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Rapid up- and down-regulation of pheromone signalling due to trail crowding in the ant *Lasius niger*

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Abstract

Social insects often respond to signals and cues from nest-mates, and these responses may include changes in the information they, in turn, transmit. During foraging, *Lasius niger* deposits a pheromone trail to recruit nestmates, and ants that experience trail crowding deposit pheromone less often. Less studied, however, is the time taken for signalling to revert to baseline levels after conditions have returned to baseline levels. In this paper we study the behaviour of *L. niger* foragers on a trail in which crowding is simulated by using dummy ants — black glass beads coated in nestmate cuticular hydrocarbons. Ants were allowed to make four repeat visits to a feeder with dummy ants, and thus crowding, being present on the trail on all visits (CCCC), none (UUUU) or only the first two (CCUU). If dummy ants were always present (CCCC), pheromone deposition probability was low in the first two visits (54% of ants deposited pheromone) and remained low in visits 3 and 4 (51%). If dummy ants were never present (UUUU) pheromone deposition probability was high in the first two visits (93%) and remained high in visits 3 and 4 (83%). If dummy ants were present on the first two visits but removed on the second two visits (CCUU) pheromone deposition probability was low in the first two visits (61%) but rose in the second two visits (69%). This demonstrates that even after pheromone deposition has been down-regulated due to crowding in the first two visits, it is rapidly up-regulated when crowding is reduced, although it does not immediately return to the base line level.

1. Introduction

Social organisms need to appropriately respond to information from group members. This is exemplified in the organisation of social insects, where the colony responds collectively to changes in the environment or to changing colony needs (Hölldobler & Wilson, 2009). Such collective responses may be caused by individuals collecting information about colony needs directly and responding accordingly. For example, scouts from starved *Lasius niger* colonies deposit more trail pheromone than scouts from well fed colonies when encountering large amounts of food (Mailleux, 2006), and ants in starved nests are more likely to be successfully recruited (Cassill, 2003; Mailleux et al., 2011). Western Honey bees *Apis mellifera* are able to both up- and down-regulate the tasks of nectar receiving and foraging in response to changes in the amount of nectar available (Kirchner, 1993; Nieh, 1993; Seeley, 1995; Anderson & Ratnieks, 1999).

Regulation of social insect foraging systems is complex, with individuals modulating their behaviour depending on information from nest mates, gathered both from signals and cues. A signal is way of conveying information specially evolved for that purpose, while a cue conveys information but did not evolve to do so, and may be not even under selection (Seeley, 1989). In the honey bee, regulation of the foraging system involves both direct signals (e.g., foragers make waggle dances to recruit additional foragers and tremble dances to recruit additional nectar receivers) and cues (nectar foragers experiencing short time delays or many simultaneous receivers during unloading are more likely to make waggle dances, while those experiencing long delays and few receivers are more likely to make tremble dances) (Seeley, 1995; Anderson & Ratnieks, 1999; Farina, 2000; De Marco, 2006; Grüter & Farina, 2009). Ant foragers, and the colony's whole foraging system, also respond to both cues and signals, and signals may have more than one effect. Trail pheromones are signals with multiple effects. Similarly to the honey bee waggle dance, these include up-regulating the number of foragers and directing recruits to the resource (Wilson, 1962; Hangartner, 1969). In addition, trail pheromones can also act as a reassurance signal, allowing faster walking and route memorisation (Van Vorhis Key et al., 1981; Beckers et al., 1992; Czaczkes et al., 2011, 2012b). As in the honey bee, regulation of the foraging system is complex, with the production and responses to the main recruitment signal, trail pheromone, themselves being affected by both

cues and other signals. For example, the response of *L. niger* workers in the nest to trail pheromone is affected by hunger, with starved workers responding to lower pheromone levels than satiated workers (Mailleux, 2006). The amount of pheromone deposited by ants is also regulated according to several factors. Workers feeding at a low-molarity sucrose feeder deposit less pheromone than those feeding at high-molarity feeders (Beckers et al., 1990, 1993; Reid et al., 2013). The volume of food ingested, food type, presence of brood in the nest, and the amount of pheromone on the trail also affect pheromone deposition (Mailleux et al., 2000, 2003; Portha et al., 2004; Czaczkes et al., 2012b).

