

Size–abundance relationships in Florida ant communities reveal how ants break the energetic equivalence rule

JOSHUA R. KING Biology Department, Central Connecticut State University, New Britain, Connecticut, U.S.A.

Abstract. 1. Ants are among the most abundant terrestrial organisms, yet little is known of how ant communities divide resources because it is difficult to measure the number of individuals in colonies and the density of colonies.

2. The body size–abundance relationships of the ants of five upland ecosystems in Florida were examined. The study tested whether abundance, energy use, and total biomass were distributed among species and body sizes as predicted by Damuth's energetic equivalence rule. Estimates of average worker body size, colony size, colony mass, and field metabolic rates were used to examine the relationships among body sizes, energy use, and total biomass.

3. Analyses revealed significant variation in energy use and did not support the energetic equivalence hypothesis. Specifically, the energy use and total standing biomass of species with large workers and colonies was much greater than smaller species.

4. These results suggest that larger species with larger colonies account for a disproportionate fraction of the total abundance and biomass of ants. A general model of resource allocation in colonies provides a possible explanation for why ants do not conform to the predictions of the energetic equivalence rule and for why ants are so abundant.

Key words. Colony number, colony size, Formicidae, metabolic theory of ecology, total standing biomass.

Introduction

Damuth (1981) first hypothesised that population density relates inversely to individual metabolic requirements and, as a consequence, energy use remains independent of body size across a large range of animal body sizes. This hypothesis is based on the observation that resource use by an individual, Q is proportional to its metabolic rate, B , and increases with body size, M , as $Q \propto B \propto M^{3/4}$, while total abundance per unit area, N , is a negative function of body size such that $N \propto M^{-3/4}$ across a broad range of taxa, life histories, and body sizes. Given these data, Damuth (1981, 1987) concluded that total energy use by a population, Q_{Tot} is a product of individual energy use and population density which scales inversely to body mass and thus, $Q_{\text{Tot}} \propto QN$, $Q \propto M^{3/4}$, $N \propto M^{-3/4}$, so $Q_{\text{Tot}} \propto M^{3/4} M^{-3/4} \propto M^0$. This relationship

has since been described as the 'energetic equivalence rule' (EER; Nee *et al.*, 1991).

The EER is an important hypothesis because it explains how the metabolism of individuals may affect population level processes in allometric scaling theory in ecology (Enquist *et al.*, 1998; Brown *et al.*, 2004). Predictions of the EER have been tested using many different organisms and across a range of biological scales with mixed results (Enquist *et al.*, 1998; Blackburn & Gaston, 1999; White *et al.*, 2007). In sum, empirical evidence has consistently shown that individual energy use increases with body mass raised to 0.75 power (Kleiber, 1932; Peters, 1983; Gillooly *et al.*, 2001; Brown *et al.*, 2004; Savage *et al.*, 2004) and population density has sometimes, but not always, related inversely as body mass raised to -0.75 power (Damuth, 1981, 1987; Peters, 1983; Maurer & Brown, 1988; Nee *et al.*, 1991; Pagel *et al.*, 1991; Blackburn & Lawton, 1994; Greenwood *et al.*, 1996; Blackburn & Gaston, 1997; Enquist *et al.*, 1998; Cyr, 2000; Enquist & Niklas, 2001; Belgrano *et al.*, 2002; Russo *et al.*, 2003; Meehan *et al.*, 2006).

Variability in body size–abundance relationships among different taxa can be influenced by the scale of the analysis

Correspondence: Joshua R. King, Biology Department, Central Connecticut State University, 1615 Stanley Street, New Britain, CT 06050, U.S.A. E-mail: kingjor@mail.ccsu.edu

(White *et al.*, 2007). Body size–abundance relationships among plants tend to be consistent across scales (Enquist *et al.*, 1998; Enquist & Niklas, 2001). In contrast, among animals, at local and regional scales there tend to be fewer significant relationships than at geographic scales (Blackburn & Gaston, 1999; White *et al.*, 2007). Nevertheless, if energetic equivalence is truly a general rule of community structure, then it should apply across scales and both within trophic groups and across phylogenetic divisions (Damuth, 1981; Pagel *et al.*, 1991; Blackburn *et al.*, 1993a,b; Russo *et al.*, 2003; Brown *et al.*, 2004; Tilman *et al.*, 2004; Meehan *et al.*, 2006).

Eusocial insects and the EER

Damuth (1981, 1987) included only a small number of terrestrial arthropods, including three species of ants, in his studies. Eusocial insects, and particularly ants, warrant further analysis because they are among the most abundant terrestrial organisms on earth. In mid to low latitude terrestrial habitats, eusocial insects may comprise one-third or more of the entire animal biomass, exceeding total vertebrate biomass, and ants alone comprise greater than 50% of that biomass (Wilson, 1971; Hölldobler & Wilson, 1990).

Community-level studies have traditionally estimated the population density of ants by counting individual ants in samples. When considered as individual workers, ants do appear to conform to the predictions of the EER, in that population density declines as worker body size increases (Janzen & Schoener, 1968; Damuth, 1981, 1987; Stork & Blackburn, 1993; Siemann *et al.*, 1996, 1999; Meehan *et al.*, 2006). As metabolic rates of individual ants have been shown to scale with body mass as approximately $M^{0.8}$ (Peakin & Josens, 1978; Nielsen, 1985; Porter & Tschinkel, 1985; Lighton & Fielden, 1995), the EER predicts that the density of ants should scale with body mass as $N \propto M^{-0.8}$. Additionally, standing stock of biomass (W) should scale as $W \propto M^{0.25}$, which is the inverse of the mass specific rate of metabolism which scales as $M^{-1/4}$ (Damuth, 1981; Brown *et al.*, 2004).

