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The Scaling of Growth, Reproduction and Defense in Colonies of Amazonian Termites

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Abstract

Phenotypes can evolve through life-history tradeoffs. Termites have been the first eusocial insects on Earth, prompting life history evolution at the colony level. Despite this, termite life-history allocation strategies are poorly known. Here, we addressed this issue using novel data on three common species from the diverse, yet understudied Amazonian termite fauna: *Neocapritermes braziliensis*, *Labiotermes labralis* and *Anoplotermes banksi*. Using Oster and Wilson's optimal caste ratio theory and Higashi et al.'s termite caste allocation theory as frameworks, we assessed how termite colonies should invest in growth (immatures), reproduction (alates) and defense (soldiers) as they accumulate workers. We also examined whether soldier loss in soil-feeding Apicotermitinae (*A. banksi*) may have affected allocation strategies. We found that: (1) the scaling of immature number was isometric in the three species, contrary to the leveling off expected under resource limitation; (2) colonies of all sizes were equally likely to produce any number of alates, rather than having a size threshold for reproduction; (3) the scaling of soldier number was unrelated to alate production, but varied from isometry in *N. braziliensis* to negative allometry in *L. labralis* despite their similar defense strategies; (4) *A. banksi* had more immatures per worker and a higher maximum alate number per worker than the other species, suggesting that soldier loss may have allowed higher relative investment in colony growth and, possibly, reproduction. Termites can provide novel insights into life-history allocation strategies and their relation to social evolution, and should be better incorporated into sociobiological theory.

Introduction

Organisms often need to allocate resources simultaneously to growth, maintenance and reproduction. However, investing in one function often limits investment into other functions, so that selection optimizes phenotypes under the constraint of life-history tradeoffs (Reznick, 2014). In eusocial organisms such as ants and termites, individuals differentiate into specialized castes that combine into highly cooperative colonies, suggesting that selection can optimize collective phenotypes (Hölldobler & Wilson, 2009). Thus, tradeoffs may arise at the colony level, shaping resource allocation to different functions and, possibly, to different castes (Oster & Wilson, 1978; Lepage & Darlington, 2000; Poitrineau *et al.*, 2009). Resource limitation could occur due to depletion of local resources, or due to the need of foragers to travel increasingly larger distances and for a longer time. In any case, foraging efficiency should decline as colonies grow, thus limiting colony productivity (Naug & Wenzel, 2006; Poitrineau *et al.*, 2009). This predicts that the number of newborns in a colony should level off as the number of workers increases (Thomas, 2003; Kramer *et al.*, 2014).

Assuming resource limitation, optimal caste ratio theory predicts general patterns of caste allocation in eusocial colonies. The theory postulates that colony fitness is maximized by first producing workers until the colony reaches a certain population size (ergonomic phase), and then investing in sexuals (reproductive phase) (Oster & Wilson, 1978; Poitrineau *et al.*, 2009). This is because producing and maintaining a swarm of

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alates (which are often larger than workers and do not forage) is costly and, thus requires a large workforce. Thus, the probability of colony reproduction should increase suddenly beyond a threshold colony size. Further, many eusocial species have evolved a caste solely committed to colony defense, the soldiers (Tian & Zhou, 2014). Optimal caste ratio theory predicts that soldier number should increase in breeding relative to non-breeding colonies, with a concomitant shift in the way soldier number scales with worker number (Oster & Wilson, 1978). In non-breeding colonies, mortality should be less costly to larger colonies relative to smaller ones, as the former can partly dispose with their workforce. Thus, soldier number should scale sublinearly with worker number (i.e. negative allometry), reflecting a relatively lower investment in defense by larger colonies. Conversely, in breeding colonies, the larger commodity represented by sexuals should increase the fitness costs of mortality, particularly in larger colonies. Thus, soldier number should scale superlinearly with worker number (i.e. positive allometry), reflecting a relatively higher investment in defense by larger colonies (Oster & Wilson, 1978).

