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TASK-RELATED ENVIRONMENT ALTERS THE CUTICULAR HYDROCARBON COMPOSITION OF HARVESTER ANTS

DIANE WAGNER,[1,*] MADELEINE TISSOT,[2,†] and DEBORAH GORDON[2]

[1]*Department of Biological Sciences*
University of Nevada
Las Vegas, Nevada 89154-4004, USA

[2]*Department of Biological Sciences*
Stanford University
Stanford, California 94305-5020

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Abstract—Within a colony of harvester ants (*Pogonomyrmex barbatus*), workers in different task groups differ in the hydrocarbon composition of the cuticle. Foragers and patrollers, which spend extended periods of time outside the nest, have a higher proportion of saturated, unbranched hydrocarbons (*n*-alkanes) on the cuticle than nest maintenance workers, which spend only short periods of time outside the nest. We tested whether these task-related differences in ant cuticular chemistry arise from exposure to conditions outside the nest. Nest maintenance workers experiencing daily, short-term outside exposure developed a higher proportion of *n*-alkanes on the cuticle than workers kept inside the lab. Independent manipulations of ultraviolet radiation, relative humidity, and temperature revealed that only the combination of high temperature (ca. 38°C) and low relative humidity (ca. 8%) increased the proportion of cuticular *n*-alkanes. The results indicate that warm dry conditions, such as those encountered when an ant leaves the nest, trigger changes in cuticular chemistry.

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

INTRODUCTION

A social insect colony performs many tasks, including foraging, nest construction, and feeding the young. In many social insect species, workers are not specialized

*To whom correspondence should be addressed. E-mail: dwagner@ccmail.nevada.edu
†Current address: Department of Insect Biology, University of California, Berkeley, California 94720-5020.

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to perform a particular task but change tasks throughout their lifetimes (Gordon, 1996; Franks et al., 1997). Typically, the tasks performed early in life take place entirely inside the nest, such as care of the queen and brood, while tasks that require leaving the nest are performed later in life (Wilson, 1971).

Workers of the harvester ant, *Pogonomyrmex barbatus* (F. Smith), perform four tasks outside the nest: nest maintenance, midden work, patrolling, and foraging (Gordon, 1986). Nest maintenance workers work mostly inside the nest, leaving the nest on brief trips lasting less than a minute (personal observation) to remove bits of soil and rock from the nest. Midden workers arrange organic debris on the nest mound. Patrollers choose the day's foraging location and respond to disturbances. Foragers find and retrieve food items. In contrast to nest maintenance, foraging and patrolling require a considerable amount of time outside the nest. A single trip by a forager averages 23 min, with a range of 2–165 min (Gordon and Kulig, 1996). It appears that a worker progresses from nest maintenance to foraging. Nest maintenance workers will switch to foraging when new food sources become available (Gordon, 1989). This transition occurs in one direction only: once a worker switches to foraging, it does not switch back to nest maintenance. New nest maintenance workers, if needed, are recruited from among the pool of interior workers (Gordon, 1989).

The transition to exterior work introduces harvester ants to new and extreme physiological challenges. *Pogonomyrmex barbatus* occupies arid regions of North America. Colonies are active during the warm months of the year, from March to November. Work outside the nest occurs in the daylight hours (Gordon, 1986), and soil temperatures during periods of activity are often very high (Whitford, 1976). In comparison to interior workers, exterior workers experience higher temperature, lower humidity, and direct solar radiation.

Caste differences in cuticular hydrocarbon composition have been reported for several social insect species (Howard et al., 1982; Smith and Taylor, 1990; Bonavita-Cougourdan et al., 1993; Haverty et al., 1996; Kaib et al., 2000). Previous work on *P. barbatus* demonstrated that foragers and patrollers have higher proportions of *n*-alkanes, relative to branched alkanes and alkenes, than nest maintenance workers (Wagner et al., 1998). Because harvester ant foragers and patrollers spend more time outside the nest than nest maintenance workers, the higher proportion of saturated, unbranched hydrocarbons on the cuticle might be a response to the warmer, drier conditions they face. Another possibility is that both task and cuticular composition change independently with age. The purpose of this study was to test the hypothesis that exposure to external conditions (ultraviolet light, warm temperature, low humidity, or some combination of these factors) causes an increase in the percentage of *n*-alkanes on the cuticle.

