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Social insects

Cuticular hydrocarbons inform task decisions

Social insect colonies are organized without central control, and must not only accomplish many tasks, such as foraging and nest construction, but must also respond to changing conditions by adjusting the number of workers performing each task[1,2]. Here we use chemically treated, artificial ants to show that cuticular hydrocarbons, which differ according to task, are used by workers of the red harvester ant (*Pogonomyrmex barbatus*) to recognize the tasks of the ants that they encounter. Encounters with other ants thus inform a worker's decision on whether to perform a particular task.

A mature colony of the red harvester ant, a seed-eating desert species, consists of a single queen and 10,000–12,000 workers. We focused on two task groups: foragers, who collect food; and patrollers, who scout the foraging area each morning. If patrollers do not return safely, foragers will not leave the nest to search for seeds[3]. Nest-maintenance workers are active at the same time as patrollers and do not stimulate foraging[4]. A social-insect worker can become active or switch task as conditions are altered — depending, for example, on the number of other workers who are currently engaged in a particular task[5–7].

Communication in social insects occurs mostly by chemical and tactile means[8], with cuticular hydrocarbons often acting as recognition cues[9]. A harvester ant's task decisions depend on its interaction, by antennal contact, with ants at the nest entrance[10] — ants in different task groups differ in their cuticular hydrocarbon profiles[11]. Foragers, for example, spend more time outside the nest and so are exposed to warmer, drier conditions than nest-maintenance workers, who mostly stay inside. This causes the foragers to have higher ratios of *n*-alkanes to *n*-alkenes and branched alkanes in their cuticular hydrocarbon profiles[12].

For field experiments, we used nine mature colonies at a long-term study site near Rodeo, New Mexico, in the United States[13]. We first inhibited foraging by removing returning patrollers. After 30 min of inactivity, we mimicked the flow of returning patrollers by dropping glass beads (3 mm in diameter) that had been coated with one ant-equivalent of extract into the nest at a rate of one every 10 seconds. The coating on the beads consisted of patroller cuticular lipids, patroller hydrocarbons, nest-maintenance hydrocarbons (which acted as a control for task specificity), or plain solvent (blank control). As a positive control for forager activity, we used live patrollers that were captured and then immediately returned to the nest. Cuticular lipids were extracted in 100% pentane for 10 min[9,11] and hydrocarbons were purified from cuticular lipids by using column chromatography[9].

The number of beads added to a nest was roughly equal to the number of patrollers collected. We then measured foraging activity by counting the number of active foragers outside the nest within 1 m of the entrance, every 10 min for 60 min. All colonies received each treatment in a random order; for each colony, we carried out one trial per day for five consecutive days. We normalized for variation among colonies in absolute forager number by dividing each mean number foraging per trial by the largest number of foragers ever observed for that colony.

Task-specific cuticular hydrocarbons from patrollers were sufficient to rescue foraging activity (Fig. 1). However, the behaviour is not a simple response to patroller extract alone. Our results, including preliminary data (not shown), indicate that in this patroller-mimic assay, all of the following are necessary to stimulate foraging activity: a one-ant equivalent concentration of hydrocarbon extract, location just inside the nest entrance, sequential presentation, and the time of day at which the colony is ready to begin foraging.

A brief encounter with a nestmate influences an ant's task decision because the encounter identifies the task of the other worker, cued by subtle features of other ants' hydrocarbon profiles. Encounters between ants thus provide information used for task allocation. These encounters in the aggregate produce a dynamic network that regulates the colony's behaviour.

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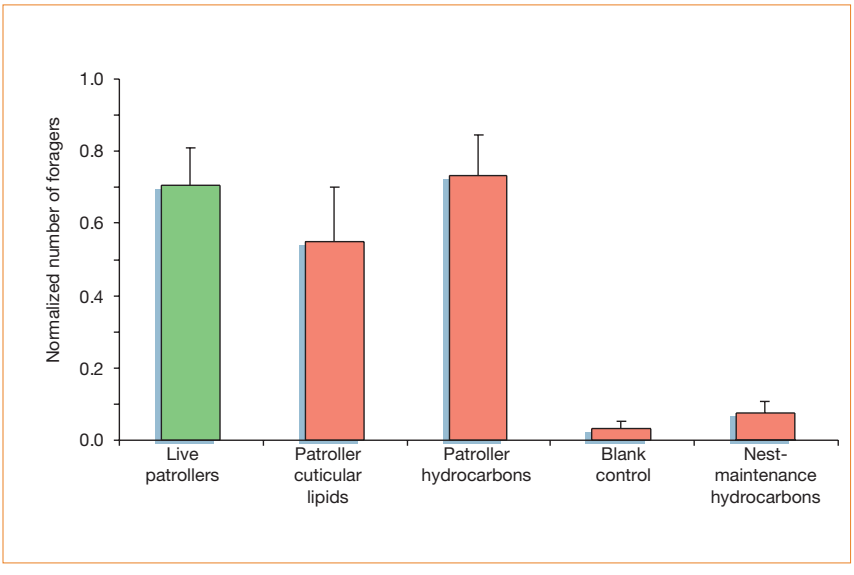

Figure 1 Task-specific cuticular hydrocarbons from patrollers are sufficient to rescue foraging activity in red harvester ants. The number of foraging ants (normalized; see text) leaving the nest is shown in response to live patrollers returning to the nest (green bars) or to different hydrocarbon-coated glass-bead ant mimics (red bars). Significantly more foragers emerged in response to live patrollers and to ant mimics treated with patroller cuticular lipids or patroller hydrocarbons than to mimics coated with blank control or nest-maintenance-worker hydrocarbons (repeated-measures analysis of variance: $F_{4,28} = 11.88$, $P < 0.0001$; $n = 9$). There was no significant difference in foraging-ant numbers among the returned live patrollers, patroller cuticular lipid and patroller hydrocarbon treatments, or between the blank and nest-maintenance hydrocarbon treatments (Tukey's post-hoc analysis). Data were transformed with an angular transformation (square-root of arcsine) for analysis.

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