



## Group size advantages to decision making are environmentally contingent in house-hunting *Myrmecina* ants



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Pooling information can allow groups to make better decisions than individuals, an idea that underlies the use of groups to make important decisions in human society. Group size is also thought to influence the accuracy of decision making in nonhuman animals, but despite the enormous variation in the size and composition of animal societies, very few studies have explored this question outside of humans. Furthermore, although both humans and animals need to make decisions in dynamic environments and models suggest that environmental conditions can alter or even invert the advantage of group size, no empirical study has addressed how the advantage of group size may vary with environmental context. In this study I investigated how group size and environmental context influence decision making using an ant model system in which colonies use a quorum-based process to decide collectively among new nesting sites. Decision making unfolded in a similar manner in colonies of different size, as quorum thresholds and task allocation scaled with colony size. Larger colonies, however, made more accurate decisions than small colonies, and in most cases did so more rapidly. There was also an influence of environmental conditions, as whereas the decision accuracy of small groups was comparable to that of large groups in benign conditions, decision making was largely ineffective in small colonies in more challenging conditions. Colonies adapted to different environmental conditions by adjusting quorum thresholds, shifting thresholds down to emphasize speed when under stress and showing a pattern of higher thresholds in complex environments. The advantage to larger colonies probably stems from their greater information collecting and processing ability, which also serves to buffer them from the negative influences of more challenging environments.

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Group-living organisms are able to combine information to make better decisions than individuals. This phenomenon, known colloquially as ‘the wisdom of the crowds’ (Surowieki, 2005), has long provided the basis for the use of groups to make important decisions in human society (Condorcet, 1785; Conratt & List, 2009; Krause, James, Faria, Ruxton, & Krause, 2011). The benefits of larger groups in decision making are also thought to apply to nonhuman animal societies (Krause, Ruxton, & Krause, 2010), but despite the enormous variation in group size both between and within animal species, this has only recently begun to receive attention (e.g. Kvajo, 2015). Many group-living organisms coordinate activities using a process of consensus decision making, allowing them to choose between mutually exclusive courses of action while maintaining group integrity

(Conratt & Roper, 2005; Sumpter & Pratt, 2009). Consensus decisions underlie a suite of actions in a wide range of species (reviewed in Conratt & List, 2009; Krause et al., 2010; Sumpter, 2010) and are typically quorum based, such that the probability of an individual performing an action increases rapidly once a critical number of individuals are already performing that action (Sumpter & Pratt, 2009). Quorum decisions help filter out individual errors and can enhance decision accuracy (Sumpter, 2010; Sumpter & Pratt, 2009; Wolf, Kurvers, Ward, Krause, & Krause, 2013). Larger groups have a greater cognitive capacity and information pool (Conratt & Roper, 2005; King & Cowlshaw, 2007; Sasaki & Pratt, 2012), and we might thus expect that, all else being equal, they should be more effective decision-making machines.

Social insects use consensus decisions to compile opinions across individuals when selecting a new home (Franks, Dechaume-Moncharmont, Hanmore, & Reynolds, 2009; Pratt, 2010; Seeley & Visscher, 2004; Visscher, 2007). This is one of the most challenging tasks an insect colony might have to perform, but must be

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undertaken whenever the current nest becomes unsuitable or during colony reproduction via fission (Cronin, Molet, Doums, Monnin, & Peeters, 2013; Pratt, 2010). Colonies rendered homeless must find and compare suitable new sites, decide collectively on a single option, and move to the new site while maintaining group cohesion. Relocating colonies face a trade-off between accuracy and speed (Franks, Dornhaus, Fitzsimmons, & Stevens, 2003) because while moving must be done as quickly as possible to limit exposure and risk, it must also be done carefully, as making the wrong choice can mean having to move again. Colonies must also balance the need for speed against the need for cohesion (Franks et al., 2013) and the relative value of different options (Pais et al., 2013; Seeley et al., 2012).

Colonies of the Japanese ant *Myrmecina nipponica* comprise 10–70 ants and make an excellent model system with which to examine the influence of group size on decision making. During the selection of a new nest site in this species, approximately half of the colony is actively involved in the decision-making process as scouts, although no decision is made until a quorum of individuals, approximately one-third of the colony, is in support of one site (Cronin, 2012). Previous studies (Cronin, 2012, 2014) suggest that in this species quorum size and the number of active scouts scales with colony size, and thus larger colonies may gain decision-making advantages via a ‘wisdom of the crowds’ effect. However, Cronin and Stumpe (2014) showed that ants in smaller colonies work harder (scout further and move faster) during colony emigrations than those in large colonies, and suggested that this may allow smaller groups to ameliorate the limitations of group size by collecting more information per capita, thus generating an equivalent information pool to larger colonies (King & Cowlishaw, 2007). However, they also noted that because individuals in small colonies are already working harder, smaller colonies may be less able to adapt to additional environmental stresses, leading to higher costs in more challenging environments.

