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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.

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; Conradt & 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 (Conradt & Roper, 2005; Sumpter & Pratt, 2009). Consensus decisions underlie a suite of actions in a wide range of species (reviewed in Conradt & 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 (Conradt & Roper, 2005; King & Cowlishaw, 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.