



## Consensus decision making in the ant *Myrmecina nipponica*: house-hunters combine pheromone trails with quorum responses

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Consensus decisions enable group-living organisms to coordinate collective tasks without the need for complex cognitive abilities or centralized leadership. Systems of nonlinear positive feedback, such as quorum responses, are thought to be integral to consensus decision processes that seek to optimize decision speed and accuracy while maintaining group cohesion, requirements typical of the house-hunting process in social insects. Studies of nest site selection in honeybees, *Apis mellifera*, and *Temnothorax* ants have revealed strong similarities in the manner in which consensus decisions are achieved, and imply a central role for quorum responses, but treatments of other species are scarce. I investigated the process of consensus decision making during colony relocation in the small colony ant *Myrmecina nipponica*. Colonies of individually marked ants were forced to relocate in experimental laboratory arenas, and given a choice of one or two alternative new sites. This species differs from other well-studied systems in using pheromone trails to navigate between old and new sites, and does not use obvious means of recruitment such as tandem running or adult transport. A quorum threshold apparently governed the switch to brood transport, which marked the final phase of the relocation. Furthermore, there was a strong relationship between inferred quorum threshold and colony size. A demonstration of the use of a quorum rule in *M. nipponica* would underline the central role of quorum responses in consensus decision making, despite interspecific variation in colony size and differing modes of recruitment and navigation.

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Consensus decision making allows group-living organisms lacking central control to select between two or more mutually exclusive actions while maintaining group integrity (Conradt & Roper 2005; Sumpter & Pratt 2009). Decisions arise as group level manifestations of individual responses to local cues in a process of self-organization, a phenomenon that features broadly in animal societies from the coordinated movements of flocks of birds to the organization of foraging in social insects (Conradt & Roper 2003; Conradt & List 2009; Pratt 2010). Consensus decisions are often characterized by quorum responses, in which an individual's propensity to perform an action is a sharply nonlinear function of the number of other individuals already performing that action (Sumpter & Pratt 2009). Quorum responses may improve the accuracy of consensus decisions and provide a mechanism for tuning decisions to variable environments (Franks et al. 2003; Passino & Seeley 2006; Pratt & Sumpter 2006), and their use is

thought to be widespread in the animal kingdom (Conradt & List 2009; Sumpter & Pratt 2009).

Decision accuracy and group cohesion are of paramount importance during the process of house hunting in social insects, as the choice of new home has important fitness consequences for all individuals and the consequences of a wrong decision can be severe (Franks et al. 2002; Pratt et al. 2005). Many social insects need to relocate when their current home is destroyed or becomes otherwise unsuitable, or during reproduction via colony fission. The house-hunting process has been well studied in honeybees, *Apis mellifera*, and *Temnothorax* ants (reviewed in Franks et al. 2002; Visscher 2007). These studies reveal that nest site choice occurs in a self-organized manner, that is, the choice of site is an emergent property of numerous distributed, semi-independent responses governed by local rules (Visscher 2007). For example, in honeybees, scouts that have found a suitable site advertise it via a waggle dance, which can encode not only locational information but also an indirect assessment of site quality. Other bees watching the dance may investigate the advertised site and subsequently contribute dances of their own. When a quorum of bees is dancing for one site, the colony's behaviour shifts rapidly and a swarm departs for the new site. In *Temnothorax*, scouts recruit other ants to

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a suitable site via tandem runs, in which naïve individuals follow scouts to the new site. Once a quorum of ants is assembled at one site, individuals begin switching to adult transport, and carry brood and the remaining majority of colony members to the new site. The body of work on these species demonstrates that quorum responses play a central role in consensus decision making, and a crucial factor in this regard may be the capacity quorum thresholds hold for tuning consensus decisions to optimize the trade-off between decision speed and accuracy (Sumpter & Pratt 2009): for example, a smaller quorum will lead to a more rapid decision, which may be favoured when the colony is under threat (Franks et al. 2003). More rapid decisions come at a cost to decision accuracy, however (Passino & Seeley 2006; Franks et al. 2009; Stroeymeyt et al. 2010), and tuning of the quorum threshold can permit adaptive tailoring of the consensus decision process to optimize this trade-off in different environmental conditions (Franks et al. 2002; Seeley & Visscher 2004; Passino & Seeley 2006).

While studies of honeybees and *Temnothorax* ants reveal interesting parallels between these two systems in the manner in which consensus decisions are achieved (Franks et al. 2002), treatments of other species have been rare. In this study, I investigated the process of consensus decision making during nest relocation in the small colony ant *Myrmecina nipponica*. This species nests in mosses and fern roots in broadleaf forests in Japan. Colonies are small (around 40 workers) and those headed by both winged and apterous queens (ergatoid, worker-like queens; Peeters 2012) can co-occur in the same population (Murakami et al. 2002; Miyazaki et al. 2005). Ergatoid queen colonies are thought to reproduce via colony fission (Ohkawara et al. 1993; Murakami et al. 2002) and thus rely on group movements to find new nesting locations. Both forms of colony are likely to have to relocate, however, as nesting substrates are ephemeral, subject to flooding, and likely to be unsuitable in winter.

A preliminary study of colony relocation in the European cousin of this species, *Myrmecina graminicola* (Buschinger 2010) suggested that, in contrast to the well-studied systems outlined above, this species relocates via the use of pheromone trails, without the use of tandem runs, adult transport or other obvious means of information transfer. Pheromone trails play an important role in effective recruitment mechanisms in ant foraging (Hölldobler & Wilson 1990), but their use is considered primarily the domain of large-colony ants (Dornhaus et al. 2012). Smaller colony ants, such as *Temnothorax*, tend to use mechanisms of tandem running or group recruitment, which are not subject to colony size because recruitment can be initiated by one individual. Furthermore, while pheromone trails have the potential to generate nonlinear feedback, potentially making their use effective in consensus decisions, pheromone trail-based choice mechanisms are subject to momentum and may be less flexible than other more adaptable

systems such as honeybee dances (Sumpter & Beekman 2003). This can lead to maladaptive results because alternatives discovered too late cannot be exploited once a trail is established (Beckers et al. 1990). While this outcome may not be too costly with respect to foraging, a suboptimal outcome during nest site selection is likely to carry much higher costs, as this places the colony at significant risk. The only two other studies of nest or aggregation site selection in trail-laying species (Jeanson et al. 2004; Evison et al. 2012) concluded that pheromones are employed adaptively during nest site selection, as has previously been demonstrated for foraging behaviour (Beckers et al. 1993). However, these studies both used large-colony species, and did not explore the possible role of quorum thresholds in consensus decision making. In this study I examined the process of consensus decision making during house hunting in *M. nipponica*, the smallest colony species so far studied in this regard. Specifically, I investigated the mechanisms of positive feedback during the nest site selection process, the possible role of quorum responses, and the influence of colony size and colony type.