L. niger foragers have also been shown to reduce pheromone deposition on crowded trails (Czaczkes et al., 2013), which may have important implications for colony-level control of foraging and maintenance of foraging flexibility (Czaczkes, data not shown). However, no information is available on possible up-regulation of pheromone deposition when crowding levels reduce. Indeed, it has been claimed that individual *L. niger* foragers rarely up-regulate pheromone deposition after down regulation (Beckers et al., 1992). The speed of response to a cue or its absence is likely traded-off against accuracy or appropriateness of the response, and thus the response speed may also inform us about whether speed or accuracy are more important for ants when deciding whether to respond to crowding (Chittka et al., 2009). This experimental study determined whether, and if so how rapidly, foraging *L. niger* workers up-regulate trail pheromone deposition after a brief experience of trail crowding that caused down-regulation.

2. Materials and methods

2.1. Housing and maintenance of the ants

Colonies of the black garden ant, *Lasius niger*, were collected on the University of Sussex campus and housed in plastic foraging boxes (40 × 30 × 20 cm) with a layer of plaster of Paris on the bottom. Each box contained a circular plaster nest (14 cm diameter, 2 cm high). Colonies were queenless with 500–1000 workers and small amounts of brood. Colonies were fed three times per week with Bhatkar diet, a mixture of egg, agar, honey and vitamins (Bhatkar & Whitcomb, 1970). Colonies were deprived of food for four days prior to each trial to give high and consistent motivation for foraging and recruitment. Water was provided ad libitum.

2.2. *Experimental method*

Crowding on a foraging trail from the nest to a food source was simulated by using dummy ants. These were black glass beads coated in nest mate cuticular hydrocarbons (CHCs), prepared as described in Czaczkes et al. (2013). Glass beads coated in cuticular hydrocarbons have been used successfully in studies on ants, including *L. niger*, to mimic both nest mates (Greene & Gordon, 2003; Ozaki et al., 2005; Czaczkes et al., 2013) and non-nest mates (Wagner et al., 2000; Ozaki et al., 2005). Cuticular hydrocarbons are sufficient to elicit appropriate behavioural responses from ants in a variety of contexts, including nest mate recognition and foraging (Lahav et al., 1999; Ozaki et al., 2005; Greene & Gordon, 2007; Martin et al., 2008). Pheromone deposition in *L. niger* was down-regulated when foragers encountered CHC-coated beads, and this effect is stronger if the beads are black rather than clear (Czaczkes et al., 2013).

Immediately prior to each trial 10 workers from the test colony were removed from the nest, chilled for 2 min at $-20°C$, and placed in a glass vial containing 500 μl pentane for 10 min to allow the CHCs to dissolve. The dead ants were then removed. The resulting solution was then dripped over 10 black glass beads (diameter 2.5 mm, height 1 mm; KnorrPrandell, Lichtenfels, Germany) in 2.5-μl drops until all the solution had been used.

A 20-cm-long, 0.5-cm-wide plastic walkway covered in printer paper was connected to the test colony via a drawbridge and led to a circa 200 μl drop of 1 M sucrose solution on a plastic feeding platform. Ten CHC-coated beads were placed on the walkway at 2-cm intervals, beginning 0.5 cm from the side of the walkway nearest the nest. A single ant was then allowed onto the walkway. As the ant was feeding from syrup drop it was marked with a dot of acrylic paint on the abdomen, and allowed to return to the nest, and then allowed to make one return trip to the feeder. *L. niger* walk with their antennae spread circa 4 mm apart. The beads were 2.5 mm wide. As a result, ants walking on the 5-mm-wide walkway made antennal contact with most of the beads. The beads were then removed, and the ant was allowed to make two more journeys to and from the feeder. Thus, each ant made two 'crowded' then two 'uncrowded' trips (CCUU). The pheromone deposition behaviours performed by each ant on each journey were counted. Pheromone deposition in *L. niger* is a stereotyped behaviour, involving the ant pausing for circa 0.2 s and pressing the tip of its abdomen against the substrate (Beckers et al., 1993), and is easily seen by eye. To control for possible

