

# Chemical cues and group association preferences in a subsocial cockroach, *Panesthia australis*

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**Abstract.** An ability to recognise and discriminate between group and non-group members is essential for most group-living species. Several different sensory modalities may be utilised for social recognition, the most notable of which is olfaction. Among insects, members of the order Blattodea (cockroaches, termites) exhibit a diverse range of social systems and provide an excellent model for examining the role of chemical communication in group discrimination. We experimentally tested the importance of chemical cues in the association preferences of the subsocial Australian wood-boring cockroach, *Panesthia australis*. Using a series of dichotomous choice trials, we found that individuals preferred conspecific odour cues over those of an unscented peatmoss control. We then gave cockroaches a choice between the odour cues of cockroaches from different logs, and found that they did not exhibit a preference for the cues of individuals from their own log versus those from different logs within the same locality. However, cockroaches exhibited a strong preference for cues taken from individuals from a geographically distant population. Our findings suggest that *P. australis* engages in group discrimination, and that patterns of association may reflect an underlying preference for unfamiliar and/or genetically dissimilar individuals in a species encumbered by restricted gene flow.

**Additional keywords:** aggregation, arthropod, chemical cue, gene flow, pheromone, sociality.

## Introduction

In group-living animals, social cohesion and the maintenance of stable aggregations are often dependent on individuals being able to recognise and discriminate between group and non-group members (Ward *et al.* 2005). A variety of different sensory modalities may be exploited for social recognition, one of the most important of which is olfaction. Chemical signals can act as valuable social cues across a wide range of taxa (e.g. fish: Brown and Smith 1994; reptiles: Bull *et al.* 2000; velvet worms: Barclay *et al.* 2000b; mammals: Bouchard 2001; amphibians: Waldman and Bishop 2004), but appear to be especially important in the communication system of insects. Chemical signals, such as cuticular hydrocarbons and aggregation pheromones, may often exhibit considerable variation within species (Higgie *et al.* 2000; Tregenza *et al.* 2000) and this, in turn, can influence the way in which individuals respond to one another (Pirk *et al.* 2001). The ability to recognise and discriminate between group and non-group members is therefore important, as it may reveal possible mechanisms underlying population genetic structuring and reproductive isolation (Wong *et al.* 2004). Yet, despite the role that chemical communication plays in social organisation, our understanding of the evolution and diversification of chemical cues remains limited, and lags far behind what is presently known about other forms of communication (Symonds and Elgar 2008).

Arthropods exhibit a diverse range of social systems (e.g. Schal *et al.* 1984; Tallamy and Wood 1986; Thorne 1997; Bourke 1999), the full spectrum of which can be found within a single order: the Blattodea (cockroaches and termites) (Roth and Willis 1960; Grandcolas 1997). Members of this order (see Inward *et al.* 2007) display a remarkable array of social complexity and organisation (e.g. Roth 1972; Brossut 1979; Schal *et al.* 1984; Gautier *et al.* 1988; Grandcolas 1997; Park *et al.* 2002), from solitary cockroaches that disperse soon after birth (e.g. *Thanatophyllum akinetum*) (van Baaran and Deleporte 2001) to the eusocial termites that live in colonies comprising tens of thousands of individuals (Inward *et al.* 2007). Between these extremes are subsocial species that exist in family groupings where one or more parents provide care for eggs and/or nymphs (e.g. *Panesthia cibrata*: Rugg and Rose 1984; O'Neill *et al.* 1987; Australian giant burrowing cockroach, *Macropanesthia rhinoceros*: Matsumoto 1992), and gregarious species that amass in dense aggregations made up of numerous nymphs and adults (e.g. German cockroach, *Blattella germanica*: Ame *et al.* 2004; Jeanson *et al.* 2005; Jeanson and Deneubourg 2007). In the light of such diversity, members of this group provide an excellent opportunity for investigating social behaviour and the role that chemical communication plays in group recognition and discrimination between, and within, populations.

