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Towards a general life-history model of the superorganism: predicting the survival, growth and reproduction of ant societies

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Social insect societies dominate many terrestrial ecosystems across the planet. Colony members cooperate to capture and use resources to maximize survival and reproduction. Yet, when compared with solitary organisms, we understand relatively little about the factors responsible for differences in the rates of survival, growth and reproduction among colonies. To explain these differences, we present a mathematical model that predicts these three rates for ant colonies based on the body sizes and metabolic rates of colony members. Specifically, the model predicts that smaller colonies tend to use more energy per gram of biomass, live faster and die younger. Model predictions are supported with data from whole colonies for a diversity of species, with much of the variation in colony-level life history explained based on physiological traits of individual ants. The theory and data presented here provide a first step towards a more general theory of colony life history that applies across species and environments.

Keywords: ant colony; life history; metabolic scaling

1. INTRODUCTION

While the theory of natural selection once seemed at odds with the ubiquity of group living observed in nature, inclusive fitness theory has since made social evolution understandable, explaining cooperative behaviour in the context of genetic relatedness [1–5]. For decades, research on ant societies has driven

advances in the evolutionary logic of inclusive fitness theory, given the cooperation displayed among related individuals to capture and use resources [6,7]. However, many of the costs and benefits of cooperation reduce to a currency of energy and thus metabolism, and few studies have sought to explain how individual metabolism shapes colony-level rates of survival, growth and reproduction. Fewer still have explored how these rates vary among ant societies whose sizes span several orders of magnitude across species and environments.

Recent studies comparing the life history and physiology of colonial and individual organisms provide insights into the factors governing the life cycles of ant societies [8–10]. These studies have shown how rates of metabolism in whole colonies, and associated rates of growth and mortality, scale as a negative allometry with 'body mass' (i.e. total worker mass) in much the same way as in individual organisms (e.g. Kleiber's 'mouse to elephant curve').

Here, we aim to provide an explanation for these observed changes in whole-colony metabolic rate, lifespan and biomass production rate with colony mass. We do so by developing and evaluating with data, a mathematical model that predicts these three scaling relationships based on two traits: (i) changes in the average mass of individual ants with colony mass, and (ii) the body mass dependence of individual metabolic rate. To do this, we measure whole-colony metabolic rates for different ant species and use data gathered from the literature. Our results reveal that systematic changes in worker and queen size with colony size can explain allometries of whole-colony metabolic rate, production rate and mortality rate with increasing colony size.

2. MODEL DEVELOPMENT AND PREDICTIONS

To develop our model, we first examine how the mean body mass and metabolic rates of workers and queens vary with colony mass (i.e. total worker mass) for diverse species. We collected much of these data in Panama (methods detailed in Shik [9]) and supplemented them with data from the literature (see the electronic supplementary material, tables S1 and S2). We performed ordinary least square (OLS) regression analyses on species means and phylogenetically independent contrasts (PICs) of genus means.

PICs were calculated using the APE package in R [11] and the chronogram from a recent molecular phylogeny of ant genera [12]. Because OLS regressions using PIC were plotted through the origin (as per Warton *et al.* [13]; see the electronic supplementary material, figure S1 and S2 for details), and because model predictions required both slopes and intercepts, we generated them using scaling of species means without phylogenetic transformation.