changes in deposition behaviour on visits three and four we also tested ants when marked beads were present during all visits to the feeder (CCCC) or none (UUUU). Treatment orders were pseudo-randomised, and each ant was removed from the colony after testing to avoid pseudo-replication. The paper overlay was exchanged, and the runway cleaned with ethanol, after every ant tested. Four ants from each colony ($N = 10$ colonies) were tested on every treatment.

2.3. Statistical analysis

Data were analysed using generalised linear mixed models (GLMM) in the statistical package R 2.9.2 (R Development Core Team, 2009). GLMMs were chosen as they can incorporate continuous variables, categorical variables, and random effects in a single model (Zuur et al., 2009). Models were fitted using the lmer function (Bates et al., 2007). Model selection followed Zuur et al. (2009): we first constructed a saturated model, including all predictor variables we had an a priori reason for testing (treatment, number of visits (1–4), experiment half (first, second), and all interactions between them). The colony test ants were from and the identity of each ant were added as random effects, so as to control for possible consistent differences between ants and colonies, and non-independence of data. Random effect structures, the way in which the randomness of a random effect is modelled, were explored and competing models compared by directly comparing their Akaike Information Criterion scores (AIC). Non-significant random effects were removed. We then explored the significance of fixed effects, and removed non-significant effects and interactions. Binomial data, whether ants deposited pheromone or not, were analysed using a binomial distribution with a loglit link function, and count data (the number of pheromone depositions per ant) were modelled on using a Poisson distribution. All p-values presented are adjusted using the Benjamini–Hochberg correction (Benjamini & Hochberg, 1995) to account for multiple testing.

3. Results

We tested whether sequence treatment (CCCC, CCUU or UUUU), position within a trial (first half, visits 1 and 2; second half, visits 3 and 4), and their interaction affected the proportion of ants performing at least one pheromone deposition. We found a significant interaction between treatment and trial

half ($Z = -3.247$, $p = 0.0035$). In the first half of the trial, ants on the CCCC and CCUU sequences were equally likely to deposit pheromone (54% vs 61% in the CCCC and CCUU trial, respectively, $Z = 3.86$, $p = 0.4$), but in the second half of the CCCC sequence ants were less likely to deposit pheromone than CCUU ants (51% vs 69%, $Z = -2.26$, $p = 0.0358$) (Figure 1A). Conversely, in the first half of the trial, ants in the UUUU sequence were more likely to deposit pheromone than ants in CCUU (93% vs 61%, $Z = 3.862$, $p = 0.00034$) (Figure 1A). This shows that crowding reduces trail pheromone laying, as expected. In the second half of the trials, there is a non-significant, but borderline, trend towards more pheromone deposition in UUUU ants than the CCUU ants (83% vs 69%, $Z = 1.933$, $p = 0.053$). This suggests a residual effect of crowding even after the crowding stops.

However, comparing within treatments between the first and second half of the trial gives less clear results. Under CCUU, there is a non-significant trend towards more ants performing at least one pheromone deposition in the final two trips ($Z = 1.907$, $p = 0.0709$), which is not significant even without correction for multiple testing ($p = 0.0565$). There is no difference in deposition likelihood between the first and second halves of the CCCC trials ($Z = -0.704$, $p = 0.555$). However, the probability of an ant depositing pheromone is significantly reduced in the second half of the UUUU treatment compared to the first ($Z = -2.575$, $p = 0.010$). These results are in line with previous research showing that depositing rates decrease in later visits (Beckers et al., 1992). Thus, the similarity between the second halves of the CCUU and UUUU treatments are probably due to a combination of a reduction in deposition likelihood in the UUUU treatment, as well as to an increase in deposition likelihood in the second half of the CCUU treatment.

