Economic investment by ant colonies in searches for better homes

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Organisms should invest more in gathering information when the pay-off from finding a profitable resource is likely to be greater. Here, we ask whether animal societies put more effort in scouting for a new nest when their current one is of low quality. We measured the scouting behaviour of *Temnothorax albipennis* ant colonies when they inhabit nest-sites with different combinations of desirable attributes. We show that the average probability of an ant scouting decreases significantly with an increase in the quality of the nest in which the colony currently resides. This means that the greater the potential gain from finding a new nest, the more effort a colony puts into gathering information regarding new nest-sites. Our results show, for the first time to our knowledge, the ability of animal societies to respond collectively to the quality of a resource they currently have at their disposal (e.g. current nest-site) and regulate appropriately their information gathering efforts for finding an alternative (e.g. a potentially better nest-site).

1. Introduction

For animals to exploit potential resources effectively and avoid danger, they should gather information to reduce uncertainty about their environment [1,2]. Assessment of available resources is a fundamental feature of decision-making at all levels of biological organization. Whether looking for potential mates, food, egg-laying-sites or nest-sites, resources will be assessed and either accepted or rejected. Information gathering is a costly behaviour; thus a fundamental question is how individuals decide on the amount of effort to put into gathering information. Social insect colonies are a great model for studying such questions, because we can count their component parts as allocated to different functions. Thus, we can quantify scouting effort simply by counting the number of individuals engaged in such a task.

Colonies of the ant *Temnothorax albipennis* will scout their environment to gather information about available nest-sites even if their current one remains intact [3]. This species has been the subject of extensive study over nest-site choice. Experimentally, an emigration may be induced by destroying their current nest and providing one or more intact nests [4]. The process starts with scouts gathering information on potential homes. When assessing nest-sites, workers look for specific attributes like floor area, thickness (ceiling height), darkness and entrance size [5]. The way workers choose the best is by weighting the value of the different attributes [5]. Ants generally prefer dark nests to thick ones and thick ones to those with narrow entrances [5].

Intriguingly, colonies will emigrate, even if their current nest remains intact [6]. This is called a 'move-to-improve' emigration as it occurs only if a considerably better nest, in comparison to the one the ants currently inhabit, is available. Such move-to-improve behaviour can be considered as a combination of two
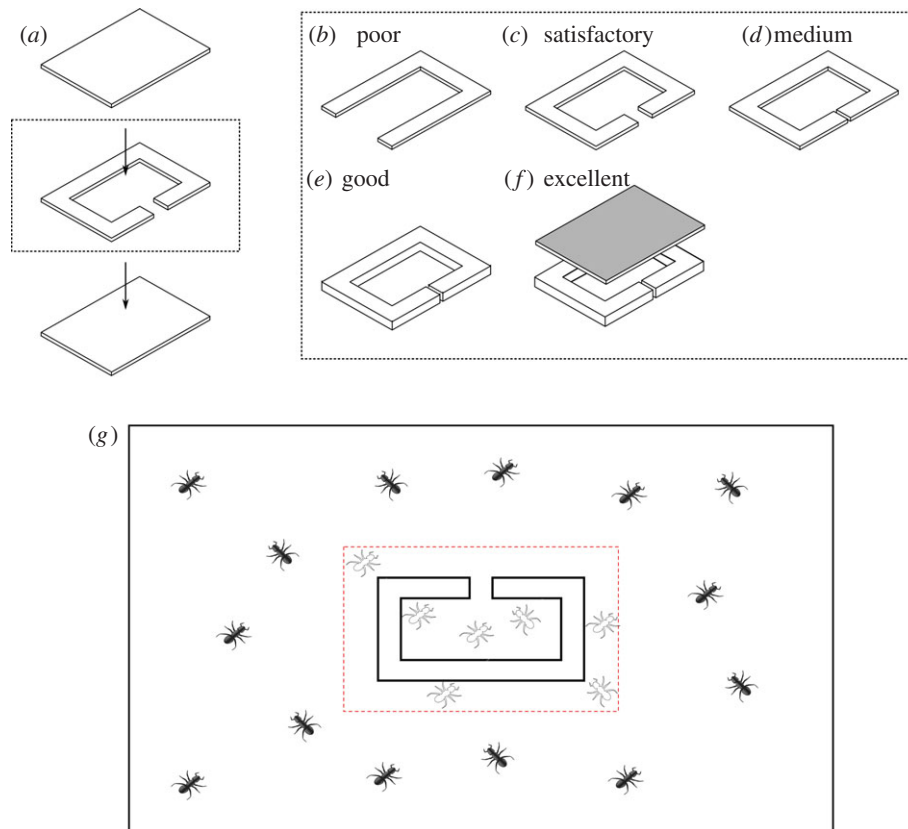
Figure 1. Nest design in the laboratory: (*a*) nests are composed of two glass slides sandwiching a cardboard perimeter; (*b*) light, thin cardboard, three walls; (*c*) light, thin cardboard, wide entrance; (*d*) light, thin cardboard, narrow entrance; (*e*) light, thick cardboard, narrow entrance; (*f*) dark, thick cardboard, narrow entrance. Cavity size is 35 × 60 mm; thin walls are 1 mm and thick walls are 2 mm; wide entrance is 4 mm and narrow entrance is 1 mm. Nest designs were based on the study of Franks *et al.* [5]. (*g*) Experimental arena (50 × 75 cm) with the test colony in one of the test nests. Black ants are scouts and white ants are non-scouts. Dotted line corresponds to the area where ants were considered as non-scouts (up to 1.5 cm away from the nest). (Online version in colour.)