Both worker and queen body mass increased as negative allometries with increasing colony mass across species (figure 1a). Specifically, worker mass scaled as $M_W = 0.08 M_C^{0.49}$ ($n = 107$; $r^2 = 0.62$) and queen mass scaled as $M_Q = 0.42 M_C^{0.53}$ ($n = 114$; $r^2 = 0.69$), where M is wet mass (mg), and the subscripts W, Q, C, denote worker, queen and colony, respectively. The exponents of these relationships, and those based on PIC, indicate that both workers and queens were absolutely larger, but relatively smaller, in larger colonies (table 1), consistent with previous reports [14,15].
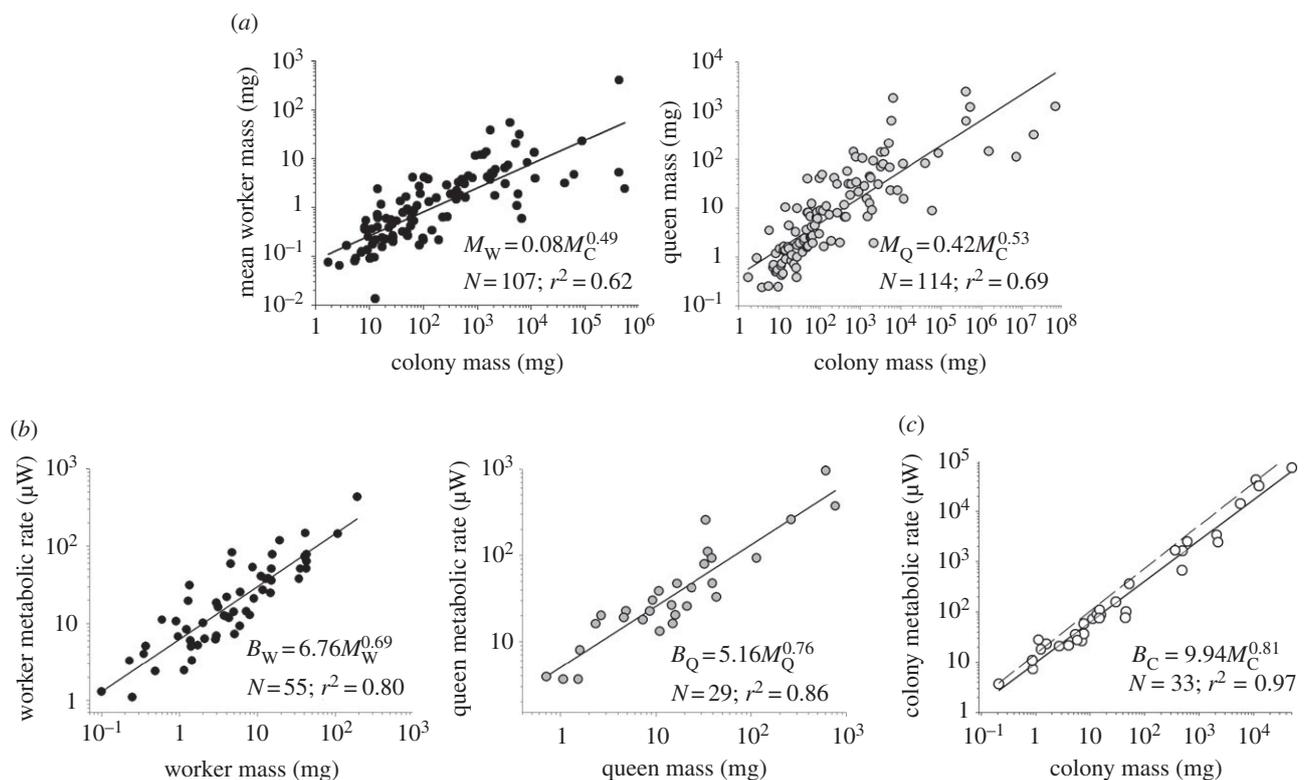
Figure 1. Interspecific relationships of (*a*) individual mass; (*b*) individual; (*c*) whole-colony metabolic rate to colony mass. Filled circles refer to workers, grey to queens, open to whole colonies. In (*c*) the solid black line is fitted to the data, and the dashed line is predicted from equation (2.1).

Table 1. Results from OLS regression for log–log scaling of ant colony traits. *n* indicates number of species (or genera for PIC) in the analysis. PIC denotes regressions based on phylogenetically independent contrasts. The coefficient values for the intercept (*a*) and slope (*b*) are provided with standard errors in parentheses. CI is the 95% confidence interval for *b*. Significance of regressions is indicated by asterisks. $**p < 0.01$, $***p < 0.001$, $****p < 0.0001$.

	species means					PIC			
	n	r^2	a	b	CI	n	r^2	b	CI
worker mass (M_W)	107	0.62	−1.07 (0.09)	0.49 (0.04)****	0.07	35	0.89	0.47 (0.05)****	0.10
queen mass (M_Q)	114	0.69	−0.37 (0.09)	0.53 (0.03)****	0.07	39	0.75	0.48 (0.03)****	0.06
worker MR (B_W)	55	0.80	0.83 (0.04)	0.69 (0.05)****	0.10	23	0.82	0.71 (0.07)****	0.15
queen MR (B_Q)	29	0.86	0.71 (0.08)	0.76 (0.06)****	0.12	18	0.93	0.81 (0.05)****	0.11
colony MR (B_C)	33	0.97	1.00 (0.05)	0.81 (0.03)****	0.05	18	0.97	0.82 (0.04)****	0.08
queen lifespan (LS_Q)	13	0.12	3.04 (0.33)	0.29 (0.24)	0.54	6	0.00	−0.18 (0.25)	0.64
colony lifespan (LS_C)	32	0.34	2.61 (0.19)	0.21 (0.05)***	0.11	15	0.66	0.29 (0.06)****	0.12
queen production (P_Q)	13	0.67	0.02 (0.34)	1.23 (0.26)***	0.57	8	0.64	1.51 (0.43)**	1.02
colony production (P_C)	25	0.94	−1.14 (0.18)	0.83 (0.04)****	0.09	14	0.84	0.84 (0.06)****	0.14

Worker and queen metabolic rates showed similar negative allometric scaling with body mass, with $B_W = 6.76M_W^{0.69}$ ($n = 55$; $r^2 = 0.80$) and $B_Q = 5.16M_Q^{0.76}$ ($n = 29$; $r^2 = 0.86$), where B is metabolic rate in microwatts (figure 1*b*). These relationships are consistent with corresponding regressions of PIC (table 1), and similar to those observed in solitary insects [8,16]. Thus, eusociality has apparently not affected the mass dependence of the metabolic rates of individual ants outside the context of the colony.

