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Synergy between pheromone trails and quorum thresholds underlies consensus decisions in the ant *Myrmecina nipponica*

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Abstract Coordination of group actions in social organisms is often a self-organised process lacking central control. These collective behaviours are driven by mechanisms of positive feedback generated through information exchange. Understanding how different methods of communication generate positive feedback is an essential step in comprehending the functional mechanisms underlying complex systems. The Japanese small-colony ant, *Myrmecina nipponica* uses both pheromone trails and an apparent quorum response during consensus decisions over a new home. Both of these mechanisms have been shown to generate positive feedback and are effective means of selecting among mutually exclusive courses of action. In this study, I investigate how pheromone trails and quorum thresholds contribute to consensus decisions during house-hunting in this species through experimental manipulations of pheromone trails, colony size and environmental context. Results demonstrate that (1) providing colonies with pre-established pheromone trails increased the number of ants finding the new site and led to higher quorum thresholds and more rapid relocations, (2) experimentally halving colony size resulted in a proportional decrease in quorum thresholds and (3) colonies relocating long distances had higher quorums than those relocating short distances. Taken together, these data indicate that pheromone trails are important for recruitment and navigation during nest site selection, but that decision making is contingent on a quorum response. Such synergy between mechanisms of

positive feedback may be a common means of optimising collective behaviours.

Introduction

In self-organised biological systems, complex emergent patterns arise as the collective product of interacting individuals responding to simple local rules. This phenomenon underlies the coordination of complex tasks in many social organisms, from the foraging networks of leaf-cutter ants to the aerial ballet of flocks of starlings (Camazine et al. 2001; Sumpter 2010). Integral to the process of self-organisation is a mechanism of positive feedback generated through the sharing of information (Nicolis and Deneubourg 1999; Sumpter and Pratt 2009). Information exchange can take various forms, from static markers such as pheromone trails (Beckers et al. 1990; Detrain and Deneubourg 2009) to vocal exchanges (Bousquet et al. 2011) and the visual displays that comprise the dance language of honey bees (Passino and Seeley 2006), and different forms of communication may be employed for different tasks (e.g. Schlegel et al. 2013). Understanding how these various forms of information exchange contribute to self-organised processes is integral to further developing our understanding of the functional mechanisms underlying complex systems.

House-hunting insects are useful model systems with which to investigate self-organised processes, because they lack the advanced cognitive abilities of some social vertebrates and are amenable to manipulative laboratory studies (e.g. Amé et al. 2006; Visscher 2007; Pratt 2010). Group cohesion is an important component of exploiting the benefits of sociality in insects, and thus group actions such as selecting a new home are usually consensus based. The process of consensus decision

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making allows groups to maintain integrity while selecting one of several mutually exclusive actions (Conradt and Roper 2005), and is found in a wide range of organisms from bacteria to humans (Waters and Bassler 2005; Dyer et al. 2008; Petit et al. 2009; King and Sueur 2011; Ward et al. 2012). Studies of the house-hunting process in several species of social insects have demonstrated interesting parallels between species (reviewed in: Franks et al. 2002; Visscher 2007; Pratt 2010). In the two most well-studied systems, honey bees (*Apis mellifera*) and *Temnothorax* ants, scouts advertise their support for candidate sites by recruiting nestmates via the waggle-dance (in honey bees) or tandem-running (*Temnothorax*). Once a quorum of individuals is at one site, a decision is made and behaviour rapidly shifts to relocation of the remainder of the colony. A 'quorum' in this sense is a threshold number of individuals performing a behaviour, above which a focal individual's probability of performing the same behaviour markedly increases (Sumpter and Pratt 2009). In this manner a step-like group-level behavioural shift can arise in response to a continuous change in signal. Use of a quorum rule can help maintain group cohesion and increase the accuracy of decisions (Pratt et al. 2002; Passino and Seeley 2006).