In this study, I shed light on how group size influences the consensus decision-making process during house hunting using *M. nipponica* as a model system. I explored four main questions. First, given that recruitment plays a key role in consensus decision making in social insects, and the efficacy and mode of recruitment can be influenced by colony size (Beekman, Sumpter, & Ratnieks, 2001; Beekman, Sumpter, Seraphides, & Ratnieks, 2004; Planqué, Van Den Berg, & Franks, 2010), I investigated whether colonies of different size employ different decision-making strategies. Second, I assessed whether groups of different size make more or less accurate decisions, as while previous studies of humans and other animals have compared decision-making accuracy in individuals and groups (Clément et al., 2013; Krause et al., 2011; Sasaki, Granovskiy, Mann, Sumpter, & Pratt, 2013), few have examined the influence of group size per se, which is arguably more pertinent in obligately social species (though see: Berdahl, Torney, Ioannou, Faria, & Couzin, 2013; Ward, Krause, & Sumpter, 2012). Third, I tested whether group size effects are environmentally contingent. Both humans and nonhuman animals must make decisions in a wide range of environments in nature, and models suggest that environmental conditions can alter or even invert the advantage of group size (Kao & Couzin, 2014; Schaerf, Makinson, Myerscough, & Beekman, 2013), yet no empirical studies have examined how the advantage of group size might vary in different environmental contexts. Finally, I explored how adaptive changes in the decision-making process in different environments are brought about at the colony and individual level. Previous studies have shown that ants can adjust quorum thresholds to emphasize speed or accuracy (Dornhaus, Franks, Hawkins, & Shere, 2004; Franks et al., 2003), while recent studies have also noted that flexibility in individual behaviour may play an important role in adaptation to different

decision contexts (Cronin & Stumpe, 2014; Doran, Newham, Phillips, & Franks, 2015) and the relative importance of these factors remains unclear.

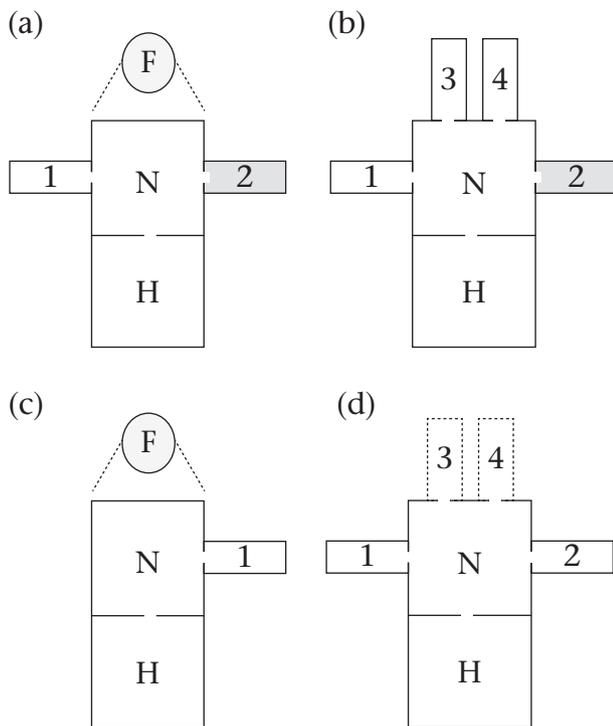
## METHODS

### Study System

Entire colonies of *M. nipponica* were collected from broadleaf forest near Chitose City in Hokkaido, northern Japan (N42° 47' E141° 34', altitude ca. 100 m) in September 2012 and 2013 and maintained in artificial laboratory nests using standard protocols (Cronin, 2012, 2013b). When required for individual tracking, ants were individually marked with differently coloured paint spots on the head, thorax and gaster. Colonies used in experimental emigrations varied in size from five to 73 ants (see [Supplementary material](#)), which spans the normal range for this species in the population studied (Cronin, 2012, 2013b, 2014). Colonies typically contained a single gynomorphic queen or one or more ergatoid queens or were in some cases orphaned (see [Supplementary material](#)). A total of 97 colonies were used in experiments, 75% of which were ergatoid queen colonies, 11% gynomorphic queens and 11% orphan. These forms can be considered equivalent in the context of this study because queens play a passive role in emigrations, and previous studies indicate that their number and type (or absence) has no observable influence on the emigration process (Cronin, 2012, 2015). This species shows no improvement in emigration performance over multiple emigrations, at least over the short term, although relocation performance can differ between colonies (Cronin, 2015). In addition, colony size varied between experiments in some cases because of mortality and new production of individuals, and thus both colony size and identity were included in analyses where appropriate.

### Colony Emigrations

Colonies must emigrate when nesting material (patches of moss, bases of ferns and soil) becomes unsuitable and during reproduction via colony fission. This process can be examined in detail in the laboratory by forcing ants to emigrate between artificial laboratory nests. Nest quality can be manipulated by modifying nest characteristics (Cronin, 2013a): ants prefer dark nests (with an opaque cover), for example, over light nests (with only a glass slide). Artificial nests in this study consisted of a circlet of foam 2 mm high with a 3 mm hole in one end covered with a 75 × 25 mm glass microscope slide (ants are ca. 3 mm long). Nests were placed in emigration arenas consisting of plastic boxes (10 × 10 cm and 3 cm high), with a floor of moist plaster, which were linked together via small holes (Fig. 1; see also Cronin, 2013b, 2015). To induce emigration in the laboratory, artificial nests were lifted from the plaster surface, exposing the colony without directly disturbing the ants. In this species, colony splitting during emigrations is extremely rare (Cronin, 2012, 2013b) and thus speed–cohesion trade-offs are of less importance than in some other species (e.g. Franks et al., 2013). In experimental trials, the relative value (quality) of available new nests was constant, and thus speed–value trade-offs were controlled for (Pirrone, Stafford, & Marshall, 2014; Seeley et al., 2012). All boxes were replaced after each emigration with ones that had been scrubbed clean and then allowed to dry for >24 h (pheromone trails in this species are effective for ~24 h; Cronin, 2013a). Colonies were selected from a pool of available colonies housed in the laboratory and randomly assigned to treatments except where certain criteria needed to be met (see experiment 2) in which case colonies were randomly selected from a subgroup fitting these criteria.