To properly assess energy use at the population level it is necessary to quantify the total density of individual ants, their mass-specific metabolic rates, and their body masses. Counting individual ants in samples does not sufficiently quantify all of these variables because ants are colonial. Their colonial life history strategy was not considered by Damuth (1987) nor has it been accounted for in any other allometric scaling theory (Hutchinson, 1959; Brown *et al.*, 2004). As they are colonial, ants have two ecologically relevant measures of size: the size of the colony and the size of individual workers (Tschinkel, 1991, 2006; Kaspari, 2005). Worker size is important because workers interact with the environment and ultimately determine, for example, the size and type of food or prey taken by the colony and the lifespan of workers (i.e. in part, each species niche); while colony size is important because, in combination with worker size, it determines the energetic requirements of the colony and also affects factors such as territory size (Hölldobler & Wilson, 1990; Tschinkel, 2006). It is also necessary to measure population density. Since each individual ant

colony functions as a large and diffuse ‘superorganism’ consisting of interacting entire organisms, colonies are the functional ecological unit that should be used to estimate population density for each species (Wheeler, 1911; Wilson, 1971; Tschinkel, 1991; Wilson & Hölldobler, 2005). Thus, to make comparisons of total biomass and population energy use relevant to the EER, it is necessary to estimate the density of colonies, the number of workers in each colony, and the mass of the individual workers.

In this study I integrated worker body mass, colony size, colony density, total biomass, and population energy use to study entire communities of ants. I focus on the ants in upland ecosystems in Florida to provide empirical data for answering questions about community scale body size–abundance patterns at a level of detail that has previously only been possible with non-social taxa (e.g. Russo *et al.*, 2003; Ernest, 2005; Meehan *et al.*, 2006). Using these data, I addressed two central questions. (i) Do ant communities conform to the predictions of the EER, such that the density of colonies scales inversely to worker body mass ($N \propto M^{-0.8}$)? (ii) Does the standing stock of total ant biomass (W), calculated by multiplying the colony size, worker mass, and colony density, scale as $W \propto M^{0.25}$? The answers to these questions will make it possible to connect variables, such as species body size and colony size to population and community levels of organisation. In the next section I use an existing descriptive model of colony-level resource allocation to provide a theoretical basis for explaining observed patterns.

A model of colony-level resource allocation

Colony-level resource allocation processes may provide a mechanistic basis for understanding the body size–abundance patterns in ant communities, much like individual biomass production provides a basis for understanding these patterns in non-social organisms (Damuth, 1981, 1987; Brown *et al.*, 2004). Oster and Wilson (1978) developed a theoretical framework to describe the optimisation of resource allocation in eusocial insects. A modified version of their general model of resource allocation within an ant colony provides a theoretical framework for understanding how worker body size and colony size may be the ultimate source of community-scale size–abundance patterns.

Like non-colonial organisms, eusocial insect colonies must gather and convert as much energy as possible into growth to maximise fitness (Oster & Wilson, 1978; Brown *et al.*, 2004; Tschinkel, 2006). Unlike non-colonial organisms, eusocial insect colonies follow a developmental pathway where interacting entire organisms are added to the superorganism; a process that parallels the self construction of organisms from molecules and tissues (Hölldobler & Wilson, 1990; Tschinkel, 2006). The ultimate currency in colony-level natural selection is the summed production of sexuals (reproductives) over time (Oster & Wilson, 1978). For claustrally founding species to generate this currency, colonies must build large populations of workers which can then be ‘cashed in’ during the breeding season through the production of sexuals (Oster & Wilson, 1978; Tschinkel, 2006). It is possible that, because many species that

use colony ‘budding’ have seasonal reproduction, this model applies to those species as well. To describe how colonies generate the energetic reserve necessary to accomplish this, Oster and Wilson (1978) formulated a simple general optimisation model of resource allocation in social insects:

$$\frac{dE(t)}{dt} = \eta(W)W - m_W W - m_Q Q - M_W[\cdot] - M_Q[\cdot], \quad (1)$$

In the model, E = energy reserve accumulation, W = workers produced, Q = queens produced, $\eta(W)$ = per capita foraging efficiency of workers, m_W = average metabolic costs of workers, and m_Q = average metabolic costs of queens. The model assumes that:

$$W, Q, E > 0 \quad (2)$$

The terms $M_W[\cdot]$ equals the rate of ‘manufacturing’ workers, and $M_Q[\cdot]$ equals the rate of ‘manufacturing’ queens, depend on the size of the worker force available for brood rearing and the fraction of resources allocated to producing workers (uW) and queens (vQ). These rate functions are modelled as:

$$\frac{dW(t)}{dt} = M_W[uE, W] - \mu W \text{ where } W(0) = W_0 \quad (3)$$

and

$$\frac{dQ(t)}{dt} = M_Q[vE, Q] - \nu Q \text{ where } Q(0) = Q_0 \quad (4)$$

The variables μ and ν are the mortality rates of workers and alate queens, respectively, and the model assumes that:

$$0 < \mu + \nu < 1 \quad (5)$$

In the model, energetic costs from the metabolic activities of workers and queens, the manufacturing costs of raising workers and queens, and the mortality of workers or departure of sexuals from the colony are compensated for by the gains in energy from worker foraging and from the standing ‘energetic reserve’ contained within the workers themselves (e.g. worker body fat). In terms of fitness, the model suggests that for colonies of a given species, increasing colony size will positively affect fitness (Oster & Wilson, 1978; Tschinkel, 2006). Increasing worker size can also positively affect fitness because larger workers may represent a larger energetic reserve or may be more effective at gathering high quality prey (Hölldobler & Wilson, 1990; Tschinkel, 2006). In this model, the nature of the pathway from energy reserves to colony biomass production and ontogenetic growth clearly does not directly parallel organismal growth, because colony growth rate is dependent on the size and number of individual organisms in the colony, each with their own mass specific metabolic rate, longevity, and energetic reserve. Revisiting the parameters of this model in the context of empirical data (see Results, below) will provide a first formulation for understanding how colony-level processes affect community level patterns in ants.

Materials and methods

Study sites and sampling

This study was carried out in five different types of ecosystem in north and central Florida on the inland region stretching from Columbia County in the north, and south into Highlands County along the Lake Wales Ridge. Ecosystems were selected as representative of some of the least disturbed remaining native upland ecosystems in peninsular Florida. Using the ecosystem criteria of Myers and Ewel (1990), I sampled in four undisturbed natural upland ecosystem types in Florida: (i) temperate hardwood forests at the San Felasco Hammock State Park, (ii) pine flatwoods at the Osceola National Forest, (iii) high pine at the Katherine Ordway Biological Preserve and (iv) Florida scrub at the Archbold Biological Station. I also included a fifth category of a human-disturbed ecosystem, consisting of previously cleared field habitats, for comparison with unaltered ecosystems. The ecosystems sampled represent a gradient of upland plant communities that include closed-canopy, hardwood forests, open-canopy pine and oak woodland, and old fields.