Recent studies of the Japanese ant *Myrmecina nipponica* (Cronin 2012, 2013) indicate that the process of nest site selection and relocation follows a similar pattern to that seen in *Temnothorax* ants and honey bees: scouts search for a new nest site and, upon finding a suitable location, begin a lengthy assessment/canvassing phase. A consensus decision is eventually achieved at a point marked by a sudden shift to brood transport, indicating the start of the final committed phase. Brood transport is always to only one destination, and is accompanied by the independent movement of the remaining adults. A strong relationship between colony size and the number of ants at the new site when the switch to brood transport occurs suggests that this switching point is regulated by a quorum threshold (Cronin 2012). However, a notable difference between this species and other house-hunting systems studied is that canvassing for a favoured site is achieved via the laying of a pheromone trail (Cronin 2012, 2013). Pheromone trails used by ants are extremely effective in regulating group processes, and this includes collective 'decisions' between mutually exclusive alternatives (reviewed in: Camazine et al. 2001; Beekman and Dussutour 2009; Detrain and Deneubourg 2009). Thus, in *M. nipponica* there are potentially two mechanisms through which consensus decisions can arise. However, previous studies on decision making in this species were largely descriptive (Cronin 2012), or focussed on group-level outcomes of information conflict (Cronin 2013), and the contribution that these two mechanisms of positive feedback make toward nest site selection remains unclear.

In this study I use experimental manipulations of the context in which nest site selection occurs to shed light on the relative importance of pheromone trails and quorum thresholds in the consensus decision process in *M. nipponica*. Firstly, by providing relocating colonies with pre-established pheromone trails in laboratory-based re-locations, I investigate the role played by pheromone trails in the decision-making process. If pheromone trails alone are sufficient for colonies to reach a decision, providing colonies with established trails should lead to more rapid decisions and reduce or eliminate the need for a quorum threshold prior to brood transport. On the other hand, if quorum thresholds play an integral role in decision making, adaptive changes in quorum threshold should be observable in different contexts. For example, the available data indicate that quorum threshold increases with colony size in *Temnothorax* (Dornhaus and Franks 2006; Franks et al. 2006; Dornhaus et al. 2008) and *Myrmecina* (Cronin 2012). However, as ant colonies typically increase in size with age, any influence of colony size may be confounded with age-related factors, and this relationship must be experimentally verified (Dornhaus and Franks 2006). In the second experiment, I therefore assess the relationship between colony size and quorum threshold by forcing relocations after manipulating colony size, with the expectation that if quorum thresholds are sensitive to colony size, colonies halved in size should have lower quorum thresholds than whole colonies. Finally, quorum thresholds can provide a mechanism through which to adaptively tailor the relocation process to different environments: *Temnothorax* ants adjust quorum thresholds to emphasise decision speed or accuracy depending on the environmental conditions (Franks et al. 2003; Dornhaus et al. 2004). In the third and final experiment, I examine if quorum threshold in *M. nipponica* is influenced by environmental context by contrasting relocations to near and far nests. Colonies relocating to far nests could be expected to reduce quorum thresholds if speed is crucial over longer distances, or may increase quorum thresholds if maintaining group integrity is of greater importance.

Methods

Colony collection and maintenance

Entire colonies of *M. nipponica* were collected from patches of moss and the bases of ferns in broadleaf forest near Chitose City in Hokkaido, northern Japan (N42°47′ E 141°34′, alt ~100 m) in September 2011 and 2012. This species is distributed throughout Japan, and colonies usually contain either a single winged queen or one or more ergatoid (worker-like) queens (Miyazaki et al. 2005). Nests are generally subterranean or found within clumps

of moss or plant roots, and consist of ~40 workers (range 10–70), each around 3–4 mm long. Colonies used in this study were typical of this species and contained between 27 and 61 ants (Table 1).

All adults and brood were carefully extracted from nests in the laboratory and transferred to artificial nests. Colonies were housed in 10×10×3 cm plastic boxes with removable lids that included a gauze-covered opening to permit airflow. Boxes contained approximately 0.8 mm of plaster that was kept moist via regular application of water. Each box contained a single nest consisting of a microscope slide covered with a red filter mounted on a 2-mm high circlet of foam with a small (3 mm) opening. Ants were kept at room temperature (~20 °C) and provided with ad libitum water in small vials plugged with tissue, sugar/water solution in vial caps, and fed mealworm pieces every few days. All ants were individually marked with different coloured spots on the head, thorax and gaster using Mitsubishi paint-marker pen paint applied with a fine brush.

