Insectes Sociaux

RESEARCH ARTICLE

Speed-versus-accuracy trade-offs during nest relocation in Argentine ants (*Linepithema humile*) and odorous house ants (*Tapinoma sessile*)

D. R. Scholes · A. V. Suarez

Abstract Animals are often forced to accommodate disturbance to their territories or nests. When nest relocation becomes necessary, it is important to efficiently evaluate alternative nest sites to choose the one most suitable under current conditions. However, if time is limiting, species may experience a speed-versus-accuracy trade-off when searching for a new home. We examined nest site selection under duress (in the form of flooding) in two species of ants: *Linepithema humile* and *Tapinoma sessile*. We predicted that if ants are able to assess and evacuate to the most suitable location, colonies should move to higher elevation, relative to their current nest site, in response to flooding. To test for a speed-versus-accuracy trade-off, we presented colonies with new nest chambers that were either higher, lower, or at the same height as their current nest and examined if their ability to efficiently choose a new site was influenced by the rate of flooding. When flooding rates were slow, both species favored the highest nest site and nearly always moved their entire nest to the same chamber. However, when the rate of flooding was doubled, colonies of *T. sessile* less often chose the highest nest site and were also more likely to split their nests between two of the available chambers. These results demonstrate a trade-off between speed and accuracy in nest site selection for odorous house ants, while *L. humile* retained their ability to adequately assess new nest sites under the conditions we presented. These patterns may arise from differences in exploratory behavior and activity between the two species. Despite having identical colony sizes, *L. humile* had approximately ten times more workers exploring the alternate nest sites 30 min into the experiment than did *T. sessile*.

Introduction

Nest site selection and territoriality are fundamental characteristics of many animals (Stamps, 1994; Adams, 2001; Visscher, 2007). While nest sites may be long-lived, animals often relocate, particularly if their current location has been altered by environmental disturbance. The process of changing nest sites may involve abandoning investments and assessing new locations, and therefore can be costly in terms of time and energy. Because nest sites can range widely in quality, the assessment of a new site can be complicated and overall suitability is often unknown. This process may be even more complex for social insects, as the colony must explore, rank, decide, and ultimately relocate to a new nest site collectively (Pratt et al., 2002; Franks et al., 2003a; Dornhaus et al., 2004; Pratt, 2005, Visscher, 2007). Once they have relocated to a new area,

D. R. Scholes · A. V. Suarez (✉)
Program in Ecology, Evolution, and Conservation Biology,
University of Illinois at Urbana-Champaign, 286 Morrill Hall,
505 S. Goodwin Ave, Urbana, IL 61801, USA
e-mail: avsuarez@life.uiuc.edu

A. V. Suarez
Department of Entomology, University of Illinois
at Urbana-Champaign, 320 Morrill Hall, 505 S. Goodwin Ave,
Urbana, IL 61801, USA

A. V. Suarez
Department of Animal Biology, University of Illinois
at Urbana-Champaign, 515 Morrill Hall, 505 S. Goodwin Ave,
Urbana, IL 61801, USA

many species expend further resources by creating a nest to protect their offspring and then defending these investments. Nests can range from simple structures to large fortresses in many eusocial insects (Wilson, 1971). Given the resources invested in such structures, social insects often only move locations as a means to avoid competition or predation, as a result of changing environmental conditions (such as humidity), as a response to variation in resources, in the event of nest damage, or in the discovery of a superior nest site (Gordon, 1992; Holway and Case, 2000; McGlynn et al., 2004; Dornhaus et al., 2004; Heller and Gordon, 2006; McGlynn, 2006).

The physical attributes of a nest site can be extremely variable, but there appear to be a few that must be present at high quality for the nest site to be considered acceptable for colony relocation (Dornhaus et al., 2004) including size, darkness, and the diameter and position of the entrance (Seeley, 1977; Herbers and Banschbach, 1995; Pratt and Pierce, 2001; Franks et al., 2003a). For example, *Temnothorax* ants and honey bees can accurately evaluate the interior area or volume of a potential nest site (Seeley, 1977; Mallon and Franks, 2000). While it is known that many factors play a role in site selection, it is often not known whether these attributes are evaluated qualitatively or quantitatively, nor whether attributes are weighted in importance (but see Franks et al., 2003a).

