

The scaling of colony size with nest volume in termites: a role in population dynamics?

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Abstract. 1. Colony size is often attributed a key role in social insect population ecology. However, in nest-building termites, colony size is a power function of nest volume, so that colonies of species with low scaling exponents tend to grow less as their nests are expanded. Thus, in such species, intercolonial differences in colony size may be less likely to develop, and changes in species total biomass may largely reflect those in colony numbers rather than colony sizes.

2. The scaling of colony biomass with nest volume in three termite species, namely *Anoplotermes banksi* Emerson, *Neocapritermes braziliensis* Snyder and *Labiotermes labralis* Holmgren was determined. Then, their nests were counted and their total biomass in plots across an Amazonian rainforest landscape was estimated. Finally, whether the strength of the relationship between total biomass and number of nests reflected species scaling exponents was examined.

3. Scaling exponents were 0.47 for *N. braziliensis*, 0.57 for *A. banksi*, and 0.83 for *L. labralis*. On the other hand, the strength of the relationship between total biomass and the number of nests (r^2) followed the opposite trend: 0.93 for *N. braziliensis*, 0.92 for *A. banksi*, and 0.53 for *L. labralis*.

4. It is suggested that the scaling of colony size with nest volume may mediate termite population dynamics: as the scaling exponent decreases across species, changes in total biomass would increasingly reflect changes in colony numbers, with an accompanying increase in the importance of colony births and deaths as opposed to colony growth.

Key words. Abundance, allometry, density, Isoptera, mound, Termitidae, Termitoidea.

Introduction

Body size is a key ecological trait, as it underlies many aspects of individual performance (Roos *et al.*, 2003). However, in social insects such as ants and termites, individuals organise into colonies, familial groups in which the majority of the brood is sterile and committed to feeding and defending the reproductives (Wilson, 1971). Colonies with more individuals

generally have superior competitive ability (Levings & Adams, 1984; Leponce *et al.*, 1997; Palmer, 2004; Walters & MacKay, 2005) and enhanced survival and reproduction (Thorne, 1983; Tschinkel, 1993; Kaspari & Vargo, 1995; Thorne & Haverty, 2000). Thus, colony size mediates colony performance in social insects as body size mediates individual performance in solitary animals, with potentially important consequences for social insect ecology (Cole, 2009).

In many social insect species, colonies build nests, housing structures that provide the colony with environmental stability and protection (Wilson, 1971). Termites in particular are known for building some of the largest and most complex nests

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among animals, and termite nests can be very abundant in the tropics (Korb, 2011). As physical structures, nests define the space where the colony development unfolds, and increments in colony size can be preceded by bouts of nest expansion (Jones, 1979). If the rate of colony growth differs from that of nest expansion, allometry between colony size and nest volume can result. Indeed, colony size has been shown to scale with nest volume to a power less than 1 (i.e. negative allometry) in almost all nest-building termite species studied so far, but the scaling exponent varies considerably among species (Josens & Soki, 2010). Such variation may have important consequences, as allometries between colony-level traits may shape social insect ecology and evolution (Tschinkel, 1993). However, the role of such allometries in termite ecology remains unknown.

One possibility is that the scaling of colony size with nest volume affects colony size variability within species. Picture a population of growing, conspecific colonies. Any intercolonial differences in growth rate (e.g. owing to different growth conditions) will tend to translate into differences in colony size. Now, in species whose scaling exponents are relatively high (≈ 1), the relationship between colony size and nest volume approximates a straight line, so that increments in colony size are roughly constant throughout nest expansion. However, in species whose scaling exponents are relatively low (< 1), the relationship between colony size and nest volume approximates an asymptotic curve, so that the rate of increase in colony size declines as the nest is expanded. Accordingly, colonies harboured by larger nests are relatively more similar in size. This suggests that, all else being equal, the lower the species scaling exponent, the less size differences should develop, given that all colonies are expected to grow slower with nest expansion. Under this scenario, colony size variability would tend to be lower in populations of species whose scaling exponents are relatively low.