Experimental relocations

Colonies were forced to relocate by removing the artificial nest. An identical nest was provided in a new box (Fig. 1) and boxes were connected by small holes. This permitted boxes to be easily switched, allowing navigation boxes
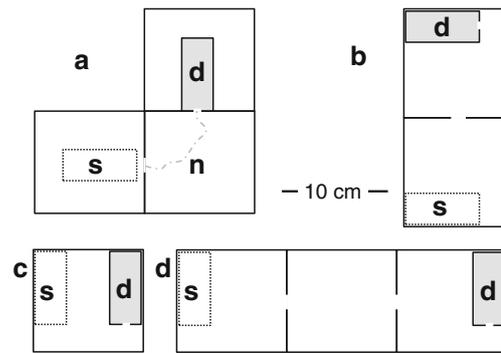

Fig. 1 Experimental setup for relocations for **a** experiment 1, **b** experiment 2 and **c** and **d** experiment 3. The original nest (*dotted line*) was removed in the source nest box (*s*) forcing ants to relocate to the new nest (*shaded*) in the destination nest box (*d*). When present, pheromone trails (example shown by *broken line*) were deposited in the navigation box (*n*) during a relocation by a different laboratory colony and the navigation box transplanted

containing established pheromone trails to be substituted in. Boxes were thoroughly washed with water between trials and sun-dried for at least 2 days, which exceeds the ~24 h effective duration of pheromone trails (Cronin 2013). Web-cameras (Elecom Ucam-DLA200H) positioned above the nest entrances were used with the motion-detection software iSpy (www.ispyconnect.com) to track entries and exits. The identity and timing of individual ants entering and exiting the new nest(s) and transporting brood were scored manually from videos.

The relocation process in *M. nipponica* can be divided into three phases (Cronin 2012). The 'search' phase is defined as the time from destruction of the nest to the first ant entering the new nest. The 'assessment' phase is defined as the time from first entry until the first brood is transported. From the first transport until the end of the relocation is termed the 'transport' phase. Relocations are completed when all brood have been transported and all ants have visited the new site. The initiation of brood transport likely defines the point at which a consensus decision has been achieved, as brood are relocated directly to only one destination site once transport commences and colony splitting does not occur. This point appears to be associated with the presence of a numerical 'quorum' of ants at the new site (Cronin 2012). The 'quorum threshold' of an ant is defined here as the number of ants present at the new site when the focal ant departs the new nest to undertake its first transport.

Quorum thresholds were calculated for all ants switching to brood transport. However, thresholds for ants switching to transport late in the relocation process may be a less accurate representation of the ant's true threshold because the number of ants present far exceeds their threshold at the time they first visit the nest. On the other hand, using only the quorum threshold for the first

Table 1 Colony characteristics for colonies used in experiments 1–3

Experiment	Colony	Colony size	Queen	Collected
1	21	42	1 WQ	2011
1	23	33	1 WQ	2011
1	25	38	1 WQ	2011
1	26	45	1 WQ	2011
1	30	39	1 WQ	2011
1	103	61	1 WQ	2011
2	21	41	1 WQ	2011
2	23	32	1 WQ	2011
2	26	42	1 WQ	2011
2	30	35	1 WQ	2011
2	52	27	1 EQ	2011
2	103	58	1 WQ	2011
3	26	34	1 WQ	2011
3	101	45	1 EQ	2011
3	203	42	3 EQ	2012
3	211	32	1 EQ	2012
3	215	49	4 EQ	2012
3	225	27	5 EQ	2012

Some colonies were used in multiple experiments and the number of workers may have changed over time. Queens are listed as EQ (ergatoid) or WQ (winged queen). Colony size includes the queen(s). Colonies were collected in September of 2011 or 2012

switching ant is subject to potential noise arising from any variation between individuals. For this reason, quorum thresholds for each colony were calculated as the mean of the thresholds for the first half of all ants switching to transport, and scatter plots incorporate only these individuals. Kernel density plots suggest that this may be a more accurate representation of individual quorum thresholds than using the mean for all transporting ants (Supplementary Material).

Experiment 1: Effect of pheromone trails on the relocation process

The importance of pheromone trails in the decision process was investigated by comparing 'normal' relocations to those primed with existing pheromone trails in six colonies (n=12 trials; Table 1). In treatment trials, colonies were provided with a navigation box containing an established pheromone trail leading to the new nest site (Fig. 1a). These trails had been established immediately prior to relocations by another laboratory colony (not used in tests). Previous experiments (Cronin 2013) have shown that trails are not colony specific and providing preformed trails can influence the decision process. Pheromone trails remain effective for approximately 24 h (Cronin 2013) and were established immediately before choice experiments. In control trials, colonies performed relocations as normal with a new clean navigation box. The order of treatment/control runs was randomised.