Once an alternate nest site is discovered during relocation, a colony member needs to effectively communicate its location or lead others to the nest (Visscher, 2007). Many ants will use chemical communication in the form of trails to lead nest mates to a new nest site while others will employ physical means of recruitment in the form of tandem running and social carrying (Hölldobler and Wilson, 1990; Pratt, 2008). In the genus *Temnothorax*, as more ants transition from recruits to recruiters, individuals arrive at a focal nest at a faster rate than other potential nests, reaching a worker quorum at a single nest site that then triggers a full colony emigration (Pratt et al., 2002). At this time, social carrying is employed, where an ant will physically carry another ant to the new nest (Dornhaus et al., 2004). The approximate midpoint of the emigration is also typically when brood and queen transfer take place (Franks and Sendova-Franks, 2000).

While the decision-making process during colony emigration may be very complex (Franks et al., 2003a), this study focuses on the final location of the colony and the implications of colony relocation. Also of importance is the role that outside factors may play in determining the decision-making process. Franks et al. (2003b) suggest that a speed-versus-accuracy trade-off may be employed during evacuations, where evacuating a disturbed nest quickly is a priority over carefully analyzing the attributes of all potential nest sites. We used the odorous house ant (*Tapinoma sessile*) and the Argentine ant (*Linepithema humile*) to determine if nest site selection is influenced by the perception of an immediate threat, flooding. In the event of a flood, it is beneficial to move the colony to higher ground. If ants are able to assess and evacuate to the "safest" location, then the ants should move higher relative to their current nest site in response to rising waters. However, their ability to do so efficiently may be hampered by the rate of flooding. Thus, we also examined how the rate of flooding interacts with the collective decision-making process, hypothesizing that under heightened flooding the ants would relocate nests more rapidly at the expense of making an optimal decision.

Methods

We chose the Argentine ant and odorous house ant for this study because of their ecological and taxonomic similarity. Both species are in the subfamily Dolichoderinae, are highly polygynous (have many queens) and polydomous (occupy many spatially separate yet interconnected nests), and are both known to move their nest sites frequently (Holway and Case, 2000; Buczkowski and Bennett, 2006; Heller and Gordon, 2006). While both are urban pests in the US, *L. humile* is a widespread invasive species native to Argentina, while *T. sessile* is not known to have established populations outside of its native range. Flooding is a particularly common form of environmental disturbance for both these species as they frequently live in riparian and urban areas. Moreover, *L. humile* is native to the flood plain regions of northern Argentina, southern Brazil and Paraguay (Wild, 2004).

We collected *T. sessile* from the University of Illinois at Urbana-Champaign campus and divided the workers and queens into 20 experimental colonies each consisting of 5 queens and 2,000 workers. Colonies of *L. humile* were collected from multiple sites in southern California and were similarly divided. Colony fragments of this size are large enough to exhibit behaviors typical of entire colonies for both species (Buczkowski and Bennett, 2008). Experimental colonies were placed into Fluon-lined plastic containers (940 cm^3) with moist mulch as nesting material. The colonies were then allowed to settle for 3–4 days. We then presented experimental colonies with three identical, alternate nest sites: one 12.5 cm higher than the focal nest, one 12.5 cm lower, and one at the same height. Each alternate nest site consisted of a plastic tub (940 cm^3) that contained three test tube nest chambers covered with a paper towel. The experimental colony was connected to the three new nests with wires of equal length. All wires emerged from the colony pointing straight up for about 15 cm and then were bent towards their final nest site. This

was done to avoid potential biases resulting from ants detecting the initial direction of their path rather than the final location of nest site.

Experimental colonies were then subjected to two experimental treatments (order determined at random) that varied in flooding rate: one with a drip rate of ~ 1 drop/s ("fast"; 4 h before the colony was completely immersed in water), and another with a drip rate of 1 drop/3 s ("slow"; 7 h before immersion). The ants were allowed to explore the nest sites throughout the trials and the number of workers at each alternate nest site was counted at regular intervals. We examined the effects of nest height on the number of workers in each container at two time periods: 30 min after water dripping began (used to quantify the initial "exploratory behavior" of each species) and after the original nest site was completely flooded (used to assess final nest site selection). We also documented if colonies ended up splitting their workers and queens between multiple nest sites at the end of the experiments. A colony was considered split if greater than 500 workers or at least one queen ended up in a second alternate nest site.

Worker counts were log transformed and statistically analyzed using an ANOVA for differences in nest site selection at the end of the experiments. Fisher's Protected Least Significant Difference (PLSD) post hoc tests were also used to examine differences between the nests at the end of each trial. Differences among species and treatments in exploratory behavior, as estimated by the number of workers in each alternate nest site after 30 min, were examined using a nested ANOVA.