If so, variation in colony-nest allometry could underlie inter-specific differences in population dynamics, because the total biomass of a social insect species in an area depends on both its number of nests and the sizes of its colonies (Adams & Levings, 1987). Thus, if a low scaling exponent is intrinsically linked to reduced colony size variability in a species, changes in its total biomass would mainly reflect changes in colony numbers. Alternatively, if variability in colony size is relatively large, colony numbers alone may not reliably inform about changes in total biomass (Adams & Tschinkel, 2001). This distinction is important because, in the first case, population dynamics would be mainly subject to processes affecting colony births and deaths, whereas in the second case, colony growth would be more important.

In the present study, this issue was addressed with three termite species in an Amazonian lowland rainforest, namely *Anoplotermes banksi* Emerson, *Neocapritermes braziliensis* Snyder, and *Labiotermes labralis* Holmgren. These are common nest-building species in Amazonia, and their colonies build single nests which are easy to locate and identify (Martius & Ribeiro, 1996; Pequeno & Pantoja, 2012). Moreover, their nests are spheroidal, which facilitates estimating their volumes. Both *A. banksi* and *L. labralis* feed on

humus and build arboreal nests close to the ground, whereas *N. braziliensis* feeds on rotten wood and builds epigeal nests.

First, we determined the scaling of colony biomass with nest volume for the three species. Then, we counted and measured their nests in 31 plots systematically distributed over a lowland rainforest landscape. By knowing the relationship between colony size and nest volume, we estimated the total biomass of each species in each plot. Then, we tested whether species with lower scaling exponents were characterised by a stronger correlation between total biomass and number of nests.

Materials and methods

Study site

Data on each species were obtained in locations in the surroundings of the city of Manaus, Amazonas State, Brazil (see below). The region is mostly covered by primary, lowland tropical rainforest. The mean daily annual temperature and mean annual rainfall between 1992 and 2002 were 26.7 °C and 2479 mm, respectively, and there is a relatively dry season (less than 100 mm of rain per month) from July to September (Research Coordination in Climate and Hydric Resources, National Institute for Amazonia Research). Local terrain is rugged, and altitude ranges from c. 50 to 120 m. Soils are classified as yellow clay latosol on higher areas, clay-sand on slopes, and sandy soils (hidromorphic podzol) in valleys. Canopy height is around 35–40 m, with some trees reaching over 45 m, and the understory is dominated by a few stemless palm species (Guillaumet, 1987).

Data on colony biomass and nest volume

Data on colony fresh biomass (g) and nest volume (dm³) were compiled from the literature for *A. banksi* and *L. labralis*, and obtained in the present study for *N. braziliensis*. In the case of *A. banksi*, colony biomass was determined by directly weighing whole colonies, whereas for *L. labralis* and *N. braziliensis*, colony biomass was obtained by multiplying the number of individuals per caste in colonies by the respective average caste body masses. Castes considered were larvae (i.e. pre-workers without wing buds), workers, soldiers, nymphs (pre-alates with wing buds and developing eyes), and alates.

The data for *A. banksi* were pooled from Martius and Ribeiro (1996) and Apolinário (2000) as they used exactly the same sampling method. Martius and Ribeiro (1996) collected nests ($n = 7$) from two primary rainforest sites: Reserva Ducke, northeast of Manaus (03°60'S, 59°59'W), in May–October 1993 and March 1994; and Reserve 1501 of the Project Biological Dynamics of Forest Fragments (PDBFF) (National Institute for Amazon Research/Smithsonian Institution), about 87 km north of Manaus. The nests were taken to the laboratory at Manaus, weighed and opened to extract all the termites, which were then collectively weighed. Two colonies were very small relative to the volume of their nests, and were identified as declining by Martius and Ribeiro (1996); these colonies were not considered in the current analysis. Apolinário

(2000) collected nests at Reserva Ducke from October 1996 to January 1997 ($n = 10$). Nests were transported to the laboratory and broken, and termites were extracted with a Berlese's apparatus. Remaining individuals were manually collected, and colony members were collectively weighed. For the present study, we estimated average caste body masses by dividing the total biomass of each caste by the respective total number of individuals. Moreover, both Martius and Ribeiro (1996) and Apolinário (2000) measured nest size in terms of mass (g). To estimate nest volume, we combined their data to the nest specific mass reported by Josens and Soki (2010) for *A. banksi* (1.20 kg/dm^3).

