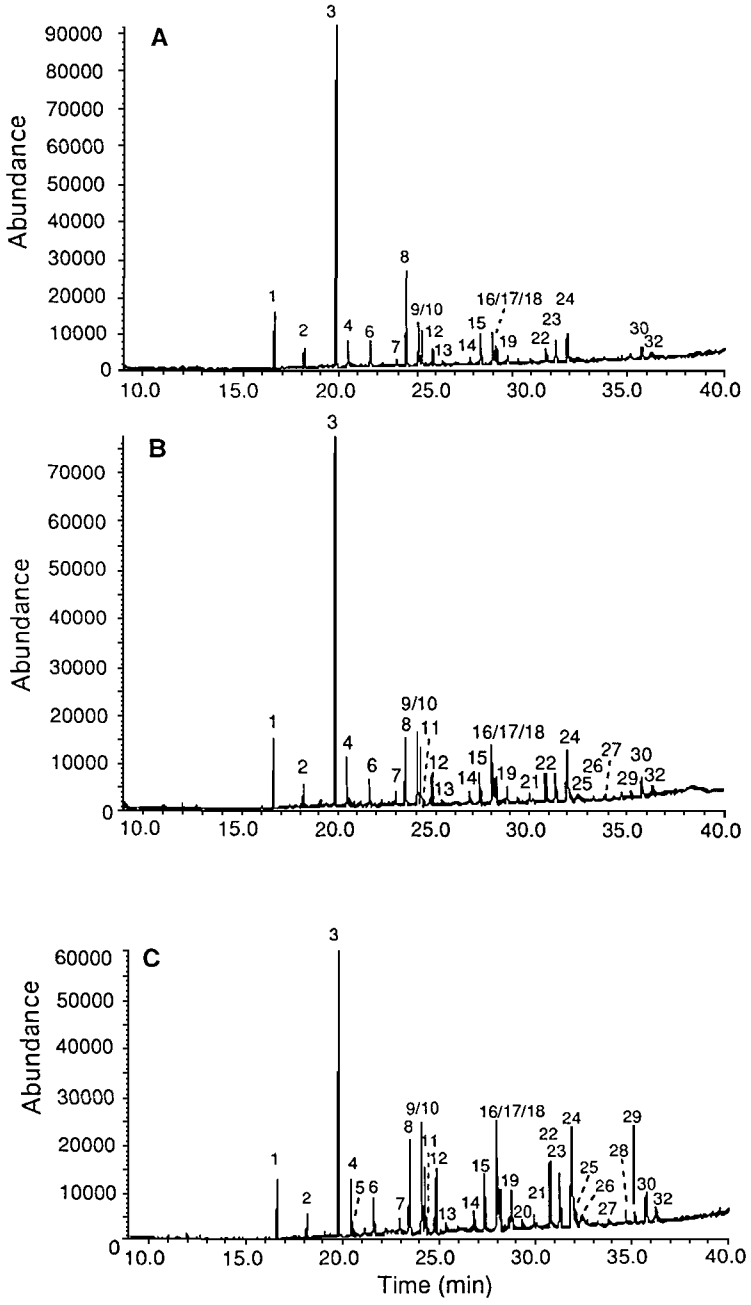
9-Methylhentriacontane	25	0.7	0.3	0.2	0.5	0.6	0.7	0.3	0.1	0.0
7-Methylhentriacontane	26	0.2	0.8	2.0	0.9	1.1	1.1	1.2	0.7	1.0
Total monomethylalkanes		27.4	26.3	29.1	26.6	27.8	0.1	27.5	28.5	29.9
Dimethylalkanes										
7,13-Dimethylheptacosane	12	3.3	3.0	4.1	3.2	3.2	4.1	2.5	3.4	4.2
7,13-Dimethylnonacosane	19	2.3	1.7	2.9	2.2	2.5	2.7	2.3	2.2	2.3
13,15-Dimethylnonacosane	21	1.1	1.3	1.0	0.3	0.9	0.6	0.8	0.6	1.3
x,y-Dimethyltriacontane[d]	24	8.1	6.9	7.4	7.4	8.3	7.8	9.0	8.4	8.1
13,15-Dimethylhentriacontane	27	0.5	0.5	0.3	0.1	0.0	0.7	0.4	0.0	0.2
x,y-Dimethyldotriacontane[d]	30	4.1	3.4	3.1	2.8	3.2	3.1	3.8	3.6	3.6
9,21-Dimethyltritriacontane	31	0.6	1.5	1.9	0.4	0.0	0.0	0.3	0.0	0.3
13,17-Dimethyltritriacontane	32	1.4	0.3	0.0	0.8	1.7	1.4	1.1	1.1	1.5
x,y-Dimethyltetratriacontane[d]	33	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
13,19-Dimethylpentatriacontane	34	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.6	0.0
Total dimethylalkanes		20.8	18.3	20.4	17.1	19.8	19.7	20.0	20.0	22.5
Alkenes[e]										
Heptacosene	7	1.1	1.3	1.6	1.0	1.3	1.2	1.2	0.7	1.6
Nonacosene	14	2.3	2.2	2.6	1.1	1.8	1.8	2	1.3	1.4
Hentriacontene	22	4.7	3.7	4.9	2.9	3.8	3.7	4.0	3.3	4.0
Tritriacontene	28	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0
Total alkenes		8.1	7.2	9.1	5.0	6.9	6.9	7.1	5.3	7.0