METHODS

Experiments were conducted at the Southwestern Research Station of the American Museum of Natural History in Portal, AZ, USA. In each experiment we exposed *P. barbatus* nest maintenance workers from 3 colonies to various combinations of the environmental conditions they would be likely to encounter outside the nest. Nest maintenance workers were collected as they left the nest carrying soil in their mandibles. The colonies from which we collected workers were large and appeared mature (5 years or older, Gordon, 1995); the nest mound of each was >1 m in diameter. In the laboratory, the workers from each colony were placed into a plastic box and provided with an aluminum foil shelter, a source of moisture, and an unlimited supply of 20% sucrose solution. On the day an experiment was to begin, a random sample of workers from each colony was killed by placing them in a freezer at -80°C. These ants were used to determine the initial cuticular hydrocarbon composition of the nest maintenance workers.

Exposure to Outside Conditions. Ants in this experiment were subjected to one of two treatments: (1) 50 min periods of exposure to outdoor conditions or (2) no exposure to outdoor conditions. Nest maintenance workers were collected from colonies S1, S6, and S7. Workers were randomly assigned to treatment and holding container. Holding containers were polystyrene dishes with plaster floors and gently sloping sides to prevent shadows on the floor of the dish when placed in the sunlight. The sides of the holding containers were coated with Fluon (Northern Products Inc., Woonsocket, RI) to prevent ants from escaping. There were 3 holding containers per treatment-colony combination, and 1–4 ants per holding container. The plaster was moistened daily with approximately 3–5 ml of water. Except during periods of active exposure, ants were provided with sucrose solution and each holding container was kept covered with a individual plastic plate.

Each morning thereafter between 1000 and 1130, food and shelters were removed from all containers. The lids were then replaced on the containers holding the indoor control ants. Ants to be exposed were carried outside in their open containers and placed on a level surface in direct sunlight for 50 min. The duration of exposure was chosen to be similar to that of two average foraging trips (about 23 min each, Gordon and Kulig, 1996). The positions of containers were rotated from day to day to prevent positional effects. After exposure, ants were returned to the lab and food and shelters were restored to all containers. Ants of the indoor control group were never put outside. Twenty days from the beginning of the experiment, all treatment and control ants were killed, by placing them into a -80°C freezer, and stored for later chemical analysis.

To measure the environmental conditions experienced by ants in the two treatments, we monitored temperature and relative humidity (RH) in holding containers that lacked ants, but that were treated in the same way as containers that

did hold ants (plaster was watered, food changed, and dishes covered as usual). We had to monitor empty containers because ants could escape by climbing onto the temperature probe. We placed two empty containers outdoors during each exposure trial and monitored temperature and humidity in them every few minutes. Temperature was measured on the surface of the plaster using a thermocouple thermometer equipped with a surface probe (Hanna Instruments, Woonsocket, RI). Temperature and RH 1 cm above the plaster surface were measured using a thermohygrometer (Oakton, Forestry Suppliers, Jackson MS #76001). Two additional empty containers were maintained inside the laboratory with the control ants. Once each day, we measured surface temperature, air temperature, and humidity inside the closed containers by inserting probes through doors in the plastic lids.

Ultraviolet Light Manipulation. We manipulated the level of exposure to ultraviolet (UV) light by placing ants outside under canopies constructed of filters that transmitted either low or high levels of UV, while monitoring temperature and humidity to assure that they did not vary among UV treatments. Low-UV canopies were constructed from plastic sheets with transmission of 0% at wavelengths less 380 nm (Lee Filters, Hampshire, UK #226). High-UV canopies were constructed of sheets with 90% transmission at 380 nm, 85% transmission at 350 nm, and 0% transmission at wavelengths less than 310 nm (Lee Filters #226). Canopies were constructed on $50 \times 50 \times 50$ cm frames made of dowels. The filter material was secured across the top and extended out 25 cm to each side. During exposure periods (1030 to 1200), the sun was high overhead and no direct sunlight reached the floor of the canopy without first passing through the filter. Reflected UV light from indirect sources could enter from the sides.

Nest maintenance workers from colonies I, K, and M were randomly assigned to high or low UV exposure, and to one of two holding containers per colony-treatment combination (1–4 ants per holding container). Each morning thereafter, ants were placed under the appropriate canopy for 50 min. All ants experienced a brief period of exposure to UV light, lasting approximately 5–10 sec, as they were carried from the laboratory to the canopies. When not underneath the canopies, ants were kept covered in the laboratory. After 11 days of daily treatments, ants were killed and stored at -80°C.