Results

When slowly flooded, nest height had a significant effect on the number of *T. sessile* workers at each height at the end of the experiment (ANOVA, $df = 2, 57$; $F = 19.94$; $P < 0.001$; Fig. 1). Post hoc tests revealed that workers preferred the highest nest site over the middle and the lowest containers (PLSD, $P < 0.001$). There was also a significant effect of nest height on the number of *L. humile* workers at each height at the end of the experiment (ANOVA, $df = 2, 57$; $F = 66.56$; $P < 0.001$; Fig. 1). Post hoc tests revealed that *L. humile* workers preferred the highest nest site over the middle and lowest nest sites (PLSD, $P < 0.001$).

In the fast flooding trials, there was also an effect of nest height on the number of workers present at each location at the end of the experiment for both *T. sessile* (ANOVA, $df = 2, 57$; $F = 3.77$; $P = 0.0289$) and *L. humile* (ANOVA, $df = 2, 57$; $F = 8.48$; $P < 0.001$) (Fig. 1). However, post hoc tests revealed that while *L. humile* workers continued their preference for the highest
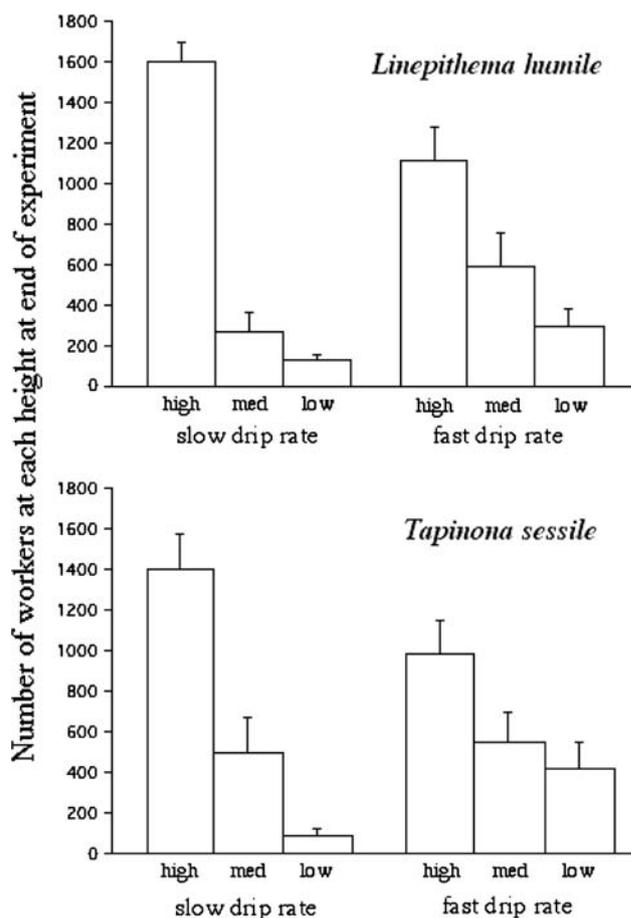
Fig. 1 The number of workers (mean ± SE) in each of three alternate nest sites separated by species (*Linepithema humile* vs. *Tapinoma sessile*) and treatment (fast vs. slow flooding). The high elevation container was favored over the medium and low container by *L. humile* workers regardless of flood rate, and by *T. sessile* when slowly flooded. However, when the flood rate was increased, the number of *T. sessile* workers in the high and medium elevation containers were not significantly different

container over the lowest (PLSD, $P < 0.001$) and the middle container (PLSD, $P = 0.014$), *T. sessile* workers preferred the highest container over the lowest (PLSD, $P = 0.01$) but not the middle container (PLSD, $P > 0.05$). Moreover, *T. sessile* often split the location of its final nest between two containers (greater than 500 workers and at least one queen in a second container) in 8 of 20 trials during the fast treatment but only 1 of 20 during the slow (chi square $= 7.025$, $df = 1$, $P = 0.008$). Unlike *T. sessile*, *L. humile* only split the final location of its workers and queens at the end of the fast experiment in 2 of 20 trials and never during the slow trials (chi square $= 2.105$, $df = 1$, $P = 0.146$).

