Energetic inequivalence in eusocial insect colonies

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The energetic equivalence rule states that population-level metabolic rate is independent of average body size. This rule has been both supported and refuted by allometric studies of abundance and individual metabolic rate, but no study, to my knowledge, has tested the rule with direct measurements of whole-population metabolic rate. Here, I find a positive scaling of whole-colony metabolic rate with body size for eusocial insects. Individual metabolic rates in these colonies scaled with body size more steeply than expected from laboratory studies on insects, while population size was independent of body size. Using consumer-resource models, I suggest that the colony-level metabolic rate scaling observed here may arise from a change in the scaling of individual metabolic rate resulting from a change in the body size dependence of mortality rates.

Keywords: energetic equivalence rule; metabolic rates; eusocial insects; mortality; allometry

1. INTRODUCTION

The energetic equivalence rule (EER) states that population-level energy use (as estimated by metabolic rate) is independent of average individual body size [1]. The metabolic rate of a population, \( B_{\text{pop}} \), is the product of the number of individuals in the population, \( N \), and the average metabolic rate per individual, \( B_{\text{ind}} \). Both \( N \) and \( B_{\text{ind}} \) are related to individual body mass, \( M \), via power functions, with exponents of \( \alpha \) and \( \beta \), respectively. This means that \( B_{\text{pop}} \) is also a power function of mass: \( B_{\text{pop}} = NB_{\text{ind}} \propto M^\alpha M^\beta \propto M^{\alpha+\beta} \). When \( \alpha = -\beta \), population-level metabolic rate is independent of body size.

Support for the EER is mixed. Population size and body mass are usually negatively related, and the exponent \( \alpha \) is frequently close to the negative of \( \beta \), lending support to the EER [1–4]. In other cases \( \alpha \) is less than \(-\beta \), suggesting that population-level metabolic rate increases with individual body mass [5–8]. In addition, the relationship between size and abundance is not always a scaling law, causing a peak in population-level metabolic rate at intermediate body sizes [9].

Standard assessments of the EER assume that the scaling of individual metabolic rate with body mass is the same for laboratory and field conditions. Metabolic scaling relations reflect mass-specific constraints on metabolism [10], and basal or resting metabolic rates have physiological constraints. For example, explanations for the scaling of basal metabolic rate with body size are based on internal factors such as the structure of cardio-vascular systems [11] or the size and number of cells in the body [12]. These hypotheses implicate an internal rate-limiting step in resource use, creating a mass-specific constraint on metabolic rate. In nature, other factors may alter the scaling, such as interactions among individuals that alter access to resources. Indeed, the scaling of field metabolic rate is often different than the scaling of basal metabolic rate [13], suggesting that ecological constraints may be present. Because of the equivocal results from allometric studies and the potential for spurious identification of EER resulting from the assumption that ecological and physiological constraints are parallel, the EER would be better demonstrated with direct measurements of population-level metabolic rate.

The EER is a theoretical mystery. Some have suggested that all populations have access to the same amount of resource, and therefore the EER is simply a natural outcome of this population-level provisioning [2,14]. Yet, it is unclear what could make the total resource supply to all populations the same. Even among plants, for which resource availability (sunlight) is arguably independent of body size, there is no guarantee that a population can access the same portion of the resource regardless of body size. It may be that some type of body size-dependent consumer–resource interaction sets the rate at which a population acquires resources, leading to a particular scaling of population-level metabolic rate with body size. This suggests that consumer–resource models may be a useful theoretical framework for understanding the EER.

In this study, I evaluate the EER for eusocial insect colonies. I analyse direct measures of whole-colony metabolic rate and find a strong positive relationship between colony-level metabolic rate and body size, indicating that the EER does not hold at this scale of aggregation. To explore this result, I analyse a consumer-resource model and show how individual metabolic rate may be influenced by ecological constraints and thereby alter the group-level metabolic scaling.

2. MATERIAL AND METHODS

I compiled data on the metabolic rates, colony sizes and body masses of eusocial insects (see data and details, electronic supplementary material; [15–23]). Metabolic rates are the measure of energy use in this study, and the values reported here reflect a range of activity levels in laboratory-reared colonies and are not consistent with basal, standard or field metabolic rate definitions. I standardized metabolic rates to 25°C using the Boltzmann factor [15]. All data represent the largest colonies from the original studies. Colonies were in a variety of stages of development but appeared to have reached saturating levels of metabolism so that the values used represent a robust snapshot of the higher levels of colony-level metabolic rate. I used average body sizes for workers or soldiers because these castes make up the bulk of eusocial insect colonies [8]. Where necessary, I calculated colony size for each colony by dividing the mass of the colony by individual mass, and I obtained individual metabolic rates by dividing whole-colony rates by colony size. I used both ordinary least squares (OLS) and reduced major axis (RMA) regression to accommodate potential error in the estimates of individual body size. All analyses used log-transformed data.

