Nesting site selection of *Temnothorax congruus* from Japanese broad-leave forests: a trade-off between nest site quality and distance from sympatric *Crematogaster teranishii* colonies

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ABSTRACT. Intra- and interspecific competition for resources such as food and nesting sites, as well as other biotic and abiotic factors, affect colony distribution of ant species. Through a series of laboratory experiments using *Temnothorax congruus* and its putative sympatric competitor *Crematogaster teranishii* we investigated whether nesting site selection by *T. congruus* is affected by the presence of *C. teranishii*. In the absence of *C. teranishii*, *T. congruus* colonies preferred plastic tubes with narrower entrances and those with fewer entrances as their nesting site. In the presence of *C. teranishii*, *T. congruus* colonies clearly avoided tubes near the *C. teranishii* nests as their nesting site, even if the tubes near *C. teranishii* nests were higher in quality than those far from *C. teranishii* nests. The mortality rate of *T. congruus* adults was higher in the presence of *C. teranishii* adults than in the absence of them.

Keywords: formicidae; competition; emigration; interspecific aggression; nest choice; trade-off

INTRODUCTION

Competition is one of the major factors regulating population density and spatial distribution of individuals (Pulliam 2000). Competition is often categorized into three types: i) exploitation competition may occur when consumption of essential resources by one organism/species subsequently reduces the gain of others; ii) interference competition may occur when one organism/species limits the other from accessing essential resources; and iii) agonistic interference competition, a form of interference competition where direct physical interaction occurs among organisms/species, and the winner occupies the resources (Reitz & Trumble 2002). When exploitation competition and/or interference competition between competing species are asymmetric,

this can lead to displacement/exclusion (Reitz & Trumble 2002). Typically, more aggressive species successfully occupy and defend essential resources at the cost of less aggressive species (Huffaker & Gutierrez 1999). As a result, many species avoid resources occupied by more aggressive competitors, in order to avoid potentially costly interactions (Schowalter 2000).

Evidence for both intraspecific and interspecific competition is common in ants (Adams 1994; Tanner & Adler 2009), and because colonies are largely sessile once settled, one aspect of colony ant life history for which competition is likely to be critical is nest site choice. Ants are known to be very choosy when it comes to nest site selection. For example, *T. albipennis* ants assess nest sites by various properties including cavity height, width, floor area and abundance

of nest entrances before making a choice (Franks et al. 2003, 2006; Robinson & Sendova-Franks 2008). Ants also take into account the presence of potential competitors when selecting a nest (Franks et al. 2007). However, both factors can affect nest choice simultaneously, and it remains unclear which (nest quality or competition) is more important and how they may interact.

In this study, we reveal the effects of two conditions, i.e., the quality of the nesting site and the presence of an interspecific competitor simultaneously, on the nesting site selection of *Temnothorax congruous*, through a series of laboratory experiments using two sympatric arboreal species, *T. congruus* and *Crematogaster teranishii*. *Crematogaster teranishii* sometimes colonizes the nesting sites of *T. congruus* (Yamaguchi 1992) and *Crematogaster* spp. can be aggressive toward sympatric ant species (Stanton et al. 2005; Izzo et al. 2009; Flanders et al. 2013). Thus, *T. congruus* and *C. teranishii* may compete with each other for nest sites and other resources.

MATERIALS AND METHODS

The myrmicine ant species *Temnothorax congruus* (Smith 1874) and *Crematogaster teranishii* (Santschi 1930) are both black-colored and small sized (2.5-3 mm in body length of the workers). They are widespread in Japan, and usually inhabit forest edges, bushes and gardens. They nest inside hollow dead branches and dead grass stems. The typical *T. congruus* colony consists of a single mated queen, approximately 200 workers and immatures (Yamaguchi 1992).

Temnothorax congruus and *C. teranishii* are frequently found from the same sites and the same localities in the Kanto District; Ibaraki, Tochigi, Gunma, Saitama, Chiba, Tokyo and Kanagawa (Kazutaka Syoji, pers. obs.).

Sampling colonies
A total of 266 colonies of *T. congruus* and 110 colonies of *C. teranishii* were sampled in Hachioji, Hino and Machida Cities (Tokyo Metropolitan area), and Sagamihara City (Kanagawa Prefecture), Japan, from November 2014 to October 2015. These colonies were used for all related preliminary trials and experiments in this study.

