# Ratio-dependent quantity discrimination in quorum sensing ants

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**Abstract** To optimise behaviour, organisms require information on the quantity of various components of their environment, and the ability of animals to discriminate quantity has been a subject of considerable recent interest. This body of research hints at generalised mechanisms of quantity discrimination in vertebrates, but data on invertebrates are still relatively scarce. In this study, I present data on the quantification abilities of an invertebrate in a novel context: quorum sensing. Quorum sensing generates a behavioural response in group-living animals once a threshold number of individuals, a 'quorum', is detected performing some key action. This process forms the basis for consensus decision-making in many species and allows group-living organisms to decide among mutually exclusive alternatives without compromising group integrity. To determine when a quorum is achieved, individuals must assess the number of group members performing the key action. Social insects employ quorum decisions to decide among potential nest sites when searching for a new home. In the Japanese ant, *Myrmecina nipponica*, quorum thresholds increase with colony size, providing an opportunity to assess the accuracy of quantity discrimination at different stimulus magnitudes. In this study, I demonstrate that the variation in individual quorum thresholds around the mean increases with increasing colony size. This indicates that the quantity discrimination ability of ants decreases with stimulus magnitude, and thus exhibits ratio dependence in the manner of Weber's Law. This may have implications for the accuracy of consensus decision-making and other collective actions in a range of group-living organisms.

**Keywords** Quorum sensing · Formicidae · Ant · House-hunting · Weber's law

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## Introduction

The optimisation of behaviour is dependent on the available information, an essential component of which is quantity. Animals frequently base decisions governing their behaviour on the number of predators, prey, potential mates, group members, or food items. The ability to discriminate quantity is thus integral to optimising behaviour in a variety of contexts (e.g. McComb et al. 1994; Agrillo et al. 2009; Aïn et al. 2009; Nelson and Jackson 2012). Studies of numerical competence originated in studies of humans and non-human primates and have only relatively recently expanded to other animals (e.g. Meck and Church 1983; Church and Meck 1984). Evidence for numeracy now exists for a range of vertebrate taxa (Meck and Church 1983; Agrillo et al. 2009; Aïn et al. 2009; Krusche et al. 2010; Bogale et al. 2011) and is suggestive of a common mode of numerical assessment across vertebrates (Feigenson et al. 2002; Agrillo et al. 2009; Brannon et al. 2010). Less is known about the capacity for numerical assessment in invertebrates, though recent studies have hinted at sophisticated abilities of quantity estimation in several species (Chittka and Geiger 1995; Wittlinger et al. 2006; Dacke and Srinivasan 2008; Gross et al. 2009; Reznikova and Ryabko 2011; Carazo et al. 2012; Nelson and Jackson 2012). Honey bees, for example, exhibit the capacity to

count landmarks and use this as a navigational aid (Chittka and Geiger 1995; Dacke and Srinivasan 2008) and can determine the number of elements in a visual pattern (Gross et al. 2009). Mealworm beetles are able to assess the number of potential mates (Carazo et al. 2009) and competing males (Carazo et al. 2012), and bumble bees can assess the duration of elapsed time (Boisvert and Sherry 2006). Given that invertebrates experience many of the same contexts as vertebrates in which quantification is likely to be beneficial (Carazo et al. 2009), it is perhaps unsurprising that their abilities of quantity discrimination are on par. We might thus expect broadly generalised mechanisms of numeracy across the animal kingdom.