3. RESULTS

The relationship between colony-level metabolic rate and body size was positive (figure 1a and table 1). Individual metabolic rate also scaled positively with body
The scaling of (a) whole-colony metabolic rate, (b) individual metabolic rate, and (c) population size with body size in eusocial insects. Ants are identified by filled circles. Fits with all data are shown with thin lines and fits with ants only are shown with thick lines. RMA fits are circles. Fits with all data are shown with thin lines and fits with ants only are shown with thick lines. RMA fits are circles. Fits with all data are shown with thin lines and fits with ants only are shown with thick lines. OLS fits are solid. See table 1 for details.

Figure 1. The scaling of (a) whole-colony metabolic rate, (b) individual metabolic rate, and (c) population size with body size in eusocial insects. Ants are identified by filled circles. Fits with all data are shown with thin lines and fits with ants only are shown with thick lines. RMA fits are circles. Fits with all data are shown with thin lines and fits with ants only are shown with thick lines. OLS fits are solid. See table 1 for details.

size (figure 1b and table 1), whereas body size and colony size were unrelated (figure 1c and table 1). Repeating the analyses with only ants indicates that none of the above results arose from combining flying and ground-dwelling organisms into one analysis (table 1). OLS and RMA regressions produced similar results.

4. DISCUSSION
In this study, I directly tested the EER for eusocial insect colonies. Rather than being independent of body mass, colony-level metabolic rate increased with mass, a pattern that is consistent with most previous studies that have not supported the EER, including one study with ants [8]. In previous studies, positive scaling of population-level metabolic rate with body size was suggested by density scaling that was shallower than the individual metabolic rate scaling under a physiological constraint. In this study, the individual metabolic rate scaling was steeper than expected from laboratory studies [24,25] and colony size was independent of body size, making for a strong deviation from the EER. A recent study on Florida ant communities found that population size and population-level metabolic rate (estimated indirectly) both increased with body size [8], suggesting that ants show energetic inequivalence at both the colony and population scales.

The steeper-than-expected (i.e. greater than 0.75) scaling of individual metabolic rate with body mass in these data suggests major differences between the mass-specific constraints of unitary insects at rest in the laboratory and active eusocial insects in colonies [10]. To understand this result, it is necessary to develop a framework for understanding how ecological interactions affect metabolic rates at both the individual and population scales. Using consumer–resource models, we can begin to understand how body size-dependent mechanisms of consumer–resource interactions can lead to particular resource use and metabolic rate patterns. In this case, I will use a standard consumer-resource model to understand how ecological factors may have influenced the scaling of individual metabolic rate and led to the positive scaling of colony-level metabolic rate with body size. The model is

\[
\begin{align*}
\frac{dR}{dt} &= g(R) - Cf(R,C) \\
\frac{dC}{dt} &= eCf(R,C) - \mu C.
\end{align*}
\]

(4.1)

In this model, two ordinary differential equations track consumer, C and resource, R densities through time. The growth function \( g \) describes the regeneration of resources. The consumers convert resources into new consumers with efficiency, \( e \), and die at mortality rate, \( \mu \). A functional response, \( f(R,C) \), links the two equations by setting the \textit{per capita} rate of resource uptake by consumers. The consumer population grows and depletes resources through time, suppressing \textit{per capita} resource uptake rate, \( f \).

A steady-state population size is reached when \( f \) is low enough that the birth rate equals the death rate. Solving the consumer equation for \( f \) when \( dC/dt = 0 \) yields the equilibrium \textit{per capita} resource uptake rate for the consumer:

\[
\dot{f} = \frac{\mu}{e}.
\]

(4.2)

Because all metabolism is fueled by food resources, the scaling of individual metabolic rate with body mass under an ecological constraint is given by the scaling of \( f \) with body mass. That scaling depends on the scaling of mortality rate and conversion efficiency with body mass.

Typically, mortality rate scales negatively with body size as \( \mu \propto M^\delta \) [26]. The scaling of \( e \) depends upon the scaling of its component parts. More completely, \( e = i_g \, e_p \, a_p \, e_c \, a_c \), where the parameters are, from left to right, the number of individuals produced per gram of production (ind g\(^{-1}\)), the efficiency of production (g J\(^{-1}\)), the allocation of energy to production (no units), the conversion rate of the assimilated mass of resources to energy (J g\(^{-1}\)), and the assimilation efficiency (no units). The only parameter in this list which is clearly body size dependent is \( i_g \), because it is the inverse of body mass. The quantity \( e_p \, a_p \, e_c \, a_c \), if multiplied by the mass of the acquired resource, is equivalent to gross growth efficiency (grams of consumer produced per gram of resource), which on average appears to be unrelated to body size [26]. In addition, there is little evidence of a body size dependence of \( e_p \) [10]. Therefore, we can substitute the scaling of \( \mu \) and \( e \) into equation (4.1) to get

\[
\dot{f} = \frac{\mu}{e} \propto \frac{M^\delta}{M^{\gamma}} \propto M^{\delta+1}.
\]

(4.3)

Table 1. Results from regressions on body size, $B$. (Parameters are for the allometric model: $y = b_0 B^a$ and are shown $\pm 95\%$ confidence intervals.)