Empirical tests of the above predictions have provided mixed results: productivity does not always level off as colonies grow (Poitrineau *et al.*, 2009; Dornhaus *et al.*, 2012; Kramer *et al.*, 2014), colony reproductive effort is often independent of colony size (Cole, 2009; Dornhaus *et al.*, 2012), and soldier allocation strategy only partially matches theoretical expectations (Walker & Stamps, 1986; Kaspari & Byrne, 1995; Dornhaus *et al.*, 2012). However, such conclusions are heavily biased towards hymenopterans, particularly ants. Termites are the oldest known eusocial organisms and the first to have evolved a soldier caste ever (Engel *et al.*, 2016), but their life-history strategies are much less known (Lepage & Darlington, 2000; Pequeno *et al.*, 2017; Korb & Thorne, 2017).

Despite this, Higashi et al. (2000) offered a quantitative theory of termite caste allocation. Within a colony, individuals are assumed to differentiate into particular castes so as to maximize their inclusive fitness, i.e. the propagation of their own genes plus those shared with colony mates. As the colony grows, the conditions affecting which castes fulfill this criterion change, thus shifting the pattern of caste allocation (Higashi et al., 2000). Two main predictions arise. First, and like optimal caste ratio theory, the probability of producing alates should increase with worker number. Second, soldier number should be proportional to extrinsic mortality rate. In species that forage outside the nest (82% of all living species; Krishna et al., 2013), this is assumed to reflect forager population size. Assuming that foragers compose a constant fraction of the worker population, soldier number is then predicted to be proportional to worker number (i.e. isometry). Yet, this theory remains largely untested. Moreover, a diverse clade of soil-feeding termites, the Apicotermitinae, lost the soldier caste (Bourguignon *et al.*, 2016), but the life-history consequences of this event are unknown.

Here, we assessed colony life-history allocation strategies using novel data on three species from the diverse, yet understudied Amazonian termite fauna: *Neocapritermes braziliensis* Snyder (Termitidae: Termitinae), *Labiotermes labralis* Holmgren (Termitidae: Syntermitinae), and the soldier-less *Anoplotermes banksi* Emerson (Termitidae: Apicotermitinae). These are among the most common nest-building termites in central Amazonia (Pequeno *et al.*, 2013; 2015; Table 1). We evaluated the following theoretical expectations (Fig 1): (1) immature number should scale sublinearly with worker number, assuming that colonies are resource-limited; (2) alate number or, alternatively, the probability of producing alates should increase with worker number, assuming that colonies need to grow to a certain size to reproduce; (3) in the species with soldiers, soldier number should be higher in breeding relative to non-breeding colonies, and scale sublinearly with worker number in the latter but superlinearly in the former, as predicted by optimal caste ratio theory; (4) alternatively, soldier number should scale isometrically with worker number, as predicted by termite caste allocation theory; (5) relative numbers (i.e. per worker) of immatures and alates should be higher in the soldier-less *A. banksi* than in the other species, assuming that soldier loss frees resources to invest in colony growth and reproduction.

Table 1. Summary of known life history and ecological traits of the Amazonian termite species *Neocapritermes braziliensis*, *Labiotermes labralis* and *Anoplotermes banksi*. Data from Dupont et al. (2009), Pequeno *et al.* (2013, 2015), Bourguignon et al. (2016), and the current study. For species pictures, see Pequeno et al. (2015).

Trait	*N. braziliensis*	*L. labralis*	*A. banksi*
Soldier type	ASM	SSM	Soldier-less
Worker body mass (mg)	3.0	4.3	0.8
Mean colony population	111,332	172,105	19,765
Food source	Fallen dead wood	Mineral soil	Organic soil
Main nest material	Soil + carton	Fine soil	Coarse soil
Preferred habitat	Sandy bottomlands	Clayish uplands	Mixed-soil slopes
Nest density (nests/ha)	14.3	3.3	43.3
Colony breeding system	Likely monogamous	Monogamous	Monogamous

*ASM: asymmetrical snapping mandibles; **SSM: symmetrical slicing mandibles.

