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Theoretical and empirical perspectives on the scaling of supply and demand in social insect colonies

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Abstract

One of the central questions in physiological ecology is how energetic constraints affect organismal performance and the dynamics of ecological systems. Social insect colonies integrate the balance of supply and demand across levels of biological organization such that the individual components are simultaneously serving as the supply transport network and also the source of energetic demand. An increasing number of studies have demonstrated that the per-capita metabolic rates of individuals within social insect colonies decrease with increasing colony size, a metabolic hypometry much like the pattern exhibited by individual organisms. An important question is thus, whether this scaling pattern is a result of an energetic supply constraint or evidence for an emergent economy of scale. This review synthesizes theoretical models and results from empirical studies on the scaling of resource supply and demand in social insect colonies. Scaling in biology is a powerful tool to unify the study of diverse concepts and organisms; increased integration of mechanistic realism into metabolic models will improve our understanding of the evolution of complex biological systems.

Introduction

The structure and function of physiological systems and the nature of ecological interactions depend on many factors, but among the most influential are the effects of an organism's size (LaBarbera, 1986; Vogel, 2004; Bonner, 2006). The development of metabolic theories in ecology represents an approach to synthesizing a broad array of biological features as dependent on the combination of a body mass allometry and the exponential temperature dependence of metabolism (Brown et al., 2004; Sibly et al., 2012). Metabolic rates represent the net power consumption induced by the sum of all chemical reactions taking place within living organisms, and consequently they correlate with many physiological, life history, and ecological characteristics. Given an organism with mass (m) and body temperature (T), its metabolic rate (R) may be estimated by the equation:

$$R = am^b e^{cT},$$

for which the mass scaling coefficient (a), scaling exponent (b), and temperature coefficient (c) may be theoretically derived or estimated by statistical curve fitting to empirical data (Peters, 1983; Robinson et al., 1983). Although the coefficients vary by activity state and taxonomic groups, the mass scaling exponent is remarkably invariant, generally $0.5<b<1$ for both intraspecific and interspecific allometries and spanning more than 10–20 orders of magnitude in body size (Hemmingsen, 1960; Glazier, 2005). The relatively conserved nature of this exponent suggests that a common mechanism may be responsible, potentially across both developmental and evolutionary time scales. Two perspectives on explaining the emergence of metabolic allometry derive from differences in its interpretation, namely whether a supply constraint or an economy of scale is responsible for larger organisms using relatively less energy (e.g., per gram) than smaller organisms. One of the central questions in physiological ecology is thus, how variation in metabolic demand and energetic constraints affect organismal performance and the dynamics of ecological systems.

Energy has long been proposed as a unifying principle in ecology due to its hypothesized roles as an environmental constraint, driver for competitive behavior, and its transformative potential (Lotka, 1945; Hutchinson, 1959; Odum, 1968; Van Valen, 1973). Global patterns in the diversity of species have been suggested to be due to the

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interactions between body size and energy gradients in temperature and primary productivity (Kaspari et al., 2004; Kaspari & Weiser, 2012). The 'metabolic theory of ecology' predicts that metabolic rates scale with mass$^{0.75}$ because organisms have evolved under pressure from natural selection for energetic optimization to minimize the costs associated with the supply of substrates for metabolism through resource transport networks (West et al., 1997; Savage et al., 2008). Metabolic rates are thus thought to be constrained according to limited energetic resources in the environment and bottlenecks in their distribution throughout an organism. The theory builds on previously developed aspects of metabolic organization including the hierarchical and fractal design of physiological systems (Sernetz et al., 1985; Goldberger & West, 1987) and the concept of symmorphosis which predicts the evolution of optimal balancing of structure and function across the cascade of steps involved in resource transport (Taylor & Weibel, 1981). Although these approaches have received substantial criticism (Dudley & Gans, 1991; Kozłowski, 1996; Price et al., 2009; Callier & Nijhout, 2012), the theory has been extended to make predictions about dynamics at higher levels of biological organization, including range distributions and biodiversity (Brown et al., 2004), the global carbon cycle (Allen et al., 2005), and the collective metabolism of eusocial insect colonies (Hou et al., 2010). The question remains, however, whether or not the foundational principle of supply constraint is responsible for these broad patterns on a mechanistic level.

As an alternative to the hypothesis of energetic constraint, metabolic allometries may be driven by variation in metabolic demands. For example, the energy budgets of many organisms, including both ectothermic poikilotherms and endothermic homeotherms, depend on rates of heat exchange across surface areas. Because the surface areas of objects that maintain their shape and density as size increases scale with mass$^{2/3}$, the costs associated with matching the demand for metabolic heat production are expected to scale similarly and be relatively lower in larger than in smaller endothermic organisms (Rubner, 1883). Variation in metabolic demand is also associated with a hypometric allometry for the cost of transport (Taylor et al., 1970; Lighton, 1985), differential growth rates with age and body size (von Bertalanffy, 1957; Ricklefs, 2003), variation in the efficiency of lipid membranes (Hulbert & Else, 2000; Hulbert, 2005), the size of energetically active organs (Hammond & Diamond, 1997), and activity patterns (Reinhold, 1999; Seibel, 2007; Glazier, 2009). Although no single mathematical theory has been developed which takes all of these factors into account, they nevertheless may all contribute to and influence the allometry of metabolic rate.