In this study we examine the role of chemical cues in the grouping habits of the Australian wood-boring cockroach (*Panesthia australis*; Family Blaberidae), a subsocial species. *P. australis* is a moderate-sized (27–36 mm), ovoviviparous, saproxylic (i.e. lives within rotting logs) species that is distributed throughout south-eastern Australia (Roth 1977). It occurs in subsocial groupings comprising a pair of adults and 12–20 nymphs of various sizes (Roth 1977; Matsumoto 1988). *P. australis* is a secondarily flightless species, and although the wings are fully developed in adults, they are broken off at the base along a line of weakness within a few days of the final moult (Roth 1977; MacEachern 2001). Logs over 30 cm in diameter may contain several complex gallery systems, potentially indicating the presence of multiple subsocial groups (Matsumoto 1988). Here we investigate whether *P. australis* is capable of recognising conspecific chemical cues and, if so, how these chemical cues might be used in group formation and social cohesion. We also examine whether *P. australis* can recognise individuals from the same log solely on the basis of chemical cues, and whether the incorporation of other cues can enhance the recognition and discrimination among social groups from different logs.

## Materials and methods

### Animal collection and housing

We collected cockroaches from an isolated patch of mixed *Eucalyptus* forest situated in central Victoria, Australia (37°16'S, 144°09'E). Additional animals were collected from a location ~500 km away at Tallaganda National Park in New South Wales, Australia (35°06'S, 149°05'E). As in studies on other saproxylic invertebrates (Reinhard and Rowell 2005), cockroaches from the same log were considered to belong to the same group as they were either found close to one another or had the potential for contact through a continuous medium. All cockroaches collected from the same log were kept together (range = 1–13 individuals) in a plastic container in isolation from cockroaches collected from other logs. Each container was filled with moistened peatmoss to a depth of 1 cm. All animals (a total of 170 individuals) were housed in the dark in a constant-temperature room maintained at 18°C and fed carrots *ad libitum*.

### Chemical preference tests

We measured the association preferences of cockroaches presented with a dichotomous choice between two Petri dishes filled to a depth of 1 cm with moistened peatmoss. These were positioned at opposite ends of an experimental arena measuring 29 × 20 × 4.5 cm (length × width × height). As in studies of chemical communication in other arthropods (e.g. Persons *et al.* 2002), peatmoss was used as substrate for the delivery of chemical cues and, in this case, was also chosen because of its resemblance to the wood mulch found inside rotten logs occupied by *P. australis*. Depending on the experiment (see below), the peatmoss in each dish was either untreated or had previously been in contact with cockroaches. To acquire the *P. australis* chemical cues, peatmoss was kept in containers with cockroaches from the same log (mean number of cockroaches ± s.d. = 3.78 ± 2.93) for one week before the commencement of experimental trials to ensure ample time for the transfer of any cues onto the substrate.

A trial began with the introduction of a cockroach (randomised with respect to sex and life-history stage) into the centre of the arena. We then conducted scan samples every 20 min over a 3-h period. During each scan sample, we recorded whether the cockroach was associating with either of the Petri dishes and, if so, which one. The focal individual was deemed to be associating with a particular chemical stimulus if it was either inside, or in contact with, the Petri dish. At the end of the observation period, we tallied the total number of times the focal animal was observed associating with each stimulus. In an earlier pilot study offering cockroaches a choice between two identical, unscented peatmoss samples, we found no evidence of any side bias (time spent with Petri dish on the left = 2.6 ± 0.58, right = 4.0 ± 0.69; paired *t*-test: *t* = -1.15, d.f. = 29, *P* = 0.26). Hence, the number of observations associated with each stimulus was taken to reflect actual association preferences. The testing arena and all equipment were washed with soapy water and ethanol between trials. All trials were conducted in the dark with the aid of a red light (Briscoe and Chittka 2001),

We conducted two sets of experiments investigating preferences based on chemical cues. First, we tested whether cockroaches actually respond to any chemical cues from conspecifics. We did so by testing the association preferences of focal individuals when offered the choice between peatmoss that had previously been in contact with other cockroaches from the same log versus unscented peat moss (*n* = 30). Second, we tested the preferences of cockroaches when presented with chemical cues from their own log members versus cockroaches from another log from either the same, sympatric, population (central Victoria; *n* = 30) or the geographically distant, allopatric, Tallaganda population (*n* = 30). In a separate experiment, cockroaches were also offered the choice between the chemical cues of cockroaches from two foreign logs, one sympatric and the other allopatric (*n* = 30).