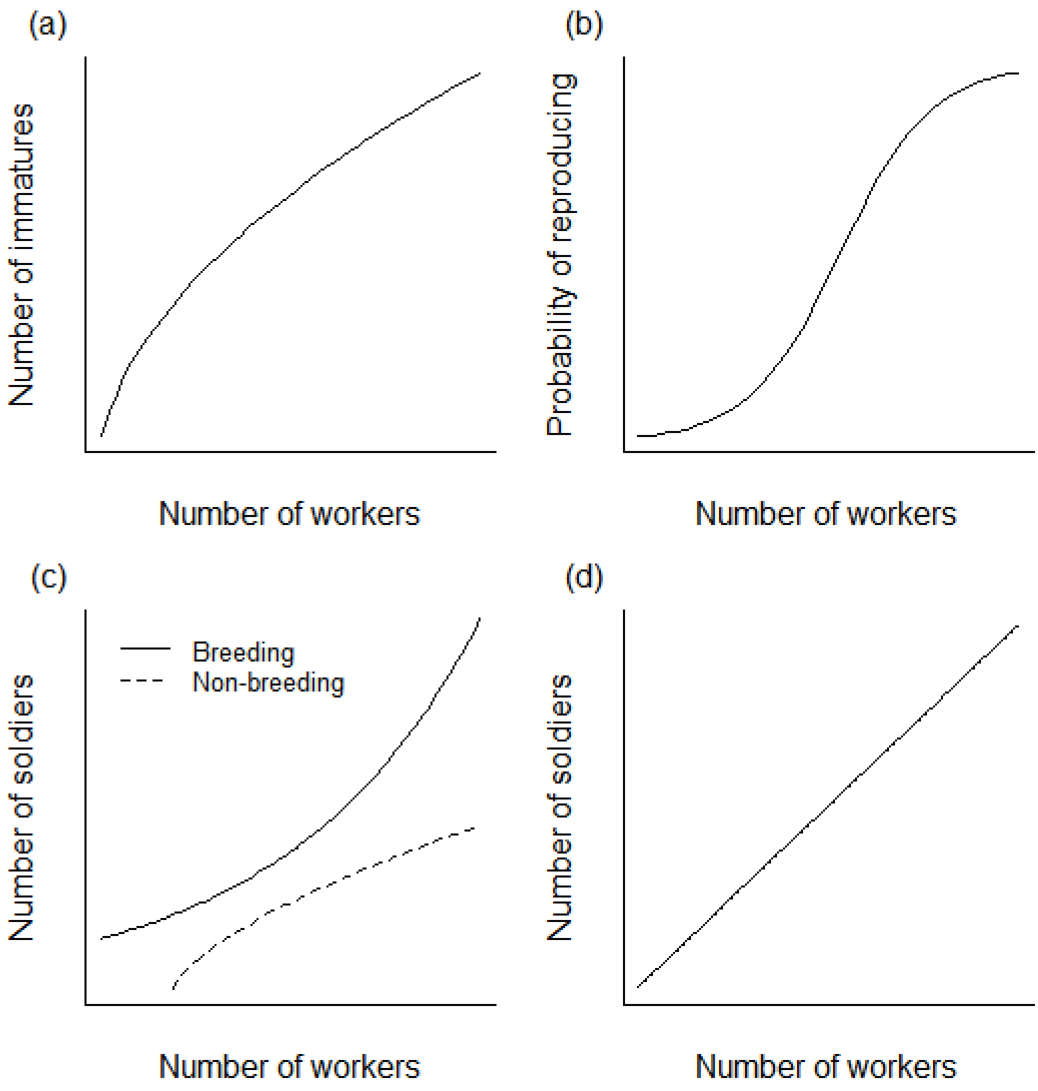

Fig 1. Theoretical scaling relationships of growth, reproduction and defense in colonies of eusocial insects. (a) If colony growth rate declines as colonies grow, the number of immatures should be a decelerating function of the number of workers. (b) If colony reproduction requires a minimum workforce, the probability of reproducing should be a sigmoid function of worker number. (c) Optimal caste ratio theory (Oster & Wilson 1978) predicts that the number of soldiers should be higher in breeding than in non-breeding colonies, and that the relationship between soldier and worker number should be a concave-up curve in the former and a concave-down curve in the latter. (d) Termite caste allocation theory (Higashi et al. 2000) predicts that soldier number should be proportional to worker number, assuming that workers are exposed to extrinsic mortality outside the nest.