We also analysed the number of pheromone depositions performed by ants in trips with at least one pheromone deposition (i.e., excluding trips where no pheromone was deposited). Of the ants that did deposit pheromone, there was no difference in the number of pheromone depositions between the CCCC and CCUU treatment in either half of the trials (first half $Z = 0.379$, $p = 0.705$, second half $Z = -1.097$, $p = 0.273$) (Figure 1B). More pheromone was deposited by depositing ants in the UUUU treatment than in the CCUU treatment in the first half of the trials ($Z = 4.53$, $p < 0.0001$), but not in the second half ($Z = 1.442$, $p = 0.224$). When comparing the number of pheromone depositions within treatments, we find that more pheromone is deposited on the second half of the CCUU treatment than the first ($Z =$
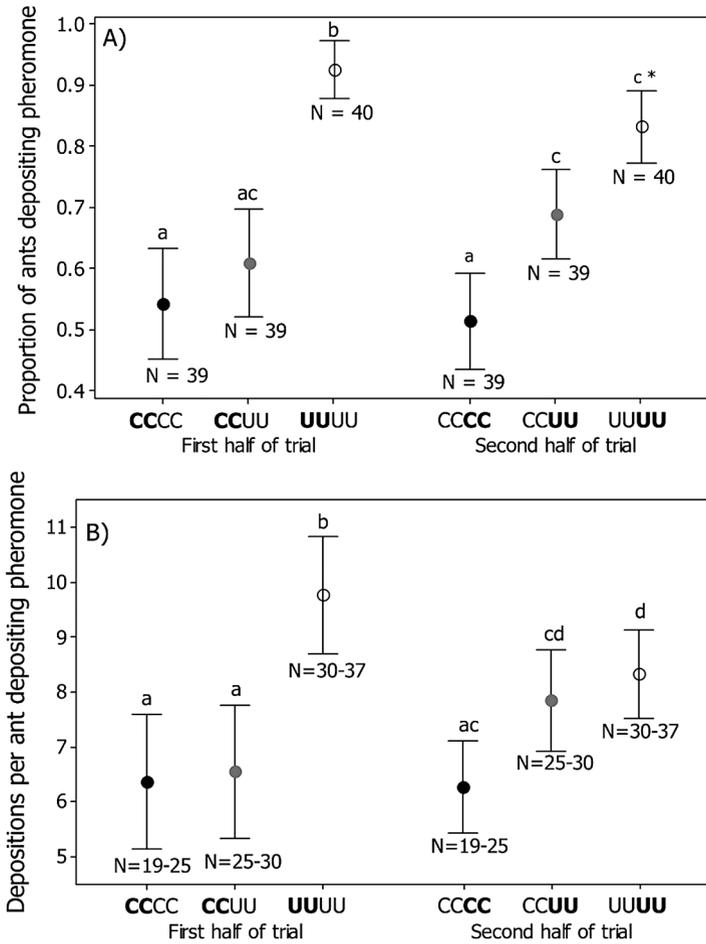
Figure 1. (A) Proportion of ants depositing pheromone and (B) pheromone depositions per ant depositing pheromone on either the first two visits (first half) or the last two visits (second half) of ants to a feeder. The path to the feeder contained either black beads covered in CHC during all four visits (CCCC), never contained any beads in any of the visits (UUUU), or contained beads for the first two trips, but not the last two trips (CCUU). Symbols signify means, bars signify 95% C.I. N = total number of ants from which the data for each group was taken. N values vary in B as not all ants deposited pheromone on each visit to or from the feeder, and those that did not are excluded from this analysis. Different letters signify significant differences using GLMM (see results). In panel A, c* indicates a borderline non-significant difference between from CCUU and UUUU in the second half of the trials (p = 0.0709 with correction for multiple-testing), and also a borderline non-significant difference (p = 0.0532 with correction for multiple testing) between UUUU in the second half of the trials and CCUU in the first half of the trials.