**Figure 1.** Experimental arenas of plastic boxes (10 × 10 cm and 3 cm high) with interconnecting holes and artificial nests constructed from foam rings atop standard microscope slides. Nests are indicated by small rectangles, with one nest randomly allocated as the preferred ‘dark’ nest (shaded). Colonies emigrated from a home nest (H), which was removed to initiate the emigration, to one of the new nests (1–4). In experiment 2, arenas were as similar as possible to permit comparison across treatments. Control and Stress trials used two-box/two-nest arenas (a) with a fan placed at F in Stress trials to blow air over the navigation chamber (N). For Complex trials, a two-box/four-nest arena (b) was used. In experiment 3, each environmental treatment had its own control. Stress trials and Stress controls used a two-box/one-nest arena (c) with a fan at F in Stress treatment trials. In experiment 3 Complex trials, treatments used a two-box/four-nest arena (d) while controls used a two-box/two-nest arena, with open spaces in place of nests at 3 and 4 (dotted lines). All nests in experiment 3 were uncovered ‘light’ nests.

Once colonies of *M. nipponica* are exposed through removal of the nest, ants begin a ‘search’ phase, during which scouts explore the available area for suitable nesting sites. When one of the ants locates a suitable site, the deliberative ‘assessment’ phase ensues, during which ants assess sites and ‘vote’ for favoured sites by laying pheromone trails, recruiting additional scouts which also independently assess the site. The assessment phase is the longest part of the emigration and lasts until a ‘quorum’ of individuals is at one new site (Cronin, 2012, 2013b; Sumpter & Pratt, 2009), as indicated by the first ant switching to brood transport. Colonies then enter a committed ‘transport’ phase, as more ants switch to transport and brood are rapidly transferred to the new site. Relocations were deemed completed when all brood had been moved to the new site. Colony splitting did not occur. Ants that made at least one visit to the new nest prior to the transport phase were classed as scouts and ants that carried at least one brood item to the new site were termed transporters. Any scout ant may switch to a transport role once it detects a ‘quorum’ of ants present at the new site. Quorum thresholds for individual ants were defined as the number of ants present in the new nest when the focal ant departed the nest to undertake its first brood transport. The quorum threshold for a given emigration event was calculated as the mean of the individual quorum thresholds for all ants switching to a transport role. Previous studies of ant emigration have employed an alternative method to estimate quorum thresholds by fitting emigration data

to a Hill function (e.g. Pratt, 2005; Sumpter & Pratt, 2009), as this provides a general means of modelling switch-like responses. For comparability with these studies, colony level quorum thresholds were also calculated using this approach by fitting emigration data to the function  $S = \frac{P^k}{T^k + P^k}$ , where  $S$  is the probability of switching to transport,  $P$  is the number of ants in the destination nest,  $T$  is the quorum threshold and  $k$  determines the nonlinearity of the response (see Pratt, 2005). This approach also served to verify that the switch in behaviour represented a quorum process as defined by Sumpter and Pratt (2009), in having a Hill parameter  $k$  of  $>2$ .

#### Experiment 1: Influence of Group Size on the Emigration Process

To assess how colony size influences the consensus decision and colony emigration process in *M. nipponica*, experiment 1 explored variation in task allocation, quorum threshold and emigration duration in colonies of different size. Emigrations were performed using 35 colonies of naturally varying size (range 8–73; mean  $30.2 \pm 15.4$ ), each performing one emigration. Emigration data were collated from earlier published studies of *M. nipponica* ( $N = 27$  emigrations; see Supplementary material) or emigrations newly performed for this study ( $N = 8$ ). In all cases emigrations used two navigable 10 × 10 cm boxes and a single new nest. As orientation of components differed slightly between experiments (Appendix Fig. A1), arena type was included as a possible explanatory factor in analyses. While in all cases a single new nest was provided, this does not remove the need for a decision to be made as ants can chose to nest anywhere in the nestbox (although artificial nests represent an outstandingly superior option). The duration of each phase, number of scouts and transporters and the quorum threshold for the emigration were quantified by tracking individually marked ants. Web-cameras (Elecom Ucam-DLA200H) positioned above the nest entrance were used in conjunction with the motion detection software iSpy ([www.ispyconnect.com](http://www.ispyconnect.com)) to track entry/exit events to/from available new nests. The identity and timing of individual ants entering and exiting the new nest(s) and transporting brood were scored manually from videos.

#### Experiment 2: Influence of Group Size and Environmental Context

To investigate the influence of colony size on decision accuracy, colonies were given the choice between a preferred ‘dark’ nest (with an opaque cover) and a ‘light’ nest (with only a glass slide; Fig. 1). To simultaneously investigate how environmental context might interact with colony size to influence decision making, three different environmental treatments were used (Fig. 1). Control emigrations were conducted under standard laboratory conditions to establish a baseline for the influence of colony size. Treatment 1 consisted of a Stress environment, which placed colonies in a time-critical environment by subjecting them to continuous gentle airflow generated by a small desk fan which clearly made ants uncomfortable and stimulated activity. Under this form of stress, emigration speed becomes emphasized as airflow heightens the risk of desiccation (see also Franks et al., 2003). Treatment 2 consisted of a complex environment, in which colonies were provided with four possible destination nests (one of which was a dark nest), generating a need to process a greater amount of information but without varying constraints on decision time. Treatments differed from the Control (Fig. 1a) only in the addition of two nests (Complex; Fig. 1b) or airflow (Stress; Fig. 1a). This experimental design allowed comparison between treatment groups as well as between treatments and controls, as results of experiment 1 (see below) suggest that small variation in arena size and shape (such as the increase in area resulting from the addition of the two nests in the Complex trials) do not influence relocation dynamics.