Materials and methods

Termite sampling

Termite colonies were sampled on different occasions in the surroundings of Manaus, Northern Brazil (92 m a.s.l.; 3°06’07’’ S and 60°01’30’’ W). Local vegetation is lowland tropical rainforest, with mean annual rainfall of 2479 mm (Research Coordination in Climate and Hydric Resources, National Institute for Amazonia Research). The terrain is rugged, alternating between clayish plateaus and sandy valleys connected through a dense drainage system.

Colonies of *N. braziliensis* (n = 16) were sampled by P. A. C. L. Pequeno in May 2010 and February 2011 in the Experimental Farm of the Federal University of Amazonas (Pequeno et al., 2013). The epigeal nests were removed from the ground and had their dimensions (i.e. height, width and thickness) measured with a tape measure, which were used to estimate nest volume according to a hemiellipsoidal shape: volume = $\pi\times$height$\times$width$\times$thickness. In casual inspections of whole nests, we observed that individuals (including reproductives) tended to occur at the bottom of nests. Thus, a cylindrical soil corer (5 cm in height and diameter) was used to collect standardized nest pieces from all over the nest surface, including the bottom. For each nest, one core was extracted for each 15 cm in nest height, so that sampling effort was proportional to nest size and accounted for heterogeneities in the distribution of castes within the nest. On average, 3.56 cores were extracted per nest, ranging from 2 to 6. Termites were manually extracted from cores and preserved in alcohol 75%. This material was transported to laboratory, where castes were sorted and counted, as follows: workers, soldiers (including presoldiers), alates (both winged nymphs and imagoes) and immatures (i.e. undifferentiated nymphs). Whole-colony caste populations were estimated by extrapolating average counts per nest core to the volume of the whole nests.

Colonies of *L. labralis* (n = 18) were sampled by J. A. Ribeiro in October 1993 and January 1995. Colonies were collected from two sites: half in Ducke Reserve, and half in a reserve of the Biological Dynamics of Forest Fragments Project (PDBFF). The arboreal nests were measured (i.e. height, width and thickness) with a tape measure, and nest volume was estimated as before. Likewise, cores with standardized volume were taken randomly from the surface of each nest with a cylindrical soil corer (10 cm in height, 3 cm in diameter), with one core for each 3.5 cm in nest height. This resulted in an average of 31 cores per nest, ranging from 16 to 62. Termite castes were extracted, sorted, counted and had their whole-colony populations estimated as before.

Colonies of *A. banksi* (n = 17) were also sampled in the two aforementioned sites in two occasions: by C. Martius and J. A. Ribeiro from May to October 1993 and March 1994 (n = 7) (Martius & Ribeiro, 1996), and by F. Apolinário from October 1996 to January 1997 (n = 10). In both cases, whole nests were taken to the laboratory and termites were exhaustively extracted either manually or using Berlese-Tullgren funnels, until no further termites were found. Then, castes were sorted as described previously, and their populations were counted.

Statistical analyses

For each species, whole-colony estimates of investment in growth, reproduction and defense were defined as the numbers of immatures, alates and soldiers, respectively (except for *A. banksi*, which is soldier-less). Then, the scaling of these traits (dependent variables) was assessed by determining how they changed with the number of workers (independent variable), which comprise the bulk of the colony and supply the resources allocated to all castes. Estimates of caste numbers obtained by extrapolation were rounded down, so that they could be modelled statistically as counts (which assumes integers).

Unless otherwise stated, analyses assumed a standard scaling function ($Y = a \times X^b$), which was linearized by taking logs of both sides ($\log Y = \log a + b \times \log X$). This allows the use of standard linear statistical models for inference. Accordingly, each dependent variable was analyzed as a function of log-transformed number of workers using a generalized linear model (GLM), assuming log link and Poisson-distributed errors corrected for overdispersion. In the case of reproduction, we also analyzed (1) the scaling of alate number only among colonies containing alates (as such relationship may only be evident during the reproductive season), and (2) the relationship between presence-absence of alates and worker number, as an indicator of probability of reproduction. In the latter case, we assumed logit link and binomial-distributed errors.

