



Breeding alters cuticular hydrocarbons and mediates partner recognition by burying beetles

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In many insects, recognition cues for social status or family membership are based on differences in cuticular hydrocarbons. In some cases these cues reflect reproductive status. Burying beetles, *Nicrophorus orbicollis*, form temporary pairs to rear a brood and, as a pair, they must defend their young and the breeding resource (a small vertebrate carcass) from conspecific intruders. Thus, a mechanism for the identification of a nonpartner is necessary for the appropriate aggressive response. Burying beetles appear to use reproductive status to identify partners. In behavioural tests of recognition, unknown individuals at the same reproductive stage were accepted as mates. In addition, males showed significantly less aggression towards unknown nonbreeding females treated with an extract of their mates' cuticular hydrocarbons. Cuticular hydrocarbon profiles of males and females on the sixth day of breeding, the most intense phase of parental care, were significantly different from those of their nonbreeding counterparts, but quite similar to each other. We conclude that these hydrocarbon profiles change during a breeding bout and mediate recognition of breeding partners. Furthermore, although juvenile hormone haemolymph titres changed dramatically during breeding, they did not directly affect hydrocarbon profiles.

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Although the major function of cuticular hydrocarbons in arthropods is to provide waterproofing, they also serve an important role as recognition signals (Howard & Blomquist 2005). Many studies of social insects have shown that cuticular hydrocarbons are the most important cues for nestmate recognition (e.g. Dapporto et al. 2006; van Wilgenburg et al. 2006; references in Howard & Blomquist 2005). Hydrocarbon profiles may even differ by caste (Kaib et al. 2000) and, in red harvester ants, are used by workers to inform their decision to perform a particular task (Greene & Gordon 2003). An important caste difference in social insects is between reproductives and nonreproductives, and hydrocarbon profiles often change in response to changing reproductive status. Profiles inform nestmates, which in turn behaviourally promote or

prevent these changes in reproductive status (e.g. Dietsmann et al. 2003, 2005; references in Howard & Blomquist 2005). Cuticular hydrocarbons can also provide cues for sex and mate recognition (crickets: Tregenza & Wedell 1997; cerambycid beetles: Ginzler et al. 2003; Zhang et al. 2003; Barbour et al. 2007; burying beetles: Steiger et al. 2007) and social status (cockroaches: Everaerts et al. 1997).

Except in the case of monogynous colonies of social insects, for which the queen is identified by her hydrocarbon profile, hydrocarbon profiles are not known to provide cues for individual identification. The ability to distinguish among individuals is commonly assumed and has often been shown in vertebrates (e.g. 'dear enemy' effect; Temeles 1994). Indeed, individual recognition is a necessary prerequisite for the complex social interactions characteristic of most vertebrates. Many insects live in stable groups, but recognition of individual characteristics appears to be rare (Tibbetts 2002). Yet in semisocial species with reproductive cooperation such as pair bonding or communal breeding, there is a need to recognize

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nestmates. In this study, we examined the basis of recognition of breeding partners in the biparental burying beetle, *Nicrophorus orbicollis*. These beetles cooperate to feed and guard larvae (Fetherston et al. 1990; Rauter & Moore 2004; Smiseth & Moore 2004; Smiseth et al. 2005) and must recognize intruders to the brood chamber to drive them off; contact pheromones appear to provide the cues to distinguish partner from nonpartner (Müller et al. 2003).

In the absence of a breeding resource, a small vertebrate carcass, and while it is being buried, neither male nor female burying beetles are aggressive towards new arrivals of the opposite sex. However, once eggs are laid, aggression by males and females is directed towards all nonpartners. If an intruder discovers and successfully takes over a carcass, it commits infanticide, then rears its own young on the resource (Scott 1990; Trumbo 1990). Males and females assist their mate to drive off intruders of either sex (Scott 1990; Trumbo 1991; Trumbo & Wilson 1993). The change in behaviour from indifference to aggression towards unknown beetles of the opposite sex probably takes place between 1 and 2 days of the discovery of a carcass (Scott 1994) and requires a mechanism for discrimination between partners and strangers.

