Allometric scaling of ant foraging trail networks

Joseph Jun,[1,2] John W. Pepper,[1] Van M. Savage,[1,3]* James F. Gillooly[4] and James H. Brown[1,4]

[1]*Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501,* [2]*Center for Complex Systems Research, Department of Physics, University of Illinois at Urbana-Champaign, 1110 W. Green Street, Urbana, IL 61801,* [3]*Theoretical Division, Los Alamos National Laboratory, Los Alamos, NM 87545 and* [4]*Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA*

ABSTRACT

The aggregation of individuals into colonies raises important questions about scaling of structure and function. We model the metabolic benefits and costs of two-dimensional, fractal-like foraging trails, such as those used by ant colonies. Total area foraged by the colony and, consequently, resource flow to the nest and rate of colony metabolism, increase non-linearly with number of foragers (F) as $F^{2/3}$. Since the cost of foraging increases linearly with F, the model predicts an optimal number of foragers and, therefore, total foraging area that maximize colony fitness or energy allocation to reproduction. The scaling of foraging may influence evolution of coloniality.

Keywords: allometry, coloniality, foraging, optimal networks, social insects.

INTRODUCTION

A major transition in organic evolution is the association of individual organisms to form colonies (Buss, 1987; Maynard-Smith and Szathmary, 1995). By remaining together and coordinating their activities, individuals create a new level of biological organization that has its own emergent informational and metabolic properties. Allometric scaling laws for individual organisms describe how body size influences structure and function (Schmidt-Nielsen, 1984; Brown *et al.*, 2000). Additional problems of scaling arise as individuals aggregate into colonies. How do critical structures and functions vary with colony size, and how do these scaling relations affect the ecology and evolution of colonial organisms?

Social insects have provided seminal insights into the causes and consequences of coloniality with respect to both information, including genetics and communication, and metabolism, including energetics of foraging, growth, maintenance and reproduction (Wilson, 1971; Bourke and Franks, 1985; Pasteels and Deneubourg, 1987; Lighton, 1989; Hölldobler and Wilson, 1990; Seeley, 1995). Important questions concern how resource acquisition and allocation scale with colony size, how foraging activities are organized for efficient resource uptake, and what limits the size of colonies and the areas that they forage.
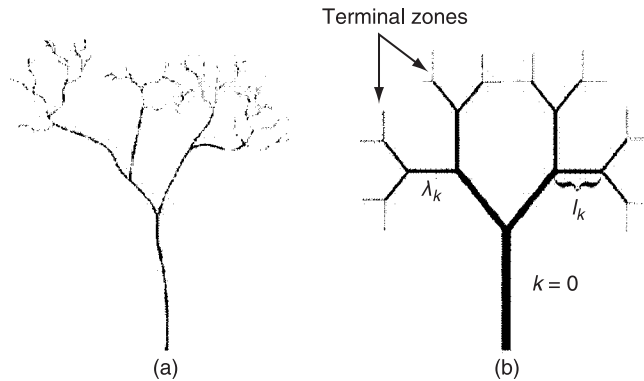

Fig. 1. (a) The trail network for the harvesting ant, *Pheidole militicida* (redrawn from Hölldobler and Wilson, 1990). (b) Schematic representation of a trail network. Line thickness represents the ant density at the kth branching level, λ_k. Here the branching ratio is $n = 2$, the number of branching levels is $T = 4$ and the number of terminal zones is $n^T = 16$.

Here we address questions about scaling of energetics and metabolism of colonies by modelling the foraging of ants. Large ant colonies typically forage along trunk trails that have a fractal-like branching structure (Fig. 1a); they can be semi-permanent structures that extend hundreds of metres (Hölldobler and Wilson, 1990). Recent models that describe the metabolic scaling of individual organisms base themselves on special features of hierarchically branched distribution networks, such as plant and animal vascular systems (West *et al.*, 1997, 1999). A similar model for ant foraging trails leads to quantitative predictions of how resource uptake and foraging area scale with the number of foragers. The model also implies that there is an optimal colony size that maximizes the rate of resource allocation to reproduction.