3.566, $p = 0.000362$). There is no difference in pheromone depositions be-
tween the two halves of the CCCC trials ($Z = -0.319$, $p = 0.75$). Less
pheromone is deposited on the second half of the UUUU trials ($Z = -3.822$,
$p = 0.00013$). Deposition rates are significantly different between CCCC
and UUUU in both halves of the trial (first half $Z = 4.029$, $p < 0.0001$,
second half $Z = 2.46$, $p = 0.0211$).

4. Discussion

As expected from previous research, crowding on a foraging trail reduced
pheromone deposition (Czaczkes et al., 2013). However, foraging workers
that had reduced pheromone deposition due to trail crowding responded
rapidly to the absence of trail crowding by increasing their pheromone de-
position probability on the first two uncrowded trips they made. Although
this response was rapid, pheromone deposition probabilities did not seem
to return to baseline uncrowded levels, although the difference between the
baseline level and the 're-up-regulated' level was not significant. A similar
pattern can be seen in the number of depositions made by pheromone-laying
ants, with pheromone deposition rates in the second half of the CCUU treat-
ment being more similar to the UUUU treatment than the CCCC treatment.
A confounding factor is the reduction in pheromone deposition probability
and number of pheromone depositions between the first and second half of
the experiment, which is noticeable in the UUUU treatment. This reduction
in pheromone deposition is likely due to a build-up of trail pheromone on the
apparatus, as high levels of pheromone on a substrate cause *L. niger* forgers
to reduce their pheromone deposition (Beckers et al., 1992; Czaczkes et al.,
2012b).

The reduction in pheromone deposition in response to trail crowding
demonstrated here and in Czaczkes et al. (2013) may play several roles
in the organisation of ant foraging. First, it may prevent the wasting of
pheromone when recruitment is already well underway, although no data
on the metabolic cost of pheromone production is available. Second, it may
allow ant colonies to maintain foraging flexibility. Due to positive-feedback
during mass recruitment in ants (Wilson, 1962; Beckers et al., 1990), trails
to food sources can rapidly become very strong. This has a tendency to
cause colonies to focus on one food source while neglecting others, and
to prevent colonies switching from an earlier discovered food source to a
later discovered source of higher quality. Both of these effects have been

demonstrated in simulations and laboratory experiments (Goss et al., 1989; Beckers et al., 1990; Nicolis & Deneubourg, 1999; Sumpter & Beekman, 2003; Grüter et al., 2012). However, this seems maladaptive, and this pattern, to our knowledge, seems not to have been reported in the field. Indeed, *L. niger* colonies can be seen foraging on multiple food sources simultaneously (Dreisig, 1988; Devigne & Detrain, 2005), which may be at least in part due to crowding at the food source (Dreisig, 1988; Grüter et al., 2012). Simulations have shown that reduced recruitment on heavily used trails can play an important role in allowing ants to switch their foraging effort to newly discovered, higher quality food sources (Czaczkes, data not shown). Lastly, the reduction of recruitment on crowded paths may allow ant traffic to be re-routed around areas experiencing heavy traffic. Other methods based on U-turning and jostling (Dussutour et al., 2004, 2006) may also play a role in traffic re-routing, but the reduction of recruitment due to crowding may allow such a re-routing when the traffic bottleneck occurs at a distance from the point where the alternative routes diverge.

Crowding at a food source does not cause a reduction in trail pheromone deposition (Grüter et al., 2012). This strengthens the suggestion that the response to trail crowding plays its main role in regulating traffic flow on the trail itself, rather than in regulating the total number of ants recruited. Crowding on the trail may also be subject to less variation than crowding at the food source, if ants spend longer travelling to and from a food source than at the food source. Furthermore, overcrowding at the food is absolute: having ants queuing to feed would not increase the overall food return rate. If the food source is uncrowded but the trail is, crowding on the trail can be reduced by routing some ants via a longer route, and would still result in a net increase in food return rate (Dussutour et al., 2006). These two types of crowding are thus disconnected to some degree, and stem from different causes. It is then perhaps not surprising that ants respond to them in different ways. Lastly, responding directly to trail crowding may give more up-to-date information (Howard et al., 1996). An ant may experience little crowding at the food source, but encounter many ants on its' return journey, suggesting that the food source will soon be crowded, and that further recruitment is not necessary. On the other hand, crowding levels at the food source should provide more precise information on how many ants are needed to fully exploit the food source. The responses of ants at the food source and on the trail are not necessarily the same, as these are quite separate parts of the system, each with their own properties and challenges. The organisation

of a foraging trail is based on individual responses, and these individual responses are location specific.