## 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 (42°47'N, 141°34'E, altitude ca. 100 m) on 15 and 20 September 2011. This site is known to host colonies headed by both winged queens and ergatoid queens (Miyazaki et al. 2010). All adults and brood were carefully extracted from the nests in the laboratory and transferred to artificial nests. Colonies were housed in plastic boxes (10 × 10 cm and 3 cm high) 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 placed 0.5 cm from one side of the box. Nests consisted of a microscope slide mounted on a 2 mm high circlet of foam with a small (3 mm) opening. Nests were covered with a removable piece of opaque card.

Colonies were of five different types: winged-queen monogynous (WQ) and polygynous (WQs) colonies ( $N = 8$  and 1, respectively), ergatoid monogynous (EQ) and polygynous (EQs) colonies ( $N = 4$  and 6, respectively), and orphan (O) colonies ( $N = 1$ ). Colony size varied between colony types, with winged-queen colonies being generally more populous (ANOVA:  $F_{4,19} = 4.43$ ,  $P = 0.015$ ; Table 1). The number of broods, defined as the number of transports recorded (see below), was highly correlated with colony size (Pearson correlation:  $r = 0.72$ ,  $P < 0.001$ ). This approach may

**Table 1**  
Demographics and relocation characteristics of different colony types used in experiment 1

	WQ	EQ	EQs	WQs	O	All
Number of colonies	8	4	6	1	1	20
Colony size	37.4±16.0	20.5±7.6	31.0±9.3	73	12	32.6±16.6
Total time for relocation ( $t_r$ )	123±45	92±29	121±52	78	96	113±43
Discovery time ( $t_0-t_d$ )	27±13	39±28	23±21	6	38	28±19
Assessment time ( $t_d-t_q$ )	72±35	27±12	69±58	48	33	59±42
Transport time ( $t_q-t_r$ )	25±5	27±16	30±13	24	26	27±10
Percentage of scouts (ants informed at $t_q$ )	49.1±16.6	47.8±21.2	59.4±17.2	47.2	50.0	51.9±16.6
Quorum threshold at $t_q$	8.8±6.5	2.3±1.0	5.7±3.7	18	3	6.7±5.8
Quorum % at $t_q$	23.3±9.2	12.7±8.0	20.3±15.1	24.7	25.0	20.4±10.9
Mean overall quorum threshold	13.8±8.4	8.19±4.7	9.48±3.5	20.76±4.3	3.8±1.2	11.7±7.1
Transporters %	41.9±10.1	55.8±11.2	45.1±11.4	27.4	58.3	45.7±12.1

All values are quoted as mean ± SD. All times are in minutes.

underestimate true brood numbers, however, as some transports of small brood items may have been missed.

Ants were kept at room temperature (ca. 20 °C) and provided with ad libitum water in small vials plugged with tissue, sugar/water solution in vial caps, and 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.

#### Experiment 1: Individual Roles and Mode of Relocation

In experiment 1, a second, identically prepared box containing a previously unused nest was attached to the occupied nestbox, and a small hole (10 mm wide × 3 mm high) was drilled between the two boxes at the level of the plaster. Nests were located at opposite sides of the arrangement, such that the distance between the two nests was approximately 13 cm (Fig. 1a). A partition prevented access to the new nestbox until video recording began, at which time the original nest was 'destroyed' by removing the microscope slide and foam. Thus all ants were 'naïve' to the new nestbox and new nest prior to the destruction of their nest. Relocations were observed once for each colony given in Table 1 ( $N = 20$ ).

#### Experiment 2: Nest Choice

In experiment 2, colonies were provided with two additional nestboxes and nests were placed at opposite sides of the occupied nestbox (Fig. 1b). One new nest was covered with a microscope slide only ('light'), while the second was also covered with red cellophane ('dark'; insects are generally considered blind to red light). Ten colonies were each used once in this experiment as follows: WQ ( $N = 5$ ), EQ ( $N = 4$ ) and O ( $N = 1$ ). All but one of these colonies had been used in experiment 1, but had overwintered for 3 months at 5 °C and 90% humidity before being returned to the conditions described above a week before choice experiments began.

#### Video Set-up

Colony relocations in experiment 1 were filmed using a Canon EOS60D digital camera with 18–55 mm lens (zoomed to fill the frame), positioned on a tripod 300 mm above the nests. At this

distance ants were individually recognizable on digital video recorded at 1920 × 1080 pixel resolution directly to computer hard disk in 10 min contiguous blocks, using the software EOS Camera Movie Record 3.1.1 (beta). In experiment 2, web-cameras (Elecom Ucam-DLA200H) positioned 5 cm above the nest entrances were used with the motion detection software iSpy ([www.ispyconnect.com](http://www.ispyconnect.com)) to track entries and exits. Video files were analysed using Kinovea ([www.kinovea.org](http://www.kinovea.org)). The identity and timing of individual ants entering and exiting the new nest(s) and transporting brood were recorded. The entire arena was visible on videos in experiment 1, making it possible to view any acts of tandem running and adult transport.

#### Statistical Analysis

Data were analysed in R version 2.15.0 (R Development Core Team 2012). Generalized linear models (GLM) and mixed-effects models (MM) were implemented using the `glm` and `lme` functions, respectively, with all possible explanatory terms initially fitted. Starting with interactions, terms were then removed in a stepwise fashion until the minimum adequate model was obtained as determined by comparison of values of AIC (Akaike information criterion). Model choice was then validated using plots of residuals (Zuur et al. 2009). Values quoted are for this minimum adequate model. Means are given as arithmetic mean ± SD unless otherwise stated.