For native ecosystems, sampling sites were located such that contiguous areas of each plant community could accommodate three large (180 m long), linear transects separated by at least 100 m from roads, fences, or edges (e.g. park boundaries or ecotones) and 1 km from each other. The three transects for disturbed field sites were located in areas adjacent to the native ecosystems (>1 km away) at Archbold Biological Station, San Felasco Hammock State Park, and Ordway Biological Preserve. In total, there were 15 transects with three transects within each ecosystem type. Ants were sampled from June through September 2001, with a standardised sampling protocol using pitfall traps and leaf-litter extraction with Berlese funnels described in detail by King and Porter (2005).

In each transect, a total of 36 pitfall and 36 litter samples were taken separately at 5 m intervals (180 m, total) in two parallel lines separated by 10 m. Pitfall traps were 85 mm long plastic vials with 30 mm internal diameter partially filled with ~15 mm of non-toxic, propyleneglycol antifreeze. Traps were buried with the open end flush with the surface of the ground and operated for 3 days. Two 0.25 m² litter samples were taken after setting pitfall traps at each litter sample point. Litter samples were obtained by collecting all surface material and the first ~1 cm of soil within quadrats. The two litter samples were pooled, larger objects (e.g. logs) were macerated with a machete, and sifted through a sieve with a 1 cm grid size. Sifted litter was placed in covered metal 32 cm diameter Berlese funnels under 40 W light bulbs. The funnels were operated until the samples were dry (~48–72 h).

Worker size

I estimated the average mass of workers (mg) for each species by drying and weighing groups of workers. I measured dry mass, as this is a functional measure of size in ants because it covaries with the size of head width and length, mouthparts, and limbs (Kaspari & Weiser, 1999; Tschinkel *et al.*, 2003;

Weiser & Kaspari, 2006). Samples were taken from one to five mature colonies capable of producing sexuals in north and central Florida and averaged for each species (King, 2007; King & Porter, 2007; J. R. King, unpublished). The average worker mass values for the majority of species were generated from two to three colonies. All ants were dried in a drying oven at 50 °C for 24 h in the presence of Drierite™, and then left out for a minimum of 24 h at room temperature to re-hydrate to room humidity before weighing to 0.0001 mg. Whenever possible, approximately 20 workers were used from each sample but samples ranged from a minimum of two workers to a maximum of 35 workers weighed per sample.

The average worker body mass values (see Appendix S1) do not account for changes in seasonal fat content or the range of worker size polymorphism within colonies. Also, for dimorphic *Pheidole* species I used only the weight of minor workers, as majors were uncommon in samples. For polymorphic species, ants were haphazardly selected to include the range of worker sizes in the sample. Twenty-three species were not weighed, because there were only one or two individuals in all samples and they were mounted as vouchers. For these species, the body weight of a similar-sized species in the same genus was rounded to the nearest fraction (10th, 100th, 1000th) of a milligram and used as an approximation. The direction and magnitude of rounding was determined by the difference in 10th of millimetres of Weber's length (a measure of mesosomal length: Brown, 1953). This approach provides an approximation of unknown weight similar to other approaches (e.g. regressive relationships, Rogers *et al.*, 1976; Kaspari & Weiser, 1999). The majority of the unweighed species were rare, appearing in less than 1% of samples.

Colony size

I estimated average mature (capable of producing sexuals) colony size, or number of workers, for each species (see Appendix S2; King & Porter, 2007). Colony sizes for 40 species were based on whole colony collections in Florida by the author or a combination of the author's data and published data on colony censuses in the literature. Every effort was made to use only data reported from the geographic region near or in Florida, and colony size estimates are inclusive of 'satellite nests' for known polydomous species (e.g. *Camponotus socius*). With the exception of five species these values are averages generated from 2 or more (up to 50) colonies, although most were generated from three to five colonies due to the difficulty of whole-colony collecting for so many species. Colony sizes for the remaining 36 species are from the literature or from an estimate based upon colony size reported for a closely related, similar species within the same genus, an estimate based on the authors' collection of a closely related species in Florida, or a combination of the two. All estimates were rounded off to the nearest 10, 100, or 1000.

Number of colonies

I used frequency of species occurrences in pitfall and litter samples as an estimate of the number of colonies in each

transect. A sample is defined as the species of ants collected in one pitfall or one Berlese funnel and there were 72 (36 pitfalls and 36 funnels) samples taken per transect, 216 samples taken per ecosystem (72 samples per transect \times 3 transects per ecosystem), and 1080 samples taken in total (216 samples per ecosystem \times 5 ecosystems sampled). If one or more workers of a species was found in a sample, then this was counted as one instance of a colony, otherwise zero instances of a colony of that species were recorded for that sample. Thus, here I define colony density, N , as the number of colonies estimated from species occurrences in litter and pitfall samples along linear transects standardised by length (180 m) and sample spacing (5 m). My reason for using a sample-based estimate of colony density, instead of worker abundance (total number of workers in pitfall and litter samples), or manual nest counts, is that I am attempting to strike a balance among (i) combining results from two different sampling methods, (ii) providing a more complete sample of the species in the fauna than manual nest counting provides, and (iii) making conservative but realistic estimates of total standing biomass of the ants in these ecosystems. I would emphasise that this is a conservative approach, as it almost certainly underestimates the total biomass of each species within the sampled space. I provide detailed justification, including supporting data, for this approach in Appendix S3.

Standing biomass and population energy use

I estimated total standing biomass, W , by multiplying worker mass \times colony size \times density of colonies. I estimated population energy use, PEU, with Lighton and Fielden's (1995) estimate of standard metabolic rate (SMR) for individual ants where, $SMR = 729M^{0.803}$ with SMR in microwatts at 25 °C and M in grams. SMR is a functional estimate of metabolic rate for use in calculating PEU for ants, as field metabolic rates (FMR) have been shown to be equivalent to resting metabolic rates in ants (Lighton & Duncan, 2002) and because, at any given time, a large portion of a mature ant colony is at rest and not actively foraging (Hölldobler & Wilson, 1990; Tschinkel, 2006). This value was then multiplied by the total biomass (worker body mass \times colony size \times number of colonies) of each species.