Data for *L. labralis* were obtained from Ribeiro (1997). Nests were collected between October 1993 and January 1995 ($n = 18$), half at Reserva Ducke and half at PDBFF Reserve of km 41. The shape of *L. labralis* nests approximates that of a hemiellipsoid with its base on the tree surface. Thus, the height, width, and thickness of each sampled nest were measured with a tape measure to estimate nest volume (see below). Subsamples were taken from each nest with an artisanal, cylindrical soil corer (10 cm in height, 3 cm in diameter). Subsamples were randomly located on the nest surface, with one subsample each 3.5 cm in nest height. This allowed a similar representation of colonies in nests of different sizes, and took into account variation in the density of individuals in different parts of the nest. Subsamples were taken to the laboratory, where all termites were manually extracted and counted. Individuals from all nests were pooled by caste and weighed. Then, the total biomass of each caste was divided by the corresponding number of individuals to determine the average caste body mass. The mean number of each caste per subsample was then extrapolated to the nest volume to determine the number of individuals in the colony. In the present study, we multiplied the number of each caste in a colony by its respective average body mass to estimate the colony biomass.

Nests of *N. braziliensis* were sampled ($n = 16$) in May 2010 and February 2011 at an area belonging to the Federal University of Amazonas (Fazenda UFAM), 38 km north of Manaus ($2^\circ 37' 17.1''$ and $2^\circ 39' 41.4''$ S, $60^\circ 03' 29.1''$ and $60^\circ 07' 57.5''$ W). A *N. braziliensis* nest resembles a hemiellipsoid with its base on the ground, so that the height, width, and thickness of each sampled nest were measured with a tape measure and used to estimate nest volume (see below). Nests were dislodged from the ground to allow access to their underside. Then, subsamples were collected from random positions all over the nest surface with a cylindrical soil corer (5 cm in height and diameter). One subsample was extracted each 15 cm in nest height. Owing to logistic constraints, subsamples could not be promptly taken to the laboratory, so termites were manually sorted in the field and preserved in alcohol 75% until they could be counted. This hampered the measurement of their fresh weight. Thus, a further colony was sampled after the main surveys to determine average body mass per caste. Individual workers ($n = 50$), soldiers ($n = 20$), and nymphs ($n = 10$) were weighed. In addition, 100 larvae were collectively weighed to determine their average body mass, because they were too small to be weighed separately.

The number of individuals in a colony was estimated by extrapolating the average numbers of each caste in the volume of a subsample to the volume of the whole nest. The resulting values were then multiplied by their respective average body masses to estimate colony biomass.

In the present study, the nest volume (V) was estimated for *N. braziliensis* using the same formula used by Ribeiro (1997) to estimate *L. labralis* nest volume:

$$V = \frac{\pi HWT}{6}$$

where H is the height of the nest, W is its width, and T is its thickness.

Data on the number of nests and their volumes in plots

Nest counts were made across a rainforest landscape of 24 km^2 at Fazenda UFAM from May 2010 to February 2011. Thirty-one plots were sampled, each measuring $250 \times 10 \text{ m}$ and with at least 1 km to any other. Additionally, each plot followed an altitudinal contour line; this minimised soil variation and its environmental correlates within plots, thus maximising between-plot variation (Costa & Magnusson, 2010). Note that, as all plots had the same area, the 'number of nests' and 'nest density' (number of nests per area unit) are equivalent in this study. In each plot, all nests of the studied species were counted. Each nest was assigned a shape (ellipsoidal or hemiellipsoidal) and had its height, width, and thickness determined with a tape measure in order to estimate its volume. For both shapes, such measurements reduce to the same aforementioned volume formula, which was then applied. Voucher specimens were collected and deposited at the Entomological Collection of the National Institute for Amazonia Research (INPA), Manaus, Brazil.

Statistical analyses

Scaling relationships are described by a power function, $Y = aX^b$, where the parameters a and b can be estimated by non-linear regression or by linear regression on log-transformed variables. The latter implies a linearised power function, $\ln Y = \ln a + b \ln X$, where \ln is the natural logarithm and the slope b stands for the exponent. However, while standard non-linear regression assumes normal, homocedastic errors, log-log regression implies lognormal, heterocedastic errors. Thus, the suitability of either method depends on the data. Accordingly, we followed the approach proposed by Xiao *et al.* (2011): for each species, colony biomass was modelled as a function of nest volume with both non-linear and log-log regression, and the two models were compared using the Akaike Information Criterion corrected for sample size (AICc). Then, the model with the lowest AICc (with a difference of at least 2 to the competing model) was favoured. The model predictive power was measured as the squared correlation between observed and predicted values (r^2) (Zheng & Agresti, 2000).

