



Research

Cite this article: Pinter-Wollman N. 2015
Nest architecture shapes the collective behaviour of harvester ants. *Biol. Lett.* **11**: 20150695.
<http://dx.doi.org/10.1098/rsbl.2015.0695>

Received: 12 August 2015

Accepted: 23 September 2015

Subject Areas:

behaviour

Keywords:

collective behaviour, foraging, network theory, *Veromessor andrei*

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2015.0695> or via <http://rsbl.royalsocietypublishing.org>.

Animal behaviour

Nest architecture shapes the collective behaviour of harvester ants

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Structures influence how individuals interact and, therefore, shape the collective behaviours that emerge from these interactions. Here I show that the structure of a nest influences the collective behaviour of harvester ant colonies. Using network analysis, I quantify nest architecture and find that as chamber connectivity and redundancy of connections among chambers increase, so does a colony's speed of recruitment to food. Interestingly, the volume of the chambers did not influence speed of recruitment, suggesting that the spatial organization of a nest has a greater impact on collective behaviour than the number of workers it can hold. Thus, by changing spatial constraints on social interactions organisms can modify their behaviour and impact their fitness.

1. Introduction

Social behaviour emerges from interaction networks which operate and form within a spatial context. Despite the defining role of spatial behaviour in the formation of interactions, because spatial proximity is necessary for an interaction to occur, spatial and ecological constraints influencing the structure and function of social networks are seldom considered in studies of social and collective behaviour [1].

The collective behaviour of social insect colonies emerges from interactions among workers. Colonies of harvester ants regulate their foraging activity through antennal interactions among workers which occur in the nest chamber closest to the nest entrance, the 'entrance chamber' [2]. The location of interactions within the entrance chamber is spatially heterogeneous [3], influencing who interacts with whom and determining the topology of the interaction network [4]. Network topology influences the speed at which information, e.g. about a food source, propagates through the colony and, therefore, the regulation of collective behaviour. Thus, spatial constraints inside the nest, which shape interactions, may affect the collective behaviour of harvester ants.

Nests of social insects are complex structures comprising chambers connected by tunnels [5]. Although much research has been devoted to understanding the simple construction rules from which complex nest structures emerge [6], we do not know how nest architecture influences collective behaviour. The structures that social insects construct have been described using networks in which chambers are nodes and tunnels are links [7]. Network theory allows the comparison of nest complexity among colonies [8]. Furthermore, network measures may provide mechanistic explanations for how various collective processes are successfully achieved inside the nest. For example, as the redundancy of connections among chambers increases, i.e. more than one path connects two chambers, so will the efficiency and robustness of information flow within the nest [7]. Similarly, higher connectivity among nest chambers may increase the speed of resource transportation [9]. Here I use network theory to analyse nest architecture and relate it to colony foraging in a natural habitat to uncover how nest architecture influences collective behaviour.

Colonies of the true harvester ant, *Veromessor andrei*, are monodomous yet often relocate among nest sites, that either they or other colonies excavated, to avoid competition with conspecifics [10] and exploit new resources [11]. The collective foraging of these colonies changes as they move among nests, suggesting that nest site impacts collective behaviour [12]. This natural relocation behaviour provides a unique opportunity for examining how the collective behaviour of a colony is influenced by the spatial constraints imposed by the architecture of different nests. Observing the behaviour of a colony at multiple nest sites naturally controls for confounding variables related to the composition of the colony, such as number of workers. Here I examine which architectural features of the nest influence collective foraging behaviour. Specifically, I ask if the speed of recruitment to food increases with: (i) entrance chamber volume, a proxy for the maximum number of ants that may occupy that chamber; (ii) connectivity of the entrance chamber, allowing recruitment of ants from a variety of locations; (iii) connectivity of all chambers, which facilitates the speed of information flow throughout the nest; and (iv) the redundancy of connections among chambers, measured as meshedness [7,9], which allows robust recruitment of ants from inside the nest.

2. Material and methods

(a) Study site

The research was conducted at the Elliot Chaparral Reserve, University of California San Diego. In March 2013, I conducted 2 m-wide transects to locate all 28 *V. andrei* colonies in an area of 100 × 300 m. Behavioural observations were conducted from 1 April to 31 May 2013. I monitored the location of all colonies three times a week as in [12] and the electronic supplementary material.