Statistical analyses

The inventory design permitted the analysis of assemblages at local (three standardised transects within each ecosystem) and regional (all data combined or 15 standardised transects total) scales. For all analyses, only records for worker ants were included, as the presence of queens or males in samples is not necessarily indicative of an established colony. Worker ants were sorted and species were identified by the author. Relationships between density of colonies, N , average worker body size (mg), M , total standing biomass (mg), W (body mass \times colony size \times number of colonies), and population energy use (PEU), Q_{Tot} ($SMR \times W$), were evaluated within ecosystems using the general linear model: $\log_{10} Y = \log_{10} a + b \log_{10} X$.

The same comparisons were also made using colony biomass (worker mass \times colony size), rather than worker body size, for each species and results were nearly identical. Therefore, only worker body size comparisons are reported. To examine the frequency distribution of species, the number of colonies and total biomass data were binned within \log_2 body mass (mg) classes.

If variation in population density is constrained by body size or colony size through ecological mechanisms, then these variables may exhibit correlation across phylogenetic history (Felsenstein, 1985). To correct for the potential effects of phylogeny, I examined phylogenetically independent contrasts among species' body size, colony density, colony size, PEU, and total standing biomass using the PDAP package in the computer program Mesquite (Midford *et al.*, 2005; Maddison & Maddison, 2007). Ideally, these comparative tests would use a complete phylogeny of ants, but such a phylogeny is not available because sampling at lower taxonomic levels is largely incomplete (Brady *et al.*, 2006; Moreau *et al.*, 2006). This limits the power of comparative analyses at the ecosystem scale because the phylogenetic relationships among many genera and most species in this study are poorly understood or unknown (Ives *et al.*, 2007). I conducted phylogenetically corrected analyses only on the full data set with all genera (27) included. I used a reduced version of Moreau *et al.*'s (2006) phylogeny of ants to assign branch lengths among higher taxonomic levels (genus and higher). Soft polytomies represented phylogenetic relationships among species and branch lengths, and therefore could not be estimated for relationships among any species and were all assigned a uniform length (Russo *et al.*, 2003; Midford *et al.*, 2005).

I did not analyse species separately by trophic groups because the vast majority of this fauna consists of dietary generalists that will feed opportunistically on a range of food types. For example, plant exudates, seeds, live insect prey, carrion, and homopteran excretions are all potential food sources. A majority of ants occupy a broad trophic level (Hölldobler & Wilson, 1990; Tobin, 1994; Kaspari, 2001). Possible exceptions include predatory genera *Pyramica*, *Strumigenys*, and *Neivamyrmex* (army ants), herbivores such as *Trachymyrmex*, and detritivores such as *Cyphomyrmex*. However, even these genera were difficult to categorise because they will opportunistically feed on a wide variety of foods (J. R. King, personal observations of laboratory colonies) or their habits were completely unknown because they are rare.

Results

A total of 76 ground-dwelling species were sampled (see Appendix S1). The richest genera were *Solenopsis* (10 species), *Pheidole* (seven species), *Camponotus* (six species), *Paratrechina* (six species), and *Pyramica* (six species). Species density was highest (ANOVA: $F = 4.93$, d.f. = 1,4, $P = 0.02$) in high pine sites (35 ± 7 ; mean \pm 1 SD) followed by Florida scrub (29 ± 3), pine flatwoods (27 ± 6), hammock (21 ± 4), and the disturbed field sites (20 ± 4). In support of this, rarefaction curves for pooled ecosystem data showed

that, for a specified number of samples, I captured the most species in high pine and the fewest in hammocks (data shown in King, 2004). The sampling protocol captured ~70–90% of the total fauna at both local and regional scales based on detailed knowledge of the fauna of this region (King & Porter, 2005, 2007).

In general, the density of colonies of species was not significantly related to average worker body mass and the slopes of these regression lines were not different from 0, except in Florida scrub where the slope = -0.33 (Table 1, Fig. 1). Thus, worker body mass was unrelated to colony density and the correlation was only weakly negative or positive (Table 1). Regardless of the scale of the analysis or the type of ecosystem, the slope of the relationship between worker body mass and colony density was never equal to -0.8 , the slope predicted by the EER, even at the lower limits of the 95% confidence intervals (Table 1).

Population energy use was a positive linear function of body mass for the full data set (regional scale) and for all of the ecosystems (Table 1, Fig. 1a–e). The slope of the relationship never equalled 0, the value expected under the EER, even at the lower limit of the 95% confidence intervals (Table 1). Similarly, the total standing biomass of each species was a linear function of average worker body mass (Table 1, Fig. 1a–e) for the full data set and all ecosystems. However, the slope of the relationship between worker body mass and total standing biomass was never equal to 0.25, the slope expected if standing biomass were the inverse of the mass specific rate of metabolism (Table 1).