In addition to differences in nest site selection, exploratory behavior (as measured by the number of workers in the three alternate nesting sites after 30 min) of the two species differed significantly (Fig. 2). Specifically,
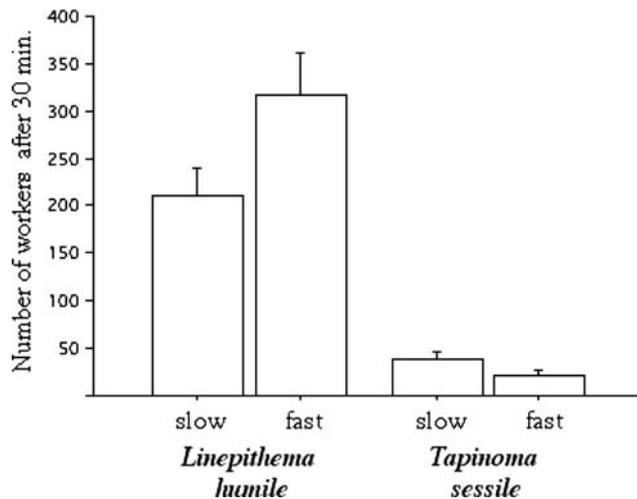
Fig. 2 The number of workers (mean ± SE) exploring the three alternate nest sites 30 min after the trails began. The number of *L. humile* workers is approximately ten times higher than *T. sessile* (see Table 1)

Table 1 ANOVA results for differences in exploratory behavior (the number of workers in each of the three alternate nest sites) by species and flooding rate 30 min after the flooding began

Factor	DF	*F* value	*P* value
Drip rate	1	3.06	0.084
Species	1	80.59	0.001
Drip rate × species	1	5.6	0.021
Residual	76		

L. humile had an order of magnitude more workers exploring the alternate nest sites after 30 min than *T. sessile* (Table 1). However, there were no differences between the fast and slow treatments within each species in the number of exploring workers after 30 min (Table 1).

Discussion

While both species favored the higher nest site when the flooding rate was slow, there were differences between species in nest site selection and colony cohesion when the flooding rate increased. We also found differences in exploratory behavior between the two species. These results suggest the species studied can relocate to higher elevations when given enough time to appropriately assess potential nest sites. Intuitively, the proper response to flooding is movement to high ground, but small animals are more severely constrained by information on local topography. Moreover, social insects must make a collective decision when relocating or risk subdividing their worker force when colonies are split. Based on these results, ants

are able to assess a location's height relative to their starting height, regardless of the path's initial direction (as all wires emerged from the colony pointing straight up). Thus, it appears that ants are capable of integrating the vertical trajectory of paths and move their colonies upward when threatened from below.

Argentine ants generally responded more efficiently to flooding than odorous house ants, although both species preferred the highest container to the lowest in both fast and slow trials. For example, while workers of both species overwhelmingly chose a single nest in the slow flooding treatment, *T. sessile* colonies often split (40% of trials) between two nests when flooded quickly while *L. humile* colonies rarely fissioned (10% of trials). While we assume that colony splitting is a sub-optimal response to disturbance in our experiment, in nature splitting may be beneficial in many circumstances (as has been argued for polydomy generally) as a means of increasing home range size, responding to the presence of parasites, food or nest sites, and changing patterns of relatedness among group members (Banschbach and Herbers, 1996; Holway and Case, 2000; Foitzik et al., 2004; McGlynn, 2006; Seppa et al., 2008). Because *L. humile* and *T. sessile* are highly polygynous, colony splitting may not represent a reproductive dead end, although colony budding as an adaptive response typically only occurs in natural populations much larger than those used in this study. These trials serve as a preliminary test of the speed-versus-accuracy theory, as detailed by Franks et al. (2003b). Evidently, the fast flooding trials exceeded some critical rate in which the speed of relocation outweighed accuracy in nest choice for *T. sessile* as they did not prefer the higher container over the middle container that was at the same height as the original nest site. Repeating these experiments at faster rates of flooding may determine the threshold at which Argentine ants also are unable to relocate their nest accurately.