Colonies were found by gently splitting dead branches/stems of *Hydrangea* spp. (Hydrangeaceae) and bamboo grass, and then each nest was put into a plastic container and carried back to the laboratory. Because sampling activities were conducted in abandoned green spaces in/around residential zones, no permission for such activities was required. The colonies were then kept inside an artificial climate chamber (NK system, BIOTRON, LPH200) at 27 ºC.

Preparation for experiments
A total of 93 colonies of *T. congruus* and artificial 50 colonies of *C. teranishii* were used for the following experiments. All of the *T. congruus* colonies were queenright; the median number of the workers and larvae + pupae per a *T. congruus* colony was 59 (interquartile range: 39 to 80) and 58 (interquartile range: 35 to 88), respectively.

At least 24 hours prior to the experiments, each colony of *T. congruus* together with the nest was transferred separately into a plastic petri dish (87 mm in diameter, 15 mm in height) with lids. Each nest occupied by a *C. teranishii* colony was destroyed, and 50 workers were transferred into a plastic petri dish (87 mm in diameter, 15 mm in height) with an artificial nest material (black-colored plastic drinking straw: 6 mm in diameter, 50 mm in length). The walls of petri dishes were coated with talc powder (hydrated magnesium silicate, $Mg_3Si_4O_{10}(OH)_2$) to prevent ants from escaping. Honey water (ca. 20 % honey solution) was always available except during the experiments mentioned below. One randomly selected colony of each species was used in each experimental trial, and each colony was used only once.

Design of experimental arena and artificial nests
The experimental set-up is shown in Figure 1. Five plastic petri dishes (87 mm in diameter, 15 mm in height, with a lid and talc-coated wall; hereafter referred to as "sites") were placed in a white plastic container (250 mm in width, 320 mm in length, 115 mm in height, with a lid and talc-coated walls; hereafter referred to as the "arena"). Sites were connected with arched white plastic strips (5 mm in width, 10 mm in length, 3 mm in thickness, 2.5 cm in height of arc; hereafter referred to as "bridges"). Ants can move from

one site to another only via bridges because the talc-coated walls of the areas prevent ants from otherwise climbing out.

Three types of artificial nesting sites were made from black-colored plastic <u>drinking straws</u> (hereafter referred to as "straws"): "Straw A", 50 mm in length, 6 mm in diameter, with entrances at both ends; "Straw B", 50 mm in length, 6 mm in diameter, with entrances at both ends and a pair of additional entrances (5 mm in diameter) at the middle; "Straw C", 50 mm in length, 13 mm in diameter, with entrances at both ends. Diameter of straw A is very similar to the natural nests of *T. congruus* and *C. teranishii* from our field experience. *T. congruus* ants usually stay in middle of the straw A from preliminary trials observations. Straw B was made as lower quality nest site than straw A, as holes made the middle of the straw less attractive. In many cases, *T. congruus* and *C. teranishii* colonies can not be found in the field from the nests which have larger diameter than that of straw A. So straw C also represents a low quality nest site for these ants.

These straws were fixed to the bottom of the sites using an electric hot glue gun.

Prior to each trial, the arenas, sites and bridges were washed with 100 % ethanol and plain water in order to remove influence of previous trials (such as effects of residual pheromone). New straws were used for each trial.

Experiment 1: effect of nest quality

In order to evaluate the effect of nest quality, the following trials were done under the absence of *C. teranishii*. A *T. congruous* colony was driven from their nest and released into site 3, and then two types of straws were placed in sites 2 and 4, with the positions of the two types of straws alternated to avoid biases from spatial preference (Pratt et al. 2001; McLeman et al. 2002) in the following manner: (i) Straw A vs. Straw B: Straw A in the site 2 and B in 4 (11 trials), and Straw B in the site 2 and A in 4 (11 trials), and (ii) Straw A vs. Straw C: Straw A in the site 2 and C in 4 (10 trials), and Straw C in the site 2 and A in 4 (11 trials).