forces: repulsion and attraction. The quality of the current nest must be such that it 'pushes' the ants to scout (i.e. gather information from) the environment for a better home. At the same time, the quality of a potential new nest must be such that it 'pulls' the scouting ants inside. For an emigration from an intact nest-site to be beneficial, the 'resultant' of these two forces (push and pull) should take into account emigration costs such as exposure to predators. Here, we only investigate the influence of repulsion on colonies' collective information gathering about potential nest-sites. We do so by manipulating the quality of their current nest in the absence of a new one.

2. Material and methods

(a) Ant colonies
Experiments were carried out on 15 colonies, collected in September 2011 from Dorset, UK. Colonies were cultured in nests made of two glass slides and a cardboard perimeter sandwiched between them. Each nest was kept in a square Petri dish 10 × 10 × 1.9 cm coated with Fluon to prevent ants from escaping. The ants were fed once a week with honey solution, water and dead *Drosophila* flies. All colonies had one queen, 84–214 workers and 55–212 brood items.

(b) Counting scouts
We used five nest qualities, each with a different set of attributes (figure 1) which we called 'poor', 'satisfactory', 'medium', 'good' and 'excellent'. We moved each of the 15 colonies to each of the five nest types, 2 days before testing. Colonies were induced to move into the experimental nest by opening their current nest in the presence of the experimental one. On the day of each experiment, the experimental nest with the resident colony was placed in the middle of the arena (74 × 50 × 7 cm) and allowed to settle for 45 min. During this time, water and food were placed on top of the nest, where colonies were already accustomed to find food. The number of ants outside the nest was counted every 10 min for 5 h, that is a total of 31 time points for each colony per treatment. When an ant was within a 1.5 cm perimeter around the nest (figure 1), it was considered to be patrolling or foraging and was not counted. We considered every other ant counted as being a scout (number of non-scouting ants = colony size − number of scouts). Each colony experienced all five different nests according to a Latin square design.