THE NETWORK MODEL FOR ANT FORAGING TRAILS

The model considers a colony containing worker ants of a single species in a given environment. Each individual forager travels along trails between the nest and a foraging zone, where it searches for food items. These types of networks are believed to arise as adaptations that enhance the collection of certain kinds of food resources, defence against predators and parasites, communication by chemical and tactile signals and other benefits (Hölldobler, 1976; Hölldobler and Lumsden, 1980; Acosta *et al.*, 1995). The trails form a hierarchical branching network that originates in a single trunk at the nest, at branching level $k = 0$. Each branch splits into n branches at each of T branching levels, and the network terminates in n^T foraging zones (Fig. 1b). Each branching level has a characteristic length, l_k, and density (per unit length) of foragers, λ_k.

We make several assumptions to characterize the geometry and dynamics of the network:

(a) There is a constant rate of resource supply per unit area per unit time.

(b) Resources are harvested, transported to the nest and consumed with minimal time lags. Consequently, transient, non-steady-state dynamics, such as temporary resource depletion (overharvesting) and storage of resources in the colony, are ignored.

(c) The metabolic rate of the ant colony, B, is proportional to the resource intake rate, which, in turn, is proportional to the rate of resource supply, $\dot{R}$, so that $B \propto \dot{R}$. Losses of resources are ignored: all resources available in the environment are harvested and all harvested resources are consumed. B includes all energy use by the colony. Net gains from foraging are allocated to some combination of growth (production of additional foragers) and reproduction (production of alates).

(d) Individual foragers are equivalent. They travel at constant speed, v, and are similar in size, behaviour and metabolic rate.

(e) The smallest branches end at foraging zones of fixed area and have invariant flow rates.

(f) The non-overlapping foraging zones of the trail termini are densely packed; they completely fill the colony foraging area.

(g) The trail network is hierarchical and fractal-like. It can be characterized by scale factors (Fig. 1b):

$$\text{length ratio: } \gamma_k \equiv \frac{l_{k+1}}{l_k} \tag{1}$$

$$\text{forager density ratio: } \beta_k \equiv \frac{\lambda_{k+1}}{\lambda_k} \tag{2}$$

(h) The branching ratio of the paths, n, remains constant, which means that there is a total of n^T terminal branches and foraging zones. Assumptions (g) and (h) can be relaxed to permit asymmetrical space-filling branching without affecting our results (Turcotte *et al.*, 1998).

(i) We assume that all ants leaving the colony complete a circuit to a foraging zone and back (i.e. that deaths and incomplete forays have a negligible effect on the flux of foragers). Together with assumption (d) and time-averaging to smooth out stochastic fluctuations, this means that the flux of foragers through the trail network is conserved.

These assumptions lead to two important properties of the model:

1. *Space-filling*: each level of branching divides the total foraging area into non-overlapping sub-areas whose sizes are determined by the branch lengths at level k. Following the model of West *et al.* (1997), but for two dimensions, this leads to the following relationship for sizes and numbers of branches as a function of k:

$$n^k l_k^2 = n^{k+1} l_{k+1}^2 \tag{3}$$

$$\gamma_k \equiv \gamma = \frac{l_{k+1}}{l_k} = n^{-1/2} \tag{4}$$

2. *Flux-preserving*: since the flux of foragers is conserved across branching levels, we can relate the total flux of foragers returning to the nest, $\dot{Q}_0$, to the flux at each level:

$$\dot{Q}_0 = \lambda_0 v = n^k \lambda_k v = n^{k+1} \lambda_{k+1} v = n^T \lambda_T v \tag{5}$$

$$\beta_k \equiv \beta = \frac{\lambda_{k+1}}{\lambda_k} = \frac{1}{n} \tag{6}$$

Using these properties, we derive the scaling exponent, which relates the total number of foragers, F, to the properties of the network:

$$F = \sum_{k=0}^{T} \lambda_k l_k n^k = n^T \lambda_T l_T \frac{1 - (n\beta\gamma)^{-(T+1)}}{1 - (n\beta\gamma)^{-1}} \tag{7}$$