## RESULTS

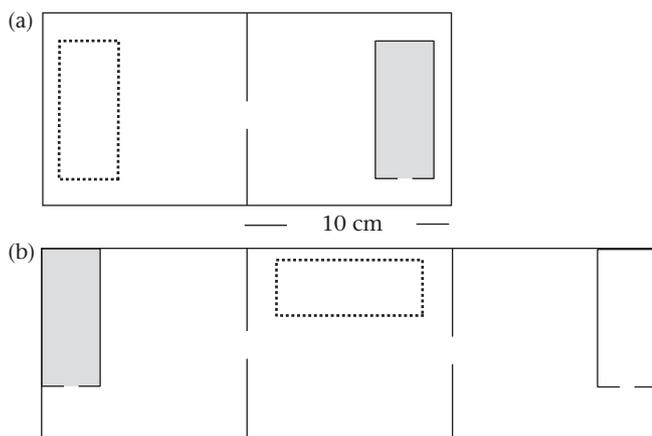
#### Outline of the Relocation Process

The relocation process was divided into three main phases as follows: discovery phase: from destruction of the initial nest ( $t_0$ ) to discovery of the new nest, that is, entry of the first worker into the new nest ( $t_d$ ); assessment phase: from discovery of the new nest ( $t_d$ ) to when the first worker achieved a quorum and switched to transporting ( $t_q$ , see below); transport phase: from achievement of a quorum ( $t_q$ ) to completion of the relocation, that is, when all brood had been relocated and all ants had visited the new nest at least once ( $t_f$ ). Total relocation time was defined as  $t_f - t_0$ . In the following account, ants that had visited new nests are termed 'informed' while those with no direct knowledge of the new nest(s) are termed 'naïve'. Ants were defined as 'scouts' when they were informed as of  $t_q$ , while others were considered 'nest ants'.

Ants initially moved individually and appeared thigmotactic (i.e. attracted to physical boundaries), as suggested by Buschinger (2010) for *M. graminicola*, and photophobic. Movement gradually became canalized during the assessment phase, from dispersed individual searching towards a single two-way trail that did not necessarily take the most direct route between the new and old nests. This suggests that scouts were laying a pheromone trail, although deposition behaviour could not be directly observed. Movement along trails could clearly be observed once transport of brood had begun, and ants transporting brood and naïve ants almost always followed the established path. Scouts also appeared to use trails to navigate to both new nests in experiment 2, but trail fidelity was clearly lower prior to the onset of brood transport.

#### Experiment 1: Individual Roles and Mode of Relocation

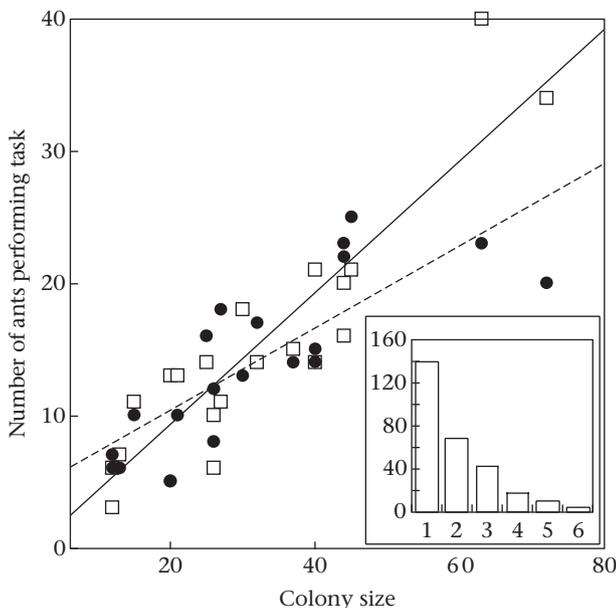
The final data set for experiment 1 comprised  $317 \pm 156$  observations of entry/exit events (range 94–572, total 6336) by  $30.1 \pm 14.6$  individuals (range 12–57, total 644) from 20 colonies. Nest relocations took 60–221 min, with phases distributed as



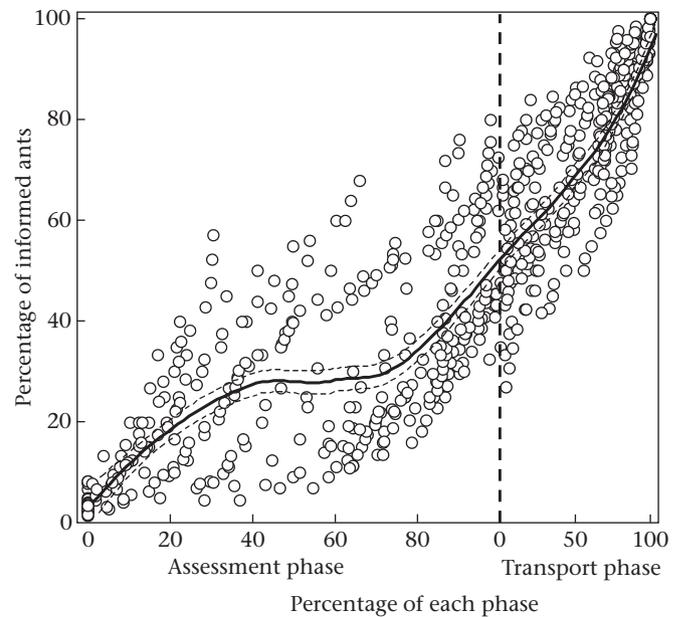
**Figure 1.** Experimental set-up for (a) experiment 1 and (b) experiment 2. Boxes were connected by a small hole drilled between the two at the level of the substrate. Old nest: dotted lines; new 'light' nest: solid line; new 'dark' nest: solid line and grey shading.

follows: discovery: 6–73; assessment: 13–183; transport: 12–50 (see also Table 1 for average times). The influence of colony factors on total relocation time was investigated using GLM for each phase of the relocation and over the entire process, with colony type and colony size as explanatory variables. The minimum adequate model indicated the only significant effect was of colony size on discovery time, which was shorter in larger colonies (GLM:  $t_{19} = -2.679, P = 0.015$ ). There were no significant effects on overall relocation time. Colony type had no significant effect and thus all types are pooled in the following analysis except where noted (see also Table 1).