We designed straws to represent a hierarchy of nest quality. However initial results indicated that ants did not discriminate between Straws B and C. These can thus be considered as equally 'bad' nests, whereas straw A was a 'good' nest. Our analysis does not report on tests between Straws B and C.
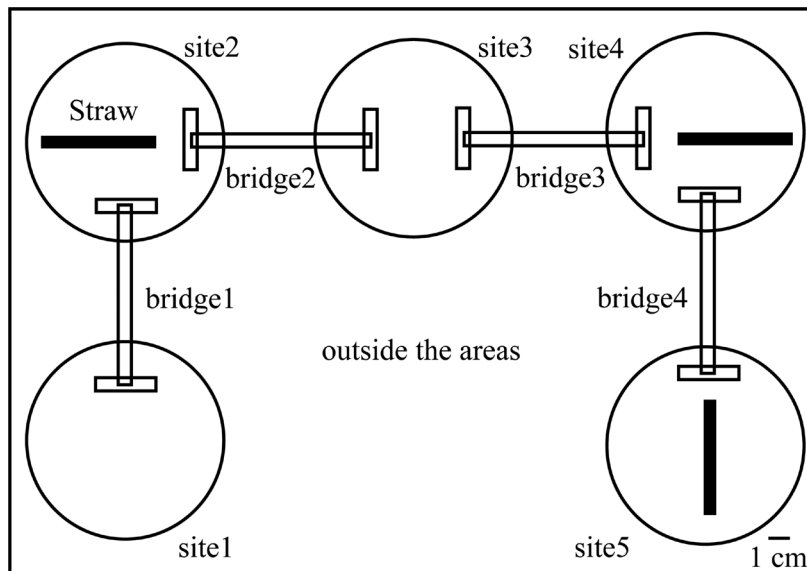

Fig. 1. The construction of the arena in the experiments. This construction was used throughout all experiments. Sites indicated by straws used various straw nest types (see Methods).
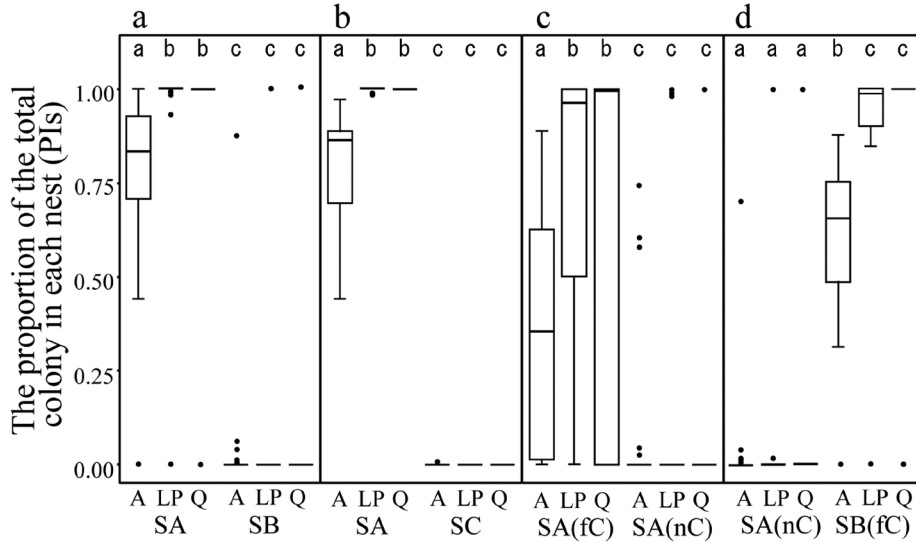
Fig. 2. Results of experiment 1 - 3. Results of experiment 1 (a & b), experiment 2 (c) and experiment 3 (d) are plotted using box plot. Different letters on the top of the box indicate groups which differ significantly for following tests within each experiment. The y-axis indicates the proportion of the total colony in each nest (PIs). Letters on the x-axis indicate the straw types, distance from the *C. teranishii* and castes (SA, straw A; SB, straw B; SC, straw C; (fC), far from the *C. teranishii*; (nC), near the *C. teranishii*; A, adult workers; LP, larvae + pupae; Q, queen). *Boxes* indicate the interquartile range; *horizontal lines* within boxes indicate the medians; *whiskers* include all points to 1.5 times the interquartile range; *short horizontal lines* indicate the maximum value and the minimum value within 1.5 times the interquartile range; *Solid circles* indicate the outliers.