All animals are thought to possess at least two independent mechanisms of numerical assessment (Agrillo et al. 2009; Krusche et al. 2010). The first of these, subsidisation, describes the spontaneous awareness of differences between small quantities and is typically limited to very low numbers (3–4), whereas the second, analogue magnitude discrimination, enables estimation of larger relative quantities (Gallistel and Gelman 2000; Nelson and Jackson 2012). This latter mechanism is characterised by ratio-dependence, and thus exhibits scalar variability (Feigenson et al. 2002; Jordan and Brannon 2006; Brannon et al. 2010), a phenomenon described by Weber's law, which states that the threshold of discrimination ('just distinguishable difference') between two stimuli is a function of their ratio, and thus increases with stimulus magnitude (Gibbon 1977; Gallistel and Gelman 2000; Feigenson et al. 2002). For example, if an animal is able to distinguish the difference between 8 and 10 objects (a distinguishable difference of ≥2), the same animal would be able to discriminate between quantities of 16 and 20, but not 16 and 18. Ratio dependence has been found in a wide range of taxa, and to apply to a range of perceptions, including tactile stimulus (Weber 1834), visual quantification of number (Emmerton and Renner 2006; Jordan and Brannon 2006; Buckingham et al. 2007; Baker et al. 2011; Bogale et al. 2011), auditory discrimination (Augustin and Roscher 2008), task repetition (Fetterman and Killeen 2010), sucrose concentration (Nachev et al. 2013), visual contrast (Scholtyssek and Dehnhardt 2013), and abstract concepts such as the estimation of price (Dehaene and Marques 2002). Ratio dependence also applies to quantification of group size. For group-living species, adaptive tuning of group size is important because group size is frequently linked to fitness (e.g. Cockburn 1998; Clutton-Brock 2002; Luque et al. 2013). An ability to quantify or estimate the number of individuals in the group is thus essential for optimisation of group size. Lions and primates make conflict-based decisions based on relative group size (McComb et al. 1994; Kitchen 2004), while the ability of fish to select the larger of two shoals depends on the ratio

between them rather than their absolute size (Buckingham et al. 2007; Gómez-Laplaza and Gerlai 2011). Insects are paragons of social behaviour and group living, and thus might be expected to exhibit group-size quantification abilities that parallel the range of sophistication of their social systems. Ratio-dependent quantity discrimination in social insects could have implications for the performance of a range of collective actions which require tracking quantities in order to optimise behaviour, such as resource allocation during colony fission, the coordination of foraging, and consensus decision-making.

Group-living organisms in a wide range of taxa must make behavioural decisions that affect the entire group while maintaining group cohesion. This is often achieved via a decentralised process known as a consensus decision-making, in which a group response emerges as the product of the actions of multiple individuals (Sumpter and Pratt 2009). Consensus decisions frequently employ a 'quorum' mechanism, whereby the probability of an individual undertaking an action increases markedly once a threshold number of individuals is already performing that action. Honey bees, for example, will initiate swarming once 10–15 scouts are in a single location (Visscher 2007). Quorum thresholds can be adjusted to suit environmental conditions (Franks et al. 2009) and are in at least some cases proportional to group size (Dornhaus and Franks 2006; Cronin 2013b). Being able to adaptively quantify the number of individuals present is thus integral to effective quorum decisions. Several species of social insects serve as model systems for studies of consensus decision-making, and studies often make use of the site selection process during house-hunting, in which bees and ants employ a quorum process to decide among new sites (Visscher 2007; Pratt 2010). Colonies that find themselves without a suitable home send out scouts to find a new location. These scouts 'vote' on available sites by recruiting nestmates to their favoured site. Once the number of scouts at one site reaches a threshold, a quorum is achieved. This triggers a phase shift, and individuals rapidly undergo a behavioural switch to conclude the relocation. The quorum threshold marks the critical number of individuals required to bring about the change of behaviour for that focal individual. To sense when a quorum has been achieved, individuals must compare the currently perceived quantity of individuals present to some internal quorum target threshold at which a behavioural change will be triggered. This judgement of when a target level has been achieved may be subject to error in discrimination ability in a ratio-dependent manner, leading to increasing individual error in the accuracy of judging the quorum point as the size of the quorum increases. This may influence the accuracy of consensus decision-making if individual choice is not entirely independent. That is, if first choices are erroneous, subsequent