The number of ants acting as scouts was strongly dependent on colony size (Fig. 2; regression:  $R^2 = 0.822, P < 0.01$ ), with on average just over half of the colony involved in assessment of the new nest ( $52 \pm 17\%$  of ants had been to the new nest as of  $t_q$ ). The rate at which ants found the new nest over the assessment phase is summarized in Fig. 3. The overall trend is one of a saturation curve for the first 75% of the phase. This pattern is characteristic of a memoryless stochastic process (Nouvellet et al. 2010) in which the chance of any ant finding the new nest is independent of how many others have already done so, suggesting individuals initially find the nest on their own without recruitment or positive feedback. The last quarter of the assessment phase, however, exhibits a substantial increase in the rate at which individuals find the nest, suggesting the introduction of some mechanism of positive feedback (see also Appendix Fig. A1). This aligns well with observations described above of the gradual forming of a pheromone trail, and suggests that scouts found the new nest independently at first, but gradually switched to trail following as a pheromone trail became established. This increase in the number of ants finding the new nest also coincides with an increase in the percentage of individuals in the new nest (Fig. 4), suggesting it is the arrival of novel individuals that produced this latter increase. Although there was also an increase in the length of individual visits to the new nest over time during the assessment phase (Pearson correlation:  $r = 0.165, P < 0.001$ ), this was gradual.

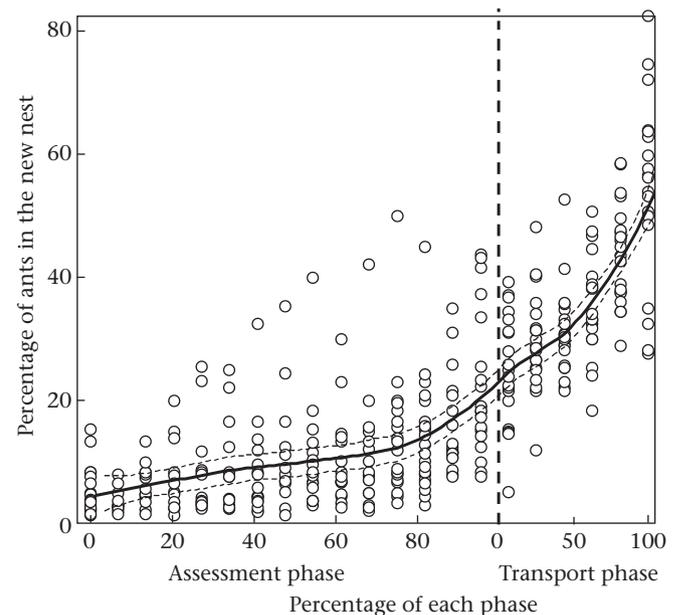


**Figure 2.** Relationship between colony size and (1) number of scouts (informed ants at  $t_q$ ; open squares and solid line) and (2) total number of transporters (filled circles and dashed line). Lines show linear regressions (see text). Inset: number of transports per individual.



**Figure 3.** Percentage of informed individuals over scaled time before and after  $t_q$  for all 20 colonies in experiment 1. The X axis is divided into percentage time for the assessment phase (left of dashed vertical line) and transport phase (right of dashed vertical line). In each case event data from each colony have been scaled as a percentage of the phase length for each colony. Dots represent the first entry to the new nest for each individual. The difference in axes lengths between the phases is based on the overall relative mean lengths of each phase. The overall trend is described by the LOESS line with  $\alpha = 0.5$ . Dashed lines indicate 95% confidence intervals.

Following a long assessment phase, the switch to brood transport was relatively rapid. The association between this switch and the increase in individuals at the selected site suggests it is governed by a quorum threshold (see below). A subset of individuals



**Figure 4.** Percentage of ants in the new nest over scaled time before and after  $t_q$  for all 20 colonies in experiment 1. The X axis is divided into percentage time as in Fig. 3. Dots represent the mean number of ants in the new nest for each colony at intervals of 5% of the phase duration. The overall trend is indicated by the LOESS line with  $\alpha = 0.5$ , and dashed lines indicate 95% confidence intervals.

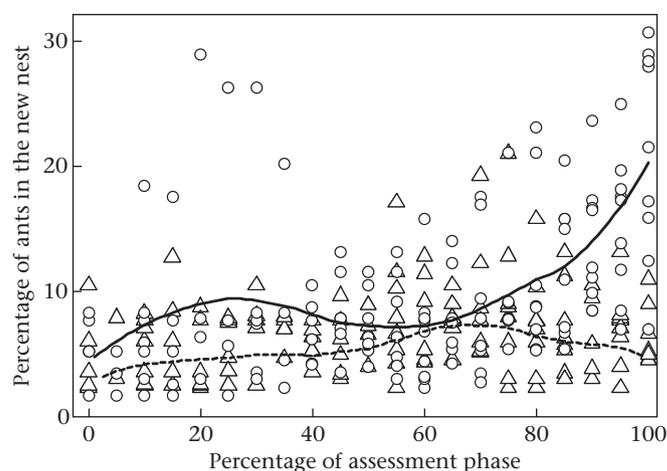
carried individual brood items to the new site. There were  $27.4 \pm 13.0$  transport events (range 9–51, total 547) by  $14.2 \pm 6.3$  transporting ants (range 5–25, total 284). As was the case for scout ants, the number of transporting ants was highly dependent on colony size (Fig. 2; regression:  $R^2 = 0.65$ ,  $P < 0.01$ ), with on average  $46 \pm 12\%$  of the colony population (range 25–67%) each performing  $1.93 \pm 0.07$  transports (range 1–6; Fig. 2 inset). There was some suggestion that this colony size relationship was a saturating one, however (Fig. 2). Ants informed at  $t_q$  comprised 74% of all transporting ants, and accounted for 83% of all observed transports. Naïve ants occasionally performed transports during their maiden voyage to the new nest (29 of 548 transports = 5.3%). There were also six instances ( $N = 3$  colonies) of transports by ergatoid queens (all in polygynous EQs colonies) and one case of transport by a winged queen (in the one polygynous WQs colony).