Experiment 2: effect of distance from *Crematogaster teranishii* nest

In order to evaluate the effect of distance from the *C. teranishii* nest, the following trials were done: a straw A was placed in site 2 and 4; a *T. congruus* colony was driven from their nest and released in the site 3, and a straw containing a *C. teranishii* colony was placed in site 1 (10 trials) or in site 5 (18 trials). Thus, the distance from the *T. congruus* colony to the two straws was always the same, and the distance from the *C. teranishii* colony to one straw was always three times farther than to the other straw.

Experiment 3: effect of nest quality vs. effect of distance from *Crematogaster teranishii* nest

In order to compare the effect of nest quality and that of distance from the *C. teranishii* nest, the following trials were done: a straw A was placed in site 2, and a straw B in site 4; a *T. congruus* colony was driven from their nest and released in the site 3, and a containing a *C. teranishii* colony was placed in the site 1 (11 trials). To avoid biases

from spatial preference, the following trials were also done: a straw A was placed in the site 4, and a straw B in the site 2; a *T. congruus* colony was released in site 3, and a straw nested by a *C. teranishii* colony was placed in the site 5 (11 trials).

Statistical analyses

After 24 hours, living and dead workers, queen and larvae + pupae of *T. congruus* in each straw, on each site, on each bridge, and outside the sites and bridges were counted. As an index of nesting-site preference (hereafter abbreviated as PI), the proportion of the number of workers, queen or larvae + pupae in each straw to the total number of the workers, queen or the larvae + pupae in the colony was calculated; the PI of queens was 0 or 1 because all of the colonies used in the present study were monogynous.

PIs were then compared within each experiment using Kruskal-Wallis rank sum tests followed by pairwise Mann-Whitney U tests. A Bonferroni correction was applied to the significance level due to there being multiple compari-

sons. A Pearson's Chi-squared test with Yates' continuity correction was used to compare number of workers, queen and larvae + pupae in the nests within each test (Experiment 1 - 3).

In the same way, we compared the mortality rate and number of dead adults across treatments. All statistical analyses were conducted using R v. 3.2.0 and EZR v. 1.28 on R commander (Kanda 2015; Fox 2005; R Core Team 2015).

RESULTS

Experiment 1: effect of nest quality

PIs of living workers, queen, and larvae + pupae were significantly higher in straw A than in B (Kruskal-Wallis rank sum test; Chi^2 = 103.19, N= 22, df = 5, P < 0.0001 Figure 2a), and in straw A than in C (Kruskal-Wallis rank sum test; Chi^2 = 122.49, N = 21, df = 5, P < 0.0001; Figure 2b).

The number of workers, queen and larvae + pupae in straw A and straw B was significantly different (Chi-squared test; workers, Chi^2 = 1422.5, df = 1, p < 0.0001; larvae + pupae, Chi^2 = 2503.4, df = 1, p < 0.0001; queen, Chi^2 = 32.82, df = 1, p < 0.0001). The number of workers, queen and larvae + pupae in the straw A and

straw C were significantly different (Chi-squared test; workers, Chi^2 = 2117.4, df = 1, p < 0.0001; larvae + pupae, Chi^2 = 2470.1, df = 1, p < 0.0001; queen, Chi^2 = 38.1, df = 1, p < 0.0001).

Experiment 2: effect of distance from *Crematogaster* nest

PIs of living workers, queen, and larvae + pupae were significantly higher in the straw far from the *C. teranishii* nest than in the straw near the *C. teranishii* nest (Kruskal-Wallis rank sum test; Chi^2 = 53.36, N = 28, df = 5, P < 0.0001; Figure 2c).

The number of workers, queen and larvae + pupae in the straw far from the *C. teranishii* and straw near the *C. teranishii* was significantly different (Chi-squared test; workers, Chi^2 = 444.14, df = 1, p < 0.0001; larvae + pupae, Chi^2 = 1348.9, df = 1, p < 0.0001; queen, Chi^2 = 9.75, df = 1, p < 0.01)

Experiment 3: effect of nest quality vs. effect of distance from *Crematogaster* nest