### Role of multiple cues

In nature, a wide range of potential cues are likely to be available to individuals for group discrimination (e.g. visual, behavioural, tactile, auditory and chemotactile cues). Accordingly, we decided to retest the association preferences of cockroaches when offered a choice between cockroaches from their own log versus cockroaches from other logs. However, this time we allowed focal animals access to all possible cues (*n* = 30 per experiment). The methods for measuring association preferences here were similar to those used in the chemical preference experiments but rather than using peatmoss-filled Petri dishes, we used two wire mesh cages (1 mm aperture; enabled visual, behavioural, tactile, auditory and olfactory interaction), each of which housed a stimulus cockroach selected randomly from the population of interest. The focal cockroach, in this regard, was deemed to be associating with a particular cage if it was physically touching the cage.

### Statistical analyses

Data were checked for normality and, where appropriate, were square-root transformed for the purpose of analyses using paired *t*-tests. All tests are two-tailed and data showing the number of

times observed associating with alternate stimuli are presented as mean  $\pm$  1 s.e.

## Results

### Chemical preference tests

When offered a choice between peatmoss that had previously been in contact with other cockroaches from their own log versus unscented peatmoss, we found that cockroaches spent significantly more time associating with the former (paired  $t$ -test:  $t = 3.22$ , d.f. = 29,  $P = 0.003$ ) (Fig. 1).

Cockroaches did not prefer the chemical cues of their own log-mates over cockroaches from other logs from the same sympatric population (paired  $t$ -test:  $t = 0.027$ , d.f. = 29,  $P = 0.97$ ) (Fig. 2a). However, when the choice was between the chemical cues of their own log-mates and those taken from the geographically distant Tallaganda population, cockroaches preferred the foreign cues (paired  $t$ -test:  $t = -2.215$ , d.f. = 29,  $P = 0.035$ ) (Fig. 2b). Intriguingly, when the choice was between the chemical cues of cockroaches taken from two foreign logs, one from the same sympatric population and one from the allopatric Tallaganda population, we found that cockroaches showed no preference for one over the other (paired  $t$ -test:  $t = 1.03$ , d.f. = 29,  $P = 0.311$ ) (Fig. 2c).

### Role of multiple cues

As in the chemical preference experiment, despite having access this time to multiple cues, cockroaches still did not show a significant preference when offered the choice between log-mates and non-log cockroaches from the same population (paired  $t$ -test:  $t = 0.40$ , d.f. = 29,  $P = 0.69$ ) (Fig. 3a). Similarly, when presented with multiple cues, cockroaches still preferred to associate with individuals from the allopatric Tallaganda population over those from their own log (paired  $t$ -test:  $t = -2.06$ , d.f. = 29,  $P = 0.049$ ) (Fig. 3b). However, this time, when presented with a choice between the two foreign groups, individuals spent significantly more time associating with members from the Tallaganda population over those from their own population (paired  $t$ -test:  $t = -3.12$ , d.f. = 29,  $P = 0.004$ ) (Fig. 3c).

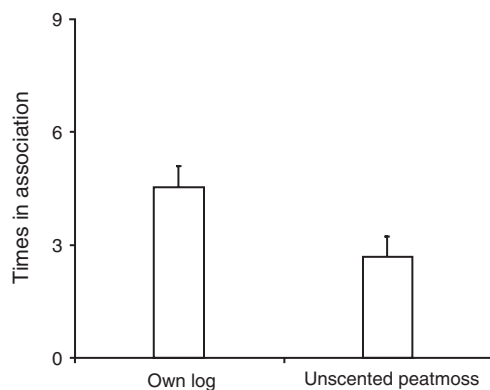


Fig. 1. Number of times cockroaches spent associating (mean  $\pm$  s.e.) with the chemical cues of own log members versus unscented peatmoss.