The purpose of this review is to compare and contrast the relative effects of supply constraint and variation in energetic demand on the scaling of social insect colonies. Social insect colonies, including ants, bees, wasps, and termites, are characterized as eusocial when they have evolved a reproductive division of labor, communal brood care, and an overlapping of generations. The eusocial superorganisms may not be the most species-rich taxa on the planet, but by any measure of biomass or energy flux they have an extraordinary ecological impact (Wilson, 1987; Folgarait, 1998). Although colonies are composed of physically independent members, many aspects of social insect biology suggest that a whole colony is effectively a functionally integrated organism. Just as the separate cells making up individual organisms are supplied by physiological transport networks, patterns of connectivity emerge within social insect colonies as well (Figure 1). Resource transport and information exchange among the members of social insect colonies takes place through dynamic and spatiotemporally variable interaction networks (Wilson & Hölldobler, 1988; Fewell, 2003; Gordon, 2007). Honeybees transport the nectar and pollen from individuals that forage to developing larvae through a network of trophallaxis exchanges (Naug, 2008, 2009; Feigenbaum & Naug, 2010). Seed harvester and leaf-cutter ants transmit not only resources but also information about colony energetic state through interaction networks based on physical antennation patterns (Greene & Gordon, 2007; Bollazzi & Roces, 2011; Pinter-Wollman et al., 2011; Waters & Fewell, 2012). Has the evolution of these dynamic and self-organized networks within social insect colonies enabled them to break energetic constraints faced by unitary or individual organisms, or have they evolved alternative economies of scale? To begin to address this question, we may consider whether or not there are general patterns for how metabolic rates, behavioral patterns, and nutrient supply rates scale with colony size.

Scaling of metabolic rate in social insect colonies

Honey bee colonies were the first social insect systems shown to exhibit a metabolic allometry in a series of papers which demonstrated not only the empirical scaling pattern but also a convincing theoretical mechanism. As individual bees are capable of endothermy and their colonies behaviorally thermoregulate to establish a homeothermic environment in which to rear brood, the surface area law of heat loss applies and net metabolic demands decrease with increasing swarm, cluster, and colony sizes (Southwick, 1982, 1985). Homeothermy within the subterranean nests of ants and termites is

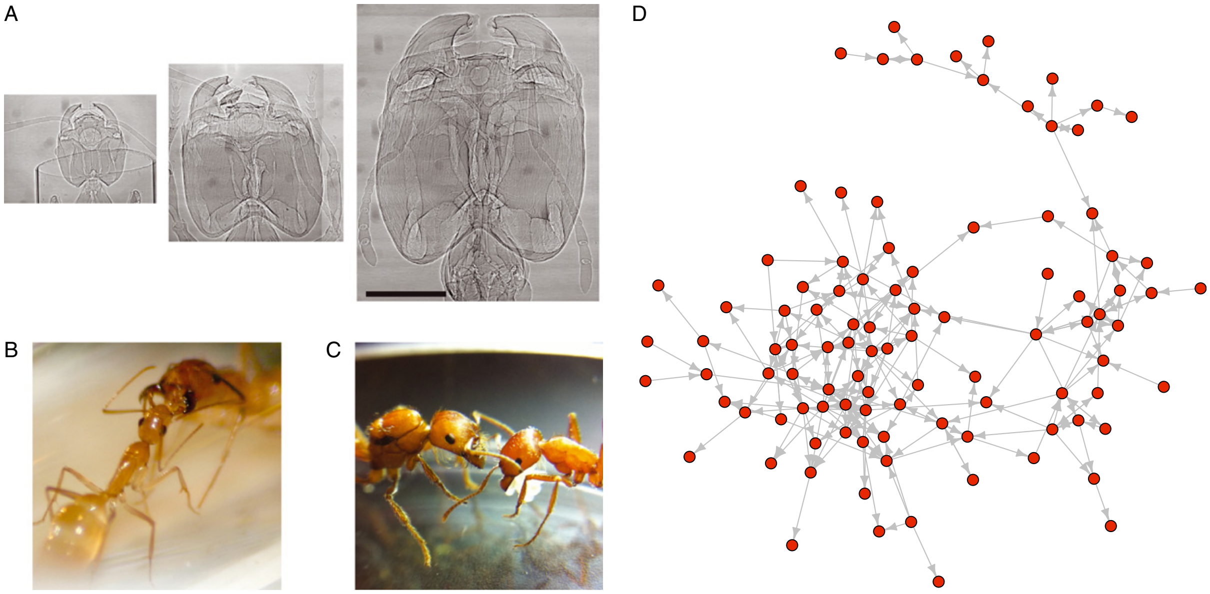

Figure 1 Communication networks and physiological transport systems function in social insects across a range of scales in biological organization. (A) Branching tracheal systems such as the one visualized here (*Pheidole rhea* Wheeler worker castes; scale bar = 1.0 mm) provide conduits for the transport and exchange of respiratory gasses. (B) Trophallaxis, photographed here between a major and minor worker of the ant species *Camponotus festinatus* (Buckley), involves the exchange of both nutrients and information about the colony's energetic state (Mc Cabe et al., 2006). (C) Patterns of physical interaction may also communicate information, such as the antennation between a worker and a queen in a colony of the seed-harvester ant *Pogonomyrmex californicus*. (D) The patterns of interaction between the individuals within a social insect colony may be aggregated and studied as communication networks, such as the one visualized here for *P. californicus* (Waters & Fewell, 2012).