(c) Statistical analysis
We analysed the effect of nest quality and time on the number of scouting ants with a generalized linear mixed model for a binomial response with a logit link using the glmer() function of the 'lme4' package in R (v. 2.15.2) [7,8]. The response variable was the proportion of scouting ants. The predictors were nest quality (a fixed factor), time (a covariate), colony (a random factor) and the interaction between nest quality and time. The best model included random variation of colony around the fixed effect of nest quality, the effect of time and the interaction between nest quality and time (see the electronic supplementary material). We ran the best model with polynomial, sum and treatment contrasts to test, respectively, for significance of a linear trend, average effect and differences between the levels of nest quality and its interaction with time.
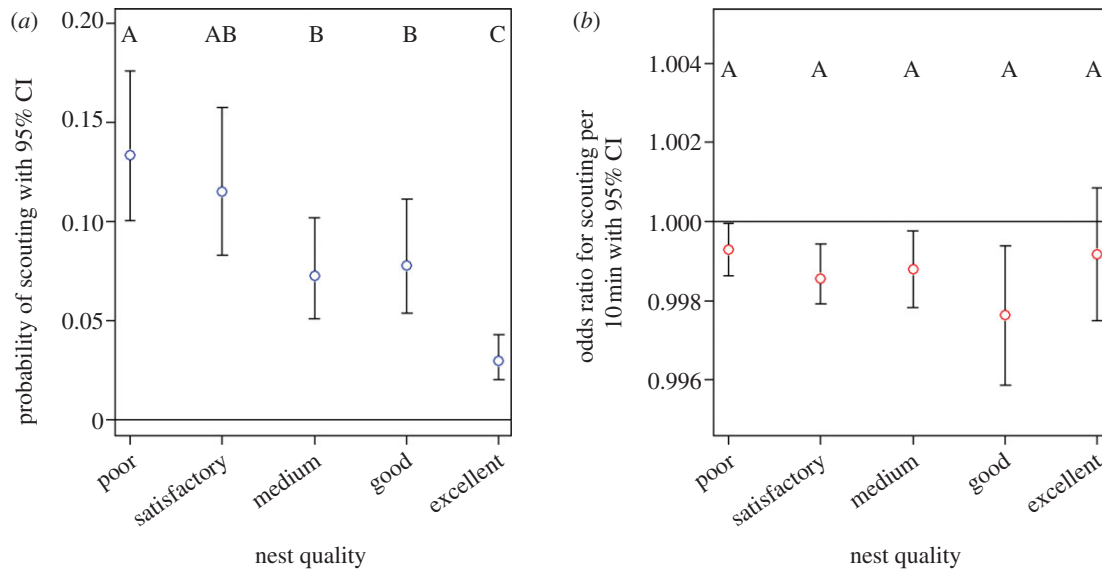
Figure 2. Results from a generalized linear mixed model for binomial data with a logit link: (*a*) the probability of an ant scouting for each currently occupied nest; (*b*) the odds ratio of scouting in one 10 min period versus the next 10 min period up to 5 h (for exact values, see the electronic supplementary material); horizontal lines stand for a probability of 0 or an odds ratio of 1, respectively, and 95% confidence intervals (CIs) straddling these lines represent no significant effect; different letters above the 95% CIs represent significant differences in pairwise comparisons at $\alpha' = 0.05/4 = 0.0125$ to correct for the four comparisons per each nest quality. (Online version in colour.)

For tests of significance, we used the z-test and associated p-values in the output of the function glmer(). To correct for four comparisons per level of nest quality or per interaction between nest quality and time, we used an adjusted significance level $\alpha' = 0.05/4 = 0.0125$. We calculated probabilities and odds ratios from the parameters of the best model (see the electronic supplementary material).

For graphical representation of the results, we used the R packages 'lattice' v. 0.20–13 [9] and 'gplots' [10].

3. Results

The probability of an ant scouting was affected significantly by nest quality ($z = -21.399$, $p < 0.0001$) and time ($z = -4.332$, $p < 0.0001$). Over all the five nest qualities, the average probability of an ant scouting was 0.077 and it decreased on average by 0.001 with each successive 10 min.

For each nest quality, the probability of an ant scouting was significantly different from zero (figure 2*a*). There was a significant linear decrease in the probability of an ant scouting with increasing level of nest quality (contrasts: linear, $z = -7.095$, $p < 0.0001$; quadratic, $z = -1.744$, $p = 0.0811$; cubic, $z = -1.414$, $p = 0.1572$; quartic, $z = -1.929$, $p = 0.0537$). The average probability of an ant scouting was 0.134, 0.115, 0.072, 0.078 and 0.030 for nests of poor, satisfactory, medium, good and excellent quality, respectively. Furthermore, for the lowest nest quality, the probability of an ant scouting was significantly different from that for the nests of medium, good and excellent quality. For the satisfactory, medium and good nest qualities, the probability of an ant scouting was significantly different from that for the excellent nest (figure 2*a*). The probability of an ant scouting decreased over time for all nest qualities except the highest. When nest quality was excellent, the odds ratio for an ant scouting in successive 10 min intervals was not significantly different from 1 (figure 2*b*). There was no significant difference between the values for this odds ratio for any of the pairwise comparisons between nest qualities (figure 2*b*).