#### Experiment 2: Selection between Two Alternative Nests

Data for experiment 2 comprised 562 ± 398 observation of entry/exit events (range 92–1214, total 5622) from  $30.4 \pm 14.5$  individuals (range 12–57, total 301) from 10 colonies, nine of which were used in experiment 1. Relocation behaviour in experiment 2 unfolded in the manner of experiment 1. However, assessment phases (in the nine colonies used in both experiments) were longer than in experiment 1 (mean of  $135 \pm 71$  min versus  $60 \pm 40$  min: Wilcoxon signed-ranks test:  $Z = -2.310$ ,  $N = 9$ ,  $P = 0.021$ ). This difference may be explained by the larger area to be assessed in experiment 2. The length of discovery and transport phases did not differ between experiments. No preference was shown for 'dark' or 'light' nests, with half of the trials resulting in selection of each. The first nest found was selected in 50% of cases. There were no instances of split colonies. Although occasional transports back to the brood pile were observed, no transports to the 'wrong' nest occurred.

As for experiment 1, approximately half of the colony was involved in the assessment process, with  $56 \pm 19\%$  ants informed of at least one new nest at  $t_q$ . Of these informed individuals,  $38 \pm 31\%$  visited only the finally accepted colony,  $10 \pm 11\%$  visited the rejected colony and  $53 \pm 35\%$  visited both colonies. At the end of the relocation, on average only half of the colony had visited both sites ( $48 \pm 50\%$ ), and only half of the transporting ants ( $51 \pm 27\%$ ) had visited the alternative nest site. These data, and the observation of further occasional transports by completely naïve individuals (eight of 228 transports), indicate that direct comparison is not essential for initiating the switch to a transporting role. The roles of scouts and nest ants were relatively consistent in the nine colonies used in both experiments: 64% of ants maintained the same role (34% of ants on average were informed at  $t_q$  in both experiments, that is, they acted as scouts, while 30% were naïve). The remaining 36% of individuals switched roles, although this may underestimate the extent of role conservatism in that it only accounts for activity up to  $t_q$ .

The number of ants in both new nests over the assessment period is summarized in Fig. 5, which shows that the average proportion of scouts in each nest was similar until a point around 75% of the assessment phase. At this time, the number of ants rapidly increased in the finally accepted nest up to the point at which transports began. This replicates the trend observed in experiment 1, including the jump in rate at 75% of the phase length, despite the fact that the assessment phase was longer in experiment 2. As in experiment 1, there was also an increase in the duration of visits to either new nest over the duration of the assessment phase, but this trend did not differ between rejected and accepted nests (GLM: time:  $t_{1519} = 2.27$ ,  $P = 0.023$ ; nest choice:  $t_{1519} = 0.096$ ,  $P = 0.924$ ). This supports the idea that the increase in



**Figure 5.** Percentage of ants in the finally accepted nest (circles and solid line) and rejected nest (triangles and dashed line) over percentage time of the assessment phase for all 10 colonies in experiment 2. Points represent the mean number of ants in each nest for each colony at intervals of 5% of the assessment phase duration. The LOESS line is fitted at  $\alpha = 0.5$  over all colonies. Confidence intervals (resembling those shown in Fig. 4) are omitted for clarity.

number of individuals leading to quorum is the result of additional ants arriving at the accepted nest, rather than individuals modifying their visit duration.

#### Quorum Thresholds

Brood transport was always to a single destination and was achieved relatively rapidly following a long assessment phase. This shift to transport was also characterized by a notable increase in speed by transporting ants, a rapid accumulation of transporting ants, and occasional tactile stimulation of passive ants by transporting ants returning to the original nest site. This suggests that the switch to brood transport represents a genuine phase shift, which does not occur until a consensus has been reached over the new nest site. This makes adaptive sense because relocation of brood no doubt carries considerable risk. This phase shift was associated with concurrent changes in the number of individuals in the new nest consistent with a quorum response, specifically (1) the switch occurred after a marked increase in the number of ants at the new nest in experiment 1 (Fig. 4), and this increase was clearly a decisive factor between the accepted and rejected nests in experiment 2 (Fig. 5), and (2) there was a strong relationship between quorum threshold and colony size (see below), suggesting quorum thresholds may be conditional.

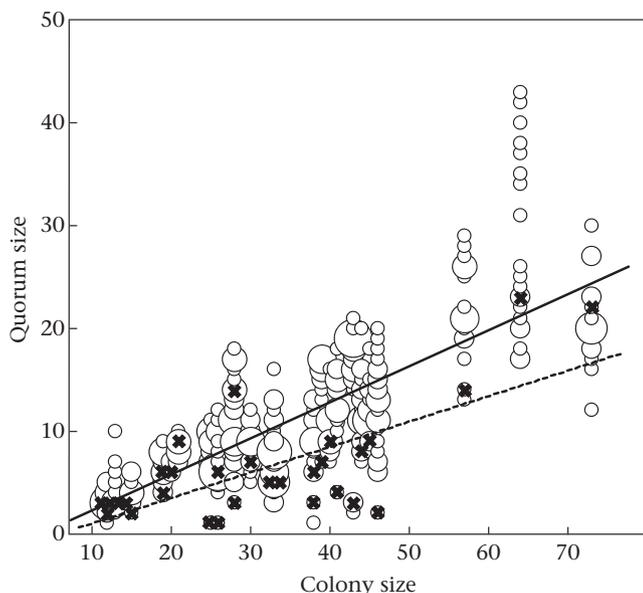
Quorum thresholds were calculated as the number of ants present in the new nest immediately prior to a focal ant's departure from the nest on a trip that culminated in her maiden brood transport to the new nest. The first of these for each colony during a given relocation event was designated the time at quorum,  $t_q$ . Some ants ( $N = 29$  of 284 total transporters) made transports without having visited the new nest, and are excluded from the analysis below. These naïve transports usually occurred late in the transport phase, and may be the result of additional feedback mechanisms (see below). Quorum thresholds at  $t_q$  (when the first switch to transport occurred) ranged between 1 and 24 with a mean of  $6.7 \pm 5.8$  ants, or  $20.4 \pm 10.9\%$  of the adult population of the colony. Over all transporting ants, the mean threshold was  $11.7 \pm 7.1$  ants, or  $31 \pm 11\%$  of the colony ( $N = 255$ ). Late-arriving ants are more likely to experience new nest populations far above their actual quorum threshold, however, and thus this overall