Colonies of naturally varying size were divided into roughly even groups of small (<20 ants), medium (20–34) and large (>34) colony size. The data set comprised a total of 211 emigrations (19–25 per treatment/size group) using 92 colonies (performing 1–3 trials each). Each colony performed a maximum of one emigration in each treatment and mean colony size within each size group did not differ across treatments ( $P > 0.186$  in all cases; see [Supplementary material](#)). Because colonies face a trade-off between decision speed and accuracy ([Franks et al., 2003](#)), both duration of emigrations and frequency of selecting the ‘correct’ (i.e. dark) nest were quantified. Colonies employed in multiple trials were rested for at least 4 days between trials. Ants were not marked.

### Experiment 3: Environmental Effects on the Consensus Decision Process

To elucidate how colonies adjusted decision-making behaviour to different environmental conditions, experiment 3 compared the performance of colonies in different environments by quantifying quorum thresholds in paired trials with individually marked ants. Colonies each performed one Control and one treatment (Stress or Complex) emigration in a random order. A total of 40 emigrations were performed, comprising 10 control/treatment pairs for each environment. Four colonies were used in both groups of trials (16 trials) while 12 additional colonies were used in one or other set of trials (24 trials). Colonies were not reused within 48 h of completing an emigration and were of average size ( $34 \pm 12$  ants; range 21–62; see [Supplementary material](#)). Quorum thresholds were quantified by fitting emigration data to a Hill function following [Pratt \(2005\)](#).

Because the focus of experiment 3 was a comparison of quorum thresholds between treatment and control conditions rather than among treatments, treatment–control pairs were independent and used different designs for each environment, and also differed to those used in experiment 2. Because of these differences, controls were conducted separately for both sets of trials and are thus not directly comparable between treatment groups. Stress trials were conducted with a single destination nest ([Fig. 1c](#)). In Complex trials, there was no ‘dark’ nest, to remove possible bias in emigrations to preferred or nonpreferred nests ([Fig. 1d](#)), and in Control runs for complex emigrations, open spaces (glass slides set on the plaster to form walls) were provided in place of nests 3 and 4 so that the total available navigable area was equal to the Complex treatment.

### Statistical Analyses

All analyses were performed in R version 3.1.2 ([R Core Team., 2014](#)). Mixed-effects models were implemented using the `lme4` package. Corrections for multiple tests were applied following [Benjamini and Hochberg \(1995\)](#). Results are given for comparison between models with and without the factor of interest using likelihood ratio tests (LRTs; [Pinheiro & Bates, 2000](#)).

Analyses of emigration dynamics (experiment 1) were conducted using mixed-effects models with colony size as a covariate and arena type as a random factor. In all cases duration data were square-root transformed and treated assuming normal errors with `lmer`, whereas numbers of scouts and transporters were treated assuming Poisson errors using `glmer`. Analyses of decision accuracy (experiment 2) were performed with `glmer` using a binomial response variable (selection of the dark or light nest) and assuming binomial errors, whereas analyses of log-transformed durations used `lmer` and assumed normal errors. In both cases size group (a factor of three levels as defined above) and treatment were

included as factors, with colony as a random factor. Separate tests within treatment or size group sets were conducted using generalized linear models (GLMs) and followed by Tukey tests.

The percentage of successes was also compared against a value of 50% (chance for two-nest trials in Stress and Control experiments) using exact binomial tests (success was compared to 50% for Complex trials despite the four nests for consistency with other trials). Quorum thresholds derived from fitting emigration data to a Hill function (see above) were compared between treatment–control pairs (experiment 3) using `glmer`, with colony size and treatment as factors, colony as a random factor, and assuming Poisson errors. Duration of relocations in experiment 3 were analysed using `lmer` on square-root transformed data assuming normal errors, including colony as a random factor to account for paired trials.

## RESULTS

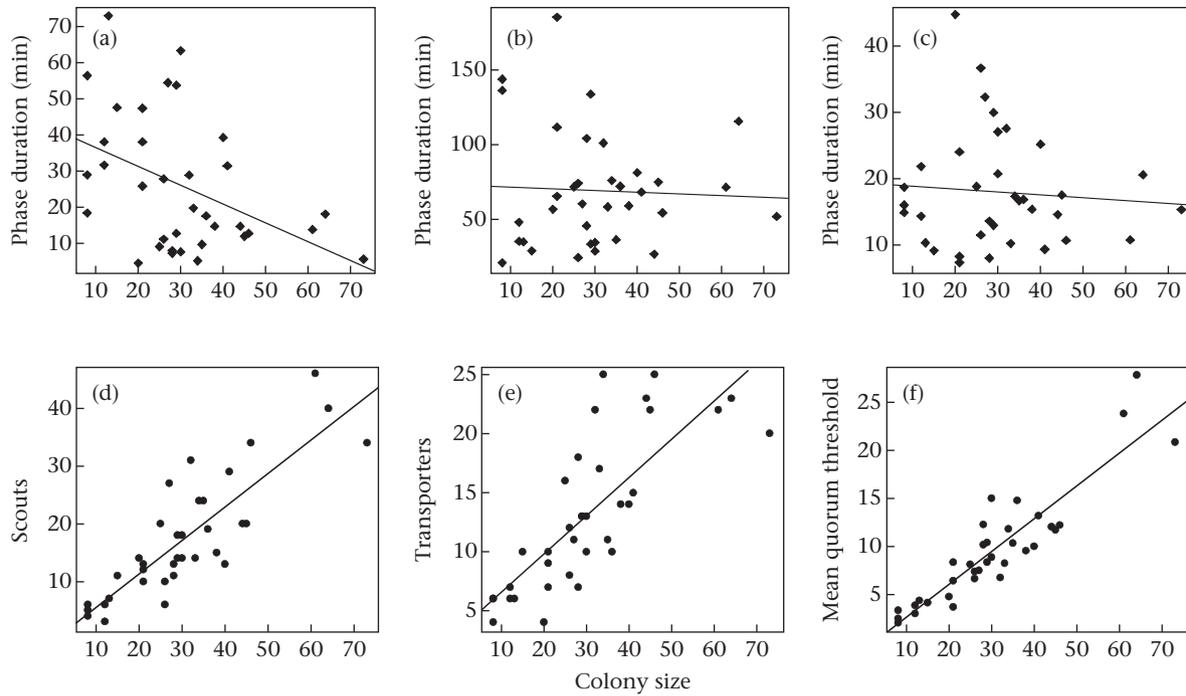
### Experiment 1: Influence of Group Size on the Emigration Process