(b) Collective recruitment to food

To measure how quickly colonies recruited to food, I placed a piece of 1 cm³ of apple 10–15 cm from the nest entrance and any active foraging trails during the morning foraging activity period (07.30–10.00 h) [13]. I counted the number of ants on the apple every minute for 20 min. This number increased over time and then saturated producing a nonlinear relationship between number of recruited ants and time (electronic supplementary material, figure S1). To quantify speed of recruitment, while taking into account its nonlinear nature, I fitted the following expression to the number of ants at the apple over time: $N(t) = N_{\max} \times t / (T_{50} + t)$, where N_{\max} is the maximum number of ants recruited, T_{50} is the time at which 50% of N_{\max} ants were recruited and t is time. I used the inverse of T_{50} ($1/T_{50}$) as the speed of recruitment and only considered trials for which $N_{\max} \geq 4$, thus excluding 22 out of 154 trials which ended after a colony concluded its morning activity. Experiments never started before foraging activity began and there was no relationship between N_{\max} and the time of day a colony was sampled (regression of N_{\max} versus time nested in colony: $t = -0.18$, $p = 0.86$). Each colony was assayed for recruitment to food once a week and because residency duration at a nest site varied, this resulted in one to eight trials (mean = 2.9) for each colony at each of its nest sites (electronic supplementary material, figure S2). Because recruitment speed did not significantly differ among trials (ANOVA: $F_7 = 0.65$, $p = 0.7$) or change with weather (linear regression: temperature $t = 0.44$, $p = 0.66$, dew point: $t = -0.74$, $p = 0.46$), I used the average recruitment speed at each nest site. See the electronic supplementary material, table S1, for observed N_{\max} and T_{50} values.

(c) Nest relocations

Nest relocations occurred throughout the study period. A given colony occupied one to eight unique nest sites and moved on average 10.58 m up to eight times during the two months of the study. Of the 28 colonies and 106 nest sites, I obtained both behavioural data and nest casts from 32 nest sites occupied by 17 different colonies. The electronic supplementary material, figure S2 illustrates the observation regime which allowed monitoring the behaviour of the same colony at multiple nest sites, producing an unbalanced block design.

(d) Nest casts

To obtain measurements of nest architecture, I created plaster casts of vacated nests post relocation, see the electronic supplementary material and figure 1.

(e) Network measures

(i) Entrance chamber

To examine whether collective recruitment is influenced by the number of chambers the entrance chamber is connected to, I calculated its connectivity as degree. If more than one entrance chamber was identified because there were multiple nest entrances, the mean value of their degree was used.

(ii) Global network measures

To examine whether collective recruitment to food is influenced by global patterns of connections among all chambers in the network, I calculated: (i) average degree—the average number of connections of all chambers in the cast; and (ii) meshedness, a measure of connection redundancy which is the number of observed cycles (figure 1*d*) in a network ($m - n + 1$; m , number of links; n , number of nodes) divided by the number of the maximal possible cycles in a planar network ($2n - 5$) [7,9].

(f) Statistics

To determine the relationship between recruitment speed at a nest site and entrance chamber degree, average chamber degree, cast meshedness, entrance chamber volume and the volume of chambers connected to the entrance chamber, I used mixed-effect models with colony as a random effect.

3. Results

Speed of recruitment increased with chamber connectivity, both of the entrance chamber (figure 2*a*) and mean connectivity of all chambers (figure 2*b*). There was a significant positive relationship between the number of chambers, the entrance chamber was connected to (entrance chamber degree) and the speed of recruitment (general linear mixed model (GLMM): $F = 4.61$, $p = 0.05$; figure 2*a*). Furthermore, there was a significant positive relationship between recruitment speed and the connectivity of all chambers (average degree) (GLMM: $F = 6.13$; $p = 0.03$; figure 2*b*).

As the redundancy in connections among chambers increased, so did the speed of recruitment to food. The proportion of cycles in the network of chambers (meshedness) positively correlated with recruitment speed (GLMM: $F = 4.46$, $p = 0.05$; figure 2*c*). Interestingly, I did not detect a significant relationship between recruitment speed and the volume of the entrance chambers (GLMM: $F = 0.66$,