**Table 1** Source of data collated for this study

| Experiment | Colonies used | Mean colony size | Relocations performed | New nests provided | Citation |
|---|---|---|---|---|---|
| 1 | 20 | 33 | 20 | 1 | Cronin (2012) |
| 2 | 10 | 30 | 10 | 2 | Cronin (2012) |
| 3 | 6 | 38 | 6 | 1 | Cronin (2013b) |
| 4 | 6 | 26 | 9 | 1 | Unpublished |
| 5 | 3 | 8 | 3 | 1 | Unpublished |
| 6 | 5 | 27 | 5 | 1 | Unpublished |
| 7 | 6 | 32 | 6 | 2 | Unpublished |
| 8 | 6 | 29 | 17 | 1 | Cronin (2013b) |
| 9 | 6 | 39 | 6 | 1 | Cronin (2013b) |
| 10 | 6 | 29 | 6 | 2 | Unpublished |

Listed are the experiment from which data were sourced (see below); number of colonies used in each case; mean number of ants in colonies used; number of relocations performed; and whether or not there was a choice of new nests. Citations are provided for published studies and details for individual relocations are provided in the supplementary material. All relocations were conducted in standard conditions. Relocation experiments were: (1) simple relocation baseline study; (2) baseline relocation with choice of nests; (3) control relocations for tests of pheromone trails on choice; (4) detailed examination of individual effort during standard relocations; (5) basic relocations conducted specifically for small colonies; (6) first relocations of several sequentially conducted for analyses of learning; (7) control relocations for influence of stress tests; (8) split and whole colonies in colony size versus quorum tests; (9) long-distance relocations in short- versus long relocation tests; (10) relocations with choice among nests of different quality. In total, 40 colonies were used for 88 relocations. Some colonies were used in multiple experiments, but each was used only once within any given experiment, and thus, 'colonies used' is equivalent to relocations performed. See the supplementary material for more detail on each relocation

choices may follow this lead and result in a sub-optimal outcome in the manner of an information cascade (Giraldeau et al. 2002; Cronin 2013a).

Previous studies of the Japanese small-colony ant, *M. nipponica*, have indicated that larger colonies employ higher quorum thresholds (Cronin 2012, 2013b), providing an opportunity to investigate if ant's assessment of the quorum point is also subject to ratio dependence as predicted by Weber's law. In this study, I collate quorum threshold data from multiple *Myrmecina* house-hunting studies to analyse the influence of quorum threshold (stimulus strength) on variation in thresholds within colonies (discrimination accuracy) and demonstrate that this ability is ratio dependent.

## Methods

### Colonies used in experiments

*Myrmecina nipponica* is a small-colony ant found in wet temperate forests throughout Japan. Colonies consist of approximately 20–40 ants with one winged queen or one or more ergatoid (worker like) queens (Miyazaki et al. 2005). Colonies were collected from near Chitose, Hokkaido, Japan, between 2011 and 2013 and housed in standard laboratory conditions. This species can be kept easily in artificial colonies ($10 \times 10 \times 3$ cm plastic boxes floored with plaster) and induced to relocate to a new nest by

removal of its present nest. For details on general methods, collection and maintenance of colonies see (Cronin 2012, 2013b).

### Data collation

Quorum threshold data from experiments on colony relocation behaviour in *M. nipponica* were collated from several recent studies (see Table 1 for details). All relocations were conducted in similar conditions: colonies were presented with one or two possible new nest sites in identical nesting boxes connected via small holes (Fig. 1) and had their nest in the source box removed. During these studies, two types of relocations were performed; those in which ants relocated to a single new nest and those in which ants had a choice between two possible new nests. In this study, I combine these data and include 'choice' as a possible explanatory factor in analyses. A total of 40 colonies were used for 88 relocations.