The emigration process was remarkably similar in colonies of different size. Although larger colonies had shorter search times (LRT:  $\chi^2 = 7.22$ ,  $P = 0.007$ ), the same amount of time was spent in site assessment (LRT:  $\chi^2 = 0.007$ ,  $P = 0.94$ ) and brood transport (LRT:  $\chi^2 = 0.005$ ,  $P = 0.94$ ; [Fig. 2a–c](#)). Most of the emigration time was spent in the deliberative assessment phase (median 66%; range 26–84,  $N = 35$ ) whereas the discovery and transport phases were of comparable duration (17%, 4–62; 17%, 4–43), and overall duration of emigrations did not vary with colony size (LRT:  $\chi^2 = 2.08$ ,  $P = 0.15$ ).

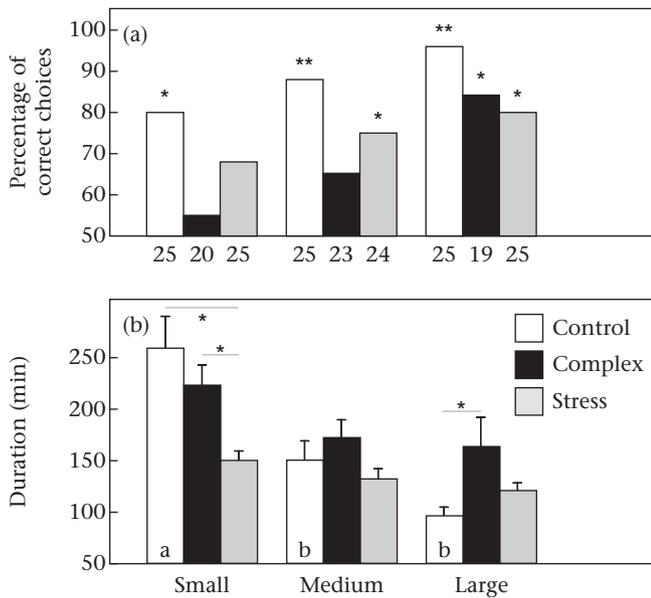
Larger colonies employed more scouts (LRT:  $\chi^2 = 143.3$ ,  $P < 0.001$ ; [Fig. 2d](#)) and transporting ants (LRT:  $\chi^2 = 52.7$ ,  $P < 0.001$ ; [Fig. 2e](#)), and also used higher quorum thresholds, whether these were calculated as the mean quorum thresholds of all switching ants (LRT:  $\chi^2 = 60.6$ ,  $P < 0.001$ ; [Fig. 2f](#)) or obtained after fitting data with a Hill function (LRT:  $\chi^2 = 33.973$ ,  $P < 0.001$ ), and indeed, these two measures were highly correlated (Pearson correlation:  $r = 0.89$ ,  $P < 0.001$ ; [Appendix Fig. A2](#)). The results of fitting data to a Hill function ([Appendix Fig. A3](#)) also support claims that *M. nipponica* uses a quorum-based decision process ([Cronin, 2012, 2013b](#)) in forming a highly step-like response, with a mean Hill parameter of 3.76 (thus exceeding the threshold of 2 for a quorum process; [Sumpter & Pratt, 2009](#)). There was no effect of the random factor (arena type) in any analysis ( $P > 0.35$  in all cases), indicating small differences in the size and shape of emigration arenas did not influence emigration dynamics.

### Experiment 2: Influence of Group Size and Environmental Context

Over all trials in experiment 2, larger colonies made more accurate decisions (LRT:  $\chi^2 = 7.15$ ,  $P = 0.028$ ) and decision accuracy differed between treatment groups (LRT:  $\chi^2 = 9.13$ ,  $P = 0.010$ ; [Fig. 3](#)). There was no interaction effect (LRT:  $\chi^2 = 1.22$ ,  $P = 0.874$ ). Analyses within each group indicated that there was no significant difference in success between treatments within each size group (Tukey test:  $P > 0.17$  in all cases) or between size groups within treatments (Tukey test:  $P > 0.14$  in all cases). However, whereas under Control conditions, colonies in all size groups had high accuracy ( $\geq 80\%$ ) and chose the correct nest significantly greater than half the time (i.e. chance for a two-nest choice; [Fig. 3a](#)), decision accuracy was notably lower under Complex and Stress treatments. As a result, only large and medium colonies selected the correct option significantly more than half of the time under Stress conditions, and large colonies alone did under Complex conditions.



**Figure 2.** Colony size versus phase durations and task allocation in experiment 1. (a) Duration of search phase, (b) duration of assessment phase and (c) duration of transport phase as a function of colony size; (d) scout and (e) transporter ant numbers as a function of colony size; (f) association between colony size and mean quorum thresholds. In all cases, each point represents one of a total of 35 emigrations under normal, benign laboratory conditions.