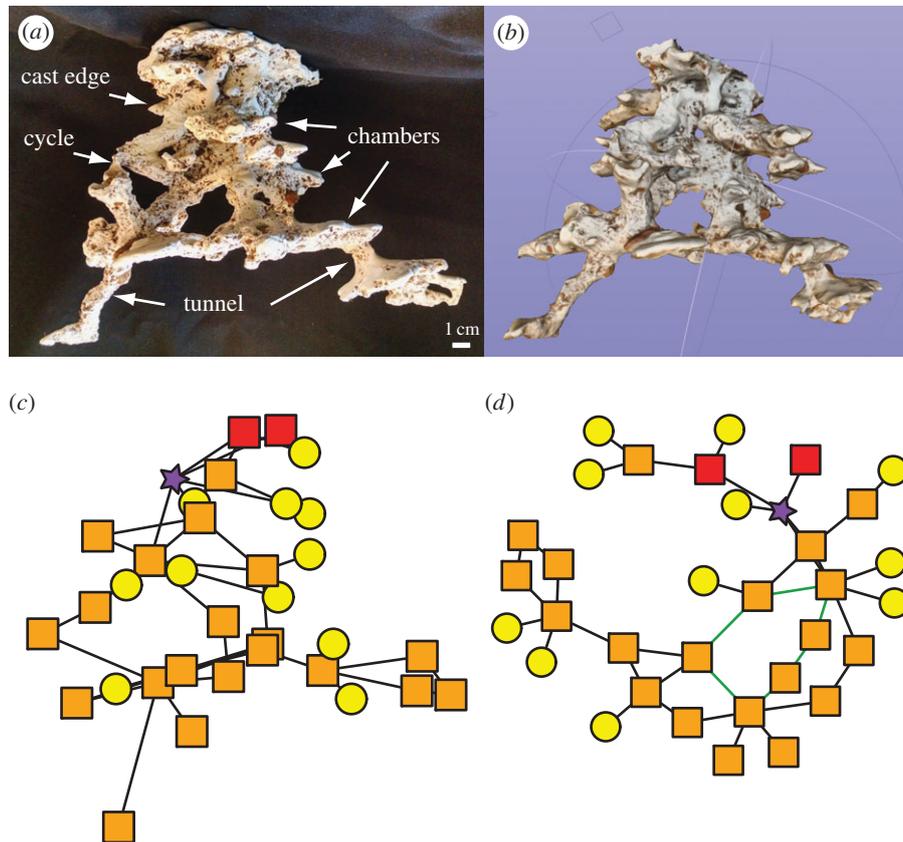


Figure 1. Cast of a nest site. (a) Image of a plaster cast. (b) Three-dimensional digitized object of the cast. (c,d) Network representations of a nest (red squares, nest entrances; orange squares, chambers; purple star, entrance chamber; yellow circles, cast edges and links, tunnels). Nodes are laid out based on spatial position (c) or (d) using the Fruchterman–Reingold algorithm (igraph R package) to enhance visibility of network features. Links in green form a cycle. (Online version in colour.)