expected for many species, but endothermy has been documented in only certain special cases (Rosengren et al., 1987; Franks, 1989; Roces & Núñez, 1989; Bollazzi & Roces, 2002; Penick & Tschinkel, 2008).

Is there a similar effect of group size on the per-capita metabolic rates of non-thermoregulating groups of ants? The first studies to investigate this demonstrated that for groups of ants, per-capita metabolic rates did not depend on group size (Brian, 1973; Lighton, 1989; Fonck & Jaffe, 1996). However, these studies focused at least in part on groups of ants extracted from their colony and thus removed from many of the social regulatory mechanisms that may otherwise influence their metabolic activity. From a methodological standpoint though, measuring whole colonies of social insects such as ants or termites is a daunting task, especially when obtaining repeatable measures of the metabolic rates of individual insects is already challenging itself (Lighton et al., 1993; Vogt & Appel, 1999; White et al., 2013). Individual ants behave differently when removed from their colony environment and so, to accurately test for an effect of group size, it is desirable to at least start with whole colonies, including the queen and brood. This can be done by collecting colonies from the field or by collecting queens following their mating flight and rearing colonies in the laboratory, but there are tradeoffs associated with either approach. Field collected colonies are more likely to have a natural composition with respect to age distributions and caste partitions, but collection of the whole colony may be difficult, and the collected colony will be more prone to the stressful environment of plastic nest boxes and respirometry chambers. Rearing colonies in the laboratory may minimize handling disturbance, alleviate some of the stress of being introduced to a new artificial environment, and reduce the probability of damage to the colony from its collection in the field, but the rearing can require an extensive commitment and offers no guarantee that the resulting colonies successfully develop into their reproductive stage or fully mature sizes.

Having overcome many of these technical obstacles, several recent studies have demonstrated that whole ant colonies exhibit metabolic hypometry (Figure 2, Table 1), both for intraspecific (Jaffe, 2010; Shik, 2010; Waters et al., 2010; Cao & Dornhaus, 2012) and interspecific allometries (Hou et al., 2010; Shik et al., 2012). Although the social insect allometry is generally the same as for individual organisms, there are no standard conditions for comparative analyses of whole-colony metabolic rates. The mammalian scaling data are compiled with rigorous criteria for