Both ecological and taxonomic characteristics of the study species may have been factors in the observed decision-making process and final nest selection. Both *L. humile* and *T. sessile* are species known for being very mobile and highly accommodative nesting ephemerally almost anywhere (Newell and Barber, 1913; Holway and Case, 2000; Buczkowski and Bennett, 2006; Heller and Gordon, 2006). With these attributes, it seems reasonable that these species are also well adapted to responding to disturbance efficiently and accurately. Particularly in the event of flooding, evolutionary history may be a factor in the response of *L. humile* to disturbance. The Argentine ant is native to South America, most commonly found in the flood plains between the rivers Parana and Uruguay, so the development of a flood response strategy is critical to survival (Wild, 2004; LeBrun et al., 2007). It should be

noted that not all Dolichoderine ants will move their nests rapidly to high ground in response to flooding; preliminary tests with *Forelius mccooki*, a species common to the deserts and dry scrub habitats of southern California revealed that when colonies are slowly flooded in a manner similar to the experiments reported here, workers will readily drown rather than relocate (A. V. Suarez, pers. obs.).

The initial exploratory behavior also differed between species, with Argentine ants consistently having more workers exploring the alternate nest sites early in the experiment. Their ability to rapidly explore new environments (Gordon, 1995), including the discovery of novel food resources, has been implicated in their success (Holway, 1999). Specifically, unlike native ants that often exhibit trade-offs between discovery and recruitment abilities, introduced Argentine ants excel at both (Human and Gordon, 1996; Holway, 1999). Differences in search rate or foraging tempo may help explain why Argentine ants are such successful colonizers of new environments while the ecologically similar *T. sessile* has not become a widespread invader. Future research could compare the evacuation process (as done here) to the general emigration process (e.g., Dornhaus et al., 2004) and examine the exploratory behavior of the two species in more detail. For example, the population within a new nest may result from several factors including the stay duration within the nest, the walking speed of workers traveling between the old and the new nest, and the intensity of recruitment to each potential site. Performing trials in the absence of flooding (or with another type of disturbance) could also serve as a control for this study. However, the difficulties in containing known pest species in the experimental setup during a potentially long emigration prevented the addition of such experiments.

Repeating the trials with larger deviations in available nest heights could result in a greater proportion of colonies preferring high ground, while decreasing the difference in heights may help characterize the ants' vertical sensitivity during evacuation by locating the "critical height" of preferred nests. It would also be worth identifying the mechanisms by which ants assess their relative height. One mechanism of detecting vertical position is phototaxis. Because the primary natural light source (the sun) is elevated relative to the organism, moving toward light is nearly always associated with moving to a higher position (including in the lab where light fixtures are overhead). Organisms that live underground, however, cannot use light as a reliable indicator of position but still seem to detect their spatial orientation. Fossorial organisms may be using gravitaxis instead. Future work investigating the relative roles of light and gravity in vertical sensitivity could be investigated by repeating this experiment while varying the position of light sources or gravitational fields.

Finally, it would also be worthwhile repeating this study with colonies that vary in size. For example, previous studies on *Temnothorax albipennis* revealed that roughly one-third of workers actively recruit to new nest sites during colony emigration (Pratt et al., 2002). Couzin et al. (2005); however, established that the larger the group, the smaller the proportion of informed individuals needed to achieve accuracy in decision-making. Because colonies of *L. humile* and *T. sessile* can range over 3 or more orders of magnitude, it would be interesting to examine the number and fraction of active recruiters across a wide range of colony sizes.

References

Adams E.S. 2001. Approaches to the study of territory size and shape. *Annu. Rev. Ecol. Syst.* **32**: 277–303

Banschbach V.S. and Herbers J.M. 1996. Complex colony structure in social insects. 1. Ecological determinants and genetic consequences. *Evolution* **50**: 285–297

Buczkowski G. and Bennett G.W. 2006. Dispersed central placed foraging in the polydomous odorous house ant, *Tapinoma sessile*, as revealed by a protein marker. *Insect. Soc.* **53**: 282–290

Buczkowski G. and Bennett G.W. 2008. Aggressive interactions between the introduced Argentine ant, *Linepithema humile* and the native odorous house ant, *Tapinoma sessile*. *Biol. Inv.* **10**: 1001–1011

Couzin I.D., Krause J., Franks N.R. and Levin S.A. 2005. Effective leadership and decision-making in animal groups on the move. *Nature* **433**: 513–516

Dornhaus A., Franks N.R., Hawkins R.M. and Shere H.N.S. 2004. Ants move to improve: colonies of *Leptothorax albipennis* emigrate whenever they find a superior nest site. *Anim. Behav.* **67**: 959–963

Foitzik S., Backus V.L., Trindl A. and Herbers J.M. 2004. Ecology of *Leptothorax* ants: impact of food, nest sites and social parasites. *Behav. Ecol. Sociobiol.* **55**: 484–493