(a) *Predicting colony metabolic rate*
We can now generate a prediction for the interspecific scaling of whole-colony metabolic rate with colony mass observed in recent studies [8,10]. To do so, we assume that whole-colony metabolic rate is equal to the sum of individual metabolic rates, such that $B_C = NB_w$, where worker number, N, is estimated as M_C/M_W. By substituting $M_W = 0.08M_C^{0.49}$ and $B_W = 6.76M_W^{0.69}$ into $B_C = NB_w$, we arrive at the prediction that

$$B_C = 6.76\left(\frac{M_C}{M_W}\right)(M_W^{0.69}) = 14.79M_C^{0.85}. \qquad (2.1)$$

Equation (2.1) is intended to apply to mature colonies across species, where changes in the body mass of individuals through the ontogeny of a colony are not relevant.

(b) *Predicting colony lifespan*
We also generate a prediction linking colony lifespan and colony mass. Estimates of colony lifespan range from months to decades across ant species [17], while colony lifespans increase as a negative allometry
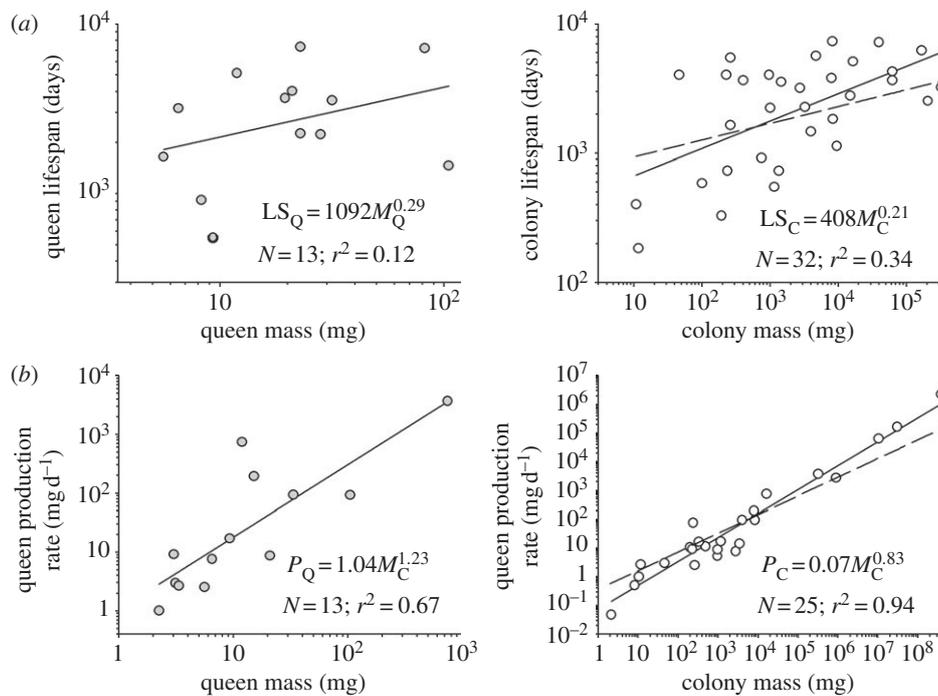
Figure 2. Interspecific relationships of (*a*) queen and colony lifespan to colony mass, and (*b*) the scaling of individual and colony biomass production rates. Solid black lines are fitted to the data. The dashed line in (*a*) is predicted from equation (2.3), and (*b*) it is predicted from equation (2.5). Symbols are defined as in figure 1.

with colony mass [8]. We first assume that queen lifespan (LS_Q in days) is inversely proportional to queen mass-specific metabolic rate, an extension of the rate-of-living hypothesis [18–21] such that

$$LS_Q = \frac{fM_Q^{0.76}}{M_Q} = fM_Q^{0.24}, \qquad (2.2)$$

where f is a taxon-specific constant that must be measured. Next, we assume that colony lifespan for monogynous (single queen) colonies can be estimated from the lifespan of the queen, LS_Q, such that $LS_C = LS_Q$. These two assumptions, combined with the relationship between queen mass and colony mass shown in figure 1*a*, yield the following prediction for the scaling of colony lifespan with colony mass:

$$LS_C = f(0.42M_C^{0.53})^{0.24} = 0.81fM_C^{0.13}. \qquad (2.3)$$

(c) *Predicting colony production rate*
Finally, we generate a testable prediction linking biomass production for queens and colonies, *P*, with colony mass based on two simplifying assumptions. First, based on scaling observed for individual animals [21,22], we assume that the total energy allocated to egg production for a queen is some constant fraction of her total metabolism such that $P_Q \propto B_Q$, and thus:

$$P_Q = P_0 M_Q^{0.76}, \qquad (2.4)$$

where P_0 is a normalization constant, and P_Q is the mass of eggs produced per queen per day (mg day^{-1}). Second, we assume that $P_C = P_Q$, where $M_C =$ (total worker mass)/(number of queens in colony). We then substitute $P_Q = P_C$ and $M_Q = 0.42M_C^{0.53}$ into equation