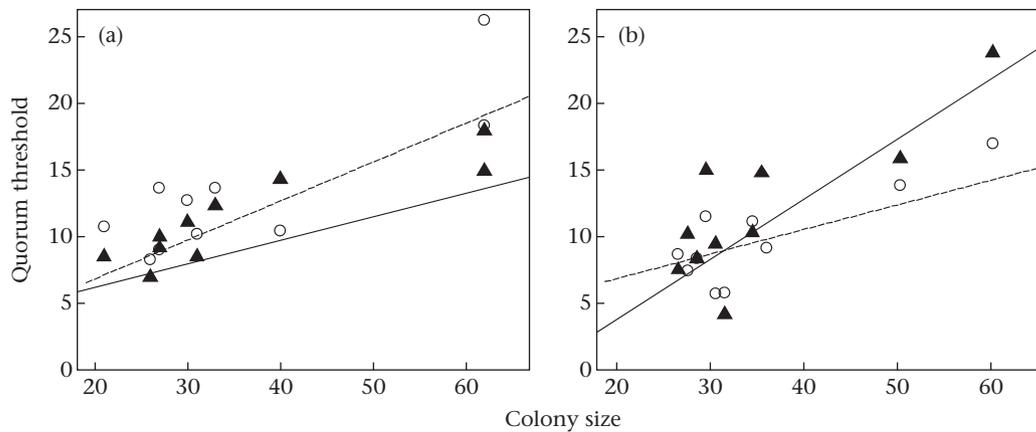
**Figure 3.** Influence of colony size on (a) decision accuracy and (b) decision speed under different treatment conditions in experiment 2. Treatment (environmental) conditions are indicated by shading: white = Controls; black = Complex; grey = Stress. Colony size is grouped into small (3–19 ants), medium (20–34 ants) and large (35+ ants). Asterisks in (a) indicate significant results of binomial tests against a value of 50% after corrections for multiple tests. Asterisks in (b) indicate differences between treatments within size groups as indicated by Tukey tests, whereas letters on bars indicate differences between size groups within treatments (those not shown were nonsignificant; see main text). \* $P < 0.05$ ; \*\* $P < 0.01$ . The number of emigrations is given below the bars in (a). Error bars in (b) indicate SD.

In addition to making more accurate decisions, larger colonies made faster decisions (LRT:  $\chi^2 = 28.97$ ,  $P < 0.001$ ), emigration duration varied between treatments (LRT:  $\chi^2 = 10.66$ ,  $P = 0.005$ ) and there was also a significant interaction between these factors

(LRT:  $\chi^2 = 15.70$ ,  $P = 0.003$ ; Fig. 3b). Stress emigrations were faster than Complex emigrations overall (Tukey test:  $P = 0.003$ ), but neither treatment differed from Controls (Stress:  $P = 0.207$ ; Complex:  $P = 0.241$ ). Post hoc tests within treatments indicated that medium (Tukey test:  $P = 0.003$ ) and large ( $P < 0.001$ ) groups were faster than small groups but only under Control conditions (other comparisons all  $P > 0.067$ ). Within size groups, Stress relocations were faster than Control (Tukey HSD:  $P < 0.001$ ) and Complex ( $P = 0.012$ ) emigrations in small colonies, while there was no difference between treatments for medium colonies ( $P = 0.735$ ). In large colonies, Stress emigrations were no faster than Controls ( $P = 0.252$ ), and Complex emigrations were slower than Controls (Tukey HSD:  $P = 0.011$ ), possibly indicating a coordination cost to larger groups under more challenging conditions.

*Experiment 3: Environmental Effects on the Consensus Decision Process*

Ants used lower quorum thresholds (as obtained by fitting emigration data to a Hill function) under Stress conditions than in Controls (Fig. 4;  $\chi^2 = 6.55$ ;  $P = 0.038$ ), while the opposite pattern (higher quorums) was observed under Complex conditions (although in this case it was marginally nonsignificant; LRT:  $\chi^2 = 5.64$ ;  $P = 0.059$ ). Larger colonies in both cases used higher quorum thresholds than smaller colonies (LRTs:  $\chi^2 = 16.73$ ,  $P < 0.001$  for Complex and  $\chi^2 = 20.91$ ,  $P < 0.001$  for Stress). In addition, there was a pattern of larger colonies modifying their absolute quorum threshold in response to the change in environmental conditions to a greater degree than smaller colonies, although this was significant in only one of two cases (LRT for the interaction effect for Complex:  $\chi^2 = 1.84$ ,  $P = 0.175$ ; and Stress:  $\chi^2 = 5.81$ ,  $P = 0.016$ ). This pattern supports previous work indicating that the quorum quantification abilities of ants follow Weber's law (Cronin, 2014), and thus a greater absolute change is required to be detectable in larger colonies. Scout and transporter



**Figure 4.** Scatterplot showing the influence of (a) Complex and (b) Stress environments on quorum thresholds obtained by fitting emigration data to a Hill function in experiment 3 in relation to colony size. Control conditions are indicated by open circles and solid lines whereas treatment conditions are indicated by black triangles and broken lines.

numbers were not significantly different between treatments in either case (LRT:  $P > 0.27$ ).

## DISCUSSION

Larger colonies of house-hunting *M. nipponica* made more accurate decisions than small colonies and did so more rapidly, demonstrating that ant colonies can benefit from a ‘wisdom of the crowds’ effect when selecting among new nest sites. Similar benefits to larger groups have been demonstrated in a wide range of taxa and tasks: birds navigate more accurately (reviewed in Faria, Codling, Dyer, Trillmich, & Krause, 2009), fish more frequently avoid predators (Ward, Herbert-Read, Sumpter, & Krause, 2011) and better track the environment (Berdahl et al., 2013), honeybee swarms make more accurate decisions over new nest sites (Schaeff et al., 2013), bats benefit from foraging collectively (Cvikel et al., 2015) and passerines show a higher rate of innovation and efficiency in problem solving (Liker & Bókony, 2009; Morand-Ferron & Quinn, 2011). Most studies, however, have been limited to a single decision-making context (but see Sasaki et al., 2013 for a demonstration of the differential abilities of individuals and groups in a dynamic context), whereas models predict that environmental conditions can alter or even invert the group size advantage (Kao & Couzin, 2014; Schaeff et al., 2013). This study demonstrates that larger groups maintain an advantage in decision accuracy in a range of environments. None the less, while small groups had comparable decision accuracy to larger groups under benign conditions, they could not make effective choices in more challenging environments, indicating that the advantages of group size can indeed be environmentally contingent.