Experiment 2: Effect of colony size on quorum threshold

To investigate the importance of the number of ants present on the decision-making process, the relationship between colony size and quorum threshold was clarified through experimental manipulation. Six colonies were forced to relocate in a two-box setup (Table 1; Fig. 1b). Each colony performed three relocations: once for the entire colony, and once each for two equally sized colony subgroups. To create subgroups, workers and brood were divided as equally as possible between two new nests (A and B), with 'A' subgroups containing the queen. The order of trials was randomised such that whole colonies were run first for some colonies and last for others. Subgroup trials were run at least 24 h (and less than 48 h) after colony division. Subgroups were allowed to reunite by joining both subgroup nest boxes following subgroup trials. Trials using the same colonies (whole or subgroups) were performed at least 2 days apart.

Experiment 3: Effect of environmental context on the relocation process

To investigate how the relocation process, and in particular quorum thresholds, might differ in different environmental contexts, six colonies were forced to relocate in two different experimental arenas (Table 1). In 'short' treatments, colonies relocated to a new nest within the same box (Fig. 1c), while in the 'long' treatment, colonies had to relocate to a nest in a third nest box via a central navigation chamber (Fig. 1d). Phase durations, quorum thresholds, and numbers of scouts and transporting ants were assessed.

Statistical analysis

Data were analysed in R version 2.15.2 (R Core Team 2012). Linear mixed-effect models were implemented using the lme function, with treatment and colony size as independent variables and colony as a random factor. Analyses of quorum thresholds and scout/transporter numbers assumed a Poisson error distribution whereas analyses of durations assumed normal errors. Duration data that were not normally distributed as determined by Shapiro–Wilk tests were successfully log transformed to fit the assumptions of normality. In figures and analyses of full colonies and subgroups in Experiment 2, subgroup data were first pooled as the mean of both subgroups. Colony size of the split group was used in all analyses of A and B subgroups. Means are given as arithmetic mean ± standard deviation unless otherwise stated.

Results

As in previous studies of nest site selection in this species (Cronin 2012, 2013), ants visited both candidate nests in choice experiments and, although occasional reverse transports (from the new nest to the site of the old nest) were observed, brood transport was always to only one destination nest and colony splitting did not occur. This suggests that brood transport only commences once a consensus decision has been achieved and is a valid indicator of this decision point.