PIs of living workers, queen, and larvae + pupae were significantly higher in the straw B far from the *C. teranishii* nest than in the straw A near the *C. teranishii* nest (Kruskal-Wallis rank sum test; Chi^2 = 92.35, N = 22, df = 5, P < 0.0001; Figures 2d).
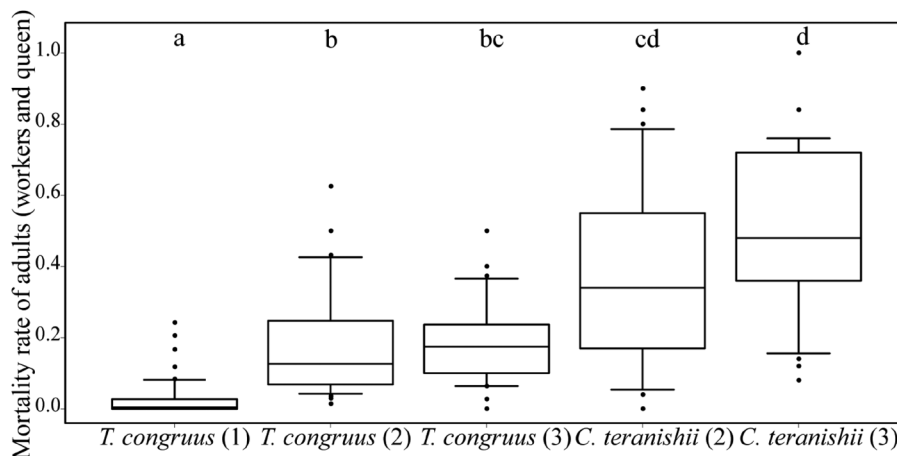

Fig. 3. The mortality rate of adults in the experiment. Different letters on the top of the bars indicate groups which differ significantly following multiple tests. The y-axis indicates the mortality rate of adults (workers and queen). The numbers of the x-axis within the brackets indicate the experiment numbers. Samples sizes were as follows: *T. congruus* (1), N = 43: *T. congruus* (2), N = 28: *T. congruus* (3), N = 22: *C. teranishii* (2), N = 28: *C. teranishii* (3), N = 22. *Boxes* indicate the interquartile range; *horizontal lines* within boxes indicate the medians; *whiskers* include all points to 1.5 times the interquartile range; *short horizontal lines* indicate the maximum value and the minimum value within 1.5 times the interquartile range; *Solid circles* indicate the outliers.

The number of workers, queen and larvae + pupae in the straw B far from the *C. teranishii* and straw A near the *C. teranishii* were significantly different (Chi-squared test; workers, $Chi^2 = 1305.8$, df = 1, p < 0.0001; larvae + pupae, $Chi^2 = 2929.5$, df = 1, p < 0.0001; queen, $Chi^2 = 24.77$, df = 1, p < 0.0001).

Mortality rate of adults (workers and queen)
Mortality rate of adults during the trials differed significantly between experiments in *T. congruus* (Kruskal-Wallis rank sum test; $Chi^2 = 83.69$, df = 4, P < 0.0001; Figure 3). The number of dead adults and mortality rate of *T. congruus* were significantly higher in the presence of *C. teranishii* than in the absence of *C. teranishii* (experiment 1 vs. 2; Chi-squared test, $Chi^2 = 331.56$, df = 1, p < 0.0001; Mann & Whitney U test, p < 0.0001: Experiment 1 vs. 3; Chi-squared test, $Chi^2 = 360.32$, df = 1, p < 0.0001; Mann & Whitney U test, p < 0.0001). There was no significant difference in the number of dead adults and mortality rate of *T. congruus* between experiment 2 and experiment 3 (Chi-squared test, $Chi^2 = 1.53$, df = 1, p = 0.22; Mann & Whitney U test, p = 1).

The mortality rate of *C. teranishii* colonies workers was higher experiment 3 than in experiment 2 also (Kruskal-Wallis rank sum test; $Chi^2 = 83.69$, df = 4, P < 0.0001; Figure 3). The number of dead adults in *C. teranishii* colonies was also significantly higher in experiment 3 than in experiment 2 (Chi-squared test; $Chi^2 = 42.99$, df = 1, p < 0.0001). However, there was no significant difference in the mortality rate of *C. teranishii* between experiment 2 and experiment 3 (Mann & Whitney U test, p = 0.82).