Temperature and humidity measurements were taken from two containers per treatment that lacked ants, as described above. These containers were moved outside and inside along with the ant containers. We took multiple measurements of temperature and RH from each dish while the ants were outside, and one measurement per day of conditions inside closed containers in the laboratory.

Temperature and Humidity Manipulations. We manipulated temperature and humidity in a 2×2 factorial experiment conducted in the laboratory. Each experimental treatment combination was administered in a plastic chamber, $50 \times 35 \times 20$ cm (length $\times$ width $\times$ depth) in size. Two chambers, one maintained at high

humidity and one at low, sat on a silicone rubber-laminated heating mat attached to a temperature controller (Thermolyne, Dubuque, IO), and two chambers sat on the desktop at room temperature. We defined high temperature as 35–40°C, moderate temperature as room temperature (25–30°C), high humidity as 95–100% RH, and low humidity as 10–30% RH. We created high RH in two chambers by sprinkling approximately 100 ml of water onto the chamber floors, and created low RH by sprinkling approximately 100 ml of desiccant crystals (Drierite, Fisher #07–577) on the floors in a similar manner. Desiccant crystals were regenerated and replaced daily. Chambers were cleaned and dried daily. We rotated chambers through treatments to prevent confounding chamber with treatment effects.

Ants from colonies I, J, and K were assigned randomly to treatment and holding containers. There were 1–5 ants per holding container and 2 holding containers for each treatment-colony combination. Chambers were prepared each morning and were considered ready to use when the temperature in the "warm" chambers was approximately 40°C, the relative humidity in the "dry" chambers was 10–20%, and the RH in the "moist" chambers was 90–100%. Containers holding ants were placed into the chambers between 1000 and 1130 hours. There was an equilibration period, lasting 5–10 min, during which chambers were returned to the target temperature and humidity. Ants were then kept in the chambers for another 50 min. Air temperature and RH inside the chambers were measured by inserting probes into small holes in the chamber walls. Whenever the probe was withdrawn, rubber stoppers were quickly inserted into the holes. The experiment continued for 11 days, after which all ants were killed and stored at −80°C.

Chemical Analysis. Chemical analyses were conducted at Stanford University. Frozen ants were transported to Stanford University on dry ice and stored at −80°C. Methods of extraction and analysis are described in detail in Wagner et al. (1998). We extracted the cuticular lipids from each ant separately by immersion in 1 ml of pentane. The mixture was gently shaken during the first minute of soaking. After 10 min soaking, the fluid was transferred to a clean vial and dried under a stream of N_2. The residue was dissolved in 50 μl of chloroform. Aliquots of 1 μl were introduced by splitless injection onto a SPB-1 fused silica capillary column (30 m, 0.25 mm ID, 0.5 μm film thickness; Supelco, Bellefonte, Pennsylvania); samples were purged after 1 min. The carrier gas was He, flowing at 1 ml/min. The injector was maintained at 300°C. The oven was set at 170°C during injection, raised quickly to 220°C at 25°C/min, then more slowly to 300°C at 3°C/min. Samples of a standardized mixture of hydrocarbons were interspersed among ant samples to confirm the consistency of elution times.

We identified unknown compounds, and confirmed the identity of peaks with retention times and relative positions known from previous work, by analyzing the mass spectra of peaks from a small sample of ants frozen at the time of collection. Lipids were extracted from 3–5 ants from each experiment and the extracts treated as described above. Approximately 2–4 μl were injected onto a capillary column

(DB-1, J&W Scientific, Folsom, CA, USA) and analyzed on an HP 5890/5970 GC/MS. Instrument temperatures and run times were the same as above, except the oven was raised to a final temperature of 310°C. We used Nelson et al. (1980 and *in press*) as references when identifying compounds. For each experiment, we used only those compounds that composed at least 0.5% of the total ion abundance in the data analysis.

Data Analysis. The dependent variable for all statistical analyses was the proportion of *n*-alkanes in the total ion abundance for each ant. Data were arcsine square root-transformed when necessary to meet the assumption of normality. For each experiment, we tested the effect of treatment and colony on proportional abundance of *n*-alkanes using a two-way factorial analysis of variance. For the outside exposure and UV manipulation experiments, we compared the average daily temperature and RH experienced by ants in the two treatments of each experiment using paired *t*-tests.