Since $n\beta\gamma < 1$ and $T \gg 1$, equation (7) is closely approximated by:

$$F \approx l_T \lambda_T \frac{(\beta\gamma)^{-T}}{1 - n\beta\gamma} = l_T \lambda_T \frac{n^{(3T/2)}}{1 - n^{-1/2}} \tag{8}$$

Based on assumptions (d) and (e), λ_T and v are constants, so equation (5) implies that $\dot{Q}_0$ is proportional to the total number of foraging sites, n^T. Furthermore, based on equation (8) and assumptions (e) and (h), n^T scales as $F^{2/3}$ and, therefore, by assumption (c) resource acquisition and metabolic rate scales as $B \propto \dot{Q}_0 \propto n^T \propto F^{2/3}$. This implies that colony metabolism is given by $B(F) = B_0 F^{2/3}$, where B_0 is a normalization factor. B_0 will vary with characteristics of the ant species, such as forager size, and of the environment, such as resource availability.

OPTIMAL COLONY SIZE: ENERGETIC CONSTRAINTS AND PREDICTIONS

The scaling of the trail network, net resource uptake and colony metabolism as a function of forager number leads to predictions for maximal and optimal colony size (Fig. 2). The net rate of energy gain, $\dot{G}$, from foraging is simply $\dot{G} = B - \dot{C}$, where $\dot{C}$ is the rate cost of foraging. Therefore, $\dot{C}$ is the cost of collecting food, and the total metabolic rate of the colony minus this cost of foraging represents the rate of energy accumulation that can be allocated to growth and reproduction. Based on assumption (d), it follows that this cost, $\dot{C}$, increases linearly with the number of foragers. From this assumption and equation (8), which implies that $B \propto F^{2/3}$, we can derive an expression for the net rate of energy gain:

$$\dot{G} = B_0 F^{2/3} - \dot{C}_0 F \tag{9}$$

where both B_0 and $\dot{C}_0$ are normalization constants.

Gross energy intake rate per forager, therefore, decreases with increasing number of foragers, $(B/F) \propto F^{-1/3}$. Consequently, there is an optimal number of foragers, $F_{opt} = ((2/3)(B_0/\dot{C}_0))^3$, which maximizes the net rate of energy gain so that $\dot{G} = \dot{G}_{max}$ (Fig. 2). Since $\dot{G}$ represents the rate at which energy can be allocated to other components of fitness such as colony growth (production of sterile castes) and reproduction (production of alates), the colony should grow until it reaches optimal size; then, all further net energy intake should be allocated to production of reproductives. This means that the optimal colony size is substantially smaller than the maximum possible colony size at which all incoming energy would be allocated to maintenance and none would be available for reproduction. Although our model is expressed in terms of the number of foragers, if the energetic costs of producing and maintaining other castes are known, it should be possible to develop expressions for optimal numbers of other castes and hence for total colony size. This model has features in common with previous attempts to understand energetic consequences of colony size (Oster and Wilson, 1978; Hölldobler and Lumsden, 1980; Torres and Trainor, 1993), but it differs in its explicit application of allometric scaling theory.
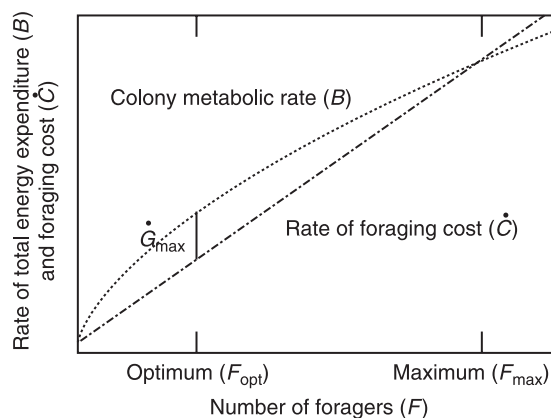
Fig. 2. Rate of energy intake B (dotted line) and expenditure $\dot{C}$ (dashed and dotted line) as a function of number of foragers F. The rate of net energy gain, $\dot{G} = B - \dot{C}$, is maximized at $F = F_{opt}$ and is zero at $F = F_{max}$.