DISCUSSION

Factors affecting nest site selection of *Temnothorax congruus*
The results of experiment 1 suggest that *T. congruus* colonies prefer straws that are narrow and have a small number of entrances (i.e., straw A). *Temnothorax albipennis* also prefers nests with narrow entrances (Franks et al. 2003, 2006), and these may provide defensive and survival advantages to the colonies. In nature, tube-like structures such as dead branches/stems of *Hydrangea*

spp. and bamboo grass often have many holes and cracks. In nature, stems of bamboo grass nests have only one entrance and *T. congruus* colonies build collars to reduce the entrance size. So usage of structures containing holes may increase the risks of desiccation (Bollazzi and Roces 2007) and/or invasion by intra and interspecific competitors (Franks & Partridge 1993) and may require additional costs for maintaining/repairing the nest (Franks 1992). Thus, the fitness of *T. congruus* colonies may be improved by evaluating the quality of tube-like structures and avoiding low-quality ones.

Experiment 2 suggests that *T. congruus* colonies prefer nesting sites far from *C. teranishii* nests. *Crematogaster* spp. are aggressive to sympatric ant species (Stanton et al. 2005; Izzo et al. 2009; Flanders et al. 2013), and *C. teranishii* colonies sometimes use nesting sites which were previously occupied by *T. congruus* colonies (Yamaguchi 1992). Thus, the avoidance of *C. teranishii* colonies could reduce the future risks of competition for food, nesting sites, and/or other resources.

Both physical and biotic factors can affect nesting site selection in ant colonies (Franks et al. 2003, 2006, 2007, 2008), but experiment 3 suggests that the presence of *C. teranishii* affects nesting site selection of *T. congruus* more strongly than the quality of nesting sites.

Mortality rate of adults and aggressive behaviors
The results of experiments 2 and 3 reveal that the mortality rate of *T. congruus* adults was higher in the presence of *C. teranishii* than in their absence. This seems to be caused by aggressive behaviors of the *C. teranishii* workers toward the *T. congruus* workers.

The *T. congruus* workers were exposed to a high risk of encountering the *C. teranishii* workers during scouting nesting sites, carrying nest mates, and tandem running. So, the presence of the *C. teranishii* workers may affect the efficiency of the nesting site selection and emigration process by *T. congruus* colonies.

Despite the apparent threat posed by *C. teranishii*, the mortality rate of workers was higher in *C. teranishii* than in *T. congruus*. This could be partly caused by *T. congruus* ants resistance to aggression of *C. teranishii*. Some *C. teranishii*

workers were killed by biting of some *T. congruus* workers in experiment 2 and 3.

     Temnothorax congruus workers often became immobile when encountering *C. teranishii* workers (Syoji & Eguchi 2015). Although some *T. congruus* workers showed mandible opening behavior toward encountering *C. teranishii* workers (which is thought to be a threat behavior; Guerrieri & D'Ettorre 2008), immobility behavior was much more frequently observed than mandible opening behavior. Thus we conclude that *T. congruus* ants prefer to avoid *C. teranishii* ants during nest site selection even though perhaps they can resist the aggression of *C. teranishii* ants.

CONCLUSION

In this study, we revealed that *T. congruus* nest site selection was much more affected by the presence of *C. teranishii* than by nest quality. This suggests that, at least with regard to the range of nest types selected, the avoidance of the aggressive interference from *C. teranishii* workers is more important than the quality of nesting sites during a nest site selection.

ACNOWLEDGMENTS

REFERENCES

Adams ES, 1994. Territory defense by the ant *Azteca trigona*: Maintenance of an arboreal ant mosaic. *Oecologia* 97(2): 202 – 208.

Bollazzi M and Roces F, 2007. To build or not to build: Circulating dry air organizes collective building for climate control in the leaf-cutting ant acromyrmex ambiguus. *Animal Behaviour* 74(5): 1349 – 1355.

Case TJ and Gilpin ME, 1974. Interference competition and niche theory. *Proceedings of the National Academy of Sciences of the United States of America* 71: 3073 – 3077.

Fox J, 2005. The R Commander: A Basic Statistics Graphical User Interface to R. *Journal of Statistical Software* 14(9): 1 – 42.

Franks NR, Dornhaus A, Hitchcock G, Guillem R, Hooper J and Webb C, 2007. Avoidance of conspecific colonies during nest choice by ants. *Animal Behaviour* 73(3): 525 – 534.

Franks NR, Dornhaus A, Fitzsimmons JP and Stevens M, 2003. Speed versus accuracy in collective decision-making. *Proceedings of the Royal Society of London*, *Series B* 270: 2457 – 2463.

Franks NR, Dornhaus A, Metherell BG, Nelson TR, Lanfear SAJ and Symes WS, 2006. Not everything that counts can be counted: ants use multiple metrics for a single nest trait. *Proceedings of the Royal Society of London*, *Series B* 273: 165 – 169.