The 15 colonies varied predominantly around the average probability of an ant scouting (s.d. for the random effect of colony ranges between 0.637 and 0.774 for the five nest qualities). Colonies varied 100 times less around the odds ratio of an ant scouting in successive 10 min intervals (the s.d. for the random effect of colony ranges between 0.0012 and 0.0034 for the five nest qualities; see the electronic supplementary material, tables S5–S11).

4. Discussion

We show for the first time to our knowledge the collective ability of an animal society to respond, in a quantitative way, to quality differences in a currently held resource as opposed to a target one. We found an inverse relationship between the investment *T. albipennis* colonies put into gathering information on potential new homes and the quality of their current nest (figure 2*a*).

This result demonstrates that colonies are able to rank the quality of the nests they currently occupy by allocating the appropriate number of individuals to scout for an alternative. Furthermore, this also demonstrates a remarkable ability to invest in information gathering according to resource utility, in an economical way.

The average probability of an ant scouting over all five nest qualities decreased over time. This relationship was significant within poor, satisfactory, medium and good nest qualities but there was no significant difference when comparing between nest qualities (figure 2*b*). The worst and best nest qualities were those with the weakest or indeed no relationship between probability of scouting and time. This is fully consistent with the following interpretation: at the two extremes of nest quality, the ants would either keep looking for a better nest with the same high probability, owing to the very low quality of their current home, or simply remain satisfied in the best quality case, and maintain their base activity level. The decrease in scouting over time, in the intermediate nest qualities can be explained by the finite arena size (figure 1*g*). Once colonies have searched all the available space thoroughly they are likely to decrease their effort.

The ability to gather information about resource values differs between animal species. Some like scorpionflies, show no evidence that resource quality affects their behaviour [11]. However others, like hermit crabs will invest more in a fight with another crab if the latter's shell has a higher quality, although we do not know whether they will invest more in a fight when their own shell is of low quality [12]. This paper shows a new approach to the study of information gathering in animals: our focus is on the currently held resource as opposed to a potential one. We hope our results will stimulate future studies at both the individual and collective level to test whether other species are also able to adjust their information gathering effort according to differences in a currently held resource.

References

1. Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW. 2005 Information and its use by animals in evolutionary ecology. *Trends Ecol. Evol.* **20**, 187–193. (doi:10.1016/j.tree.2005.01.010)

2. Dall SRX, Johnstone RA. 2002 Managing uncertainty: information and insurance under the risk of starvation. *Phil. Trans. R. Soc. Lond. B* **357**, 1519–1526. (doi:10.1098/rstb.2002.1061)

3. Stroeymeyt N, Giurfa M, Franks NR. 2010 Improving decision speed, accuracy and group cohesion through early information gathering in house-hunting ants. *PLoS ONE* **5**, e13059. (doi:10.1371/journal.pone.0013059)

4. Pratt SC. 2010 Nest site choice in social insects. *Encycl. Anim. Behav.* **2**, 534–540. (doi:10.1016/B978-0-08-045337-8.00127-3)

5. Franks NR, Mallon EB, Bray HE, Hamilton MJ, Mischler TC. 2003 Strategies for choosing between alternatives with different attributes: exemplified by house-hunting ants. *Anim. Behav.* **65**, 215–223. (doi:10.1006/anbe.2002.2032)

6. Dornhaus A, Franks NR, Hawkins RM, Shere HNS. 2004 Ants move to improve: colonies of *Leptothorax albipennis* emigrate whenever they find a superior nest site. *Anim. Behav.* **67**, 959–963. (doi:10.1016/j.anbehav.2003.09.004)

7. Bates DM, Bolker B. 2012 lme4: linear mixed-effects models using S4 classes. R package v. 0.999999-0. See http://cran.r-project.org/web/packages/lme4/index.html.

8. R Development Core Team. 2012 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

9. Sarkar D. 2008 *Lattice: multivariate data visualization with R*. New York, NY: Springer.

10. Warnes GR *et al*. 2012 gplots: various R programming tools for plotting data. See http://cran.r-project.org/web/packages/gplots/index.html.

11. All AM, Terms J. 1984 Fighting and assessment in *Harpobittacus* scorpionflies. *Soc. Study Evol.* **38**, 204–214.

12. Arnott G, Elwood RW. 2008 Information gathering and decision making about resource value in animal contests. *Anim. Behav.* **76**, 529–542. (doi:10.1016/j.anbehav.2008.04.019)