[a] Ants were collected while they were performing three tasks: foraging (F), patrolling (P), and nest maintenance (N). The number of ants analyzed per sample appears in parentheses.

[b] Total ion chromatograph (TIC) peak numbers correspond to those in Figure 1.

[c] One of the five most abundant compounds, used in statistical comparisons.

[d] x · y-methylation branch points undetermined.


A
B
C
Abundance
Time (min)
10.0
15.0
20.0
25.0
30.0
35.0
40.0

were also present in small quantities (< 1% on average). It is possible that other lipid components were present, but only in trace quantities. Figure 1 shows representative chromatograms for the three task groups.

Ants from different colonies and task groups expressed the same set of cuticular compounds (Table 1). However, there were differences in the relative abundance of those compounds. Colonies differed somewhat in the proportions of the four major classes of hydrocarbons on the cuticle ($\lambda = 0.79$, $\chi^2 = 17.4$, $df = 8$, $P = 0.03$); however, classification based on the discriminant analysis scores from these four classes of compounds was poor, misclassifying fully 48% of individuals overall (6/24 ants in colony 1, 18/29 in colony 2, and 14/27 in colony 3 were misclassified). Colonies differed more strongly in the relative proportions of the five most abundant cuticular hydrocarbon compounds ($\lambda = 0.33$, $\chi^2 = 83.0$, $df = 10$, $P < 0.001$). Prediction of colony membership on the basis of discriminant scores from the five single compounds led to an overall misclassification frequency of 21% (6/24 ants in colony 1, 4/29 in colony 2, and 7/27 in colony 3 were misclassified).

Despite the variation among colonies, the cuticular hydrocarbon profiles of ants in different task groups differed in a similar fashion both within and among colonies. For example, nest maintenance workers in all colonies tended to have relatively low levels of *n*-alkanes and relatively high levels of branched alkanes, in comparison to other task groups (Figure 2). All further analyses are based on individuals' deviations from their colony means, for each compound or class of compounds. This enables task group differences within colonies to be combined across colonies. We use the term "Standardization" to identify this part of the data analysis.

Initial inspection of the data using principal components analysis suggested that nest maintenance workers differed in hydrocarbon profile from foragers and patrollers, but foragers could not be distinguished from patrollers. On the basis of this observation, we compared task groups by using two discriminant analyses: nest maintenance workers versus foragers and patrollers, and foragers versus patrollers.

The relative abundance of *n*-alkanes, monomethylalkanes, dimethylalkanes, and alkenes on the cuticle differed significantly between nest maintenance workers and foragers/patrollers ($\lambda = 0.62$, $F_{4,75} = 11.25$, $P < 0.001$; Figure 3a). Predicted classification based on discriminant scores from this analysis misclassified 21% of workers (5/23 nest maintenance workers and 12/57 forager/

FIG. 1. Representative chromatograms of ants collected while they were performing one of three tasks: (A) foraging; (B) patrolling, or (C) nest maintenance. All three ants were from the same colony.