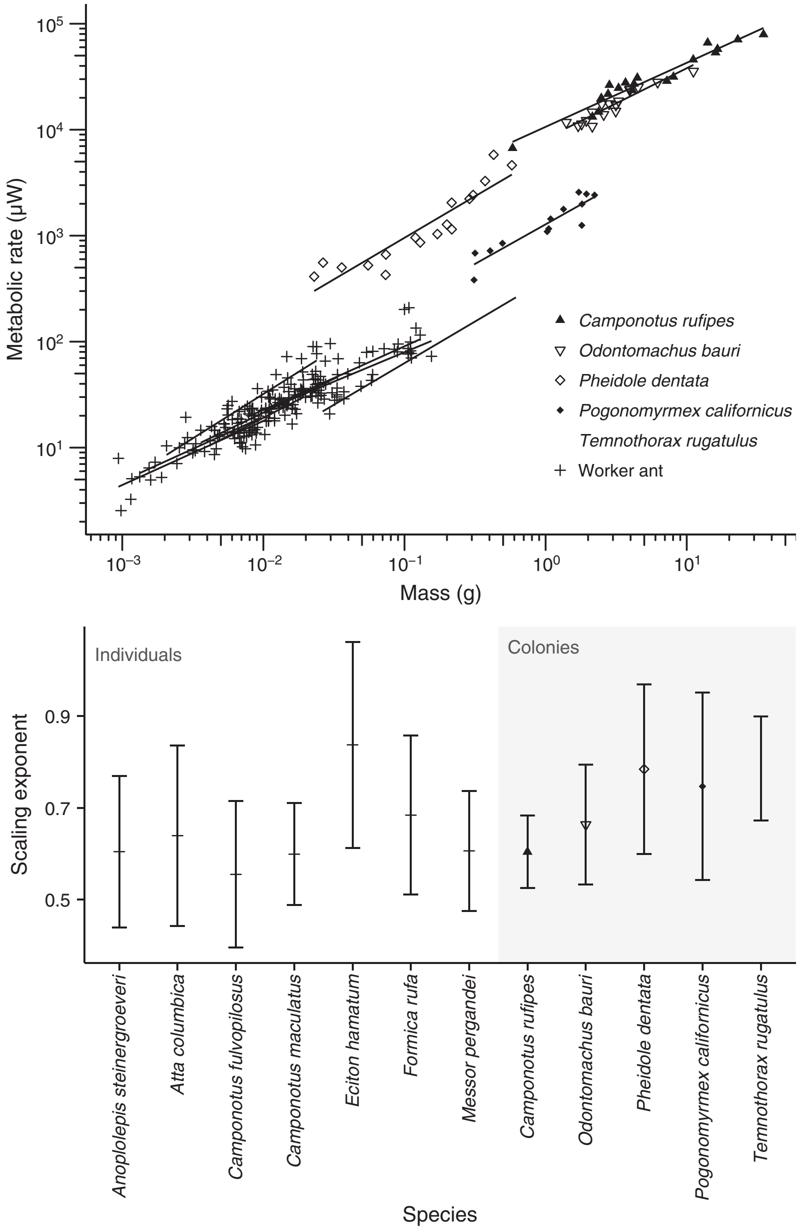

Figure 2 The scaling of metabolic rate in individual ants with body size and whole ant colonies with colony size follows an allometry with variable coefficients and a relatively constant hypometric scaling exponent. Sources for these data and statistical summaries for the individual regression lines may be found in Table 1.

organisms having been measured according to ‘basal’ or ‘standard’ conditions with respect to activity, nutritional state, and temperature. Whereas it may be possible to standardize feeding and temperature protocols for work with social insects, colonies generally do not disengage from behavior and the published works represent measures that might be classified as active, functioning, or field metabolic rate allometries.

Why might the per-capita metabolic demands of individuals within ant colonies decrease with colony size? Colony size can have a profound influence on the composition of individuals within a colony and the distribution and organization of their work (Oster & Wilson, 1978; Anderson & McShea, 2001; Dornhaus et al., 2012). In many species, average worker sizes increase with colony age, and in some polymorphic species, as colonies age and grow in size, morphological castes develop among the workers through genetic mechanisms, environmental conditions (e.g., seasonality), and the social regulation of food quantity and quality fed to larvae (Anderson et al., 2008). Through these processes, larger colonies may exhibit changes in the mean, variance, and modality of size distributions. These may be associated, for example, with groups of workers especially small for tending fungus

Table 1 Summary of regression models plotted in Figure 2

Data	Slope ± SE	95% confidence interval	Intercept ± SE	F-ratio	R^2	Source
Individual ants						
Anoplolepis steinergroeveri	0.60 ± 0.08	0.43–0.77	2.46 ± 0.19	$F_{1,26} = 56.7$	0.68	Chown et al. (2007)
Atta columbica	0.64 ± 0.10	0.44–0.84	2.61 ± 0.18	$F_{1,25} = 45.1$	0.64	Chown et al. (2007)
Camponotus fulvopilosus	0.56 ± 0.08	0.40–0.71	2.46 ± 0.11	$F_{1,22} = 52.2$	0.70	Chown et al. (2007)
Camponotus maculatus	0.60 ± 0.06	0.49–0.71	2.56 ± 0.09	$F_{1,48} = 117.8$	0.71	Chown et al. (2007)
Eciton hamatum	0.83 ± 0.11	0.61–1.06	3.18 ± 0.22	$F_{1,23} = 59.7$	0.72	Chown et al. (2007)
Formica rufa	0.68 ± 0.08	0.51–0.85	2.65 ± 0.17	$F_{1,18} = 68.9$	0.79	Chown et al. (2007)
Messor pergandei	0.61 ± 0.06	0.48–0.74	2.50 ± 0.15	$F_{1,19} = 94.2$	0.83	Chown et al. (2007)
Whole colonies						
Campotnotus rufipes	0.60 ± 0.04	0.53–0.68	4.03 ± 0.03	$F_{1,17} = 259.4$	0.94	Jaffe (2010)
Odontomachus bauri	0.66 ± 0.06	0.53–0.79	3.92 ± 0.03	$F_{1.15} = 117.2$	0.88	Jaffe (2010)
Pheidole dentata	0.78 ± 0.08	0.60–0.97	3.76 ± 0.08	$F_{1,15} = 81.83$	0.85	Shik (2010)
Pogonomyrmex californicus	0.75 ± 0.09	0.54–0.95	3.11 ± 0.03	$F_{1,11} = 64.8$	0.85	Waters et al. (2010)
Temnothorax rugatulus	0.79 ± 0.06	0.67–0.90	2.58 ± 0.05	$F_{1,27} = 202.0$	0.88	Cao & Dornhaus (2012)

gardens, or ones especially large, potential for colony defense or processing food items.