Experiment 1: Effect of pheromone trails on the relocation process

Quorum thresholds were significantly higher when colonies were primed with pheromone trails (Fig. 2a; z=2.28, P=0.023), whereas there was no effect of colony size (z=0.97, P=0.33). Relocation times were significantly shorter overall for relocations in which colonies were provided with pheromone trails (t_5=−2.61, P=0.048), and analyses of each phase indicated that this was mainly because of a shorter search phase (Fig 3a; search: t_5=−5.46, P=0.003; assess: t_5=−2.02, P=0.099; transport: t_5=−0.28, P=0.79). In addition to higher quorum thresholds, there were significantly more scouts in trials with trails (Fig. 4; z=2.19, P=0.029), indicating a recruitment influence of trails on ants finding the new nest.
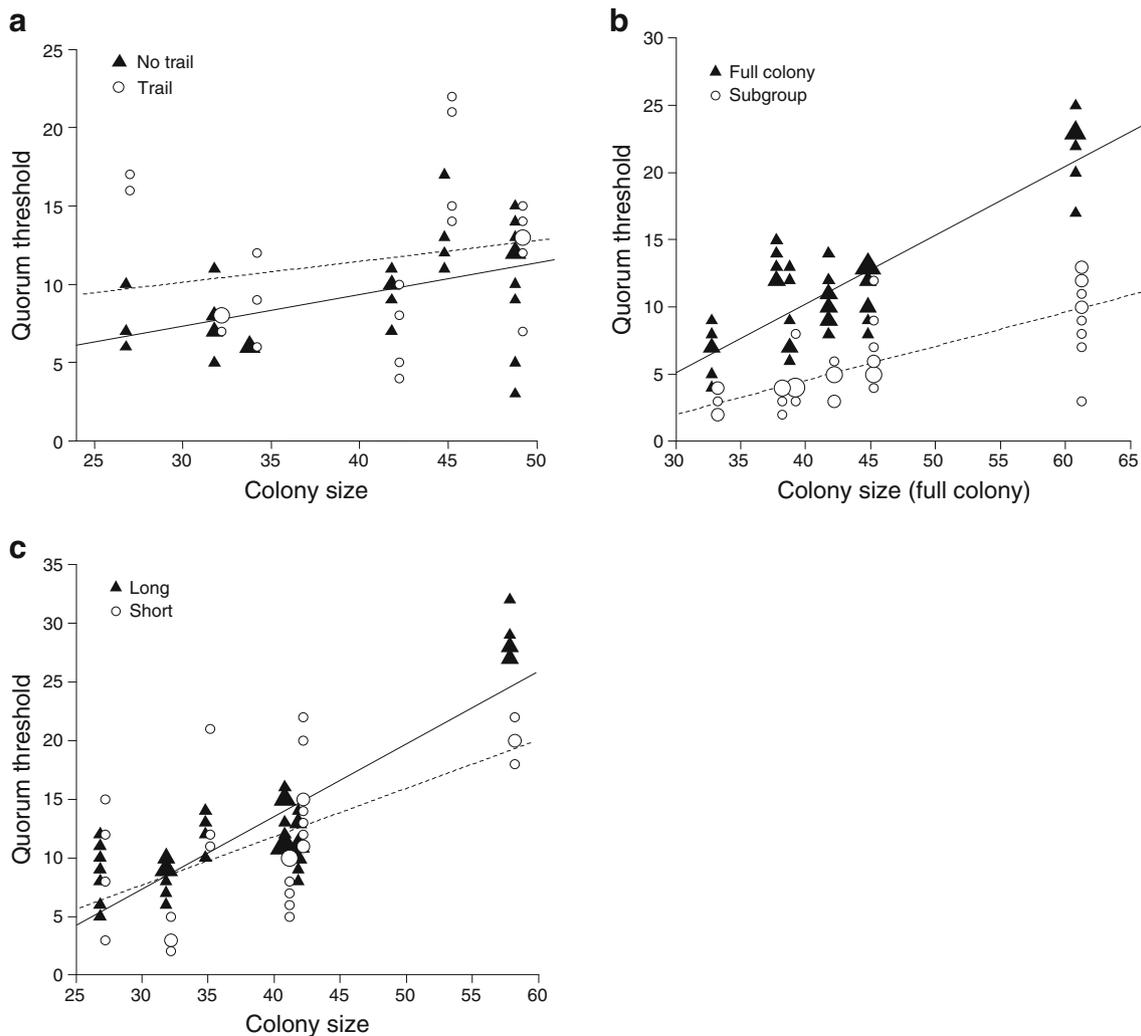
Fig. 2 Relationship between colony size and quorum thresholds. Data are presented for the first half of all switching individuals in each relocation (see main text). **a** Experiment 1, colonies relocating without established trails ($n=6$) are indicated by *black triangles* and the *solid regression line*, whereas colonies supplied with an established trail ($n=6$) are indicated by *white circles* and the *dashed regression line*. **b** Experiment 2, full colonies ($n=6$) are indicated by *black triangles* and the *solid regression line* whereas subgroups ($n=12$) are indicated by *white circles* and the *dashed regression line*, x-axis indicates size of full (non-split) colonies. **c** Experiment 3, long-distance relocations ($n=6$) are indicated by *black triangles* and the *solid regression line* whereas short-distance relocations ($n=6$) are indicated by *white circles* and the *dashed regression line*. The *size of points* indicates the number of repeated points

There was, however, no difference in the number of transporting ants ($z=-0.51$, $P=0.61$).

Experiment 2: Effect of colony size on quorum threshold

Quorum thresholds increased significantly with colony size in both full colonies and subgroups (Fig. 2b; $z=8.13$, $P<0.001$) and were higher in full colonies compared to subgroups ($z=-2.37$, $P=0.018$). There was also a significant interaction between these factors ($z=3.19$, $P=0.002$). The duration of relocations did not differ overall or for any phase of the relocation (Fig 3b; overall $t_4=-0.56$, $P=0.61$; search: $t_4=0.86$, $P=0.44$; assess: $t_4=-0.88$, $P=0.43$; transport: $t_4=2.42$, $P=0.07$) and there was no significant difference in the number of ants acting as

scouts and transporters between full and split groups when controlling for colony size (Fig. 4; scouts: $z=0.81$, $P=0.421$; transporters: $z=-0.95$, $P=0.342$).