The advantage to larger colonies in decision accuracy probably stems from the fact that they are able to field more scouts and use higher quorums, allowing them to collect and collate more information than smaller colonies in the same period of time. Emigrations unfolded in much the same way across a range of colony sizes, and this can be explained by the fact that although larger colonies employ more scouts, they also use higher quorum thresholds, and therefore the same amount of time is required to reach a quorum decision. Similarly, the increase in transporter ants with group size balances the fact that larger colonies have more brood to move (Cronin, 2012), and these results reflect patterns observed in other emigrating ants (Dornhaus & Franks, 2006; Franks, Dornhaus, Best, & Jones, 2006). Quorum responses represent a form of switch, allowing group level decisions to be made while maintaining group cohesion and simultaneously filtering out individual errors.

Quorum building results from recruitment by individual ants ‘voting’ for favoured sites, and in this sense resembles a competition among candidate sites for achievement of a quorum (Pratt, 2010). We might thus expect a link between quorum thresholds and colony size, because increasing quorum thresholds without increasing the number of scouts could result in no decision, while the reverse could lead to a premature and inaccurate decision (Conradt & Roper, 2005; Franks et al., 2006). Thus, under benign conditions, although more scouts can reduce search time in larger colonies, assessment time is similar because it is moderated by the quorum threshold. Higher quorum thresholds allow collection of more information, however, and this can lead to more accurate decision making.

The results of this study align with previous studies indicating that colonies respond to environmentally induced urgency by using lower quorum thresholds to emphasize speed over accuracy (Dornhaus et al., 2004; Franks et al., 2009, 2003; Passino & Seeley, 2006). This ‘any port in a storm’ response may be useful when finding shelter rapidly is more important than finding the optimal nest. As these ants nest in impermanent substrates such as moss clumps and fern stems in areas subject to flooding, such emergency evacuations are likely to occur from time to time. In addition, data presented here indicated a pattern of increased quorum thresholds in response to environmental complexity. Increased quorums could lend colonies an enhanced capacity to collect and collate information in environments with higher processing demands (such as that represented by multiple candidate nest sites), or could serve as a response to an increased risk of colonies splitting among multiple candidate sites. However, such a response is likely to come at a cost to the colony as ants that are scouting cannot perform other tasks such as brood care.

This study used unmanipulated colonies that naturally differed in size, and in doing so assumes that the goal of emigrating colonies does not change with colony size. This assumption seems valid in that it is unlikely that colonies of different size differ in preference between light and dark nests, whereas other characteristics such as nest size are more likely to be colony size dependent (e.g. Pratt & Pierce, 2001; but see Seeley, 1977). However, as some authors have noted, group size can be confounded with additional parameters such as age and experience (Dornhaus, Powell, & Bengston, 2012). None the less, group size appears to have clear and pronounced effects on the decision-making process in *M. nipponica* (Cronin, 2013b, 2014; Cronin & Stumpe, 2014) and, while studies of other species have demonstrated an influence of experience on nest emigration in some contexts (e.g. Langridge, Franks, &

Sendova-Franks, 2004), the available evidence indicates no such effect in *M. nipponica* (Cronin, 2015). Finally, manipulating colony size produces artificial entities by altering group composition, and this may have unpredictable effects on how highly integrated processes such as consensus decision making unfold. For example, while there is evidence for individuals outperforming groups in humans (Clément et al., 2013; Krause et al., 2011) and ants (Sasaki et al., 2013), the response of isolated individuals in obligately social animals may not be directly comparable to groups because isolation is an unusual context, and the mechanics and accuracy of decision making are likely to be state dependent (Fischer, Bessert-Nettelbeck, Kotrschal, & Taborsky, 2015; Schuck-Paim, Pompillo, & Kacelnik, 2004).

The consistent decision-making benefit to larger groups demonstrated here contrasts with the variation in relative performance of groups and individuals in *Temnothorax* ants with changes in decision context (Sasaki et al., 2013), although as the authors of that study noted, this can be ascribed to differences in the manner in which decisions in groups and individuals are achieved. This pattern also contradicts models that predict that smaller groups may be advantaged in more complex environments because environmental information obtained by different individuals is frequently correlated, eroding the advantage generated by information diversity in the wisdom of the crowds effect (Kao & Couzin, 2014). This suggests that the decision-making strategy employed by these ants is robust to the risks of negative information cascades and correlated information (Kao & Couzin, 2014; Sasaki et al., 2013), possibly in part because ants prefer private information over social information (Cronin, 2013a). A large part of the advantage to large groups appears to be derived from their greater capacity to adapt to more challenging conditions, and this may be because the greater information collection and processing capacity of the larger workforce buffers them from the effects of more challenging environments. This group level advantage may be augmented by adaptive strategies employed at the individual level. For example, solitary fish and those in smaller groups move slower than those in larger groups when faced with a choice of direction (Ward et al., 2011), which may allow them to collect more information about their environment before making a decision. Similarly, individual *Temnothorax* ants move faster or recruit sooner when emigrating to new nests of higher relative value (Doran et al., 2015). Cronin and Stumpe (2014) showed that ants in small colonies of *M. nipponica* work harder than those in larger colonies during the process of consensus decision making, and suggested this may allow small colonies to ameliorate the costs of small group size in decision making through increasing per capita information and thus the total information pool. There is some support for this idea in this study, as under benign conditions, small colonies were able to maintain decision accuracy comparable to large colonies. However, as noted by Cronin and Stumpe (2014), this capacity to increase individual effort is likely to be limited, and this may help explain the relatively poor performance of smaller colonies under more challenging conditions. The findings presented here have implications for weighing the virtues of democratic versus despotic leadership, because even though despotic decisions may be favourable in some contexts (Conradt & Roper, 2007; Katsikopoulos & King, 2010) consensus-based decisions may be more robust in dynamic environments because they can buffer against environmental heterogeneity.