### Consensus decisions via quorum

During the house-hunting process, scout ants (approximately 50 % of the colony; Cronin 2012) travel repeatedly between the new site and the site of the former nest. Brood transport to the new site does not begin until a consensus decision has been reached, and this occurs only once a quorum of ants is present at the new site (Cronin 2012, 2013b). Once a quorum has been achieved, behaviour
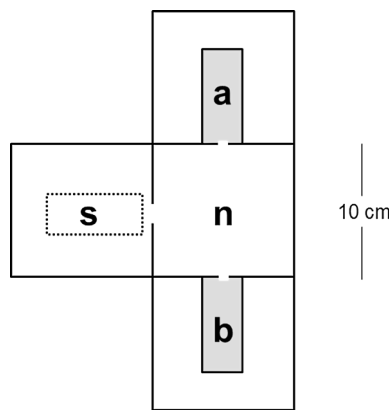
**Fig. 1** Example of typical experimental arena, showing orientation of the source box and location of original source nest (*s*), navigation box (*n*), and destination boxes containing new nests (*a* and *b*). In choice trials, both *a* and *b* boxes were included, while in non-choice trials, only one option was provided

rapidly shifts as formerly scouting individuals begin to transport brood to the new site, concluding the relocation. The quorum threshold for each ant is defined as the number of ants present at the destination site at the time the focal ant departs the site to undertake its first brood transport. Quorum thresholds were determined for all individual ants switching to transportation by video tracking the behaviour of individually marked ants using web-cameras positioned above nest entrances (see Cronin 2012, 2013b). This permitted quantification of the number of ants present in the new nest, and individual entry and exit events including brood transport. The number of switching ants (those detecting a quorum of ants present and switching from scouting to brood transport) in each relocation ranged from 3 to 24 (mean ± SD: 10.6 ± 5.3) and was correlated with colony size (Pearson's correlation: $r = 0.55$, $P < 0.001$). Late-arriving individuals are a potential source of bias, because the number of ants present may greatly exceed their internal quorum target threshold. To account for this, quorum thresholds were used from only the first half of all switching ants in each relocation (with fractional divisions rounded up), following Cronin (2013b). The final dataset comprised quorum threshold data from 483 switching ants.

Weber's law states that the minimum distinguishable difference between two quantities is proportional to the magnitude of the stimulus. This is summarised in the expression $\Delta a/a = k$, where $\Delta a$ is the 'just distinguishable difference' in a stimulus of magnitude $a$ and $k$ is a constant, the Weber fraction (Augustin 2008, 2009). With respect to quorum sensing, a constant Weber fraction is represented by increasing variation in quorum thresholds among individual ants with increasing mean quorum threshold. Weber fractions for each relocation were calculated as the average absolute difference (AAD) in individual quorum thresholds

from the arithmetic mean for that relocation, divided by the mean.

Statistical analysis

Data were analysed in R version 3.0.2 (R Core Team 2013) using mixed effects model procedures (*lme*). As some colonies were used in repeated trials, colony was included as a random factor. Data were in all cases log + 1 transformed to fit the assumptions of normality following examination of plots of residuals. Full models were applied initially and reduced in a stepwise manner until the minimal adequate model was obtained following Zuur et al. (2009). Final model selection was based on plots of residuals and assessment of Aikake information criterion and included only colony size and choice as factors. Regression lines provided in figures are for simple linear regressions and serve only to illustrate trends.

## Results

Quorum thresholds and colony size

There was a strong positive relationship between colony size and the mean quorum threshold (Fig. 2; $t_{46} = 7.173$, $P < 0.001$). In addition, in relocations in which colonies were provided with a choice of new nests, there was a suggestion that the mean quorum threshold was higher than
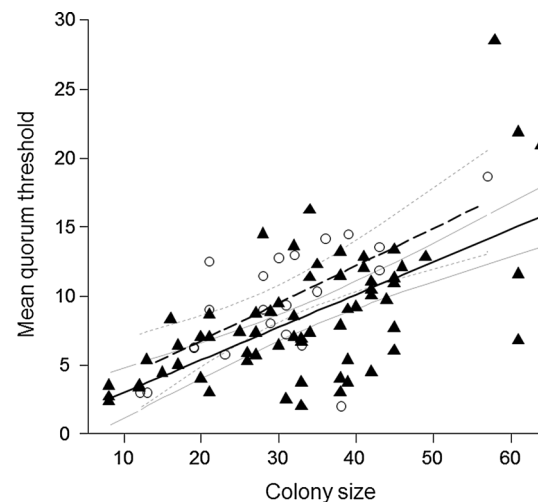