Franks NR, Hardcastle KA, Collins S, Smith FD, Sullivan KME, Robinson EJH and Sendova-Franks AB, 2008. Can ant colonies choose a far-and-away better nest over an in-the-way poor one? *Animal Behaviour* 76(2): 323 – 334.

Franks NR, Mallon EB, Bray HE, Hamilton MJ and Mischler TC, 2003. Strategies for choosing between alternatives with different attributes: Exemplified by house-hunting ants. *Animal Behaviour* 65(1): 215 – 223.

Franks NR and Partridge LW, 1993. Lanchester battles and the evolution of combat in ants. *Animal Behaviour* 45(1): 197 – 199.

Franks NR, Wilby A, Silverman BW and Tofts C, 1992. Self-organizing nest construction in ants: Sophisticated building by blind bulldozing. *Animal Behaviour* 44(PART 2): 357 – 375.

Flanders BJ, McKillup SC and McKillup RV, 2013. Temporal stability of a mosaic of two competitively exclusive arboreal ants in a tropical mangrove forest. *Insectes Sociaux* 60(2): 173 – 178.

Guerrieri FJ and D'Ettorre P, 2008. The mandible opening response: Quantifying aggression elicited by chemical cues in ants. *Journal of Experimental Biology* 211(7): 1109 – 1113.

Huffaker CB and Gutierrez AP, 1999. *Ecological Entomology*, 2nd edn. John Wiley and Sons, New York.

Izzo TJ, Bruna EM, Vasconcelos HL and Inouye BD, 2009. Cooperative colony founding alters the outcome of interspecific competition between amazonian plant-ants. *Insectes Sociaux* 56(4): 341 – 345.

Japanese Ant Database Group, 2003. Japanese Ant Image Database. Downloaded from http://ant.edb.miyakyo-u.ac.jp/J/index.html on 6 April 2016.

Kanda Y, 2013. Investigation of the freely available easy-to-use software ‚EZR‘ for medical statistics. *Bone Marrow Transplantation* 48(3): 452 – 458.

McLeman MA, Pratt SC and Franks NR, 2002. Navigation using visual landmarks by the ant *leptothorax albipennis*. *Insectes Sociaux* 49(3): 203 – 208.

Pulliam HR, 2000. On the relationship between niche and distribution. *Ecology Letters* 3(4): 349 – 361.

Pratt SC, Brooks SE and Franks NR, 2001. The use of edges in visual navigation by the ant *Leptothorax albipennis*. *Ethology* 107: 1125 – 1136.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Downloaded from http://www.R-project.org/.

Reitz SR and Trumble JT, 2002. *Competitive displacement among insects and arachnids.*

Robinson EJH and Sendova-Franks AB, 2008. Can ant colonies choose a far-and-away better nest over an in-the-way poor one? *Animal Behaviour* 76(2): 323 – 334.

Sasaki T and Pratt SC, 2011. Emergence of group rationality from irrational individuals. *Behavioral Ecology* 22(2): 276 – 281.

Santschi F, 1930. Trois notes myrmcologiques. *Bulletin et Annales de la Socit Entomologique de Belgique* 70: 263 – 270.

Schowalter TD, 2000. *Insect Ecology: an Ecosystem Approach.* Academic Press, San Diego, California.

Smith F, 1874. Descriptions of new species of Tenthredinidae, Ichneumonidae, Chrysididae, Formicidae, &c. of Japan. *Transactions of the Entomological Society of London* 7(4): 373 – 409.

Stanton ML, Palmer TM, and Young TP, 2005. Ecological barriers to early colony establishment in three coexisting acacia-ant species in kenya. *Insectes Sociaux* 52(4): 393 – 401.

Syoji K and Eguchi K, 2015. Immobility behavior of *Temnothorax congruus* (Formicidae: Myrmicrinae). *ARI* 37: 39 – 46.

Tanner CJ and Adler FR, 2009. To fight or not to fight: Context-dependent interspecific aggression in competing ants. *Animal Behaviour* 77(2): 297 – 305.

Yamaguchi T, 1992. Interspecific interference for nest sites between *Leptothorax congruus* and *Monomorium intrudens*. *Insectes Sociaux* 39(2): 117 – 127.