Both the response to crowding, and the response to a sudden lack of crowding, are very rapid. This is at first glance surprising, as the foraging system is likely to suffer from a high degree of stochasticity, since there is no reason to expect the ants using a trail to be evenly spaced, and indeed recruitment in the nest may cause ants to leave the nest in waves. Thus, if by chance a forager experiences many head-on encounters during a foraging trip on an otherwise underused trail it may reduce its pheromone deposition inappropriately. Conversely, if a forager experiences few head-on encounters during a foraging trip on an otherwise busy trail it may inappropriately maintain pheromone deposition. However, recruitment and foraging in many ants including *L. niger* is a group activity, and thus the appropriate level at which to examine collective behaviours is the collective response. While each ant responds individually to the crowding level they sense, their response is made either by strengthening or not strengthening the pheromone trail, which is a pooled social information source available to all foragers on the trail. While each ant samples the trail once, and responds appropriately, the collective response of the colony to crowding levels on the trail is a result of the integrated sampling of many ants over an extended period of time. The time over which the information is integrated is an aspect of how rapidly the trail pheromone decays. Thus, individual ants respond rapidly to crowding (and other environmental changes) by up or down regulating pheromone deposition (Czaczkes et al., 2013) but colony-level information sources integrate information over a longer time-frame. However, individual social insects may also respond very slowly in some situations: honey bees may repeatedly return to unproductive feeders for up to a week before abandoning a feeding location (Al Toufailia et al., 2013b). Social insects can also respond to highly stochastic cues by increasing measurement effort: for example, honey bee waggle-dances from more distant food sources show more scatter in angular information, and so dance-followers respond by increasing dance-following duration, i.e., sampling time (Al Toufailia et al., 2013a).

Integrating response to environment changes over different time scales can provide flexibility in the short term and robustness in the longer term (Flack, 2012; Pinter-Wollman et al., 2013). *L. niger* colonies can in fact react to trail use levels by changing pheromone deposition rates on three different timeframes. The response to crowding levels described here and in Czaczkes et

al. (2013) is the most rapid, and leads to almost immediate changes in behaviour. The response of foragers to trail pheromone levels, wherein on paths strongly marked with pheromone trail recruitment is suppressed (Beckers et al., 1992; Czaczkes et al., 2012b), is intermediate in timing. This response is modulated according to variation over tens of minutes or hours, as set by the evaporation rate of the pheromone (Beckers et al., 1993; Evison et al., 2008). Lastly, *L. niger* foragers also adjust their pheromone deposition behaviour according to home-range marking levels. Home-range markings in *L. niger* are cuticular hydrocarbons laid down passively over a surface as an ant walks (Yamaoka & Akino, 1994; Devigne & Detrain, 2002). They are non-volatile, and so are likely stable over many hours or days. The pheromone-deposition response of foraging ants to home-range markings is complex, and related both to the presence of trail pheromone markings and the travelling direction (to or from the nest) of the forager (Devigne et al., 2004; Czaczkes et al., 2011, 2012a). These three complementary components have similar roles, but integrate information over very different time periods. This may be analogous to the way the mammalian brain uses both a rapid but inaccurate mechanism and a slow but accurate mechanism to make decisions (Carpenter & Williams, 1995; Trimmer et al., 2008). Such mechanisms are likely to interact with each other to produce an appropriate response based on information integrated over an appropriate time frame (Trimmer et al., 2008).

Acknowledgements

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