Experiment 3: Effect of environmental context on the relocation process

Quorum thresholds were higher in long relocations than short (Fig. 2c; $z=-1.99$, $P=0.046$) and increased with colony size ($z=5.14$, $P<0.001$). There was no effect of treatment on the overall time taken for relocations, but search phases were significantly shorter in short trials (Fig. 3c; overall: $t_3=-0.87$, $P=0.45$; search: $t_3=-11.17$, $P=0.0015$; assess: $t_5=-0.51$, $P=0.63$; transport: $t_5=-0.40$, $P=0.70$). The number of scouts
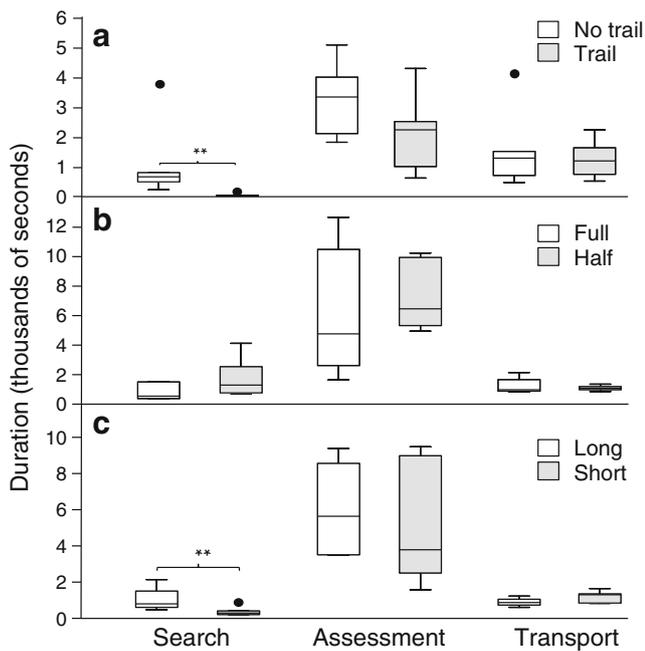
Fig. 3 Box plots for duration of search, assessment and transport phases. *Boxes* indicate upper and lower quartiles, the *horizontal line* indicates the median while *whiskers* indicate boundaries for the maximum/minimum points within 1.5× the interquartile range. Outliers are indicated by *points*. **a** Experiment 1: colonies relocating without established trails (*white bars*) and those primed with trails (*grey bars*); **b** experiment 2: full colonies (*white bars*) and split groups (*grey bars*); **c** experiment 3: long-distance (*white bars*) and short-distance relocations (*grey bars*). Asterisks indicate statistically significant differences (**P*<0.05; ***P*<0.01; see also main text)

did not differ between treatments (Fig. 4; $z=-0.12$, $P=0.90$), though there were significantly more transporting ants in long treatments ($z=-2.37$, $P=0.018$).

Discussion

Positive feedback associated with pheromone trails allows ant colonies to focus foraging effort where it is most needed (Nicolis and Deneubourg 1999; Beekman and Dussutour 2009) and at least to some extent to do so in dynamic environments (Dussutour et al. 2009a, 2009b). Pheromone trails thus are an effective means of collectively reaching a 'decision' between alternative actions (Camazine et al. 2001). For example, *Lasius niger* colonies are able to employ trail pheromones to exploit proteinaceous or sucrose baits depending on colony requirements (Portha et al. 2002). In house-hunting *Myrmecina*, providing colonies with pre-established trails can strongly bias choices between equivalent nests (Cronin 2013), and more ants were attracted to new nests to which pheromone trails lead in *Monomorium pharaonis* (Evison et al. 2012), suggesting trails can also have an important role in nest site selection. Data presented here however, indicate that while trails are important in directing
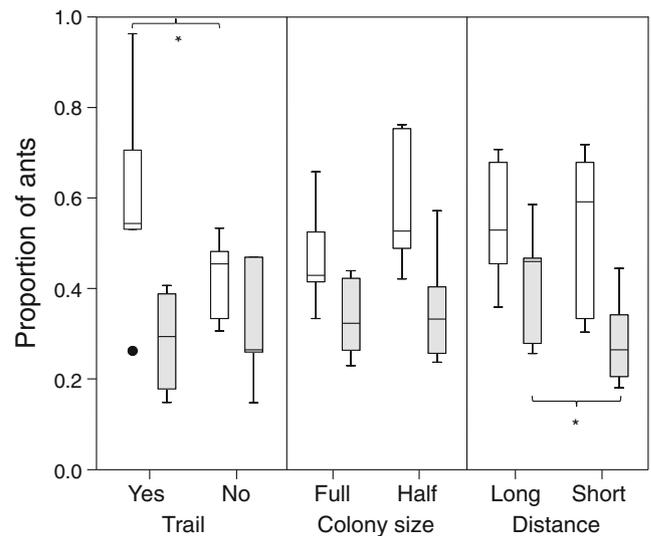