**Fig. 2** Relationship between colony size and mean quorum threshold over 88 relocations. *White circles* and the *dashed line* indicate relocations with a choice between two new nests ($r^2 = 0.43$; $n = 22$), whereas *black triangles* and the *solid line* indicate relocations to a single new nest ($r^2 = 0.43$; $n = 66$). Confidence intervals (95 %) are indicated by *solid* and *dashed grey lines*, respectively
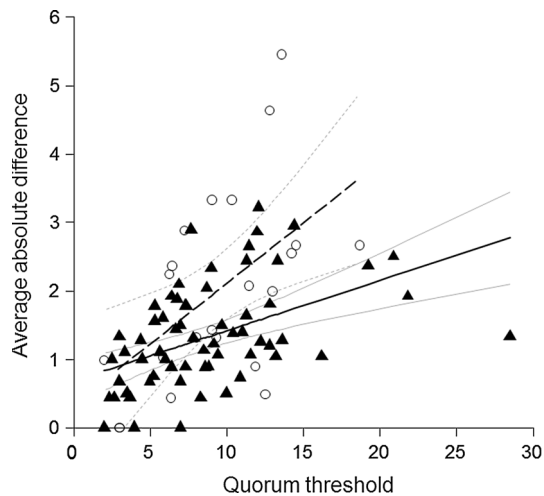
**Fig. 3** Relationship between average absolute difference between individual quorum threshold and mean quorum threshold. *White circles* and the *dashed line* indicate relocations with a choice between two new nests ($r^2 = 0.25$), whereas *black triangles* and the *solid line* indicate relocations to a single new nest ($r^2 = 0.22$). Confidence intervals (95 %) are indicated by *solid* and *dashed grey lines*, respectively

in relocations in which only a single new nest was provided ($t_{46} = 1.996$, $P = 0.0519$).

### Variation in quorum thresholds with colony size

Weber's law predicts that the minimum detectable difference in a signal increases proportionally with the signal strength. Thus, as quorum threshold increases, we would expect increasing variation in individual quorum
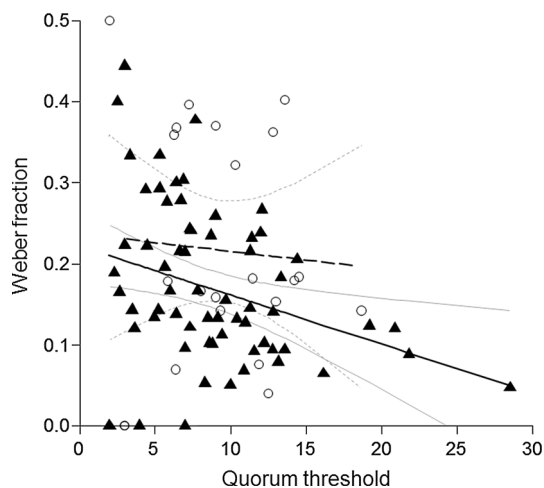


**Fig. 4** Relationship between Weber fraction and mean quorum threshold. *White circles* and the *dashed line* indicate relocations with a choice between two new nests ($r^2 = 0.05$), whereas *black triangles* and the *solid line* indicate relocations to a single new nest ($r^2 = 0.08$). Confidence intervals (95 %) are indicated by *solid* and *dashed grey lines*, respectively

thresholds. The AAD in quorum thresholds increased with the mean quorum threshold as expected from Weber's law ($t_{46} = 5.321$, $P < 0.001$; Fig. 3), and this effect was more marked in relocations involving a choice between two new nests ($t_{46} = 2.048$, $P = 0.0463$).