RESULTS AND DISCUSSION

The model offers insight into the metabolism of ant colonies, such as how energetics constrain colony growth and result in optimal and maximal colony size. Previous qualitative cost–benefit models predicted an optimal colony size (Oster and Wilson, 1978), but our allometric model makes explicit quantitative predictions for how the number of foragers determines the income of energy available for colony growth and reproduction. Figure 2 can also be interpreted in terms of colony foraging area, which corresponds to rate of energy intake. Foraging area grows slower than linearly with increasing numbers of foragers, as $F^{2/3}$. This is a fundamental constraint of the network: as larger colonies use larger areas, each forager spends proportionately more time travelling between the nest and its foraging zone, and the colony has a greater proportion of its foragers in transit as opposed to searching for food. This scaling limits colony metabolism and affects the allocation of energy and resources to growth and reproduction, similar to the way that constraints of vascular supply limit metabolic rate and allocation to growth and reproduction in individual organisms.

We are well aware that many ant species do not conform exactly to all assumptions of our model. For example, workers may vary in size, travel speed and size of food particles transported. Like any model, ours is a deliberate oversimplification of a more complex reality. Some of the assumptions, which were made for simplicity, can be relaxed without changing the predicted scalings. For example, assumption (a), that there are equal rates of resource supply per unit area, can be relaxed so long as there is an average rate of supply to the colony foraging area that is constant with respect to the total number of foragers in the colony. Assumption (c), that all available resources are harvested and then consumed, could be relaxed by incorporating terms for losses. If a model is useful, it should capture the fundamental essence of pattern and process and lead to increased understanding of how nature – in this case, an ant colony – works. We believe that our model does help to explain and to ask new questions about the functional organization and scaling relations of ant colonies.

Our model makes predictions about foraging efficiency, net energy return from foraging and colony foraging area as functions of the number of foragers. We are unaware of studies

of ant colonies that provide data of sufficient precision to test these predictions quantitatively. What is known about ants that use trunk trails for foraging is consistent with the model. The geometry of foraging trails is often fractal-like (Fig. 1a) (Hölldobler and Wilson, 1990). For the desert harvester ant, *Pogonomyrmex barbatus*, approximately four trunk trails tend to leave a colony entrance (Gordon and Kulig, 1996). Our model considers only one trunk trail, so that a multiplicative constant is necessary to describe colonies with multiple trunks.

Information that colonies grow logistically to some approximately constant size (Hölldobler and Wilson, 1990) is consistent with an optimal number of foragers. For example, in *P. barbatus* the number of foragers and total colony foraging area increase rapidly after colony founding, reach relatively stable levels after 3–5 years, and then maintain these values for the life of the colony, which may be 15–20 years (Gordon, 1992, 1995; Gordon and Kulig, 1996). According to Lighton (1989), the cost of foraging (total energy expenditure by foragers) apparently does increase linearly with the number of foragers, as the model assumes (e.g. Fig. 2). Additionally, one cost of foraging that has been measured – mortality of foragers due to fighting with neighbouring colonies – varies linearly with the number of foragers (Gordon and Kulig, 1996), which is again consistent with the assumption of our model.

This study raises interesting questions about how the metabolic and informational systems of colonies are integrated. Our model does not explain why ants should use trunk trails in the first place. An alternative foraging strategy would have each forager travelling directly to and from its foraging site by the straightest path. Honeybees and some ants that maintain small colonies use such individual foraging. The advantages of using fractal-like trunk trails include: (i) the space-filling property facilitates efficient harvesting of resources throughout the colony foraging area; (ii) the pheromone and tactile cues used to mark the trails transmit information that facilitates navigation to and from the nest and recruitment to resources; (iii) maintenance of semi-permanent major trunks promotes rapid, efficient travel; (iv) trunk trails help avoid competition for strictly central-place foraging (Hölldobler, 1976; Hölldobler and Lumsden, 1980; Acosta *et al.*, 1995).

