Original article

Density-body mass relationships: Inconsistent intercontinental patterns among termite feeding-groups

Cecilia A.L. Dahlsjö [a, b, g, *], Catherine L. Parr [c], Yadvinder Malhi [a], Patrick Meir [d, e], Homathevi Rahman [f], Paul Eggleton [b]

[a] Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK
[b] Soil Biodiversity Group, Department of Entomology, The Natural History Museum, London, UK
[c] Department of Earth, Ocean and Ecological Sciences, School of Environmental Sciences, University of Liverpool, Liverpool L69 3GP, UK
[d] School of Geosciences, University of Edinburgh, Edinburgh, UK
[e] Research School of Biology, Australian National University, Canberra ACT 0200, Australia
[f] Institute for Tropical Biology and Conservation, University Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia
[g] Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Czech Republic

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ABSTRACT

Allometric relationships are useful for estimating and understanding resource distribution in assemblages with species of different masses. Damuth's law states that body mass scales with population density as $M^{-0.75}$, where M is body mass and -0.75 is the slope. In this study we used Damuth's law ($M^{-0.75}$) as a null hypothesis to examine the relationship between body mass and population density for termite feeding-groups in three different countries and regions (Cameroon, West Africa; Peru South America; and Malaysia SE Asia). We found that none of the feeding-groups had a relationship where $M^{-0.75}$ while the data suggested that population density-body mass relationships for true soil-feeding termites in Cameroon ($M^{2.7}$) and wood-feeding termites in Peru ($M^{1.5}$) were significantly different from the expected values given by Damuth's law. The dominance of large-bodied true soil-feeding termites in Cameroon and the absence of fungus-growing termites from Peru suggest that these allometric patterns are due to heterogeneities in termite biogeographical evolution. Additionally, as these feeding-groups have higher population density than expected by their body masses it may be suggested that they also have a higher energy throughput than expected. The results presented here may be used to gain further understanding of resource distribution among termite feeding-groups across regions and an insight into the importance of evolutionary history and biogeography on allometric patterns. Further understanding of population density-body mass relationships in termite feeding-groups may also improve understanding of the role these feeding-groups play in ecosystem processes in different regions.

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1. Introduction

1.1. Allometric scaling laws

Body mass is one of the most studied physiological traits in ecology as, among other things, it influences metabolic rate, abundance, and growth rate (Brown et al., 2004). The relationship between body mass and energy flow is important for understanding resource distributions within assemblages with species of different masses (Damuth, 1981; Eggleton et al., 1998; Lewis et al., 2008; Maurer and Brown, 1988). According to metabolic scaling theories the metabolic rate is a power law function of body mass (Brown et al., 2004). The species-specific metabolic rate of the individual $\dot{B}$ is calculated as

$$\dot{B} = \overline{M}^{b} \qquad (1)$$

where $\overline{M}$ is the average mass of a species and b is the scaling exponent.

* Corresponding author. Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK.
E-mail addresses: cecilia.dahlsjo@ouce.ox.ac.uk, c.dahlsjo@gmail.com (C.A.L. Dahlsjö), kate.parr@liverpool.ac.uk (C.L. Parr), yadvinder.malhi@ouce.ox.ac.uk (Y. Malhi), pmeir@ed.ac.uk (P. Meir), homa.ums@gmail.com (H. Rahman), p.eggleton@nhm.ac.uk (P. Eggleton).

It is frequently observed across a range of organisms that b ~0.75, a relationship referred to as Kleiber's law (Kleiber, 1947). The West, Brown, and Enquist (WBE) model suggests that the mechanism behind this law is the regulation of metabolic rate by the geometry of vascular networks that supply cells with energy from mammalian aortae to vascular systems in plants (West et al., 1997). This is supported by the mass scaling exponent $b \sim 0.75$ for the cross-section area of aortae or tree trunks (West et al., 1997). Critics of this law have argued, however, that the scaling exponent is not always 0.75 (Chown et al., 2007; Riveros and Enquist, 2011). An alternative model, the cell size model (Chown et al., 2007), suggests that Kleiber's law is only true at a wider interspecific level with a range of scaling exponents between 0.6 and 1.0 found within species or genera (Chown et al., 2007).

The energy flow in a species population (total metabolic rate) can be described as the product of species-specific metabolic rate $\dot{B}$ and population density of a species N:

$$\dot{B}_{tot} = \dot{B} \cdot N \tag{2}$$

N is proportional to $\overline{M}^{-a}$, where $\overline{M}$ is the average mass of a species and a is the power law coefficient of the relationship between population density and mean individual mass. It is commonly observed that smaller organisms have higher population density while larger organisms have lower population density. The power constant a is frequently observed to be ~ -0.75 described as Damuth's law (Damuth, 1981).