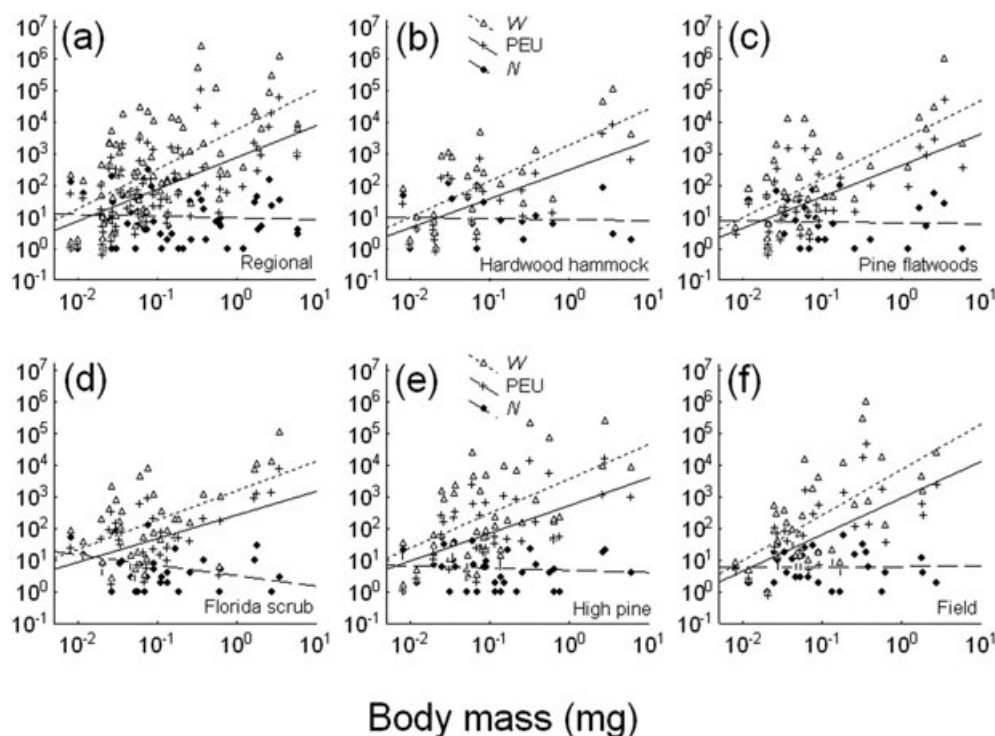
Average colony size was a slightly positive linear function of average worker body mass (Fig. 2a). This pattern suggests that species with larger workers tended to have colonies of equal or slightly larger size than species with smaller workers. The mean body mass of the species with the largest workers, *Camponotus socius*, was nearly 750 times heavier than the workers from the species with the smallest workers, *Solenopsis tennesseensis*. Regionally and for ecosystems, diversity was high among intermediate sized species (see Appendix S1, Fig. 1a). Among intermediate sizes, species of *Pheidole*, *Solenopsis*, and *Paratrechina* had the greatest number of colonies. The most abundant large species were from the genera *Odontomachus* and *Camponotus* (see Appendix S1). Population energy use was a positive, linear function of colony size (Fig. 2b). Colony size accounted for nearly 60% of the variability in population energy use when all species were considered. This pattern (Fig. 2b) and the relationship of worker size and population energy use (Table 1, Fig. 1a) both show that population energy use is primarily a function of the sum of individual metabolic rates as would be expected given the nature of this analysis.

The regression of phylogenetically independent contrasts of the relationship between worker body mass (mg) and the density of colonies, worker body mass and colony size, worker body mass and population energy use, and worker body mass and total biomass (mg) were all significant for the full data set (Table 2). These results show that all of these variables are correlated with worker body size after the effects, if any, of phylogeny are removed. The slopes of all of these relationships were all positive and body mass explained some of the

Table 1. Ordinary least squares regression statistics for the relationship between worker body mass (mg) and the density of colonies, worker body mass and population energy use, and worker body mass and total biomass (mg) for the full data set (regional) and for each ecosystem.

	<i>n</i>	Slope (SE)	95% CI of slope	Probability slope = -0.8	Probability slope = 0	Probability slope = 0.25	Correlation coefficient
<i>Density of colonies</i>							
Regional	76	-0.05 (0.12)	-0.29, 0.19	<0.0001	0.67	0.0154	-0.049
Hardwood hammock	25	-0.03 (0.20)	-0.44, 0.37	0.0007	0.87	0.1648	-0.348
Pine flatwoods	35	-0.03 (0.16)	-0.35, 0.29	<0.0001	0.85	0.0840	-0.035
Florida scrub	35	-0.33 (0.16)	-0.65, -0.01	0.006	0.05	0.0009	-0.338
High pine	40	-0.07 (0.13)	-0.34, 0.20	<0.0001	0.61	0.0222	-0.083
Field	33	0.01 (0.15)	-0.29, 0.31	<0.0001	0.95	0.1064	0.011
<i>Population energy use</i>							
Regional	76	1.00 (0.16)	0.69, 1.32	<0.0001	<0.0001	<0.0001	0.595
Hardwood hammock	25	0.92 (0.21)	0.47, 1.36	<0.0001	0.0003	0.0051	0.664
Pine flatwoods	35	0.99 (0.20)	0.58, 1.40	<0.0001	<0.0001	0.0009	0.648
Florida scrub	35	0.74 (0.20)	0.33, 1.15	<0.0001	0.0008	0.0199	0.540
High pine	40	0.88 (0.21)	0.44, 1.31	<0.0001	0.0002	0.0058	0.553
Field	33	1.15 (0.26)	0.63, 1.68	<0.0001	<0.0001	0.0014	0.627
<i>Total biomass (mg)</i>							
Regional	76	1.25 (0.20)	0.86, 1.64	<0.0001	<0.0001	<0.0001	0.595
Hardwood hammock	25	1.14 (0.27)	0.59, 1.69	<0.0001	0.0003	0.0029	0.664
Pine flatwoods	35	1.23 (0.25)	0.72, 1.74	<0.0001	<0.0001	0.0005	0.648
Florida scrub	35	0.93 (0.25)	0.42, 1.44	<0.0001	0.0008	0.0111	0.540
High pine	40	1.09 (0.27)	0.55, 1.63	<0.0001	0.0002	0.0031	0.553
Field	33	1.43 (0.32)	0.78, 2.09	<0.0001	<0.0001	0.0008	0.627

The standard error (SE) and 95% confidence interval (CI) of each slope are given as are the Pearson's correlation coefficient for each regression.

**Fig. 1.** Relationships between average worker body mass (mg) and number of colonies (*N*), population energy use (PEU), and standing biomass (*W*) in (a) the region (the full data set), (b) hardwood hammock, (c) pine flatwoods, (d) Florida scrub, (e) high pine, and (f) fields. Lines are ordinary least squares regressions for each of the relationships. All data were \log_{10} transformed.