### Quorum sensing and ratio dependence

Strictly speaking, the property of scalar variance requires that the variation around the mean vary linearly with the mean, and thus we would expect the Weber fraction to remain constant with increasing stimulus magnitude. However, Weber fractions for quorum thresholds declined with increasing mean quorum threshold ($t_{46} = -2.074$, $P = 0.0437$; Fig. 4). There was no effect of choice ($t_{46} = 1.736$, $P = 0.0892$).

## Discussion

The above data demonstrate a clear positive association between quorum threshold and colony size in *M. nipponica*. Thus, scout ants from large colonies visiting potential new nest sites must quantify larger groups of nestmates to assess whether a quorum has been achieved. The average difference between individual and mean quorum thresholds varies in a ratio-dependent manner, such that this difference increases with colony size (and thus quorum size). This suggests ants are employing an analogue magnitude mechanism to quantify the number of nestmates present (Feigenson et al. 2002; Brannon et al. 2010), and this variation results from stimulus-magnitude-dependent limitations on the ants ability to discriminate quantity (i.e. Weber's law). The observed pattern could also stem from greater variation between nestmates in individual internal quorum target thresholds in larger colonies. However, this is unlikely for the following reasons. Firstly, studies of this and other species have shown that ants are able to tune quorum thresholds to different environmental contexts (Franks et al. 2009; Cronin 2013b). Individuals can thus modify their internal target threshold and do so to optimise collective behaviour in an adaptive manner. It seems unlikely that subtle changes such as this would be possible if there was marked variation among nestmates internal target thresholds. Secondly, although individual variation could be derived from colony-size-related differences in genetic diversity, *M. nipponica* is monandrous and monogynous (or functionally monogynous in ergatoid colonies; Ohkawara et al. 1993; Murakami et al. 2000), and thus genetic variation is unlikely to increase with colony size in a consistent manner. The observed patterns could also be linked to an experience effect, in that large colonies are more likely to contain individuals with a broader

distribution of experience (Dornhaus et al. 2009). However, *M. nipponica* colonies in which colony size has been artificially manipulated perform relocations in an equivalent manner to unmanipulated colonies; quorum thresholds are adjusted proportionately to colony size, but there is no observable influence of experience (Cronin 2013b; Cronin and Stumpe unpub.). Thus, the most parsimonious explanation is that the increasing variance is a result of discrimination errors on the part of individual ants.

Weber's law predicts that the minimum detectable difference between two reference values will be a constant proportion of the stimulus magnitude (Gibbon 1977; Augustin 2009). As a result, a plot of Weber fractions versus stimulus magnitude will be a line with a slope of zero. In quorum sensing *Myrmecina*, the Weber fraction was a declining function of quorum threshold, indicating that larger colonies outperformed small colonies with respect to the expectations of Weber's law. Decreasing Weber fractions with increasing stimulus magnitude are commonly found in auditory discrimination (e.g. Augustin and Roscher 2008), and a similar trend has been shown for brightness discrimination in seals (Scholtyssek and Dehnhardt 2013). Furthermore, Nachev et al. (2013) reviewed previously published data on discrimination of sugar concentration in various animal and showed that whereas the magnitude effect was less than that predicted by Weber' law in bees, the opposite trend was observed in several vertebrates. Deviations from zero slope have been accommodated for by a range of modifications to Weber's law (Augustin 2009). However, recent reviews suggest that the relationship between stimulus intensity and discrimination ability may only rarely conform to the constant ratio specified in Weber's law and is probably in most cases a more complex function that varies in a species-and-ecological-context-specific manner (Masin 2009; Nachev et al. 2013).