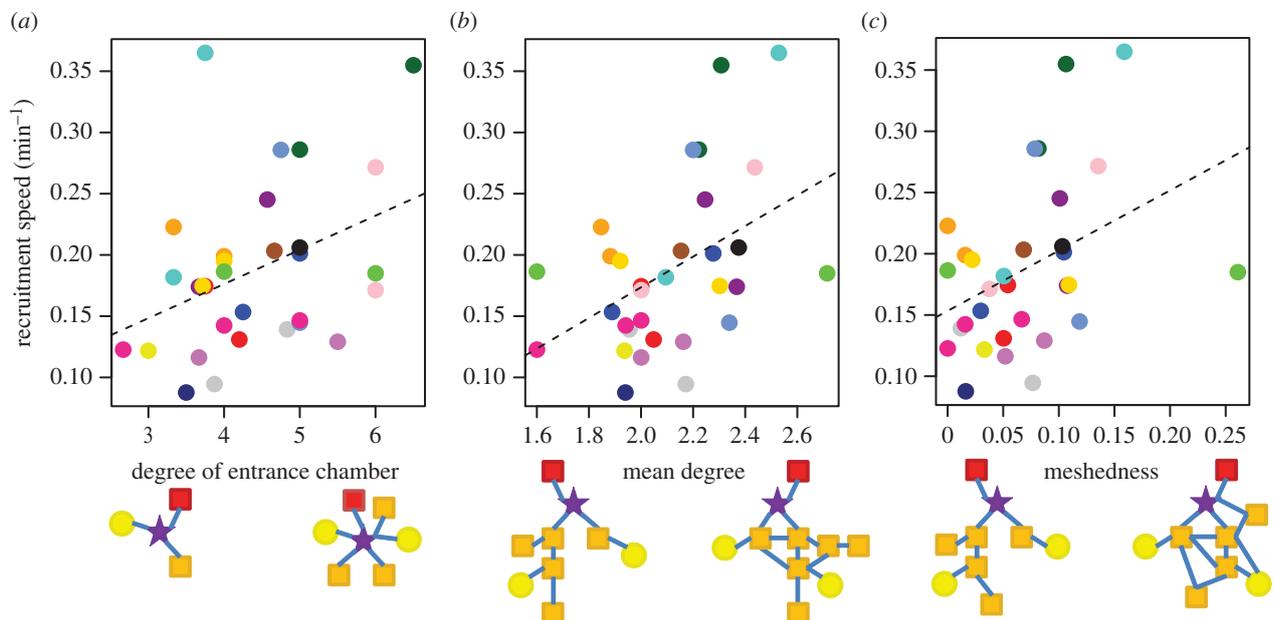


Figure 2. Nest architecture influences collective behaviour. Recruitment speed increases with connectivity of the entrance chamber (a); mean connectivity of chambers (b); and redundancy of connections, i.e. meshedness (c). Each point represents a colony in a particular nest site and each colony is depicted in a different colour. (Online version in colour.)

$p = 0.43$) even though this volume negatively correlated with entrance chamber degree (GLMM: $F = 8.8$, $p = 0.01$), and there was no relationship between recruitment speed and the volume of chambers connected to the entrance chambers (GLMM: $F = 0.5$, $p = 0.48$). See the electronic supplementary material, figure S4. These findings suggest that the spatial organization of the nest's chambers has a greater

impact on the collective behaviour of the colony than the number of workers these chambers can potentially hold.

4. Discussion

Uncovering the relationship between nest structure and colony function provides insights on how architecture

shapes collective outcomes by affecting social interactions. My findings suggest that the structure of the top part of a nest, and not the number of ants the chambers can hold, determines the dynamics of collective foraging. As the number of chambers an entrance chamber is connected to increases, so does the variety of locations from which ants can be recruited to outside work, thus influencing the availability of foragers at the entrance chamber which can affect foraging regulation [3]. Furthermore, the more connections among network nodes, i.e. nest chambers, the faster the spread of information, for example, about a new food source, throughout the network and therefore recruitment speed [4]. Finally, higher redundancy of connections among chambers, measured as meshedness [7,9], provides alternate routes, increasing the robustness of recruitment of ants from inside the nest for example, if a path is temporarily blocked. These field-based observations lay a foundation for further controlled laboratory experiments that are needed to establish the causative relationship between nest structure and collective behaviour. Past studies examined how nest architecture buffers the physical environment by regulating temperature or gas exchange [14] and the age distribution of workers within a nest [15]. However, this is, to my knowledge, the first study that directly links naturally occurring nest architecture and the collective actions of the colony that resides in it.

There is an intricate feedback between the collective behaviour of the colony and the nest structure in which it resides because colonies construct their nest or select vacated nests that were constructed by them or other colonies. However, nest selection or construction are collective processes that operate at a different timescale from the foraging activity that is affected by nest architecture. This timescale separation allows the analysis of the effects of nest architecture on collective foraging. Colonies that construct the nest into which they

relocate experience little change in architecture [16] and may therefore retain their foraging dynamics. However, if colonies relocate into existing nests, as examined here, the architecture of successive sites will differ (figure 2) and foraging behaviour will change as colonies relocate [12]. Although evidence for nest remodelling by *V. andrei*, in the form of fresh dirt pellets outside the nest entrance, has been observed after rain (personal observations), this study was conducted at a dry site [11] and evidence for remodelling was never observed while this work was conducted. One might reason that colonies will remain for a longer duration in nests that facilitate rapid recruitment to food. However, I detected only a non-significant positive relationship between recruitment speed and a colony's tenure at a particular nest site (Pearson's correlation: $r = 0.03$, $p = 0.87$) most likely because many other factors, such as food availability and population density [10,11], also influence nest relocation. When an incipient colony excavates a nest, or when colonies remodel the top part of their nest after rain, they construct a niche [17] that will influence the success of other colonies in the population. The factors that determine the structure of these nests, and whether local ecological conditions that influence foraging efficiency feedback on the excavation process, remain to be examined.

Ethics. The work conducted complies with the ethical regulations of the United States of America.

Data accessibility. Data presented are available on Dryad: <http://dx.doi.org/10.5061/dryad.35rt2>.

Competing interest. There are no competing interests.

Funding. Funding was provided by the National Academies Keck Futures Initiative and the NSF IOS grant no. 1456010.

Acknowledgements. Annamarie Go and James Huettner helped collect data, Roy Wollman assisted with data analysis and Jurgen Schulze advised on cast digitization.

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