The resulting regression equations were used to predict the biomass of colonies inhabiting all nests measured on

plots. When log-log regression was preferred over non-linear regression, predictions were back-transformed to the original scale of the data and multiplied by the exponential of half the error variance to correct for bias in antilog transformation (consistent I estimator in Hayes & Shonkwiler, 2006). Then, predicted colony biomasses were summed by plots to estimate total biomass for each species. Therefore, the total biomass of a species in a plot (B_{tot}) can be seen as the product between its number of nests (N) and its average colony biomass (\bar{B}_{col}):

$$B_{tot} = N\bar{B}_{col}$$

Next, a linear regression with total biomass in a sampling plot as a response variable and the respective number of nests as a predictor was carried out for each species to assess how much of the among-plot variation in the former was accounted for by the latter. All analyses were performed in R 2.15.1 (R Development Core Team, 2012), with support of packages 'drc' and 'nlwr' (Ritz & Streibig, 2007, 2008).

Results

Complete counts of individuals from *A. banksi* nests averaged $19\,765.2 \pm 13\,504.99$ individuals per nest (mean \pm SD), ranging from 909 to 48964. Subsampling of *N. braziliensis* and *L. labralis* nests to estimate colony size involved averages of 31 ± 12.09 and 3.41 ± 1.37 subsamples per nest (mean \pm SD), respectively, ranging from 1 to 6 in *N. braziliensis* and from 16 to 62 in *L. labralis*.

In *N. braziliensis*, the mean (\pm SD) number of individuals per subsample within nests was 372.78 ± 453.99 , and varied from 92.6 to 1849.5 across nests. Variability in subsamples from the same nest (SD) ranged from 45.16 to 1399.36 individuals. Estimated colony size averaged $111\,332.2 \pm 84\,817.56$ individuals (mean \pm SD), ranging from 12\,069.09 to 294\,420.74.

For *L. labralis*, the mean (\pm SD) number of individuals per subsample within nests was 392.74 ± 221.21 . Variability in the number of individuals in subsamples within nests (SD) ranged from 83.4 to 741.8 individuals. The estimated colony size averaged $172\,105.9 \pm 123\,318.6$ individuals (mean \pm SD), varying from 23\,449.1 to 422\,429.

Body mass was highest in most castes for *L. labralis* and lowest for *A. banksi* (Table 1). In the three species, colony biomass increased with nest volume, with a moderate to high predictive power (Fig. 1). However, while non-linear regression fitted the data better than log-log regression for *A. banksi* (AICc = 83.59 and 97.56, respectively), log-log regression was favoured over non-linear regression for *N. braziliensis* (AICc = 213.33 and 219.07, respectively) and *L. labralis* (AICc = 247.80 and 260.25, respectively). Among the studied species, the scaling exponent was relatively high for *L. labralis* ($b = 0.83$, 95% CI = 0.56–1.1), intermediate for *A. banksi* ($b = 0.57$, 95% CI = 0.38–0.76), and low for *N. braziliensis* ($b = 0.47$, 95% CI = 0.15–0.80).

Total biomass increased with the number of nests in *N. braziliensis* ($F_{1,29} = 376.1$, $P < 0.0001$), *A. banksi*

Table 1. Body mass (mg) (mean \pm SD) of castes of the studied termite species.

Species	Larvae	Worker	Soldier	Nymph	Alate
<i>Anoplotermes banksi</i>	0.3	0.8	–*	2.5	2.1
<i>Neocapritermes braziliensis</i>	0.4	3.0 ± 0.4	6.6 ± 0.3	8.0 ± 0.3	–**
<i>Labiatermes labralis</i>	1.4	4.3	18.0	7.2	49.7

Mean caste body masses presented without SD were calculated by dividing the pooled biomass of the caste in the whole sample of nests by the respective number of individuals. *: the caste does not occur in the species. **: the caste did not occur in any of the sampled nests.