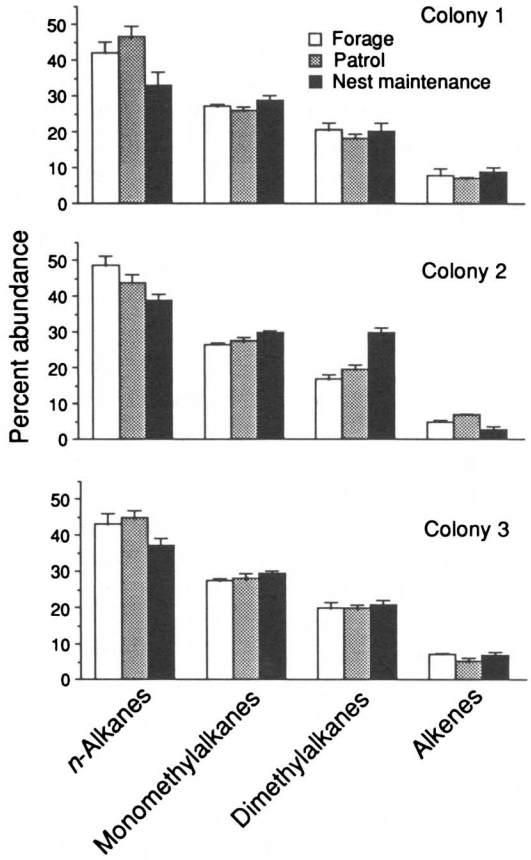


FIG. 2. Mean proportional abundance of major classes of cuticular hydrocarbons from *Pogonomyrmex barbatus* workers in three colonies. Sample sizes range from 5 to 10 per colony/task. Bars are standard errors.

patrollers). In general, workers performing nest maintenance expressed relatively lower concentrations of *n*-alkanes, and relatively higher concentrations of methyl-branched alkanes and alkanes, than foragers and patrollers (Figure 4). There was no significant difference among the three task groups in the proportion of long-chain *n*-alkanes (more than 28 carbons) to total *n*-alkane ion abundance ($F_{2,77} = 2.8$, $P = 0.08$; overall mean $= 0.25 \pm 0.1$ SE, $N = 80$).

Nest maintenance workers and foragers/patrollers differed in the relative abundance of the five most abundant compounds as well ($\lambda = 0.67$, $F_{5,74} =$

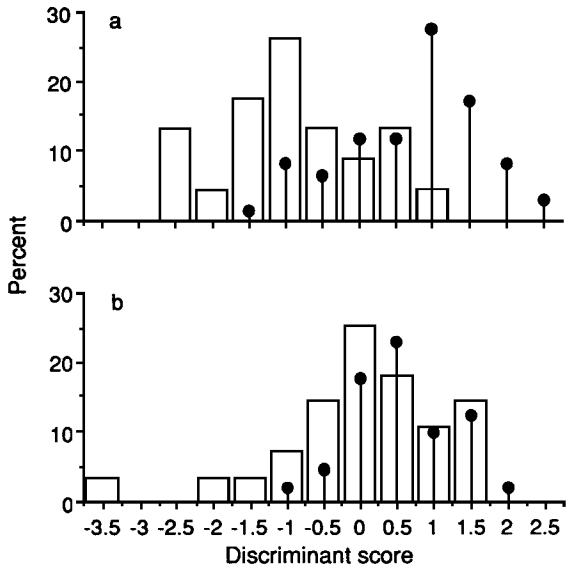


FIG. 3. Frequency distribution of linear discriminant analysis scores for ants of three task groups. Discriminant analysis yielded a new variable that was a linear function of the proportional abundance of the four major hydrocarbon classes (alkanes, monomethylalkanes, dimethylalkanes, and alkenes). The discriminant scores shown here are the position of each ant along this new axis. Similarity in discriminant scores reflects overall similarity in chemical composition. Graph (a) compares the scores of nest maintenance workers (bars) and the group composed of foragers and patrollers (spikes); graph (b) compares the scores of foragers (bars) and patrollers (spikes). See text for significance tests.

abundance of the five most abundant compounds as well ($\lambda = 0.67$, $F_{5,74} = 7.1$, $P < 0.001$). Not all compounds contributed equally to this result. The proportion of the most abundant compounds, *n*-pentacosane, *n*-heptacosane, and 13-methylheptacosane, varied considerably between nest maintenance workers and forager/patrollers, while 7-methylheptacosane and *n*-nonacosane varied little (Figure 5). Prediction of task group (nest maintenance versus forage or patrol) from discriminant scores based on the five most abundant compounds misclassified 25% of workers (4/23 nest maintenance workers and 16/57 foragers/patrollers).