value may be inflated. None the less, mixed-effects model analyses (with colony as a random factor) indicate that ants that began transporting later made more nest visits before transport (MM:  $t_{198} = 101.3$ ,  $P < 0.001$ ), and had a higher latency between their first entry and first transport (MM:  $t_{198} = 12.3$ ,  $P < 0.001$ ) suggesting that late transporters may indeed have different quorum requirements to earlier ones.

Quorum thresholds in experiment 2 were similar to those in experiment 1, both at  $t_q$  and overall ( $6.2 \pm 4.3$  ants, range 3–14, or  $22 \pm 12\%$  of the colony at  $t_q$ ; and  $12.4 \pm 7.1$  ants, or  $34 \pm 13\%$  of the colony overall). The influence of experimental treatment and colony size on individual quorum thresholds over both experiments (for  $N = 361$  transporting ants) was examined with a mixed-effects model in R, with colony as random factor. This analysis suggested that quorum threshold did not vary between experiments but was highly dependent on colony size ( $t_{338} = 10.74$ ,  $P < 0.001$ ). An equivalent analysis on proportionate quorum thresholds (percentage of the colony comprising the quorum) had no significant effects. This relationship is summarized in Fig. 6. Overall individual quorum thresholds and colony ( $t_q$ ) quorum thresholds are both highly dependent on colony size (regressions: overall:  $R^2 = 0.57$ ,  $P < 0.001$ ,  $0.755 + (0.351 \times \text{workers})$ ;  $t_q$ :  $R^2 = 0.51$ ,  $P < 0.001$ ,  $0.714 + (0.248 \times \text{workers})$ ).

### Relocation of Queens

Queens in monogynous colonies moved at the end of the migrations (last 15% of all first entries, or on average  $69 \pm 28\%$  of the way through the transport phase;  $N = 12$  colonies in experiment 1) and usually made only one trip to the new nest, whereas queens in polygynous colonies moved at any time during the relocation, sometimes making multiple trips. This contrasts with other monogynous ant species in which queens relocate in the middle of the emigration, ostensibly for reasons of safety (Franks & Sendova-Franks 2000; Pezon et al. 2005; Avargues-Weber & Monnin 2009). Why this rationale seemingly does not apply in *M. nipponica* is unclear, although the risk of getting lost may



**Figure 6.** Relationship between quorum threshold and colony size. Dots indicate individual quorum thresholds over all individuals, with dot size proportional to number of overlapping points. Crosses indicate first quorum events for each colony (i.e. at  $t_q$ ). Regression lines are given overall (solid line) and for  $t_q$  (dashed line; see text).

outweigh the benefits of safety in numbers, favouring a later emigration. Although clearly not part of the regular colony relocation process, three cases of adult transport or attempted adult transport were observed. All cases involved the transport of ergatoid queens, which appeared unable to relocate on their own. In two cases, workers were unable to pick up queens and queens eventually made their own way to the new nest. In the remaining case, a worker successfully transported an ergatoid queen from within the new box into the new nest. In all cases workers had clear difficulty in picking up and positioning the carried adult, suggesting this behaviour is not well honed. In the instances observed, queens were grasped from above and the front and held between the head and alitrunk, although unsuccessful efforts to grasp queens from behind around the petiole were also observed.

### DISCUSSION

*Myrmecina nipponica* employs a multistep process enabling colonies to maintain group cohesion while selecting and relocating to a new nest site following destruction of their old nest. The evidence from 30 observed relocations and choice experiments suggests this is achieved via a consensus decision process that combines the use of pheromone trails and quorum responses, although the role of both of these mechanisms must be clarified with further experimental tests. The relocation process consists of at least three distinct phases: search, assessment and transport. In the search phase, ants move independently about the arena searching for suitable aggregation sites. Once a promising site has been found, individuals assess the site, with approximately half of the scouts visiting both nests. During this time, ants also repeatedly return to both the newly discovered site and the site of the old nest, apparently laying pheromone trails to favoured sites. These trails lead to the accumulation of other ants at the new site, and once a sufficient number of ants (approximately 20% of the colony) is located in the new nest, brood transport ensues, and remaining ants relocate by themselves by following trails. Pratt et al. (2005) described four analogous phases in the relocation behaviour of *Temnothorax albipennis*: search, assessment, canvassing and committed. In *M. nipponica* it was not possible to distinguish between assessment and canvassing because vote casting (via trail laying, as opposed to tandem runs or waggle dances) is cryptic, and it is thus difficult to assess at which point canvassing becomes active (see also Buschinger 2010). The increase in arrival rate of new ants at around three-quarters of the assessment phase suggests trails become effective around this time and implies ants must begin laying trails sometime prior to this. A further distinction from *Temnothorax* is the lack of adult transports; although these were observed on a few occasions, they were employed only in the case of wayward queens, were crudely effected, and clearly not part of the normal relocation process. While the accumulation of individuals at the new site was apparently a result of navigation via pheromone trails, the role of pheromone trails in directly stimulating activity oriented towards relocation remains unclear. This raises the question of what trigger causes passive ants to emigrate once a quorum has been achieved. One possibility is tactile stimulation, as transporting ants returning to the brood pile were occasionally observed running over brood and ants assembled there while rapidly shaking from side to side. This action stimulated activity in recipients, and may be akin to the buzzing runs of honeybees (Camazine et al. 1999). Tactile stimulation is important for recruitment in other social insects in both a foraging and migratory context (Hölldobler 1971; Wilson & Hölldobler 1986; Nieh 2004) and additional work should quantify the efficacy of this behaviour in *M. nipponica*. Once transport of brood has begun,

additional positive feedback mechanisms may stimulate activity in the remaining passive ants, including (1) reduction in the number of brood at the site of the old nest, (2) the presence of brood at the new nest, (3) encounters with transporting ants and (4) movement of the queen.