<table>
<thead>
<tr>
<th>dependent variable</th>
<th>$r^2$</th>
<th>$p$</th>
<th>$b_0$</th>
<th>$a$</th>
<th>$b_0$</th>
<th>$a$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>all data combined</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>population-level energy use</td>
<td>0.80</td>
<td>&lt;0.001</td>
<td>12.9</td>
<td>1.36</td>
<td>25.16</td>
<td>1.53</td>
</tr>
<tr>
<td>individual energy use</td>
<td>0.96</td>
<td>&lt;0.001</td>
<td>0.02</td>
<td>1.50</td>
<td>0.02</td>
<td>1.53</td>
</tr>
<tr>
<td>population size</td>
<td>0.04</td>
<td>0.58</td>
<td>665</td>
<td>-0.13</td>
<td>57.3</td>
<td>-0.73</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(51–8730)</td>
<td>(-0.68 to 0.4)</td>
<td>(0.66–17 300)</td>
<td>(-1.64 to 0.71)</td>
</tr>
<tr>
<td><strong>only ants</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>population-level energy use</td>
<td>0.86</td>
<td>0.002</td>
<td>6.9</td>
<td>1.37</td>
<td>11.73</td>
<td>1.48</td>
</tr>
<tr>
<td>individual energy use</td>
<td>0.93</td>
<td>&lt;0.001</td>
<td>0.003</td>
<td>1.18</td>
<td>0.004</td>
<td>1.22</td>
</tr>
<tr>
<td>population size</td>
<td>0.28</td>
<td>0.22</td>
<td>2178</td>
<td>0.20</td>
<td>5357</td>
<td>0.37</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(310–15 276)</td>
<td>(-0.16 to 0.56)</td>
<td>(72–22 126)</td>
<td>(-0.35 to 0.63)</td>
</tr>
</tbody>
</table>

In conclusion, direct tests of the EER are difficult to conduct, but data on eusocial insects provide a unique opportunity. Colony-level metabolic rates increased with average body size, indicating that the EER does not hold at this scale. Understanding the EER will require the development of new theory that connects the metabolic rates of individuals to population-level traits. Consumer-resource models may be useful in this regard and yield novel and interesting hypotheses about body size-dependent processes in nature.

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**Figure 2.** How mortality can alter individual metabolic rate. An initial steady-state, point $A$, has an equilibrium population size, $K_1$, and per capita resource uptake rate, $f_1$. If the mortality rate increases, the population declines in size, causing $f$ to increase and birth rates to increase until they are equal to the higher mortality rate. At this point, a new steady-state is produced at point $B$.

Equation (4.3) shows that the scaling of metabolic rate for individuals in a population context is primarily dependent on the mortality rate scaling. The scaling of $f$ under this ecological constraint (meaning constrained by resources in the context of a population) will parallel the scaling of individual metabolic rate under a physiological constraint if $\delta = \beta - 1$. The scaling of lifespan is often about $1 - \beta$ [26]. The scaling of morality rate is the inverse of the scaling of lifespan ($\beta - 1$), indicating that $\delta$ may satisfy this condition for many groups. This suggests that many cases of the EER previously identified by the condition that $\alpha = -\beta$ are correct, unless other mortality factors such as size-specific predation are at play.

Equation (4.3) also suggests that the steep scaling of individual metabolic rate in this study is generated by a positive scaling of mortality rate with body mass, which contrasts with the usual negative scaling of mortality rate with body mass. What this means is that higher mortality causes the population to stop growing at higher levels of $f$ for larger species, making the individual metabolic rate scaling steeper. This is easiest to understand if we consider what happens to a population at steady-state that experiences an increase in mortality rate (figure 2). An increase in mortality rate leads to a decrease in abundance, which increases $f$ until birth rate equals the heightened mortality, making $f$ and the metabolic rate higher.

In conclusion, direct tests of the EER are difficult to conduct, but data on eusocial insects provide a unique opportunity. Colony-level metabolic rates increased with average body size, indicating that the EER does not hold at this scale. Understanding the EER will require the development of new theory that connects the metabolic rates of individuals to population-level traits. Consumer-resource models may be useful in this regard and yield novel and interesting hypotheses about body size-dependent processes in nature.