RESULTS

Chemical Analysis. We found between 21 and 30 cuticular lipid compounds on individual ants in the three experiments. All but two of these compounds had been identified in previous studies (Wagner et al., 1998; Wagner et al., 2000). Compounds included normal alkanes, mono- and di-methylbranched alkanes, alkenes, and esters. We were unable to identify two novel compounds found in trace amounts (each constituted $<1\%$ on average) on ants in the UV exposure experiment. The mass spectra of these unknown compounds indicated that they were not *n*-alkanes. No novel compounds were produced in response to experimental manipulation; rather, changes in *n*-alkane abundance reflected changes in the relative abundance of common compounds.

Exposure to Outside Conditions. During periods of exposure, ants placed outside experienced significantly higher temperatures and lower RH than those kept inside. The mean (range) conditions in containers during exposure and inside containers within the laboratory were as follows: air temperature 34.3°C (25.0–41.0) outside and 25.1°C (21.1–28.5) inside (t_{19}, paired by day, $= -11.6$, $P < 0.0001$); surface temperature 27.0°C (21.0–30.2) outside and 24.6°C (21.0–26.9) inside (paired $t_{19} = -6.2$, $P < 0.0001$); RH 42.4% (16.2–78.1) outside and 87.4% (75.4–97.0) inside (paired $t_{19} = 12.3$, $P < 0.0001$). The sun was obscured by clouds during 7 of the 20 days of exposure.

Mean percentages of cuticular hydrocarbon compounds in this experiment are listed in Table 1 (see Figure 1 for a representative chromatogram). Outside exposure led to an increase in the proportion of *n*-alkanes on the harvester ant cuticle (Figure 2, Table 1). The cuticular lipids of ants that were exposed to outside conditions for 50 min/day contained a significantly higher percentage of *n*-alkanes

TABLE 1. AVERAGE PERCENT COMPOSITION OF CUTICULAR HYDROCARBONS FROM EXPOSED AND CONTROL *P. barbatus* WORKERS

Compound	TIC Peak no.[a]	Colony S1		Colony S6		Colony S7	
		Control	Exposed	Control	Exposed	Control	Exposed
Alkanes							
n-Tricosane	1	6.9	9.1	5.7	6.7	4.2	7.2
n-Tetracosane	2	1.5	1.6	1.5	1.5	1.0	1.4
n-Pentacosane	3	30.7	33.5	24.2	26.9	20.6	27.9
n-Hexacosane	5	1.6	1.5	1.6	1.7	1.2	1.6
n-Heptacosane	7	5.0	5.1	4.2	3.8	3.7	4.5
n-Nonacosane	12	2.1	2.4	2.4	2.1	2.1	2.3
n-Hentriacontane	18	3.0	3.4	3.4	2.7	2.8	2.8
Total alkanes		50.8	56.6	43.0	45.5	35.7	47.6
Alkenes							
Heptacosene	6	2.2	1.8	2.2	2.0	3.4	2.6
Nonacosene	11	2.0	1.7	2.1	1.9	3.3	2.7
Hentriacontene	18	3.8	3.3	4.6	2.9	6.6	5.2
Total alkenes		8.1	6.8	9.0	6.8	13.3	10.5
Monomethylalkanes							
13-Methylpentacosane	4	2.7	2.3	2.9	3.3	4.3	3.0
13-Methylheptacosane	8	4.5	3.8	4.2	4.3	5.4	4.5
7-Methylheptacosane	9	4.2	3.9	3.4	3.2	4.5	4.3
15-Methylnonacosane	13	4.1	3.7	5.0	4.1	4.4	4.2
9-Methylnonacosane	14	1.5	1.4	2.8	1.8	1.8	1.8
7-Methylnonacosane	15	1.9	2.0	1.8	1.6	2.1	2.5
15-, 13-, 11-, 9-Methylhentriacontanes	19	5.8	5.5	6.8	6.0	6.1	5.1
7-Methylhentriacontane	20	1.6	1.2	2.0	1.8	1.9	0.2
17-, 15-, 13-, 11-, 9-, 7-Methyltritriacontanes	21	2.1	1.9	2.5	2.1	2.0	2.0
Total monomethylalkanes		28.3	25.7	31.3	28.2	32.5	27.6
Dimethylalkanes							
7,13-Dimethylheptacosane	10	2.2	1.9	1.9	2.0	3.1	2.0
7,13-Dimethylnonacosane	16	1.0	0.9	1.0	1.1	1.4	1.0
Total dimethylalkanes		3.3	2.7	2.9	3.0	4.5	3.0