Group coordination in social animals relies on positive feedback, but nonlinear feedback such as quorum responses may be necessary for consensus decisions, when maintenance of group cohesion is of paramount importance (Sumpter & Pratt 2009). The two best studied systems, those of honeybees and *Temnothorax* ants (reviewed in: Franks et al. 2002; Sumpter 2006; Visscher 2007), employ systems of linear feedback that culminate in a sharply nonlinear quorum response (Sumpter 2006). A clear difference between these systems and that of *M. nipponica* is the mode of recruitment: whereas honeybees employ the waggle dance and *Temnothorax* use tandem running, the accumulation of individuals at the new site during relocations in *M. nipponica* appears to be a result of the use of pheromone trails. While pheromone trails are important in optimizing foraging effort in many ants (Hölldobler & Wilson 1990; Sumpter & Beekman 2003), it is generally assumed that they are used by large-colony species (Dornhaus et al. 2012). Pheromone trails can be employed adaptively and elicit nonlinear responses on their own (Sumpter & Beekman 2003), allowing colonies to choose effectively between foraging and aggregation sites (Beckers et al. 1993; Jeanson et al. 2004). However, pheromone trail-based choice mechanisms may suffer from inflexibility compared to more adaptable mechanisms such as the honeybee dances, leading colonies to become committed to earlier options over preferable alternatives discovered later (Beckers et al. 1990; Sumpter & Beekman 2003). The potential for this to influence decisions over nest choice in *M. nipponica* remains unclear: while no preference for the first-discovered nest was found in experiment 2, as might be expected in a momentum-dominated process (Beckers et al. 1990), the formation of temporary maladaptive 'mills' (Deneubourg & Goss 1989) during the relocation process in some colonies hints that pheromone trail use could result in suboptimal outcomes in some circumstances.

The use of pheromone trails and quorum responses would seem a strong combination to facilitate group cohesion and, indeed, in the choice experiments there were no examples of colony splitting as has been reported in other relocating ants (Franks et al. 2006; Evison et al. 2012). While both candidate nests received numerous visits, a quorum was achieved at only one of them as evidenced by the absence of brood transports to the rejected nest. The available data do not permit an assessment of how quorums are detected by ants, but a likely mechanism is the rate of encounters between individuals in the new nest, which is density dependent and can thus serve as a proxy for the number of individuals present. Encounter rate is thought to have a role in mediating quorum decisions in other house-hunting ants, and guide other collective processes in ants (Pratt 2005a, b; Greene & Gordon 2007). The lack of preference between treatments in experiment 2 is likely to be an effect of choice of alternatives rather than evidence of error on the ant's part: while it is often accepted that red filters are equivalent to darkness for ants, empirical evidence suggests this is not always the case (Depickère et al. 2004). Indeed, the outcome of these trials is similar to that observed in the choice of two equivalent foraging or aggregation sites in other trail-laying species, in which presumed stochastic fluctuations of signal lead to amplification eventually resulting in the dominance of one trail over another (Beckers et al. 1993; Jeanson et al. 2004). In addition to indicating a single outstanding option, a quorum may also mark a point at which a safe, navigable trail has become established, and thus a suitable time to initiate the relocation of brood and naïve individuals. This is analogous to

*Temnothorax* using tandem runs to teach enough workers the correct route to the new site to enable an effective relocation (Franks et al. 2009), and honeybees having sufficient scouts to guide the swarm (Seeley & Visscher 2004). Pheromone trails can also optimize route choice by reorienting scouts that have taken a less-direct path, one possible function of reverse-tandem runs in *Temnothorax* (Franks et al. 2009).

There was a strong relationship between colony size and quorum threshold, suggesting that quorum thresholds are at least in some sense conditional. Conditional quorum thresholds have also been demonstrated in *Temnothorax* ants (Franks et al. 2003; Dornhaus et al. 2004), and observed quorum thresholds in honeybees and *Temnothorax* are thought to reflect a balance between competing optima for speed and accuracy (Seeley & Visscher 2004; Franks et al. 2009). A colony size relationship has also been identified in *Temnothorax* ants (Dornhaus & Franks 2006; Franks et al. 2006), and Franks et al. (2006) suggested that higher quorum thresholds in larger colonies may mitigate against colony splitting; because larger colonies also have more scouts, there is a greater probability of finding multiple alternative new sites and attaining a quorum at more than one of them at once. Absolute quorum thresholds in *M. nipponica* (approximately seven ants at  $t_q$ ) were similar to that observed in *Temnothorax* (ca. 10 ants; Dornhaus & Franks 2006; Franks et al. 2006) and indeed not markedly different from that quoted for honeybees (10–15 bees; Seeley & Visscher 2004) despite the smaller colony sizes (colonies usually <40 ants in *M. nipponica* compared to 100–500 ants in *T. albipennis* and <10 000 honeybees; Seeley 1996; Franks et al. 2006). These data indicate that quorum thresholds are proportionately high in *M. nipponica*. High quorum thresholds may be associated with relatively benign conditions (Dornhaus et al. 2004), but the experimental treatment used here was similar to that employed in other relocation studies and, furthermore, in being an inhabitant of very moist areas, *M. nipponica* is particularly susceptible to desiccation, and the open arena conditions used in the experiments are unlikely to represent benign conditions for this species. In addition to *M. nipponica* having a relatively large quorum threshold, the relationship between quorum threshold and colony size in *M. nipponica* ( $0.714 + 0.248 \times \text{workers}$ ) is much steeper than that observed in *Temnothorax* ( $0.95 + 0.014 \times \text{workers}$ ; Franks et al. 2006), and the percentage of ants directly involved in the decision process (ca. 50%) is relatively high, suggesting the consensus decision process is more 'democratic' than in other species (around 5% of the colony in honeybees; Seeley & Buhrman 1999; 30% of the colony in relocating *Temnothorax*: Sumpter 2006). This may suggest quorum thresholds are key elements in the tailoring of consensus decisions in *M. nipponica*, although the interspecific trend is also in line with models predicting that smaller colonies require a larger proportion of informed individuals to make accurate decisions (Couzin et al. 2005).