1.2. Allometry in termites

Termites are one of the most important invertebrate decomposers, particularly in the tropics where their abundance and range of feeding-groups are high (Bignell and Eggleton, 2000; Donovan et al., 2001a; Eggleton et al., 1999, 1996) partly due to their symbiotic relationship with gut biota (Hongoh, 2010). The termite gut is a specialised habitat for bacteria, archaea, and protists which, along with termites' specialised guts and mandibles (wood-feeders), make them highly efficient decomposers (Eggleton, 2011; Hongoh, 2010). Termites have been categorised into five feeding-groups depending on the humification (decomposition) of the material they feed on (Donovan et al. 2001a,b). These feeding-groups range from wood-feeding termites, which feed on sound dead wood, to true soil-feeding termites, which feed on soil organic matter in mineral soil with no visible plant remains (Table 1). The difference in particle size of the diets of humus-feeding (FGIII) termites and true soil-feeding (FGIV) termites, although no difference in isotope composition has been found (see Bourguignon et al. (2011) for C and N stable isotope ratios), may mean that the two feeding-groups metabolise their substrates in different ways. It is known, for example, that FGIV feeders have a more complex gut than FGIII feeding termites to allow the

Table 1
Classification of termite functional groups and respective feeding substrates within tropical rain forests. Modified from Donovan et al. (2001) and Inward et al. (2007).

Functional group	Feeding substrates
FGI	Sound wood
FGII	Wood and leaf litter
FGIIF	Wood and leaf litter on which fungi are grown and harvested (Macrotermitinae only)
FGIII	Organic material-rich soil and humus, with visible plant structures
FGIV	Mineral soil with no visible plant structures (true soil-feeding termites)

decomposition of nutritionally poorer soil (Ji and Brune, 2005). Species of *Cubitermes* (FGIV soil-feeding termites) have been shown to stabilise nitrogen in a form which plants can utilise by increasing soil ammonia content (Ngugi et al., 2011; Ngugi and Brune, 2012). Through decomposition of organic matter and the construction of tunnels, runways and nesting structures (e.g. mounds) termites influence nutrient availability and distribution which affects water and air movement through the soil and promote plant growth (Jouquet et al., 2011, 2006). These activities make termites important ecosystem engineers as they contribute to the structural and chemical composition of their habitat (Brussaard et al., 1997; Jones et al., 1994).

Eggleton et al. (1998) investigated the relationship between total metabolic rate and body mass in two termite feeding-group assemblages (wood-feeding and soil-feeding termites) in Cameroon. Their analysis showed that small to medium-bodied wood-feeding termites had higher metabolic rates (O_2 consumption per unit weight combined with population density to give energy use per unit area) than large-bodied species while large-bodied soil-feeding species had the highest metabolic rates. The latter indicates that the larger-bodied soil-feeding termites in Cameroon have a larger energy throughput (Damuth, 1981) than species of other mass classes due to their proportionally higher metabolic rate. Recent biomass estimates across the three study sites (Dahlsjö et al., 2014) show that termite biomass varies among regions with highest biomass per unit ground area being found for large-bodied soil-feeding termites (*Cubitermes*-group & *Apicotermes*-group) in Cameroon. These very large soil-feeding termites are absent from Asia and South America.

Since the Eggleton et al. (1998) study, a number of advances have been made in the field of termite ecology, particularly in the development of comparable sampling techniques and a more sophisticated feeding-group classification (Jones and Eggleton, 2000; Donovan et al. 2001a,b; Davies et al. 2003; Bourguignon et al. 2011; Hyodo et al. 2011). These developments have provided better estimates of termite diversity patterns and functional groupings. Additionally, there are now sufficient data to compare biomass and abundance patterns of assemblages from sites in the three main tropical regions (Africa, Asia, and South America) (Dahlsjö et al., 2014; Eggleton et al., 1999, 1996). These advances allow us to explore the termite population density — body mass relationship in more detail and to compare and contrast across the three major tropical continents for the first time. This paper considers population density - body mass relationships in termite feeding-groups using data from Cameroon, Peru and Malaysia. As population density is, according to Damuth's law, approximately reciprocal to individual metabolic rate (Damuth, 1981) investigating population density-body mass relationships in termite feeding-groups may enhance our understanding of the role termites play in ecosystem processes, such as nutrient turnover, availability and distribution (Jouquet et al., 2011), among regions.

In this study we (a) treat Damuth's law as a null hypothesis (Isaac et al., 2013), by testing the observed slope values for population density and body mass against the predicted value (-0.75) of Damuth's law, for three feeding-groups (true soil-feeding termites FGIV, humus-feeding termites FGIII and wood-feeding termites FGI, FGII and FGIIF) across three regions (Cameroon, Peru and Malaysia) and (b) discuss the causes of the observed patterns (biogeography and evolution) and the potential implications on ecosystem processes. We predict that the dominance of large-bodied true soil-feeding (group IV) termites in Cameroon will greatly impact on the population density - body mass relationships and is, therefore, expected to diverge from Damuth's law. The population density — body mass relationships in all other feeding-groups are expected to follow Damuth's law.