Foragers and patrollers did not differ in the proportion of *n*-alkanes, monomethylalkanes, dimethylalkanes, and alkenes on the cuticle ($\lambda = 0.92$, $F_{4,52} = 1.1$, $P = 0.3$; Figures 3b and 4). Discriminant scores based on classes

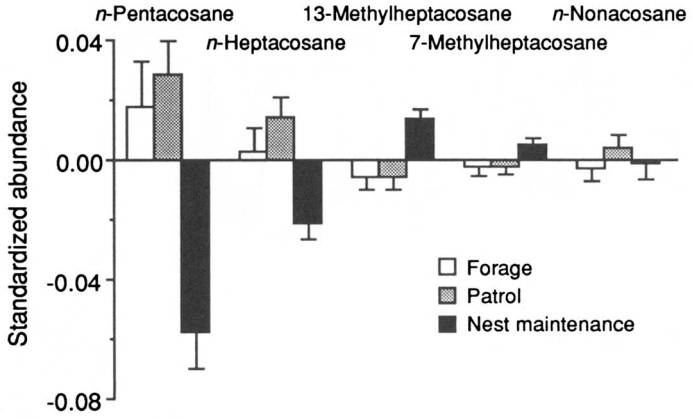


FIG. 4. Differences among task groups in the proportion of major cuticular hydrocarbon classes. Data were standardized for differences among colonies by subtracting the within-colony mean proportional abundance for each hydrocarbon class from the proportional abundance of that hydrocarbon class on each ant. A value of zero for *n*-alkanes, for example, would mean no difference between the proportional abundance of *n*-alkanes on an ant and the mean proportional abundance of *n*-alkanes for that ant's colony as a whole. Bars represent standard errors; $N = 80$ ants.

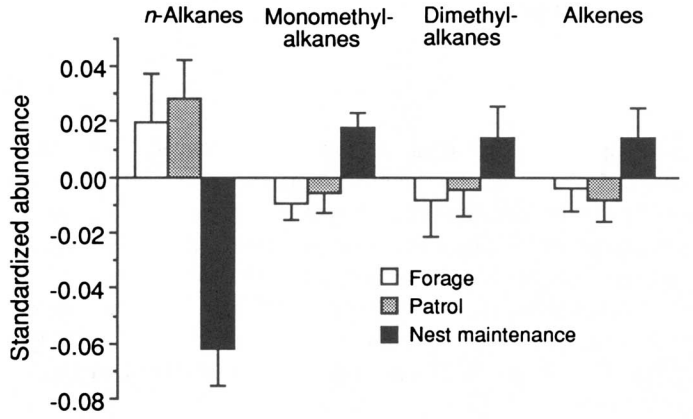


FIG. 5. Differences among task groups in the mean proportion of the five most abundant cuticular hydrocarbon compounds. Data were standardized among colonies (see Figure 4 legend for explanation of the standardization). Bars represent standard errors; $N = 80$ ants.

of compounds were poor (analysis misclassified 39% workers: 12/28 foragers and 10/29 patrollers). There was also no difference in the proportion of the five most abundant cuticular hydrocarbons on foragers and patrollers ($\lambda = 0.95$, $F_{5,51} = 0.5$, $P = 0.9$; Figure 5). Discriminant scores from this analysis misclassified 35% of workers overall, 11/28 of foragers and 9/29 of patrollers.

DISCUSSION

The results demonstrate that there are differences in cuticular hydrocarbon composition between some harvester ant task groups. Previous work showed that the extent to which one worker group actively performs a task affects the activity of other worker groups (Gordon, 1987). Brief antennal contacts with workers engaged in the same or different tasks may influence an ant's subsequent behavior. Recent laboratory work suggests such contacts do influence transitions in ant behavior from one task to another and between activity and inactivity (Gordon and Mehdiabadi, unpublished data). Task-related differences in cuticular hydrocarbon composition may permit one ant to determine the task of another during a brief antennal contact.

Contact among ants within a colony probably transfers some quantity of cuticular lipids from one worker to another, but contact among *P. barbatus* workers in different task groups was evidently not sufficient to homogenize their hydrocarbon profiles. Recent work by Soroker et al. (1995) demonstrated that hydrocarbons are regularly exchanged among workers of the ant *Cataglyphis niger*. Cuticular hydrocarbons were transferred to the postpharyngeal gland, probably through self-grooming, and then exchanged with other ants primarily through trophallaxis. Whether this exchange of hydrocarbon material was enough to eliminate differences among task groups in *C. niger* is not known. Observations of *P. barbatus* colonies dwelling in transparent nest boxes in the laboratory suggest that trophallaxis among adults is rare. Low rates of postpharyngeal hydrocarbon exchange may preserve task-related hydrocarbon differences in this species.