Fig. 4 Box plots of the proportion of ants in each colony (for adjusted colony sizes for experiment 2) acting as scouts (*white bars*) or transporters (*grey bars*) in all experiments. *Boxes* indicate upper and lower quartiles, the *horizontal line* indicates the median while *whiskers* indicate boundaries of maximum/minimum points within 1.5× the interquartile range. Outliers are indicated by *points*. *Asterisks* indicate statistically significant differences (**P*<0.05; ***P*<0.01; see also main text)

scouts to a candidate site, and could serve additional functions such as route-learning (e.g. Czaczkes et al. 2013), colonies of *M. nipponica* do not enter a committed phase (i.e. begin transporting brood) until a quorum threshold had been attained.

The recruitment effect of trails is evidenced by the increased number of scouts (more ants had found the new nest at the time of the first switch to transport) and reduced search time in relocations provided with established pheromone trails. Relocation time overall was also significantly lower in the presence of established trails. However, the length of the assessment phase did not differ significantly from relocations under control conditions, and the assessment phase remained by far the longest component of the relocation process. This suggests that ants continue to make independent assessments of the candidate sites regardless of the presence of an existing trail, and supports a recent study highlighting the importance of private information during nest site selection in this species, even in the presence of strong social information (Cronin 2013). While there was a trend of shorter assessment phases in relocations with trails, this could also be explained by more rapid achievement of quorum thresholds resulting from trail-recruitment rather than a decisive influence of the trails themselves. Quorum thresholds were higher in trials with trails, which is opposite to what might be expected if trails alone were sufficient to achieve a consensus response. These data suggest that trails serve a navigation function and act to recruit scouts to a preferred site, but are insufficient for colonies to reach a

decision on their own. The higher quorum thresholds in trials with trials may also be explained by the recruitment effect from established trails, because the actual quorum threshold of individual ants was more often exceeded, similar to the case proposed for late switching ants (see Methods and Supplementary Material). That is, providing colonies with trails may artificially inflate observed quorum thresholds, and the higher quorums in these trials should be treated with caution.

In contrast to the moderate increase in quorum thresholds observed in relocations with trails in experiment 1, the colony size manipulation in experiment 2 had a dramatic influence on quorum thresholds, which decreased proportionately when colonies were split in two. This provides experimental support for the strong relationship between colony size and quorum threshold identified in earlier studies of this species (Cronin 2012, 2013), and indicates that ants are sensitive to changes in the number of individuals present. This implies that ants are using a numerical threshold to designate the point at which to switch to transport in the manner of a quorum response, and are able to adaptively adjust this quorum threshold within 24 h. Combined with the data from experiment 1, this indicates that house-hunting *Myrmecina* employ pheromone trails for recruitment and navigation but do not commit to a choice until a quorum threshold has been achieved. A colony-size/quorum threshold relationship has also been reported in some studies of *Temnothorax* (Dornhaus and Franks 2006; Franks et al. 2006; Dornhaus et al. 2008) and a similar trend has been observed in consensus decision processes in vertebrates (Conradt and Roper 2005). Larger colonies which do not adjust quorum thresholds proportionally are more likely to achieve multiple quorums simultaneously and therefore more likely to split (Franks et al. 2006). The increase of quorum threshold with colony size is relatively steep in *M. nipponica* (Cronin 2012), and this may be indirect evidence of a high cost to colony splitting in this species. Indeed, as colony sizes are small and development of brood is slow and protracted (Cronin; unpublished data) loss of colony members and/or brood would impose high costs perhaps worthy of slower and more accurate consensus decisions.