The question of whether or not invertebrates can 'count' has received considerable attention in recent years (Chittka and Geiger 1995; Wittlinger et al. 2006; Dacke and Srinivasan 2008; Gross et al. 2009; Reznikova and Ryabko 2011; Carazo et al. 2012; Nelson and Jackson 2012). These studies have indicated that at least some invertebrates possess sophisticated methods of assessing quantity. While in some cases, it remains unclear if individuals are using true counting or instead basing assessments on summation of correlated continuous information (Franks et al. 2006b; Agrillo et al. 2011), recent studies controlling carefully for the latter have demonstrated that counting or 'proto-counting' is certainly possible in some species. For example, honey bees (*Apis mellifera*) can distinguish between numerically different sets of objects (Gross et al. 2009) and can count up to four objects during navigation to a food source (Dacke and Srinivasan 2008). Carazo et al.

(2012) showed that mealworm beetles use numerical cues to assess the number of potential competing males. On the other hand, Franks et al. (2006b) suggest that *Temnothorax* ants use ambient light levels to estimate the number of nest entrances when assessing potential nest sites rather than counting *per se*. In *M. nipponica*, individuals assessing whether or not a quorum has been achieved probably have a range of possible cues to do so. Ants could be inferring quorum thresholds based on the composition and abundance of chemical trails at the new site, the abundance of airborne chemical signals at the new site, or other metrics such as encounter rate, without needing to invoke numerical assessment. Indeed, encounter rate is a likely possibility, as previous studies have indicated that encounter rates are important in mediating collective processes including consensus decision-making in ants (Pratt 2005; Greene and Gordon 2007). However, it has been proposed that spatial, temporal, and numerical sensory information share a common system of magnitude estimation (Church and Meck 1984; Cheng et al. 1996; Walsh 2003) and thus various possible stimuli are likely to be subject to the same pattern of ratio dependence. Whatever metric is being employed, the dynamic and adaptive nature of quorum thresholds (e.g. Franks et al. 2003) suggests that the internal target value is being constantly updated depending on environmental context. This may at least partially explain why scout ants repeatedly travel between the new site(s) and the previous nest site, as this may allow ants to track the ratio of the populations until a quorum has been achieved.

Ratio-dependent discrimination implies increasing error with increasing stimulus magnitude, and this may have implications for the accuracy of various behaviours. In insects, ratio dependence has also been demonstrated in distance estimation in honey bees (Cheng et al. 1999) and may help describe the process of ant navigation on chemical trails (Perna et al. 2012). Ratio-dependent distance estimation has also been reported in a slime mold (Mori and Koaze 2013), suggesting the phenomenon does not require the presence of a neural system. With respect to quorum sensing, increasingly inaccurate quantity discrimination with increasing stimulus magnitude means that individuals are more likely to misjudge the quorum point as quorum size increases. While early and late switches should cancel each other out overall, there is a risk that an incorrect decision will be reached if initial decisions are poor and influence subsequent decisions in the manner of an information cascade (Giraldeau et al. 2002; Cronin 2013a). In general, lower quorum thresholds are associated with more rapid, and less accurate, decision-making (Franks et al. 2009; Pratt 2010), whereas higher quorum thresholds occur in more benign environments and larger colonies (Dornhaus et al. 2004; Dornhaus and Franks 2006;

Cronin 2013b). There was also a suggestion in this study that ants may employ higher quorums in more complex choices (i.e. where multiple new nests are available). It has been suggested that the use of larger quorums in *Temnothorax* ants may insure against multiple quorums being achieved concurrently at different locations, leading to colony splitting (Franks et al. 2006a), and ratio dependence may place an upper limit on the accuracy of the use of larger quorums. In addition to consensus decision-making, ratio-dependent quantity discrimination may have implications for other collective processes in social insects. For example, when insects reproduce via colony fission, resources are typically distributed among new candidate nest(s) and the parent colony, often by a small subset of the colony workforce (Chéron et al. 2011; Cronin et al. 2013). Presumably, these ants are also assessing resources allocated (adults and brood transported) to each nest against some internal metric. This may also be subject to increasing error with increasing quantity and may thus affect the distribution of colony resources among new colonies (e.g. Chéron et al. 2011).

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