Note: "Exposed" workers were placed outside daily; "control" workers were not placed outside.
[a] Total ion chromatograph (TIC) peak numbers correspond to those in Figure 1.

than those of ants kept indoors in covered containers ($F_{1,38} = 7.7$, $P < 0.01$). Colonies differed in the percentage of *n*-alkanes on the cuticle ($F_{2,38} = 9.9$, $P < 0.001$). There was no significant interaction between treatment and colony ($F_{2,38} = 0.7$, $P = 0.5$). There was a tendency for ants in both treatments to increase in the proportion of *n*-alkanes from the beginning of the experiment to the end. Ants

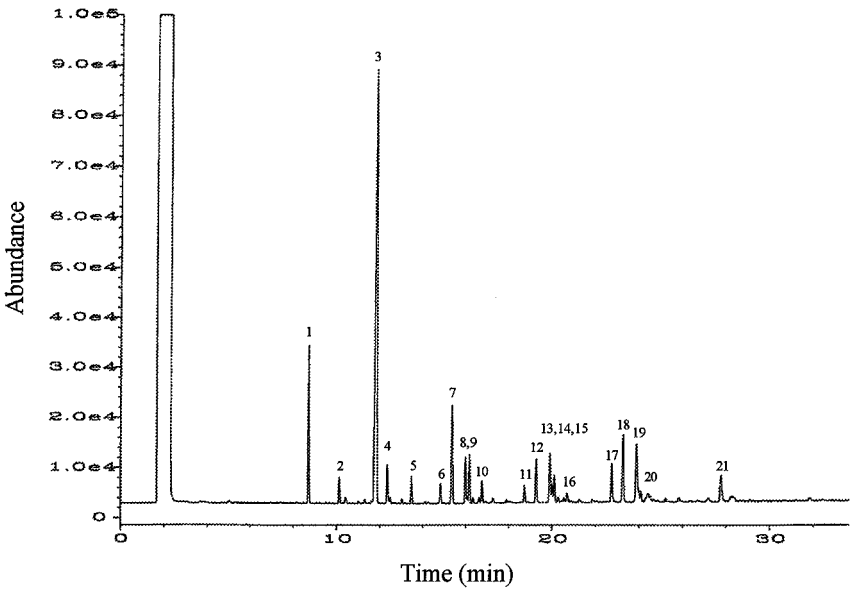

FIG. 1. Representative chromatogram of an ant in the exposure experiment. The large peak at 2 minutes is the solvent, chloroform. Numbers over peaks refer to the compounds listed in Table 1.

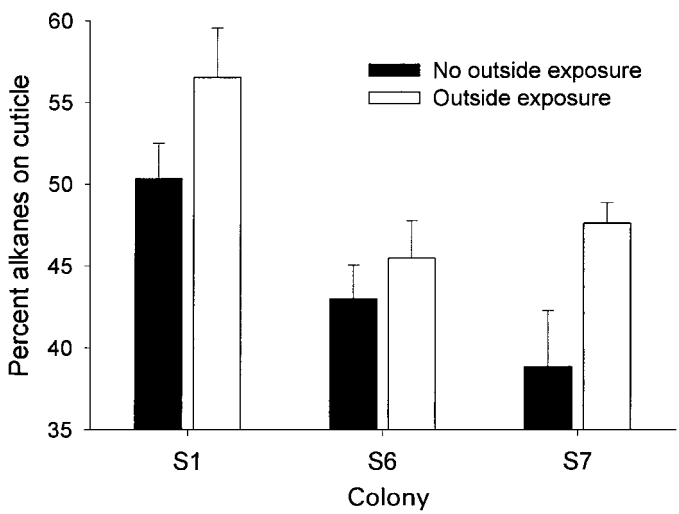

FIG. 2. Percentage of *P. barbatus* cuticular lipids composed of *n*-alkanes on ants exposed to outside conditions for 50 min/d and ants not exposed to outside conditions. Error bars show one mean standard error.

exposed to external conditions increased about 32% in *n*-alkanes over the initial state (overall mean initial % *n*-alkanes = 37.8, SE = 2.1, $N = 18$), while those kept indoors increased by about 16%.