Juvenile hormone (JH) profiles of male and female burying beetles change dramatically during breeding. Furthermore, JH directly influences cuticular hydrocarbon profiles used as recognition cues by ants as they progress from performing tasks inside to performing tasks outside the nest (Lengyel et al. 2007). Therefore, we hypothesized that the changes in chemical cues involved in partner recognition might be hormonally mediated. The discovery of a carcass triggers a two-fold increase in JH titres within 10 min and within 24 h there is a three- to four-fold increase in JH titres in females (Trumbo et al. 1995) and in males (Panaitof et al. 2004). JH haemolymph titres are highest in females (nine-fold higher than prebreeding) on the sixth day of breeding, when young larvae are being fed (Trumbo 1997). JH of paired males throughout parental care remains at about the level of the initial increase (Panaitof et al. 2004).

In a concurrent study, Steiger et al. (2007) identified cuticular hydrocarbons on the European burying beetle, *Nicrophorus vespilloides*, and found that they are highly plastic, changing with the beetles' physiological condition. In this study we confirm that partner recognition cues are based on reproductive status in *N. orbicollis*, examine cuticular hydrocarbon profiles of prebreeding and breeding males and females, and test whether changes in hydrocarbons are a direct consequence of changes in JH titres.

METHODS

Nicrophorus orbicollis were captured in Durham, NH, U.S.A., and a laboratory colony was established with new wild-caught individuals included each year. Some of the beetles used in these experiments were wild-caught soon after they emerged in late spring; others were reared in the laboratory. All beetles were maintained in small groups of conspecifics on beef kidney and mealworms at 20 °C on a 14:10 h light:dark cycle.

Behavioural Observations

Breeding pairs were each established in a plastic box (19 × 14 × 10 cm) of soil with a 30–35 g previously frozen mouse. On the fifth or sixth day after the initiation of breeding, about the time when eggs hatch and JH is at its highest level in females, the beetles were removed. Larvae were present in most but not all of the brood chambers. We performed several experiments to compare the behaviour of a beetle towards its mate versus a sexually mature, nonbreeding stranger of the opposite sex and then to establish the conditions necessary to mimic the cues for partner recognition. Each resident was observed with its mate and with only one stranger. All strangers were smaller than the opposite-sex residents with which they were tested because the willingness to attack depends on relative size (Scott 1990; Safryn & Scott 2000). First, we individually placed members of each breeding pair ($N = 15$) in arenas in a random sequence with either their mate or a nonbreeding member of the opposite sex. Second, we exchanged the members of two breeding pairs ($N = 15$) so that each male and female was observed (in random order) with their mate and with a breeding member of the opposite sex at the same reproductive stage. Third, we decapitated the breeding female and placed the body parts in 2 ml of hexane for 10 min to extract cuticular hydrocarbons (Ginzel et al. 2003; Barbour et al. 2007). We then dried the hexane and resuspended the extracted material in 10–20 µl of hexane. The breeding male ($N = 19$) was tested with a nonbreeding female to which 10 µl of hexane had been applied to her pronotum and elytra, then tested with a different nonbreeding female to which 10 µl of the hexane extraction from his mate had been applied to her pronotum and elytra.

Beetles were observed for 10 min in a neutral arena (a clean 15 cm petri dish). The behaviours scored were: contact with indifference; contact and quick withdrawal but no active aggression; aggression, which included chasing, leg biting and fighting. Generally, the same response occurred repeatedly whenever the two beetles met as they circled the arena, so the frequency of behaviours was not recorded. Also since latency to first contact varied as a function of beetle activity, frequency of aggressive acts in a 10 min period was not informative.

Cuticular Hydrocarbon Profiles

We established hydrocarbon profiles of males and females removed from the colony (prebreeding), males and females removed from the brood chamber on the sixth day after burial, and males removed from the brood chamber on the second day after burial ($N = 5$ each treatment). These times were chosen because larvae hatch on the sixth day and JH is highest in females shortly thereafter, whereas JH is highest in paired males on the second day. The cuticular hydrocarbons were extracted by soaking and gently shaking both elytra in 500 µl of HPLC grade hexane for 15 min (cuticular hydrocarbons excreted from the abdomen accumulate on the elytra; C. M. Orians, personal observation). Elytra were removed and extracts were stored at –20 °C. We injected 4 µl of each sample

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