## Discussion

Chemical cues appear to play an important role in the association preferences of *P. australis*. Like several other cockroach species (e.g. Ishii and Kuwahara 1967, 1968; Ishii 1970; Roth and Cohen 1973; Brossut 1979; McFarlane and Allie 1986; Ross and Tignor 1986; Dambach *et al.* 1994; Moore *et al.* 1995; Rivault and Cloarec 1998; van Baaran *et al.* 2002; Ame *et al.* 2004), *P. australis* was able to use the chemical cues of conspecifics to distinguish between different groups. Although *P. australis* did

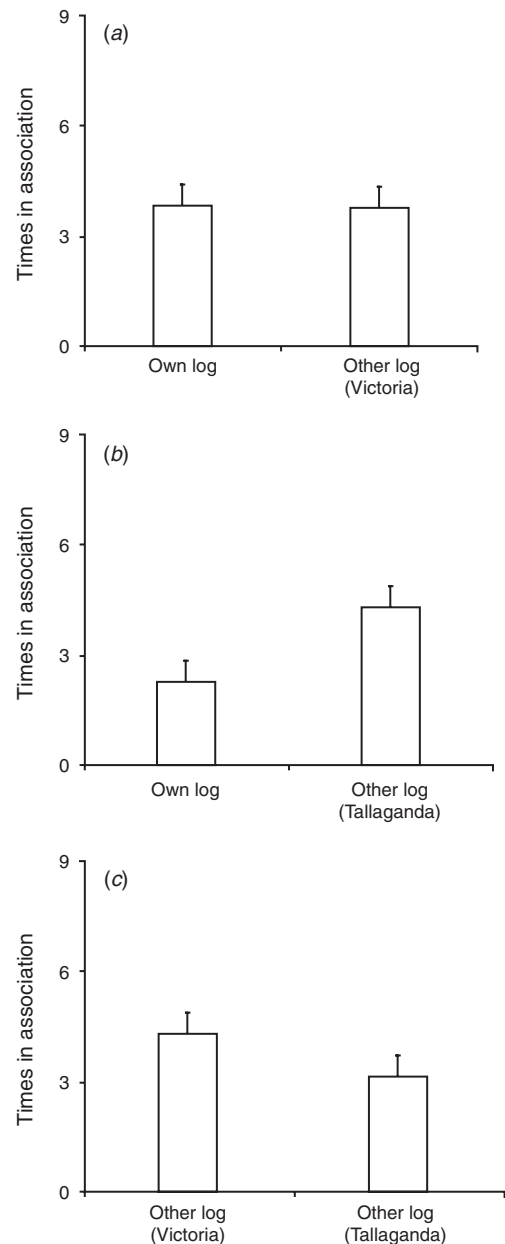
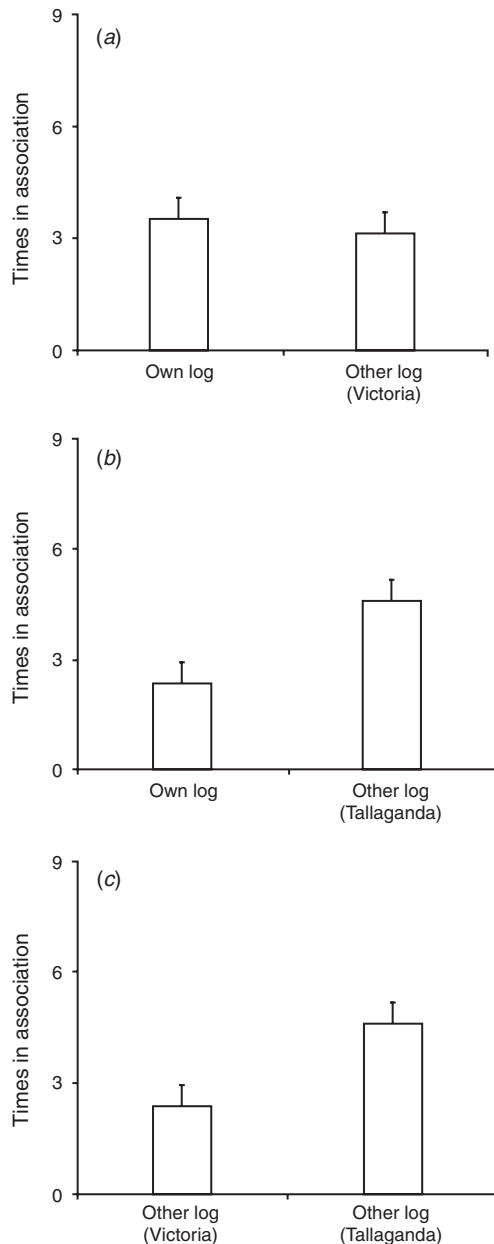