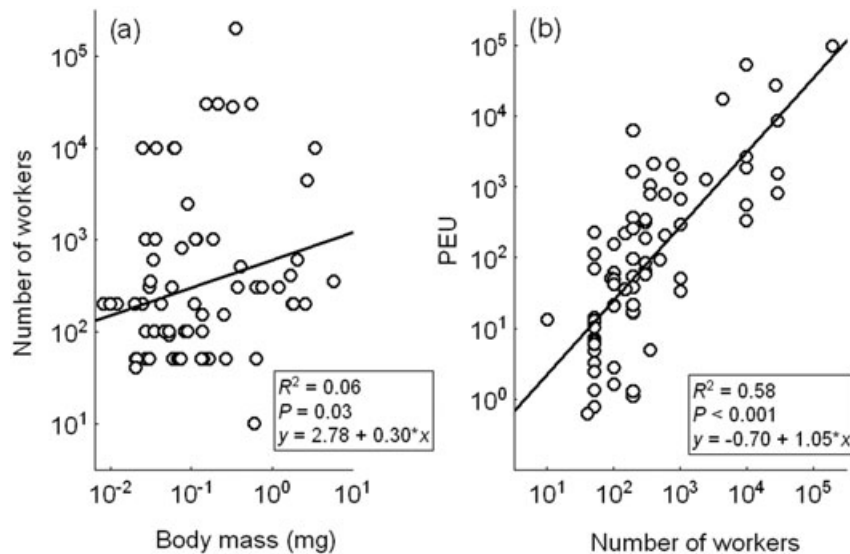


Fig. 2. The relationship between (a) worker body mass and number of workers (colony size) and (b) number of workers and population energy use (PEU) across all species in the data set. In (a), there was a positive, linear relationship between worker mass and worker number, indicating that medium and large-bodied species tend to have colonies greater in size than small-bodied species. In (b) there was a positive, linear relationship between number of workers and population energy use, indicating that number of workers predicts a large portion of the variability in population energy use.

Table 2. Ordinary least squares regression statistics for the phylogenetically independent contrasts of the relationship between worker body mass (mg) and the density of colonies, worker body mass and colony size, worker body mass and population energy use, and worker body mass and total biomass (mg) for the full data set. Significant two-tailed *P*-values indicate lack of fit between variables and thus no effect of phylogeny on the relationship.

	<i>n</i>	Slope	<i>P</i> (two-tailed)	Correlation coefficient
Density of colonies	76	0.77	0.01	0.29
Colony size	76	1.53	<0.001	0.13
Population energy use	76	2.65	<0.001	0.69
Total biomass (mg)	76	3.30	<0.001	0.69

Pearson's correlation coefficients are given and these were forced through the origin.

variation in colony density and colony size, and most of the variation in PEU and total standing biomass (Table 2).

Both the regional – (all data combined) and ecosystem – scale frequency distributions revealed that the relationship between species richness and body mass was unimodal (Fig. 3a). The relationships among the density of colonies, total biomass, and body mass were less obviously unimodal (Fig. 3b). For density of colonies–body size relationships, the mode included medium-sized species (Fig. 3b, black bars). For summed total biomass–body size relationships, the mode included the largest species and the majority of the biomass was contained in the largest body size classes (Fig. 3b, white bars). These data show that the largest body size classes account for a large majority of the total biomass of ants, despite

the fact that the density of colonies declines slightly as body size increases.

Discussion

Ant communities and the EER

The distribution of worker body size among species and their total biomass patterns were consistent among ecosystems (Fig. 3) suggesting that this is a typical feature of ant communities, at least in this region. The explanation for this pattern is that species with larger workers tended to have larger colonies (Fig. 2a) and their combined impact on resource acquisition was, accordingly, much greater than that of smaller species with smaller colonies (Fig. 2b). There have been few comparable studies of entire ant communities that include estimates of worker body size and colony size, but these results are congruent with those reported in previous studies. Geraghty *et al.* (2007) showed that colony size increases with worker size in Great Smoky Mountains National Park. There have been numerous other studies in species poor habitats in temperate zones of western Europe, which also suggest that species with large colonies are among the most abundant species in the fauna, although they do not report worker body size (Brian *et al.*, 1965; Pétal, 1968, 1980; Jensen, 1978). These studies suggest that species with large workers will sequester a majority of the available energy in ant communities because these species also tend to be abundant and have large colonies.

The sample of ant species captured in this study is representative of the entire range of body sizes that exist in the Florida ant fauna (Deyrup, 2003; King & Porter, 2005;

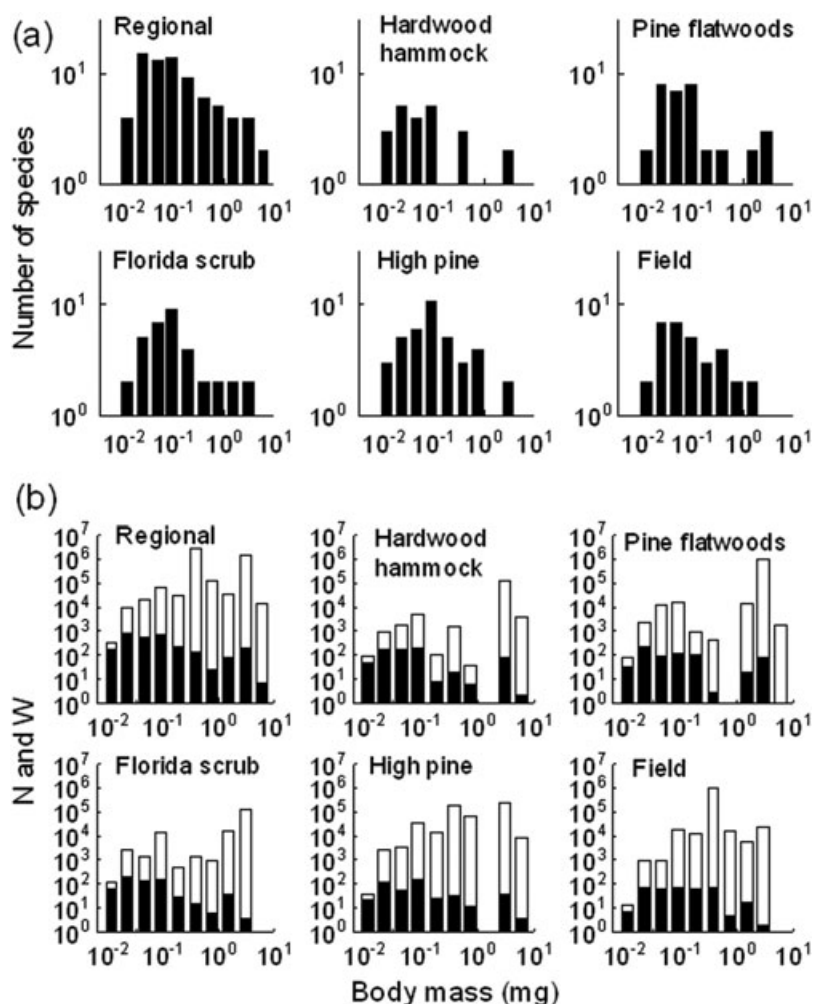


Fig. 3. The distribution of worker body mass (mg) among (a) species and (b) N , or number of colonies (black bars) in the region and for each of the ecosystems. In (b), W , or total biomass (white bars) shows the total biomass contributed by species in each of the body size bins, rather than a frequency distribution. Also, note that in (b) the bars are not cumulative totals, rather they are overlain to aid in visually comparing the frequency distribution of colonies with the summed total of biomass. Data were binned in \log_2 intervals.