How might these changes in the body mass distribution of a colony affect predictions of its total metabolic rate? Consider a simplified version of an additive model (Waters et al., 2010) for predicting whole-colony metabolic rates (R_{colony}) as the sum of the metabolic rates for a colony of N ants with masses m_i:

$$R_{colony} = \sum_{i=1}^{N} a m_i^b .$$

If individual masses are normally distributed and the average ant mass does not scale with colony size, this model predicts a metabolic isometry. Alternatively, it predicts an allometry if average masses change with colony size, as has recently been demonstrated empirically in an ant species which contains a higher proportion of large-headed ants (with lower mass-specific metabolic rates) in larger colonies (Shik, 2010). Because larger colonies may have more larger workers, and because the larger workers have a lower mass-specific metabolic rate than smaller workers, the emergent allometry at the colony level may be entirely explained by physiological variation at the individual level (Shik et al., 2012). The production of major and super-major castes and their effect on colony metabolic rate allometry is not indicative of supply constraint – to the contrary, they represent the use of surplus resources to increase per-capita energetic investment, and as a consequence the colony may benefit from their relatively lower maintenance costs in addition to the morphological and behavioral characteristics associated with their form.

It is also possible to use the additive model to predict deviations from isometry, even if the average ant size does not scale with colony size. For example, if the shape of the distribution of masses changes, it can result in increases or decreases in the predicted whole-colony metabolic rate. This can be thought of as an example of Jensen's inequality (Ruel & Ayres, 1999; Martin & Huey, 2008) applied to the concave non-linear function of metabolic allometry. The inequality explains that given a distribution of body masses, the metabolic rate estimated for an ant of average mass will be greater than the average of the metabolic rates estimated for each of the ants. Consequently, models of whole-colony metabolism should incorporate information relevant to the size distribution of the workers, larvae, pupae, and reproductive castes.

Behavioral organization can also have a strong effect on setting patterns of colony metabolic demand. Many of the behaviors engaged by workers within social insect colonies are triggered by social stimuli rather than being of independent origin. Following the early stages of colony founding, workers forage for resources, exchange information, and engage in behaviors necessary not for their own physiological demands, but rather to organize and distribute these resources throughout the colony (Hölldobler & Wilson, 1990; Robinson et al., 2008; Buffin et al., 2009). In this way, the workers exhibiting variation in response-thresholds may specialize in particular tasks leading to the emergence of division of labor as a self-organized structure within the colony.

There are both theoretical models (Merkle & Middendorf, 2004; Jeanson et al., 2007) and empirical data (Anderson & McShea, 2001; Jeanson & Fewell, 2008; Holbrook et al., 2011) to suggest that increases in colony size (both developmentally and evolutionarily) are associated with changes in the division of labor and demands for work. Although specialization does not necessarily increase energetic efficiency at the level of the individual and its task (Dornhaus, 2008), it may be associated with adaptive features at the whole-colony level. This is possible through efficient temporal allocation of tasks at the colony level (Tofts & Franks, 1992; Bonabeau et al., 1997; Beshers & Fewell, 2001) and a resilient spatial distribution of individuals within their nest (Sendova-Franks & Franks, 1994, 1995). Many of these features may contribute to an emergent hypometric scaling relationship for work (Beckers et al., 1989; Gautrais et al., 2002), so that as colony size increases, although task complexity increases and more work is being done overall, there are relatively fewer tasks required on a per-capita basis. In seed-harvesting ant colonies, *Pogonomyrmex californicus* (Buckley), mass-specific metabolic rates were shown to decrease with increasing colony size even though there were no significant changes in the average per-capita sizes or caste distributions (Waters et al., 2010). Instead, the distribution of walking speeds changed with colony size such that larger colonies exhibited a relatively greater proportion of inactive individuals (Waters et al., 2010). Correspondingly, the division of labor among the workers within *P. californicus* colonies was found to increase with colony size (Holbrook et al., 2011). The development of an energetic-state dependent reserve workforce has also been observed in *Apis mellifera* L. and *Bombus* spec. colonies (Kolmes, 1985; Cartar, 1992). Foragers in larger honey bee colonies are also able to more effectively gather and communicate information about resource locations than foragers in smaller colonies, leading to improved foraging performance (Donaldson-Matasci et al., 2013). Although one perspective suggests that metabolic hypometry is indicative of a diminishing of returns, that the investment in additional size offers relatively less in terms of performance or capability, this does not appear to be the case for social insect colonies due to their ability to minimize maintenance costs by morphological specialization, communication, and behavioral regulation.

Scaling of supply and resource limitation

Are social insect colonies subject to energetic supply constraints or optimization such as those hypothesized to limit metabolic rates in individual organisms (Hou et al., 2010; Bruce & Burd, 2012)? Two ways in which social insect colonies may become energetically constrained or resource limited as colony size increases are by a limitation in the raw availability of resources or by a limitation in the transport and effective distribution of these resources. The resources necessary for metabolism within ant colonies include oxygen and metabolic substrates in the form of proteins, fats, and carbohydrates. Additional environmental factors may include specific salts and minerals, symbionts, and physical space.