Ultraviolet Light Manipulation. Temperature and humidity did not differ under canopies composed of UV-transmitting and UV-blocking material. Air temperature averaged 36.5°C (range 29.2–41.7) in high UV treatment containers and 37.6°C (30.5–41.7) in low UV treatment containers ($t_{10} = -0.7$, $P = 0.5$); surface temperature averaged 28.9°C (26.2–32.4) in high UV treatment containers and 28.7°C (26.3–32.8) in low - UV treatment containers ($t_{10} = 1.1$, $P = 0.3$); and RH averaged 37.7% (28.4–51.2) in high UV treatment containers and 36.6% (23.3–53.5) in low-UV treatment containers ($t_{10} = 1.1$, $P = 0.3$). Canopies trapped heat, so ants in this experiment experienced warmer conditions during periods outside than ants in the general exposure experiment. While inside the laboratory, within-container air temperature averaged 24.7°C (22.3– 26.5), surface temperature averaged 24.6°C (21.9–26.8), and RH averaged 88.6% (83.0–91.1).

Exposure to UV light had no effect on *n*-alkane abundance ($F_{1,28} = 1.8$, $P = 0.2$; Figure 3). As in the previous experiment, colonies differed in percent cuticular *n*-alkanes ($F_{2,28} = 19.3$, $P < 0.001$; Figure 3) and there was no significant interaction between treatment and colony ($F_{2,28} = 0.7$, $P = 0.5$). Cuticular *n*-alkanes increased about 40% over the course of the experiment, from a mean initial value of 29.8% alkanes (SE = 1.9, $N = 17$) to a final overall mean value of 41.6% (SE = 1.7, $N = 32$).

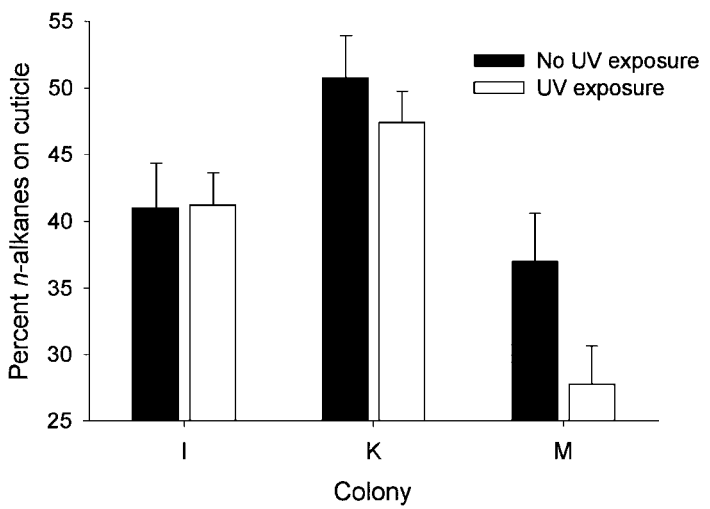

FIG. 3. Percentage of cuticular *n*-alkanes on harvester ants from different colonies exposed to sunlight that had passed through ultraviolet-transmitting and ultraviolet-blocking filters.

Temperature and Humidity Manipulation. The air temperatures and RH to which ants were exposed in this experiment averaged 38.7°C (range = 35.3–41.5) and 8.3% (4.5–12.1) in the high temperature–low RH chamber, 38.8°C (36.8–42.7) and 94.9% (78.9–99.9) in the high temperature–high RH chamber, 26.6°C (20.9–30.3) and 7.8% (4.0–18.2) in the moderate temperature–low RH chamber, and 26.2°C (21.8–28.9) and 86.0% (79.8–90.6) in the moderate temperature–high RH treatments.

The effects of temperature and humidity on cuticular composition were interdependent; in general, warm dry conditions lead to high *n*-alkane abundance (Figure 4). Humidity had a significant effect on *n*-alkane abundance, whereas temperature did not; however, the main effects must be interpreted cautiously because there was a significant interaction between temperature and humidity (Table 2). Inspection of Figure 4 indicates that low humidity affected cuticular composition only in combination with warm temperatures. Variation in humidity had little effect on *n*-alkane abundance at moderate temperatures. Colonies did not differ in *n*-alkane abundance, and there were no interactions involving colony (Table 2).