This study adds weight to the argument that quorum responses hold a central role in consensus decision making among species with diverse life history traits (Sumpter & Pratt 2009). The strong relationship between colony size and quorum threshold also supports existing empirical evidence that the quorum threshold is a key parameter in adaptive tuning of consensus responses (Franks et al. 2003; Dornhaus et al. 2004; Pratt & Sumpter 2006). However, while the use of quorums can increase the accuracy of decision making, other factors may be more important in tailoring decisions to the speed/accuracy trade-off (Pratt & Sumpter 2006). Specifically, modelling suggests that emphasis can be placed on decision speed or accuracy via varying the propensity for individuals to leave the nest to search, and the propensity for individuals to switch to recruitment. The cryptic nature of recruitment in *M. nipponica*

makes quantifying the latter of these difficult, but the potential role of these factors should be explored.

This is to my knowledge the first study that provides evidence for the combined action of pheromone trails and quorum threshold in a consensus decision-making process. In their study of *Tetramorium caespitum*, Collignon & Detrain (2010) described group mass recruitment to food sources as an 'intermediate' mechanism between standard mass recruitment and tandem running. *Myrmecina nipponica* uses a different system again, relying on pheromone trails for navigation (with a possible recruitment role) but also apparently employing a quorum rule to ratify decisions before switching to brood transport. Further studies of other species will shed light on the pervasiveness of quorum thresholds in consensus decision making. *Myrmecina* is an interesting model for analyses of consensus decision making and, in having a very small colony size and employing pheromone trails, a valuable counterpoint to other well-studied systems. Further studies on this group should investigate the role of pheromones in recruitment and the adaptive use of quorum thresholds in varied environmental conditions.

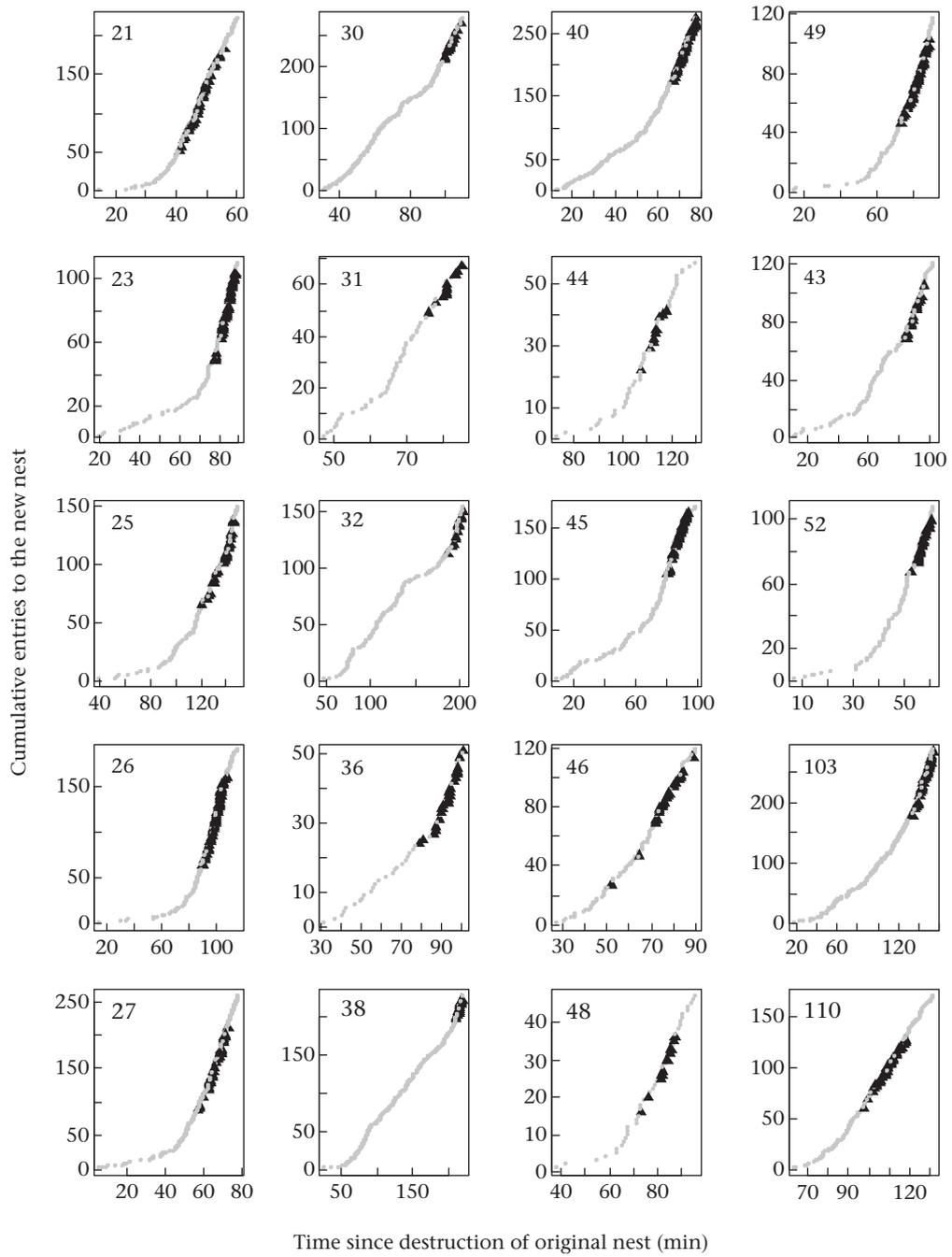
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Appendix



**Figure A1.** Cumulative number of entries into the new nest over time (min) since destruction of the original nest for the 20 colonies in experiment 1. Nontransport entries are indicated by grey dots while transports are indicated by black triangles. Colony numbers are provided in the top left of each figure.