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## Supplementary Material

Supplementary material for this article, consisting of an excel file containing emigration metrics for all experiments, is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.06.010>.

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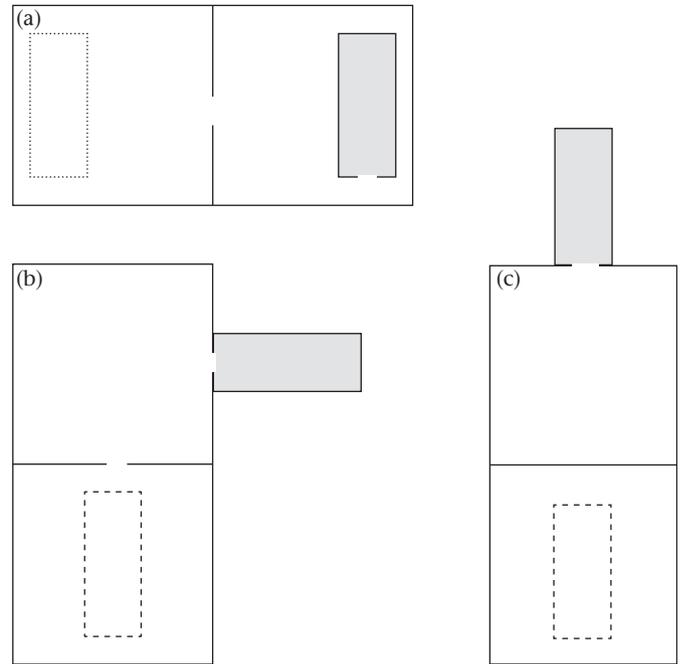
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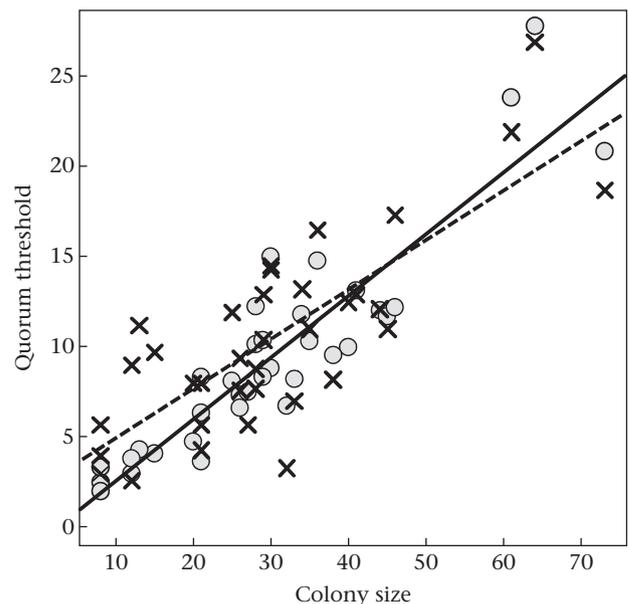
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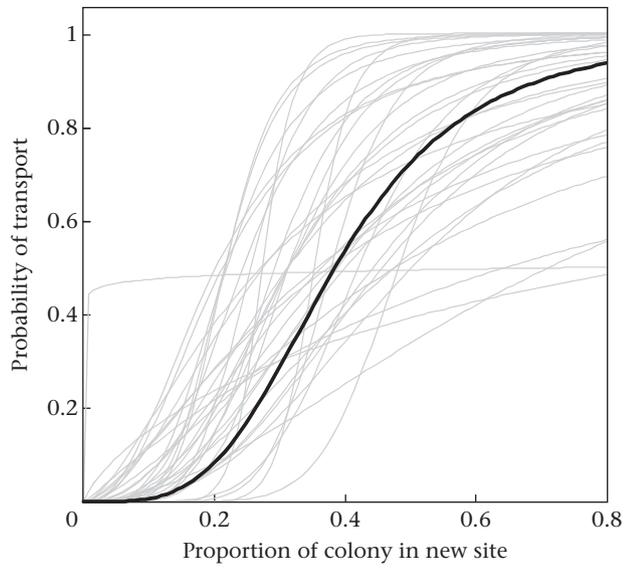
## APPENDIX



**Figure A1.** Different types of arena used in experiment 1. Dashed lines indicate sites of home nests (removed) whereas shaded areas indicate sites of new nests. Different arenas were used in different studies: (a) Cronin (2012); (b) Cronin (2015), Cronin (2014; experiment 5) and this study (Stress controls in experiment 3); (c) Cronin and Stumpe (2014).



**Figure A2.** Relationship between different measures of quorum threshold and colony size in experiment 1. Correlation between colony level quorum thresholds as fitted to a Hill function (crosses and dashed line) and calculated as the means for individual switching ants (grey circles and the solid line). Each point represents a single emigration.



**Figure A3.** Hill function plots for 35 emigrations by colonies in experiment 1 (grey lines) and plot for mean parameters over all colonies (thick black line). Emigration data were fitted to a Hill function following Pratt (2005; see also main text). Mean parameters were  $k = 3.67$  and  $Q = 38.5$ , where  $Q$  is the quorum threshold as a proportion of colony size.