There was no consistent increase in *n*-alkanes over time in this experiment; rather, the magnitude and direction of change in percent *n*-alkanes depended on treatment. The average cuticular *n*-alkane abundance of ants exposed to warm, humid conditions was about 2% lower than that of the initial sample, whereas the

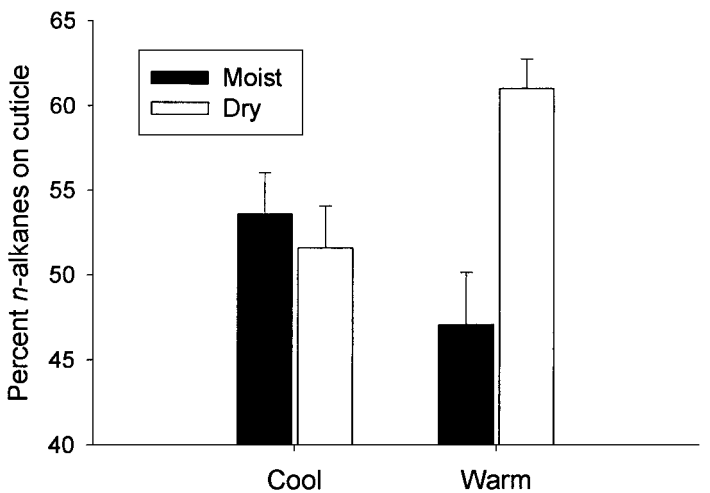

FIG. 4. Percentage of *n*-alkanes in the cuticular lipids of harvester ants subjected to combinations of temperature (warm and cool) and relative humidity (high and low). Colonies did not differ significantly in percent *n*-alkanes in this experiment and data from all colonies are combined for purposes of illustration.

TABLE 2. RESULTS OF ANALYSIS OF VARIANCE INVESTIGATING THE EFFECT OF TEMPERATURE, HUMIDITY, AND COLONY IDENTITY ON THE PERCENT *n*-ALKANES IN HARVESTER ANT CUTICULAR LIPID EXTRACTS

Source	*df*	*F*	*P*
Temperature (*T*)	1	0.1	0.8
Humidity (*H*)	1	6.6	0.01
$T * H$	1	12.6	<0.001
Colony (*C*)	2	1.6	0.2
$C * T$	2	0.1	0.9
$C * H$	2	0.6	0.6
$C * T * H$	2	1.9	0.2
Error	52		

n-alkane abundance of ants exposed to other treatments was 3–22% higher than the initial sample (initial average *n*-alkanes = 49.9%, SE = 2.4, $N = 25$).

DISCUSSION

The results indicate that environmental conditions affect the hydrocarbon composition of the harvester ant cuticle. Exposure to warm, dry conditions triggered an increase in the proportional abundance of cuticular *n*-alkanes. Exposure to UV radiation, in contrast, had little effect on cuticular *n*-alkane abundance. These results support the hypothesis that differences in exposure among task groups explains task-related differences in cuticular hydrocarbon composition. The total increase in *n*-alkane proportional abundance in exposed ants over 20 days (2–12%) was similar to differences between field-sampled nest maintenance workers and foragers reported previously (5–8%, Wagner et al., 1998). Our results corroborate those of previous studies investigating environmental effects on insect cuticular chemistry. Low RH lead to a similar increase in the relative abundance of *n*-alkanes in weevil larvae (*Oryzaephilus surinamensi*), although not in adults (Howard et al., 1995). Acclimation to warm temperatures increased the ratio of straight-chain relative to branched alkanes in the grasshopper *Melanoplus sanguinipes* (Gibbs and Mousseau, 1994).

The primary mechanism of water conservation in insects is a thin layer of lipids on the cuticle that forms a passive barrier to water loss through the integument (Hadley, 1994). In ants and many other arthropod taxa, cuticular lipid composition is dominated by various forms of hydrocarbons. The effectiveness of the cuticular lipid barrier at slowing water loss depends on its composition as well as its thickness. Hydrocarbon compounds differ in physical

properties that influence their effectiveness as waterproofing agents. Permeability to water increases sharply at compound-specific transition temperatures, probably the melting temperatures (Gibbs, 1998; Rourke and Gibbs, 1999). Double bonds and methylbranching dramatically reduce the melting point (Gibbs and Pomonis, 1995), so *n*-alkanes are thought to provide qualitatively better waterproofing than alkenes and branched alkanes of similar size. Studies of water loss in insects appear to support this hypothesis. Methylbranching and unsaturation are positively associated with water loss rate within several insect species (Hadley, 1978; Toolson, 1984). The proportional increase in cuticular *n*-alkanes detected in this study might serve to reduce water loss by ants exposed to warm dry conditions.