Oxygen is transported and exchanged within insects by both cuticular respiration and by means of a highly efficient tracheal system. Tracheal tubes branch from spiracular openings in the exoskeleton to extend throughout the body, providing sites for gas exchange proportional to the local tissue demand. Individuals exhibit a respiratory ventilation pattern (discontinuous gas exchange cycles) in which spiracles remain sealed for an extended duration, open slightly or flutter, then open wide, but only relatively briefly (Lighton, 1988, 1992, 1994; Lighton & Wehner, 1993). The physiological function of this ventilatory rhythm has been the source of longstanding controversy (Chown, 2011), but it has been hypothesized to an adaptive response to life in hypercapnic or hypoxic environments (Lighton & Berrigan, 1995; Lighton & Garrigan, 1995; Snyder et al., 1995), to prevent water loss (Kestler, 1985), to generate mass transport by absolute pressure differentials (Levy & Schneiderman, 1958), and to avoid oxygen toxicity (Hetz & Bradley, 2005). Taking advantage of both diffusive and convective mechanisms, insect tracheal systems have evolved to support impressive capacities for oxygen transport and behaviors associated with large aerobic scopes (Weis-Fogh, 1964; Snelling et al., 2011). This is possible, in part, due to the fact that the structure of tracheal networks is highly plastic, responding to variation in tissue demand and atmospheric oxygen concentration over both developmental and evolutionary time scales (Loudon, 1989; Centanin et al., 2010; Harrison et al., 2010).

One of the methods used to determine the safety margin for oxygen supply is to gradually decrease its partial pressure while observing the behavior or metabolism of organisms within this changing environment. Although the supply-limitation hypothesis predicts that deviations from normoxic supply (21 kPa O_2) should be associated with proportional increases or decreases in metabolism, this is generally not observed for resting or even moderately active insects (Joos et al., 1997; Harrison et al., 2006; Van Voorhies, 2009; Klok et al., 2010). Oxygen-enriched air also does not improve insect survival at their upper-thermal limits, suggesting that its delivery is not constrained even though increasing temperature induces a disproportionate increase in metabolic demand relative to diffusion rates (McCue & De Los Santos, 2013).

In one study, as groups of *Atta sexdens rubropilosa* Forel were exposed to a stepwise decline in oxygen partial pressure, their metabolic rates did not significantly decrease until the oxygen partial pressure was as low as 2.5 kPa; even at less than 1.0 kPa, the group metabolic rates were still a relatively large fraction (40%) of their average rate in normoxia (Hebling et al., 1992). Though these results may suggest that ants have exceptionally low oxygen demands, to the contrary, they exhibit some of the most metabolically intense tissues of any animal. Leaf-cutting ants, for example, exhibit an impressive aerobic scope, as their metabolic rates while cutting plant matter may be more than 30 times higher than their standard metabolic rates; the mass-specific metabolic rates of their mandibular muscle (193.5 W kg^{-1}) approaches that of insect flight muscle (Roces & Lighton, 1995).

As a result of the metabolism of the ants and the microorganisms with which they share their nests, the atmosphere deep within a subterranean ant colony may be prone to low oxygen concentration (hypoxia) and high carbon dioxide concentration (hypercapnia). One species of mangrove ants, which nests in an environment that periodically floods, has evolved the capacity to tolerate carbon dioxide atmospheres in sealed-off underground galleries elevated more than 300 times in concentration (Nielsen et al., 2003). In the nests of leaf-cutting ants and termites, among the largest social insect colonies, nest architecture has been shown to facilitate the ventilation of respiratory gasses (Kleineidam & Roces, 2000; Kleineidam et al., 2001; Korb, 2003). Ants may also take advantage of natural gradients in atmospheric concentrations for the organization of work and the production of preferred microclimates within the nest (Hangartner, 1969; Tschinkel, 2004).

How do patterns of growth and production depend on factors other than oxygen supply? The first workers produced by a queen are often provisioned from her own energy stores and are smaller in size than typical workers. Although this first brood of nanitics have relatively higher maintenance costs, their small size enables the queen to have an initially greater work force and this tradeoff between worker size and number has an adaptive value early in colony development (Oster & Wilson, 1978; Porter & Tschinkel, 1986). As colonies grow, they transit through ergonomic and reproductive stages in which increases in colony size follow a logistic trajectory. Because there are no physical limits on the size of a colony, the mechanisms responsible for determining and limiting its size are likely to depend on social interactions and the division of labor.

If colony growth was limited by the rate of resource acquisition, then this rate might be expected to be proportional to colony size and the available workforce. However, this does not appear to be the case. In a well-studied mutualism between colonies of *Azteca pittieri* Forel ants and *Cordia alliodora* (Ruiz & Pav.) Oken trees, the growth of the trees and their supply of nutrients and nest space for the ant colony outpaced the growth of the colonies (Pringle et al., 2012). Food supplementation increased productivity in field colonies of the fungus-tending ant *Trachymyrmex septentrionalis* (McCook), but the effect was due to an increase in growth of the colony's fungal symbiont and a change in the colony's sex allocation, not a strict result of increasing the number or size of workers (Seal & Tschinkel, 2008).