($F_{1,29} = 313.8$, $P < 0.0001$), and *L. labralis* ($F_{1,29} = 33.21$, $P < 0.0001$). The strength of the relationship was fairly high for *N. braziliensis* and *A. banksi*, but only moderate for *L. labralis* (Fig. 2). Moreover, it was negatively related to the species scaling exponent: *N. braziliensis* had the lowest scaling exponent ($b = 0.47$) and the strongest correlation between total biomass and number of nests ($r^2 = 93\%$), whereas *L. labralis* had the highest scaling exponent ($b = 0.83$) and the weakest correlation between total biomass and number of nests ($r^2 = 53\%$).

Discussion

Colony size is usually thought to be of fundamental importance in the description of social insect population dynamics because it varies by orders of magnitude, both within and between species (Adams & Levings, 1987; Adams & Tschinkel, 2001). In contrast, this study suggests that spatial variation in a social insect species' total biomass may be largely accounted for by variation in nest numbers alone. Some degree of correlation between total biomass and number of nests is to be expected as long as the latter is used to estimate the former. However, the strength of this relationship depends also on how variable the colony size is. Thus, the very strong correlations between total biomass and the number of nests observed for *N. braziliensis* and *A. banksi* across sampling plots indicate that, at the studied spatial scale, colony size contributed relatively little to variation in total biomass.

The negative allometry between colony size and nest volume found for the three studied species agrees with the general pattern reported for termites (Josens & Soki, 2010), although correlational data alone are not sufficient to infer the precise allometric mechanism; it may involve nest respiratory constraints, as suggested by the latter authors, but also several other mechanisms, such as decreased queen fertility (Lepage & Darlington, 2000). While this issue requires further study, the increase in the strength of the correlation between total biomass and number of nests as the species scaling exponent decreased is consistent with the idea that colony-nest allometry is linked to intra-specific variability in colony size. We propose that the saturating curve that characterises the relationship between colony size and nest volume in species with low scaling exponents (such as *N. braziliensis* and *A. banksi*) reflects a progressive decline in colony growth rate throughout nest expansion. As all conspecific colonies are expected to experience such a decline, intercolonial differences in growth

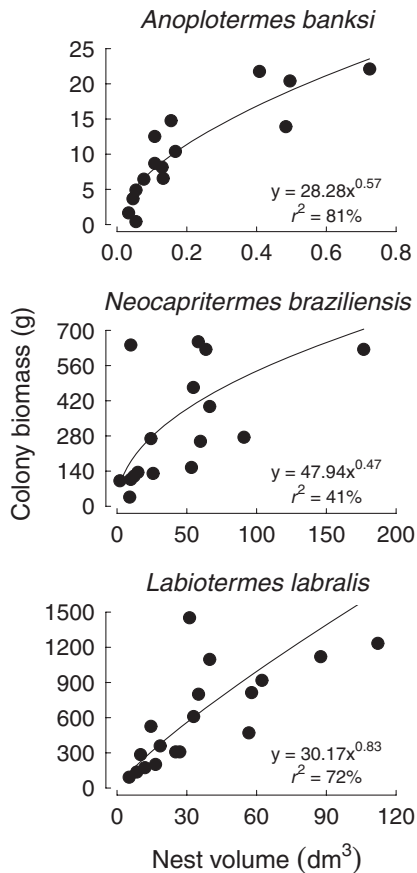


Fig. 1. Scaling relationships between colony biomass (y) and nest volume (x) for three termite species from central Amazonia. Each point represents a colony. For each species, the fit of a linear regression on log-transformed variables was compared with that of a non-linear regression using the Akaike Information Criterion corrected for sample size (AICc) to account for the error structure of the data. Log-log regression was better supported for *Neocapritermes braziliensis* and *Labiotermes labralis*, whereas non-linear regression was preferred for *Anoplotermes banksi* (see Results).

rate would be less likely to develop into large differences in size. Accordingly, colony sizes would tend to be more similar, and colony numbers would contribute relatively more to changes in total biomass.