The transition from interior work to nest maintenance not only involves short bursts of exterior work, but brings ants closer to the surface while inside the nest, where they encounter warmer, drier internal conditions. Once a harvester ant begins to work outside the nest, it tends to stay in the upper chambers of the nest near the entrance (MacKay, 1983; Tschinkel, 1999). The entrance to a *P. barbatus* nest, which can be 1–4 cm wide, is connected by wide tunnels into one or more chambers just inside the nest entrance. Strong temperature and moisture gradients have been found in *Pogonomyrmex* nests during the summer months: areas near the surface are drier and warmer than deeper areas (MacKay, 1981). After performing nest maintenance work, ants move on to tasks that entail longer periods of external exposure, such as patrolling and foraging.

In addition to treatment effects, there was a general increase in the proportion of *n*-alkanes between the initial and final sampling times in both the outside exposure experiment and the UV exposure experiment, and an increase in three out of four treatments groups of the temperature and humidity experiment. There are two plausible explanations for this trend toward increasing *n*-alkane abundance over time. First, the conditions experienced by the ants in this study, including the indoor controls, may have been drier and warmer than those they experienced in the nest prior to collection, leading to the same sort of environmentally-triggered increase in *n*-alkanes that we detected in our experiments. Second, *n*-alkane abundance may increase as an ant ages, with environment acting to enhance or temper a general increase over time. We cannot reject either of these possibilities at the present time. Working with laboratory colonies of the ant *Myrmicaria eumenoides*, Kaib et al. (2000) found that the cuticular hydrocarbon composition of ants that switched from nest work to foraging changed with age over a period of 30–40 days, whereas the composition of workers that remained in the nest was unchanged over the same period. This result suggests either that task-related changes in cuticular chemistry are triggered by an ant's environment and not its age, or that only particular task groups undergo endogenous age-related changes in cuticular chemistry. Further work is underway to test the hypothesis that the relative abundance of *n*-alkanes is related to age, as well as environment, in *P. barbatus.*

We found that most colonies differed from one another in the proportion of *n*-alkanes in the cuticular lipids of nest maintenance workers. Colony-level differences in ant cuticular lipid composition have been detected in many ant species (Obin, 1986; Bonavita-Cougardan, 1987; Vander Meer et al., 1989; Nowbahari et al., 1990; Wagner et al., 1998; Nielsen, 1999). These differences may be due in part to genetic differences among colonies. There is some evidence of a heritable component to the cuticular hydrocarbon composition of fire ants and honeybees (Ross et al., 1987; Vander Meer et al., 1985; Page et al., 1991). Differences among the colonies we measured may also reflect how recently new nest maintenance workers were recruited from the younger workers inside the nest. For example, a colony whose nest was recently trampled by a cow will have recruited nest maintenance workers to repair the damage. Such a colony may have more new nest maintenance workers than one whose nest was undisturbed. Differences among colonies in cuticular *n*-alkane composition of their nest maintenance workers may reflect, in part, variation in the duration of the nest maintenance workers' tenure in that task, and thus, in how long the workers have been exposed to warm, dry conditions.

Rates of brief antennal contact, which involve the perception of odor, influence task decisions in *P. barbatus* (Gordon and Mehdiabadi, 1999). An ant's response depends on the task of the ant it meets (Gordon and Mehdiabadi, 1999). Cuticular hydrocarbons act as the cue for nestmate recognition in *P. barbatus* (Wagner et al., 2000), as in other ant species (Lahav et al., 1999; Thomas et al., 1999). We infer that task-specific differences in hydrocarbon profiles may also permit an ant to assess the task of a nestmate it meets. Our results show that the environmental conditions associated with a task, in particular exposure to warm temperature and low humidity, can shape task-specific differences in the cuticular hydrocarbon profile. When one ant contacts another, these task-related differences in hydrocarbon composition might provide information about the other's task. Similarly, we might recognize a carpenter by the calluses on her hands, whether or not she holds a hammer.

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