The rapid change in quorum thresholds within 24 h of the colony size manipulation indicates a capacity for flexibility in the quorum response. Several other studies have also demonstrated how flexibility in quorum thresholds may allow effective consensus decision making under different environmental conditions (e.g. Franks et al. 2003; Dornhaus et al. 2004; Passino and Seeley 2006), and such flexibility may help colonies balance the competing optima of decision speed and accuracy (Seeley and Visscher 2004; Franks et al. 2009; but see also Sumpter and Pratt 2009). Colonies of *M. nipponica* exhibited (marginally) higher quorum thresholds when relocating to far nests than when relocating to near nests. This suggests that the flexibility of quorum thresholds implied by the response to the colony size manipulation may also permit adaptive modification of quorum responses to suit changes in environmental conditions in this species. Higher quorum thresholds have been linked with relocations under benign conditions when speed is not critical (Franks et al. 2003; Dornhaus et al. 2004). Consensus decisions employing higher quorums thresholds require more time, but are more accurate and are associated with less colony splitting (Franks et al. 2002, 2003, 2013; Pratt 2010). Higher quorums in longer-distance relocations may serve to delay colony relocation so that any more suitable (i.e. closer) alternative nests can be found (Franks et al. 2003). Higher quorums may also be an adaptive response to ensure enough ants know the location of the new site, given there may be a greater risk of colony splitting or getting lost, and may facilitate the accumulation of a sufficient corps of informed transporters. Pratt (2008) showed that in relocations to distant nests, *Temnothorax* ants invested more effort in recruitment (more tandem runs) and that these recruited ants performed a greater share of transports than when relocating to near nests. These data suggest that in *M. nipponica*, adaptive adjustment of quorum threshold to environmental context is likely to be more focussed on maintaining group cohesion during colony relocation than maximising speed. This idea is supported by recent work on *Temnothorax* which demonstrates that rapid decisions come at a cost to group cohesion in addition to decision accuracy (Franks et al. 2013). Contrasting short and long relocations represents only one environmental variable, however, and Franks et al. (2008) showed that *Temnothorax* ants actually preferred distant nests if they were of higher quality. Further experimental conditions may provide a more rigorous test of the adaptability of quorum thresholds in this species (e.g. Franks et al. 2003).

This study shows that *M. nipponica* employs at least two positive feedback mechanisms during house-hunting, with the recruitment influence of trails facilitating the achievement of a quorum-based response. It is possible that a third feedback component exists in the form of tactile stimulation of ants remaining with the brood pile by those already transporting (Cronin 2012) though this remains to be quantified. Similarly, the influence of trails in stimulating ants to leave the old nest site remains unknown: although more 'scouts' (ants that found the new nest before first switch to transport) were observed in trials with trails, this does not necessarily mean that more ants left the old nest site, as events at the source site were not recorded. Previous studies of social insects have demonstrated that several mechanisms of information exchange may be involved in the eventual attainment of a collective response. For example, honey bees use a combination of dance recruitment, quorum sensing, piping and beeping to effect colony swarming (Schlegel et al. 2013). In house-hunting *Temnothorax* ants, recruitment is

initially via tandem running but switches to social carrying following a quorum response (Pratt et al. 2002). In *Messor barbarus*, selection of an aggregation site is achieved via a combination of the recruitment effect of chemical trails and an aggregation process characterised by a group size effect on leaving propensity (Jeanson et al. 2004). The use of multiple communication systems could facilitate rapid and accurate decision making. For example in *M. nipponica*, the synergistic effect of trails and quorum thresholds may help to improve decision speed by drawing scouts to site of interest, while simultaneously maintaining accuracy by delaying brood transport until one site has a threshold level of support. Similarly, in *Tetramorium* ants, groups of nestmates are initially led to favoured food sites by informed scouts, before a switch to trail-based foraging (Collignon and Detrain 2010). In this way group recruitment may be a method of 'kick starting' trail-based recruitment in species that rely on trails for foraging (Beekman and Dussutour 2009) but are otherwise constrained by minimum critical masses to initiate effective trails (e.g. Beekman et al. 2001). Synergistic mechanisms of positive feedback such as these help optimise collective actions, and may aid tailoring of collective behaviours to different environmental contexts by providing multiple avenues for adaptive tuning of the collective response.

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