Fig. 2. Number of times cockroaches spent associating (mean  $\pm$  s.e.) with the chemical cues of (a) own log members versus foreign log members from the same population, (b) own log members versus foreign log members from the allopatric, Tallaganda population, and (c) foreign log members from the same population versus Tallaganda.



**Fig. 3.** Number of times cockroaches spent associating (mean  $\pm$  s.e.) with caged cockroaches when the choice was between (a) own log member versus foreign log member from the same population, (b) own log member versus foreign log member from Tallaganda, and (c) foreign log member from the same population versus Tallaganda.

not exhibit a preference for grouping with individuals from its own log over those from different logs within the same locality, it surprisingly exhibited a strong preference for individuals from ~500 km away at Tallaganda. These preferences remained unchanged (apart from an even stronger preference for foreign individuals over local individuals) even when *P. australis* had access to multiple cues. This contrasts with association preferences of other cockroach species, such as the German

cockroach, *B. germanica*, which displays a preference for the odour of individuals of its own genetic strain, and avoids odours of unfamiliar individuals (Rivault and Cloarec 1998; Ame *et al.* 2004).

A recent population genetic study of *P. australis* (MacEachern 2001) might help to elucidate the chemical preferences observed in this study. Saprophytic organisms, such as *P. australis*, are prone to the formation of small, isolated populations due primarily to the fragmented distribution of forested habitats in eastern Australia and the scattered distribution of rotting logs within these forests (e.g. Barclay *et al.* 2000a; Reinhard and Rowell 2005). The imposition that this population structure may have on population mixing in *P. australis* is further exacerbated by the species' secondary flightlessness (Roth 1977), which limits its dispersal abilities, resulting in restricted gene flow between populations, and hence substantial genetic differentiation among populations (MacEachern 2001). Thus, our finding that *P. australis* prefers the cues of individuals from foreign allopatric populations could reflect the presence of a strong inbreeding avoidance strategy in a species that occurs in small, isolated populations. Multiple subsocial groups can occur within the same log (Matsumoto 1988), and *P. australis* will readily colonise nearby logs (MacEachern 2001). This, in turn, may explain the high level of genetic variation that is present within a single log (the level of genetic variation within logs was similar to that observed within entire populations: MacEachern 2001). Thus, the failure for *P. australis* (with access to only chemical information) to exhibit a preference for individuals from its own log compared with neighbouring logs might be a result of the high levels of genetic variation within logs, and similarity to nearby logs.

Although chemical cues appear to play a pivotal role in the grouping behaviour of *P. australis*, it appears that other cues are also used. When exposed solely to chemical cues, *P. australis* did not show any preferences between foreign (i.e. other log) individuals from their own population versus those from Tallaganda. However, when offered the same choice using multiple cues, *P. australis* significantly preferred the latter. This suggests that multiple cues may be important in facilitating grouping preferences in *P. australis*.

In conclusion, we found that *P. australis* exhibits distinct association preferences when offered the choice between cues from cockroaches from the same log and individuals from an allopatric population. Social aggregation is believed to confer numerous benefits including antipredator vigilance and avoidance, increased efficiency at acquiring mates and other resources, and the conservation of heat and water (reviewed in Krause and Ruxton 2002). In cockroaches, subsocial behaviour has also been shown to promote the survival, growth and development of offspring (Matsumoto 1992; Holbrook *et al.* 2000; Park and Choe 2003a, 2003b). The potential benefits of subsocial aggregations in *P. australis* remains unknown but offers potentially rewarding avenues for future research.

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