Despite colony differences in cuticular hydrocarbon composition, *P. barbatus* task groups tended to differ from one another in consistent ways from one colony to the next. In all three colonies surveyed, nest maintenance workers relative to foragers and patrollers were characterized by a lower ratio of straight-chain alkanes to branched and unsaturated hydrocarbons. Differences in the relative abundance of many single compounds of nest maintenance workers and foragers/patrollers also tended to be consistent among colonies. Similarity among colonies in task-related hydrocarbon patterns is noteworthy, because it suggests a common mechanism may operate to produce task group differences. Unlike foragers or patrollers, nest maintenance workers perform relatively little of their

work outside the nest. Differences in the hydrocarbon composition of exterior workers (foragers) and wholly interior workers (brood-tenders) were demonstrated for the ant species *Camponotus vagus* (Bonvita-Courgourdan et al., 1993). Taken together, these results suggest that changes in the chemical composition of the cuticle may be associated with the transition between interior and exterior work.

How do task-related differences in cuticular hydrocarbon composition arise? We consider two, not mutually exclusive, hypotheses to be likely. First, both the transition to exterior work and changes in the composition of the cuticle may correlate with age (as suggested by Bonavita-Cougourdan et al., 1989). In many ant species, including several species of *Pogonomyrmex*, younger ants work inside the nest, whereas older ants perform exterior tasks (MacKay, 1983; Wilson, 1971; Hölldobler and Wilson, 1990). In response to experimental perturbation, workers of *P. barbatus* switch between external tasks in a predictable manner, from nest maintenance to foraging or patrolling (Gordon, 1989). If the distribution of this short-term task switching mirrors the way an ant moves from one task to another over the months of its lifetime, then nest maintenance workers should be younger on average than foragers and patrollers. If age is a cause of differences in cuticular hydrocarbon composition among task groups, then our data suggest that older ants produce more *n*-alkanes relative to methyl-branched alkanes and alkenes than younger ants. Similar increases in the proportion of cuticular *n*-alkanes with increasing adult insect age have been reported for the hemipteran *Triatoma infestans* (Juarez and Brenner, 1985) and the moth *Trichoplusia ni* (de Renobales and Blomquist, 1983).

Second, environmental conditions experienced by ants in different task groups may induce changes in the cuticle. Workers that perform their tasks outside the nest are likely to experience markedly different abiotic conditions from those inside the nest, including higher temperature, lower humidity, and exposure to ultraviolet light. Cuticular lipids are the primary passive barrier to water loss, and the composition, as well as the quantity, of hydrocarbons appears to play a role in the desiccation resistance (Hadley, 1994). Waterproofing is thought to result from weak molecular interactions among long-chain, nonpolar molecules (Lockey, 1976; Toolson et al., 1979; Toolson, 1982). Compounds of long chain length are generally thought to enhance desiccation resistance (reviewed by Gibbs, 1998), although this is not always the case (Gibbs et al, 1998). Both within and between species, arthropods dwelling in warm, dry environments tend to have hydrocarbons of longer chain length than their counterparts in more mesic environments (Hadley, 1977, 1978; Hadley and Schultz, 1987). Methyl-branching and unsaturation probably also affect cuticle permeability. Increases in the relative abundance of methyl-branched alkanes and alkenes in simple mixtures with *n*-alkanes result in a decrease in the melting

temperature, suggesting that both disrupt lipid packing (Gibbs, 1995; Gibbs and Pomonis, 1995) and thus may reduce waterproofing. In *Melanoplus sanguinipes*, acclimation to warm temperatures results in a greater relative abundance of straight-chain relative to branched-chain alkanes (Gibbs and Mousseau, 1994). The proportional abundance of cuticular *n*-alkanes on *P. barbatus* foragers and patrollers was about 20% higher than on nest maintenance workers. This greater relative abundance of *n*-alkanes may enhance the desiccation resistance of foragers and patrollers and is consistent with their greater exposure to the desert environment. Foragers and patrollers in this study did not, however, have alkanes of longer average chain-length than nest maintenance workers. Further work will be required to determine whether abiotic conditions are responsible for a shift toward saturated alkanes in *P. barbatus* foragers and patrollers.

Differences among task groups in cuticular hydrocarbon composition may assist in our understanding of how work is organized in social insect colonies. If *P. barbatus* can perceive cuticular hydrocarbons, differences in the composition of the cuticle among task groups may provide workers with information about the task of ants they encounter. Future work should focus on whether ants perceive and respond to task-related differences in cuticular hydrocarbon composition.

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