Foraging patterns are often independent of or non-linear functions of colony size. The rate of foraging in leaf-cutting ants (Roces, 2009; Bollazzi & Roces, 2011) and seed harvesters (Greene & Gordon, 2007; Gordon et al., 2008) depends primarily on the rate of successful (i.e., laden) foraging workers returning to the nest and their positively stimulating reserve workers which were otherwise idle. Foraging success is more dependent on the rate of interactions between individuals than the size of the colony. In *Pogonomyrmex occidentalis* (Cresson), early onset of foraging, a factor associated with genetic diversity, is a better predictor of foraging success and colony growth than colony size (Cole et al., 2008; Wiernasz et al., 2008). Colony size was also not associated with foraging activity in *Pogonomyrmex barbatus* (Smith), for which colonies with greater fitness exhibited greater restraint by not foraging during poor conditions (Gordon, 2013). As the energetic value of a single seed returned to the nest by a harvester ant may be 1 000 times greater than the metabolic costs of foraging for and returning with the seed (Fewell, 1988), it is not hard to imagine that the regulation of foraging is not probably limited by the energetics of these behaviors.

One of the ways colonies may experience supply constraint is by the egg production rates of queens. Although colonies are frequently founded by a single queen, in many species unrelated queens may found colonies cooperatively. In one genetic variant of the ant *Solenopsis invicta* Buren, the per-capita productivity of individual queens decreased with the number of queens present in a colony (Vargo & Fletcher, 1989). The same pattern was found among initial foundress associations in *Pachycondyla villosa* (Fabricius); however, after 21 weeks of growth, colonies with more queens ultimately produced significantly more workers than colonies with fewer queens (Trunzer et al., 1998). Furthermore, productivity in social insect colonies is not a simple function of queen size, number, or egg-laying rate. Variation in intracolonial oophagy (i.e., egg cannibalism), social control of egg-laying rate, and intercolonial brood raiding can all strongly affect resource availability, distribution, and colony growth patterns (Brian, 1953; Bartz & Hölldobler, 1982; Tschinkel, 1988, 1993).

Although many of these findings call into question the paradigm of simple energetic constraints, either environmental or behavioral, which may limit colony growth and performance, there is still a role for specific resources to dramatically affect colony behaviors and abundance. The availability of specific nutrients and elements including salt, water, nitrogen, and phosphorus may dramatically alter patterns of colony behavior. For many species, experiments designed using the geometric framework (Raubenheimer & Simpson, 1999) have demonstrated that colonies regulate their macronutrient intake rates, both with respect to available resources and dependent on specific demands from the colony for protein and carbohydrates (Behmer, 2009; Dussutour & Simpson, 2009; Cook & Behmer, 2010). Salt availability is a constraint to growth in both termites and ants with strong effects on decomposition processes in coastal and inland ecosystems (Kaspari et al., 2008, 2009). Species of ants that must cope with stoichiometrically imbalanced diets have benefitted from evolutionary changes in the morphology of their digestive system, the number and arrangement of malpighian tubules, and from mutualistic relationships with microsymbionts (Cook & Davidson, 2006). In a comparative study of three species of *Formica*, all maintained in the laboratory and fed ad libitum, larger colonies consumed less carbohydrate on a per-capita basis than smaller colonies, but there were species-level differences in rates of protein acquisition with changing colony size (Ayre, 1966). In a recent study of nutrient limitation in tropical litter ants (Shik & Kaspari, 2010), necromass, a primary source of their food, did not generally promote growth, but it became a limiting factor when there were increases in the space available for colony nest expansion, suggesting an interaction between resource availability and habitat expansion in the scaling of supply constraints with colony size.

Foraging in *Atta columbica*: a case study of supply and demand

Leaf-cutting ant species have evolved a complex organization that integrates nutrient selection, biomechanical constraints, ecological factors, and communication networks to produce emergent foraging patterns (Wirth et al., 2003; Bollazzi & Roces, 2011). Bruce & Burd (2012) recently reported a series of allometric scaling relationships that compare the behavior of foraging leaf-cutting ants with the size of the foraging workforce and trail geometry. They investigated the relationship between trail size (a proxy for colony size) and foraging rate (a proxy for metabolism) and found that the foraging rate (i.e., the rate of workers returning to their colony carrying a leaf fragment) increases disproportionately with the number of foraging ants. The 31-fold range in forager number was associated with only an 18-fold range in successful foraging rate and trail length was proposed as the key factor responsible for this pattern – the longer trail lengths associated with larger colonies were hypothesized to ultimately constrain their size (Bruce & Burd, 2012). This conclusion however, depends on the assumption that demand for leaf supply increases linearly with colony size. Instead, foraging patterns of leaf-cutter colonies may be the result of balancing rates of resource transport with the quality of those resources (Meyer et al., 2006) and the patterns of information transmission (Bollazzi & Roces, 2011).