Franks N.R. and Sendova-Franks A.B. 2000. Queen transport during ant colony emigration: a group-level adaptive behavior. *Behav. Ecol.* **11**: 315–318

Franks N.R., Mallon E.B., Bray H.E., Hamilton M.J. and Mischler T.C. 2003a. Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. *Anim. Behav.* **65**: 215–223

Franks N.R., Dornhaus A., Fitzsimmons J.P. and Stevens M. 2003b. Speed versus accuracy in collective decision making. *Proc. R. Soc. London, Ser. B* **270** 2457–2463

Gordon D.M. 1992. Nest relocation in harvester ants. *Annls Entomol. Soc. Amer.* **85**: 44–47

Gordon D.M. 1995. The expandable network of ant exploration. *Anim. Behav.* **50**: 995–1007

Heller N.E. and Gordon D.M. 2006. Seasonal spatial dynamics and causes of nest movement in colonies of the invasive Argentine ant (*Linepithema humile*). *Ecol. Entomol.* **31**: 499–510

Herbers J.M. and Banschbach V. 1995. Size-dependent nest site choice by cavity dwelling ants. *Psyche* **102**: 13–17

Hölldobler B. and Wilson E.O. 1990. *The Ants*. Harvard University Press. 732 pp

Holway D.A. 1999. The competitive displacement of native ants by the invasive Argentine ant: mechanisms of exploitation and interference competition. *Ecology* **80**: 238–251

Holway D.A. and Case T.J. 2000. Mechanisms of dispersed central-place foraging in polydomous colonies of the Argentine ant. *Anim. Behav.* **59**: 433–441

Human K.G. and Gordon D.M. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* **105**: 405–412

LeBrun, E.G., Tillberg C.V., Suarez A.V., Folgarait P., Smith C.R. and Holway D.A. 2007. An experimental study of competitive interactions between red imported fire ants and Argentine ants in a region of native-range sympatry. *Ecology* **88**: 63–75

Mallon E.B. and Franks N.R. 2000. Ants estimate area using Buffon's needle. *Proc. R. Soc. London, Ser. B* **267**: 765–770

McGlynn T.P., Carr R.A., Carson J.H. and Buma J. 2004. Frequent nest relocation in the ant *Aphaenogaster araneoides*: resources, competition, and natural enemies. *Oikos* **106**: 611–621

McGlynn T.P. 2006. Ants on the move: resource limitation of a litter-nesting ant community in Costa Rica. *Biotropica* **38**: 419–427

Newell W. and Barber T.C. 1913. *The Argentine ant*. USDA Bureau of Ent. Bull. 122. 98 pp

Pratt S.C. 2008. Efficiency and regulation of recruitment during colony emigration by the ant *Temnothorax curvispinosus*. *Behav. Ecol. Sociobiol.* **62**: 1369–1376

Pratt S.C. and Pierce N.E. 2001. The cavity-dwelling ant *Leptothorax curvispinosus* uses nest geometry to discriminate among potential homes. *Anim. Behav.* **62**: 281–287

Pratt S.C., Mallon E.B., Sumpter D.J. and Franks N.R. 2002. Quorum sensing, recruitment, and collective decision-making during colony emigration by the ant *Leptothorax albipennis*. *Behav. Ecol. Sociobiol.* **52**: 117–127

Pratt S.C. 2005. Behavioral mechanisms of collective nest-site choice by the ant *Temnothorax curvispinosus*. *Insect. Soc.* **52**: 383–392

Seeley T.D. 1977. Measurement of nest cavity volume by the honeybee (*Apis mellifera*). *Behav. Ecol. Sociobiol.* **2**: 201–227

Seppa P., Fernandez-Escudero I., Gyllenstrand N. and Pamilo P. 2008. Colony fission affects kinship in a social insect. *Behav. Ecol. Sociobiol.* **62**: 589–597

Stamps J.A. 1994. Territorial behavior – testing the assumptions. *Adv. Study Behav.* **23**: 173–232

Visscher P.K. 2007. Group decision making in nest-site selection among social insects. *Annu. Rev. Entomol.* **52**: 255–275

Wild A.L. 2004. Taxonomy and distribution of the Argentine ant, *Linepithema humile*. *Annls Entomol. Soc. Amer.* **97**: 1204–1215

Wilson E.O. 1971. *The Insect Societies*. Harvard University Press. 548 pp