J. R. King and S. D. Porter, unpublished) and additional sampling will not produce larger or smaller species. In a broader context, these species are among the largest and smallest body masses for ants in general (Kaspari & Weiser, 1999). The colony sizes I estimated in this study also generally represent most of the possible spectrum of colony sizes for New World ants, with the exception of the very largest colonies (e.g. leaf-cutter ants of the genus *Atta*; Hölldobler & Wilson, 1990). Therefore, these data are particularly powerful for understanding regional and local scale body size–abundance patterns and provide a basis for comparison with larger scales.

In sum, size–abundance patterns of ants did not conform to the predictions of the EER. Within the upland ant communities of Florida, mass and energy were inequitably distributed among species of different size classes such that species with large workers sequestered the largest portion of the available energy (Table 1, Figs 1, 2b and 3). The density of colonies, N , did not scale inversely to worker body mass as $N \propto M^{-0.8}$ and the standing stock of biomass, W , did not scale as $W \propto M^{0.25}$, regardless of whether the data were corrected for phylogeny or not (Tables 1 and 2). Across all animal taxa, these results are similar to other studies of animals where the predictions of

the EER were not met because the relationship between body mass and population density varies (Brown & Maurer, 1987; Maurer & Brown, 1988; Pagel *et al.*, 1991; Blackburn *et al.*, 1993a,b; Brawn *et al.*, 1995; Blackburn & Gaston, 1997, 1999; Russo *et al.*, 2003; Ernest, 2005). However, the energy use and total biomass of ants in this fauna are much more strongly skewed toward the larger species than what has been shown for many other taxa (Maurer & Brown, 1988; Pagel *et al.*, 1991). The lack of a relationship between worker body mass and colony density relationship in each ecosystem (Table 1) is of particular interest, because this is as a negative relationship for a variety of other taxa regardless of scale (mean slope approximately = -0.25 , Blackburn & Gaston, 1997).

It is possible that social insects are simply an outlier among animals because, despite their ecological importance, eusociality has evolved in only a very few animal lineages (Wilson & Hölldobler, 2005). Yet, social insects have certainly not escaped the ecological constraints on body size that other, non social organisms face. Kaspari and colleagues (Kaspari, 2001, 2004, 2005; Kaspari *et al.*, 2000a,b) have shown that species diversity and relative abundance, as well as colony density, colony size, and body size of ants are influenced

by latitudinal gradients of productivity and temperature. This seems to be due to trade-offs in colony size and worker mass such that warmer climates are associated with larger colonies of smaller workers and the most and least productive ecosystems yield smaller colonies (Kaspari, 2005). Similarly, both colony size and worker size of ants appear to conform to Bergmann's rule (decreasing size with decreasing latitude) perhaps due to increasing starvation resistance in more seasonal climates (Cushman *et al.*, 1993; Kaspari & Vargo, 1995).

It is not surprising that ants have evolved similar life-history strategies to all other non-colonial animal taxa in response to the same constraints imposed by gradients of temperature, seasonality, species interactions, and productivity. But clearly the enormous abundance of social insects relative to other animal taxa in the moderate temperate and tropical zones suggests that it is eusociality that conveys an ecological advantage at these latitudes. In one of the few comparable studies of a phylogenetically distant, non-ant, eusocial insect community, Eggleton *et al.* (1998) showed that energy use and total biomass were strongly skewed toward larger species in soil-feeding termite (Isoptera) assemblages in Cameroon (Eggleton *et al.*, 1998). In combination, this study and that by Eggleton *et al.* (1998), suggests a working hypothesis that at local scales, a small number of larger species with larger colonies will dominate energy use and total biomass in eusocial insect communities, and this pattern may be general to eusocial insect communities, regardless of taxa or latitude. Therefore, the answers as to why energy use patterns in eusocial insect communities appear to be so strongly skewed toward a small number of larger species relative to other non-colonial animal taxa, likely reside in the emergent properties of the interaction of worker size and colony size during the process of biomass production in colonies.

How worker size affects colony size in eusocial insects

Understanding how colony-level resource allocation and growth can potentially affect biomass production within colonies may explain the body size–abundance patterns in this study and provide a theoretical basis for generalising patterns to other ant communities. The relationship between body size and colony size was significant after accounting for phylogeny, suggesting that these traits have undergone correlated evolution (Tschinkel, 1991).

Like all organisms, larger body size is correlated to greater longevity and larger ants tend to live longer than smaller ants. Empirical support can be found in Tschinkel & Porter's work with the fire ant, *Solenopsis invicta*, a species with a polymorphic worker size distribution, has shown that larger workers live longer than smaller workers (described in Tschinkel, 2006). In a eusocial system this relationship has a direct impact on colony size, because egg-laying is the task of only one or a few individuals, the queen or queens in each colony. Within a colony, if the fecundity of the queen or queens remains constant, but the worker size distribution shifts toward a larger size class, then a possible result is larger colony size because worker turnover (the ratio of deaths to births) decreases (Tschinkel, 1991).

Decreasing worker turnover through increased worker longevity contributes significantly to the growth of the superorganism (Wilson, 1971). In most ant species (except for species that reproduce only through colony budding), the individual foundress rears the first brood of workers from her own body reserves, which are significantly smaller than future workers, who then take over the tasks of brood care and colony maintenance and the superorganism becomes increasingly complex (Wilson, 1968; Oster & Wilson, 1978). Early in this ontogeny, shortly after the production of the first generation of nanitic workers, worker size begins to increase. Positively correlated with colony growth, worker size subsequently increases through most of the life of a colony, skewing the worker size distribution toward larger size classes – a pattern seen in both monomorphic and polymorphic species (Hölldobler & Wilson, 1990; Tschinkel, 2006).