We note that our study was limited to three species. Still, the literature is even more silent on this subject: several previous studies measured nest numbers and total biomass for termite species, but did not assess their relation (e.g. Matsumoto, 1976; Meyer *et al.*, 2001; Jeyasingh & Fuller, 2004; Vasconcellos *et al.*, 2007; Vasconcellos & Moura, 2010). However, Lepage (1984) quantified nests and biomass of *Macrotermes bellicosus* Smeathman in five plots in the Comoé National Park, Ivory Coast. This species has one of the lowest termite scaling exponents between colony size (in number of individuals) and nest volume, 0.4 (Josens & Soki, 2010). Thus, we expected variation in its biomass to largely reflect nest numbers. Although the plots studied by Lepage (1984)

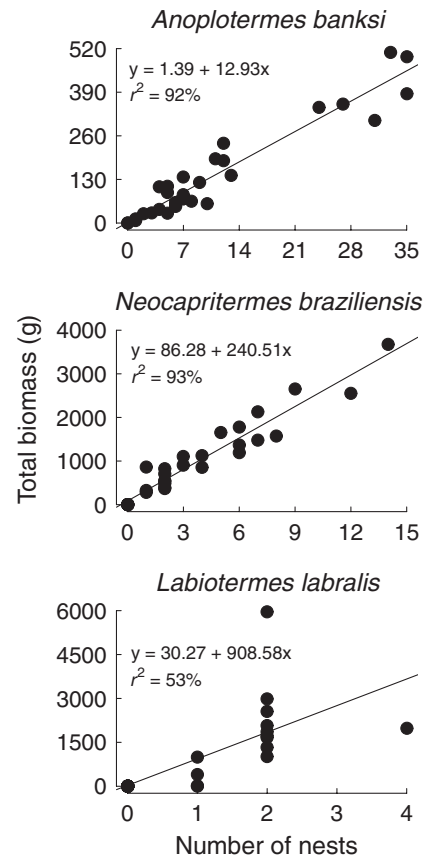


Fig. 2. Relationships between total biomass (y) and the number of nests (x) for three termite species in a rainforest landscape (24 km²) in central Amazonia. Each point represents a sampling plot (250 × 10 m). The total biomass was estimated by determining the relationship between colony biomass and nest volume for each species, and then counting and measuring their nests in each plot.

had different areas, we did find that the reported densities of live nests and biomass were strongly related ($r^2 = 0.91$).

A strong correlation between the number of nests and total biomass, as found for *N. braziliensis* and *A. banksi*, means that the latter could be predicted from simple nest counts. This is of practical importance, as quantifying termite populations and their ecosystem impacts usually requires labour-intensive methods (e.g. Eggleton *et al.*, 1996). Furthermore, it suggests that, at the studied spatial scale, the underlying population dynamics is mainly driven by colony births and deaths rather than colony growth. The number of colonies attainable by a social insect species in an area seems to depend crucially on local alate recruitment (Cole & Wiernasz, 2002). In fact, larger alate production can sustain higher colony numbers even where colony survival is relatively low (Korb & Linsenmair, 1999). Thus, we hypothesise that differences in the number of nests of *N. braziliensis* and *A. banksi* across the studied landscape mainly reflect processes affecting colony reproductive output.

One process probably influencing colony reproduction and abundance is intra-specific competition for food (Deslippe & Savolainen, 1994; Gordon & Wagner, 1997; Korb &

Linsenmair, 2001), and there is substantial natural variation in termite food sources within Neotropical rainforest landscapes (Davies *et al.*, 2003). Accordingly, young *A. banksi* nests settled away from established ones and the proportion of dead nests increased with nest abundance in a population in French Guiana, suggesting intra-specific competition (Bourguignon *et al.*, 2011). Alternatively, nest numbers may be limited by competitive exclusion by a dominant termite species (Leponce *et al.*, 1997) or by predation, particularly by ants (Leponce *et al.*, 1999). The latter is supported in the current case by a negative relation between the number of nests of *N. braziliensis* and that of dominant *Azteca* ants at another site in central Amazonia (Pequeno & Pantoja, 2012). Such processes are not mutually exclusive, although, and their different combinations represent alternative hypotheses that could be tested in future studies.

The termite colony-nest system integrates individual-level phenomena into a cohesive phenotype that is thought to lie at the core of termite ecology and evolution (Lepage & Darlington, 2000). We propose that one feature of such a phenotype, the scaling of colony size with nest volume, may have a previously unrecognised role: the lower a species scaling exponent, the more changes in total biomass may reflect changes in the number of nests, which are likely to be driven by colony births and deaths as opposed to colony growth. Thus, colony size variability and population dynamics may have a component that is predictable from an intrinsic species trait.

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