The model and this allometric approach to the costs and benefits of coloniality raise further questions about how the colony obtains, processes and uses information to regulate its size and allocate its resources to growth, maintenance and reproduction. The existence of an optimal number of foragers provides a quantitative measure of one advantage of coloniality because net energy gain, $\dot{G}$, is maximized when $F > 1$. This, in turn, raises questions about how natural selection operates to control and integrate the activities of the individuals for the metabolic welfare and evolutionary fitness of the colony. Perspectives from allometric scaling offer potentially valuable insights into other evolutionary transitions, such as those that produced multicellular organisms, colonial animals and human societies.

REFERENCES

Acosta, F.J., López, F. and Serrano, J.M. 1995. Dispersed versus central-place foraging: intra- and intercolonial competition in the strategy of trunk trail arrangement of a harvester ant. *Am. Nat.*, **145**: 389–411.

Bourke, A.F.G. and Franks, N.R. 1995. *Social Evolution in Ants*. Princeton, NJ: Princeton University Press.

Brown, J.H., West, G.B. and Enquist, B.J. 2000. Scaling in biology: patterns and processes, causes and consequences. In *Scaling in Biology* (J.H. Brown and G.B. West, eds), pp. 1–24. Oxford: Oxford University Press.

Buss, L.W. 1987. *The Evolution of Individuality*. Princeton, NJ: Princeton University Press.

Gordon, D.M. 1992. How colony growth affects forager intrusion between neighboring harvester ant colonies. *Behav. Ecol. Sociobiol.*, **31**: 417–427.

Gordon, D.M. 1995. The development of an ant colony's foraging range. *Anim. Behav.*, **49**: 649–659.

Gordon, D.M. and Kulig, A.W. 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecology*, **77**: 2393–2409.

Hölldobler, B. 1976. Recruitment behavior, home range orientation, and territoriality in harvester ants *Pogonomyrmex*. *Behav. Ecol. Sociobiol.*, **1**: 3–44.

Hölldobler, B. and Lumsden, C.J. 1980. Territorial strategies in ants. *Science*, **210**: 732–739.

Hölldobler, B. and Wilson, E.O. 1990. *The Ants*. Cambridge, MA: Belknap Press.

Lighton, J.R.B. 1989. Individual and whole-colony respiration in an African Formicine ant. *Funct. Ecol.*, **3**: 523–530.

Maynard-Smith, J. and Szathmary, E. 1995. *The Major Transitions in Evolution*. Oxford: W.H. Freeman.

Oster, G.F. and Wilson, E.O. 1978. *Caste and Ecology in the Social Insects*. Princeton, NJ: Princeton University Press.

Pasteels, J.M. and Deneubourg, J.L., eds. 1987. *From Individual to Collective Behavior in Social Insects*. Basel: Birkhäuser.

Schmidt-Nielsen, K. 1984. *Scaling: Why is Animal Size so Important?* Cambridge: Cambridge University Press.

Seeley, T.D. 1995. *The Wisdom of the Hive: The Social Physiology of Honeybee Colonies*. Cambridge, MA: Harvard University Press.

Torres, J.-L. and Trainor, L.E.H. 1993. Energy function for a model of ant colonies. *J. Theor. Biol.*, **165**: 177–184.

Turcotte, D.L., Pelletier, J.D. and Newman, W.I. 1998. Networks with side branching in biology. *J. Theor. Biol.*, **193**: 577–592.

West, G.B., Brown, J.H. and Enquist, B.J. 1997. A general model for the origin of allometric scaling laws in biology. *Science*, **276**: 122–126.

West, G.B., Brown, J.H. and Enquist, B.J. 1999. A general model for the structure and allometry of plant vascular systems. *Nature*, **400**: 664–667.

Wilson, E.O. 1971. *The Insect Societies*. Cambridge, MA: Belknap Press.