Although direct measurements of metabolic rate in naturally growing whole leaf-cutting ant colonies is empirically challenging, colony demands may be modeled to predict whole-colony metabolic rate and how it relates to allocation of foraging workers. As the energetics of foraging in leaf-cutting ant species has been relatively well studied (Lighton et al., 1987; Moll et al., 2010), it is possible to predict the relationship between supply (Table 2) and demand (Table 3) in these colonies. If whole-colony metabolic rate is modeled as an isometric additive sum of individual metabolic rates, the energetic supply from foraged leaf matter is less than the predicted metabolic demand – these colonies are effectively constrained. However, if the colony is considered as an integrated organism and modeled with a corresponding allometry, the demand for both small and large colonies (12.6–226.6 W) matches well with the observed rates of energy supply delivered by the foraging workers (12.0–223.8 W). As an alternative to the hypothesis that biophysical constraints associated with resource supply limit colony sizes, we must consider how variation in colony size and foraging patterns may also reflect differences in growth rate and resource demand.

Discussion, unanswered questions, and future directions

The metabolic rate of an organism is ultimately a snapshot of the state of a complex behavioral and physiological

Table 2 Scaling of foraging supply in leaf-cutting ants (data adapted from Bruce & Burd, 2012)

	Colony size	
	Minimum	Maximum
No. foraging workers	877	27569
Foraging mass (g)	15.3	482.5
Foraging rate (laden ants s^{-1})	0.2	3.73
Foraging supply (W)	12	223.8
Trail length (m)	18.5	157.9

Table 3 Estimates for the metabolic demand of leaf-cutting ant colonies

	Colony size	
	Minimum	Maximum
Colony size[1]	43850	1378450
Colony mass[2] (g)	767.4	24122.9
Foraging MR[2] (W)	2.6	107.1
Isometric demand[3] (W)	71.2	2238.3
Hypometric demand[4] (W)	12.6	226.6

[1] Colony size is estimated assuming only 2% of the colony is engaged in foraging.

[2] Colony masses and foraging metabolic rates are estimated using a mass distribution for *Atta columbica* (Lighton et al., 1987) and a metabolic rate allometry for *Atta vollenweideri* (Moll et al., 2012).

[3] Isometric demand is an estimate of the whole colony's metabolic rate based on summing the metabolic rates expected for each individual.

[4] Hypometric demand is calculated using the estimate of net colony mass$^{0.78}$.

system. It represents the integration of energetic supply and demand across the cells and tissues in a unitary organism or across the individuals and castes of superorganisms such as social insect colonies. How this integration takes place is in many ways a grand challenge requiring attention from both experimental biologists and theoreticians. In pursuit of this question, it is remarkable that in 1883, Max Rubner wrote:

> "Large and small dogs have a different metabolic rate, not because there are definite differences in the organization of their cells, but because the impulses originating in the skin from cooling, stimulate the cells to metabolic activity"

This passage by Rubner (1883), quoted by Kleiber (1947), suggests both ultimate and proximate explanations for metabolic hypometry. He proposed the surface law of metabolism, that nutrient intake and metabolic demands match a constant rate of heat loss per unit of body surface. He also hints at a mechanistic foundation for this in the 'impulses originating in the skin' that affect the metabolic activity of other cells. In this way, he has effectively proposed the existence of a distributed regulatory network with the capacity to integrate information about energetic supply and demand and regulate metabolic rates accordingly.

One hundred and thirty years after Rubner, do we know the mechanisms involved with the information cascade that regulates the metabolic rates of the cells within an organism depending on its size? We know many pieces of the puzzle, such as how specific nutrients affect growth or how certain genetic pathways are dependent on environmental concentrations, but on a fundamental level, we still do not know many of the basic mechanisms by which growing tissues and organisms perceive their size and know when to stop growing or how individual social insects detect the size of quorums or their own colony size (Pratt et al., 2002; Vogel, 2013). Progress in the field of physiological regulatory networks (Cohen et al., 2012), may further illuminate how information is transmitted across levels of biological organization, from signaling cascades within cells to the interactions between an organism and its environment. Investigating the interaction patterns and dynamics of social insect colonies may serve as a model to understand how similar information cascades function in collectives and in individual organisms.

Three promising areas for future study include investigating the relationship between collective behavior and metabolism, the effects of temperature on activity cycles and energy budgets, and the application of dynamic energy budget theory to modeling growth and metabolism in social insect networks. How do decision-making processes and state transitions in the behaviors of social insect colonies depend on energetic stimuli and how are these stimuli communicated? Social insect colonies offer excellent models for these investigations due to the ability to tease apart the behaviors of the different components of the colony, by considering ecological differences between individual and colonial organisms, and by taking advantage of the diversity of social complexity among the eusocial insects.

As a predictive tool, metabolic theory is useful for addressing large-scale patterns such as changes in energy flux resulting from climate warming (Dillon et al., 2010) but it has also failed to predict the thermal dependences of metabolism in active insects (Irlich et al., 2009; Waters & Harrison, 2012) and social insect community size-abundance relationships (King, 2010). Contrasts such as these highlight the value of developing metabolic theories as they can provide a framework for evaluating competing models (Martínez del Rio, 2008). Scaling in biology is a powerful tool to unify the study of diverse concepts and organisms, but we must integrate behavioral and ecological realism into metabolic models to make apparent the impact of social context and biotic interactions on metabolism.

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