Accounting for changes in worker size within the existing framework of Oster and Wilson's (1978) general model of resource allocation (equations 1–5) can explain how increasing worker size may increase colony size (Fig. 4). In their model, energetic costs from the metabolic activities of workers and queens, the manufacturing costs of raising workers and queens, and the mortality (or departure from the colony) of

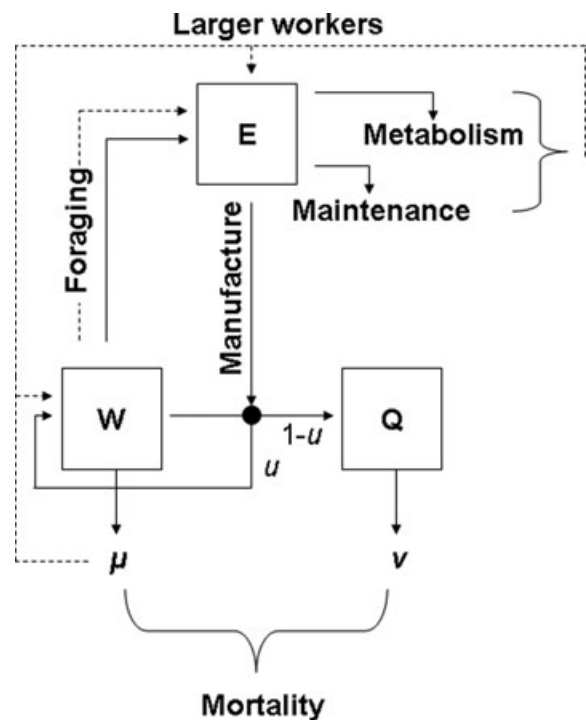


Fig. 4. A modified visualisation of Oster and Wilson's (1978) model of colony resource allocation, eqn 1, where E = energy resources, W = worker production, Q = worker production, u = the fraction of resources allocated to producing workers, $1 - u$ = the fraction of resources allocated to producing queens, μ = the mortality rate of workers, and ν = the mortality rate (or loss) of queens. Solid arrows show the allocation of resources into worker and reproductive castes while dashed arrows show the returns in energy in lower metabolic costs, greater foraging efficiency, and lower mortality rates associated with larger workers.

workers and sexuals are compensated for by the gains in energy from worker foraging and from the standing 'energetic reserve' contained within the workers themselves (e.g. worker body fat). Colonies can increase in size primarily by altering $M_W[-]$, the rate of 'manufacturing' workers. Increasing worker size makes this possible because it decreases m_W , the average metabolic costs of workers, and may also increase $\eta(W)$, the per capita foraging efficiency of workers (Tschinkel, 2006). Increasing worker size also directly affects worker turnover by reducing the mortality rate of workers, μ . Thus, under the conditions of the model, increasing worker size results in potentially great returns in energy availability from lower metabolic costs, lower worker turnover (mortality), greater energetic reserve, and increases in foraging returns (Fig. 4, dashed arrows).

There is some empirical support for this hypothesis. Tschinkel (2006) showed that, within a species (*S. invicta*), the returns predicted by the model from increasing worker size over the course of a colony life-span, result from increased colony size, territory size, foraging efficiency, and presumably, are also translated into increasing production of sexuals. Queen egg-laying rates, and egg mass are directly related to the quality and quantity of prey (Nonacs, 1991; Tschinkel, 2006), which is also affected by colony size and worker size because larger workers represent a larger energetic reserve and may be more effective at gathering high quality prey (Hölldobler & Wilson 1990; Tschinkel, 1991, 2006). Therefore, for a given species, gains in colony size can be converted directly into gains in alate production (and presumably, fitness, Tschinkel, 2006).

The model does not explain how selection constrains increases in worker body size or colony size. Sexual and worker body size is limited by the same genetic effects that determine body size for holometabolous insects in general (Abouheif & Wray, 2002). Within those constraints, ontogeny of the body size of workers and colony size is a product of direct and indirect genetic effects within the colony (Linksvayer, 2006, 2007) and the environment (Kaspari, 2005). There is evidence that selection may operate on worker size (Chew & Chew, 1980; Chew & DeVita, 1980; Gotelli & Ellison, 2002; King, 2007) such that worker mass is thus correlated with the size of food particles workers can carry, the rate and distance at which workers will forage, and desiccation resistance (Hood & Tschinkel, 1990; Kaspari & Weiser, 1999; Ness *et al.*, 2004). The body size of a species is constrained directly by genotype, local resource availability, and the energetic costs of producing individuals of different sizes under local conditions (Linksvayer, 2006, 2007; Tschinkel, 2006). While increasingly larger workers may provide many returns on investment (Fig. 4), they are nevertheless more costly to produce than smaller workers, which limits the rate at which they can be produced and the number of large workers a colony can support, although as colony size grows this constraint may be relaxed, or the energy 'spent' on sexual production (Tschinkel, 2006). Similarly, alternating investment in workers and sexuals, a strategy employed by many species, will constrain colony size, as will the effects of predation, parasitism, and density-independent factors (e.g. seasonal temperature changes; Poittrineau *et al.*, 2009). These constraints

limit the evolution of physical worker castes to only some genera and prevent, for example, the evolution of increasingly larger workers and colony sizes (Wilson, 1971; Oster & Wilson, 1978; Poittrineau *et al.*, 2009).

The data and model I present here provides a framework for understanding the mechanisms that explain how sociobiology profoundly influences the ecology of eusocial insects and, in turn, the ecosystems of a majority of the terrestrial biomes. The conversion of energy to fitness occurs at a higher level of biological organisation in ant communities. The body size of individual ants does not predict relative abundance as it does in many other animal and plant taxa, because there is a positive relationship between worker body size and colony size (Fig. 2a) and these traits are linked by colony-level resource allocation (Fig. 4). As a consequence, larger species have larger colonies, are more abundant, and make a disproportionately large contribution to the total standing biomass of ants. This first formulation of this hypothesis needs to be tested in a variety of other ecosystems across a range of latitudes, especially in the tropics. The remaining challenge is to accumulate sufficient data on colony size, worker size, colony density, whole colony metabolic rates, and resting and field metabolic rates of workers for many more species.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference:

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Appendix S1. Body mass, colony size, and occurrence data.

Appendix S2. Colony size data.

Appendix S3. Estimating colony density in ant communities with species occurrences in pitfall and litter samples.

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