(2.4) to give a prediction for whole-colony production rate as a function of colony mass:

$$P_C = P_0(0.42M_C^{0.53})^{0.76} = 0.52P_0 M_C^{0.40}. \qquad (2.5)$$

3. RESULTS AND DISCUSSION
We evaluated model predictions on whole-colony metabolic rate, lifespan and biomass production rate from equations (2.1), (2.3) and (2.5), with data from diverse species whose colonies spanned over five orders of magnitude in mass (see the electronic supplementary material, tables S3–S5). Exponents based on regressions of PIC generally strengthened our scaling results, because most exponents were within the 95% confidence intervals (CI) of those generated from regressions of species means (table 1).

As predicted by equation (2.1) ($B_C = 14.79M_C^{0.85}$), colony metabolic rate scales as a negative allometry with colony mass as $B_C = 9.94M_C^{0.81}$ ($n = 33$, $r^2 = 0.97$; figure 1*c*), with a 95% CI that contained the predicted exponent (table 1), although the intercept is about 1.5-fold lower. The match between predicted and observed relationships supports our hypothesis that a significant proportion of the change in whole-colony metabolic rate with colony mass results from changes in the mass and metabolic rates of individual worker ants.

As predicted by equation (2.2), queen lifespan scales as $LS_Q = 1091.57M_Q^{0.29}$($n = 13$, $r^2 = 0.12$; figure 2*a*), although queen mass explains only a small portion of the variation (table 1). Nonetheless, if we insert the observed scaling relationship for queen lifespan into equation (2.3) ($LS_C = 0.81fM_C^{0.13}$), we obtain a prediction linking colony lifespan and colony mass, $848.78M_C^{0.15}$, and an exponent that is within 95%

CI for the observed relationship $LS_C = 407.75M_C^{0.21}$ ($n = 32$, $r^2 = 0.34$), although this observed intercept is twofold lower (table 1 and figure 2a).

Finally, we compare the observed and predicted scaling relationships for biomass production rates of queens and colonies, P_Q and P_C. We observe that $P_Q = 1.04M_Q^{1.23}$ for queens ($n = 13$, $r^2 = 0.67$), and $P_C = 0.07M_C^{0.83}$ for colonies ($n = 25$, $r^2 = 0.94$; figure 2b). The 95% CI for the observed exponent of P_C does not contain the exponent predicted by equation (2.5) ($P_C = 0.52P_0M_C^{0.40}$) (table 1), and the positive allometric scaling of P_Q suggests that larger queens invest relatively more in biomass production than smaller queens. Thus, allocation to biomass production does not appear to be a constant fraction of total metabolism as assumed in equation (2.4) and typically observed for individual animals [21,22]. While this may be important towards understanding colony growth, it must be cautiously interpreted given the limited data.

Still, substituting the observed relationship for queen mass $M_Q = 0.42M_C^{0.53}$ into the observed relationship for queen production $P_Q = 1.04M_Q^{1.23}$, yields $P_C = 0.36M_C^{0.65}$, which agrees well with the observed relationship between colony production and colony mass. This suggests that whole-colony production is approximately a constant fraction of whole-colony metabolism because metabolism scales similarly with colony mass.

To conclude, the model developed here yields specific quantitative predictions regarding how the energy use, lifespan and production rate of colonies change with colony mass. The predictions are based on the previously unappreciated allometries between worker size, queen size and colony size, and the relationships between the metabolic rate and mass of individual ants. Moreover, the correspondence of the data with theory not only supports the model, but also explicitly links the survival, growth and reproduction of whole colonies to the physiology of individual colony members without invoking changes in group-level traits (e.g. division of labour) with colony mass.

An important caveat is that because our study uses laboratory measurements, we cannot test the extent to which the efficiencies of group living affect the metabolism and production of colonies facing complex ecological challenges. By design, the models presented here are simplified representations of a more complex reality. For example, deviations from model predictions (i.e. lower observed intercepts) may occur as a result of ecological factors such as parasitism or competition, or as a result of variably sized worker castes [23,24]. Integrating such information into this model may enable finer scale predictions about the phenomena addressed here.

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