To test the predictions of optimal caste ratio theory on soldier allocation, we followed previous studies (Walker & Stamps, 1986; Kaspari & Byrnes 1995) and used the presence-absence of alates as a covariate to represent the reproductive status of the colony (i.e. breeding vs. non-breeding). As the model predicts an independent effect of reproductive status on soldier number plus an interaction between this variable and worker number (Fig 1c), we compared a series of nested models using deviance-based *F* tests, in the following order: a model including an interaction term against a model including independent effects only, and the latter against a model including number of workers as the sole predictor. To test for deviations from isometry (i.e. $b \neq 1$) in the scalings of growth and defense, we determined whether 95% confidence intervals (95% CI) of estimated scaling exponents included 1. Predictive power (r^2) was calculated as the proportion of deviance accounted for by the fitted GLM relative to the intercept-only model.

Lastly, we looked for interspecific differences in life-history allocation strategy by comparing the numbers of immatures, alates and soldiers per worker among species. For each dependent variable, we used a GLM assuming inverse link and Gamma-distributed errors; pairwise comparisons among species were performed with Tukey's test. A single *N. braziliensis* colony contained no immatures; this observation was excluded when comparing immature:worker ratios to meet distributional assumptions. Further, because the proportion of colonies producing alates varied between species, alate: worker ratios were compared only among breeding colonies. All analyzes were performed in R 3.3.2 (R Development Core Team, 2016), with support of package "multcomp" (Hothorn et al., 2008).

Results

Species showed either similar or contrasting life-history allocation patterns, depending on the caste considered. First, there was evidence that species differed in the way they invested in immatures and soldiers across colony sizes. In *N. braziliensis*, the number of immatures scaled superlinearly with that of workers ($t = 2.52$, p = 0.02) (Fig 2a), whereas it scaled sublinearly in *L. labralis* ($t = 6.19$, p < 0.001) (Fig 2b) and *A. banksi* ($t = 4.28$, p < 0.001) (Fig 2c). Yet, scaling exponents were not statistically different from 1, so that isometry could not be conclusively rejected in any of the three species (Table 2).

Second, reproduction was unrelated to worker number, both in terms of alate number (*N. braziliensis*: $t = 1.18$, p = 0.25; *L. labralis*: $t = 0.78$, p = 0.44; *A. banksi*: $t = 0.81$, p = 0.42) (Table 2, Fig 3a,b,c) and probability of producing alates (*N. braziliensis*: $z = 1.04$, p = 0.29; *L. labralis*: $z = 1.30$, p

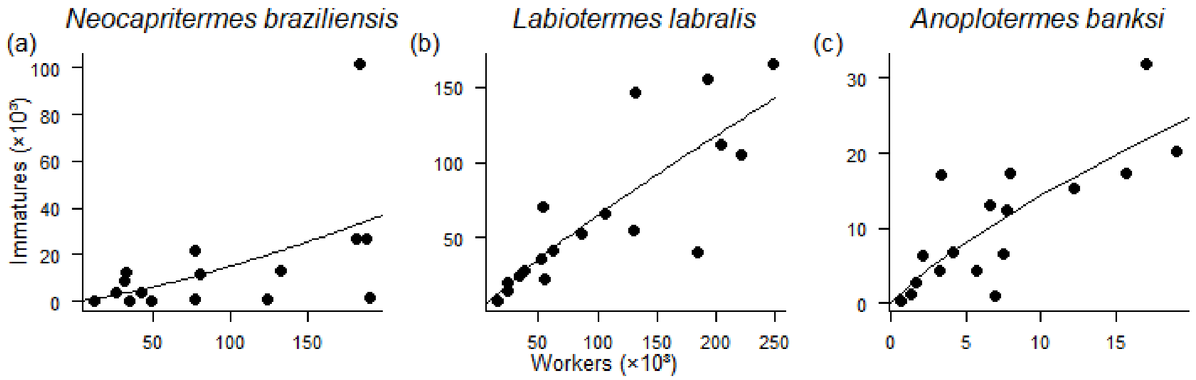

Fig 2. Whole-colony scalings of growth in three Amazonian termite species. Points represent colonies. Solid lines represent statistically significant GLM fits at the 0.05 level, as indicated in Table 2.

= 0.19; *A. banksi*: *z* = 0.44, p = 0.65) (Table 2, Fig 3d,e,f). Considering the relationship between numbers of alates and workers only among breeding colonies revealed the same result (*N. braziliensis*: *t* = 0.85, p = 0.45; *L. labralis*: *t* = 0.37, p = 0.71; *A. banksi*: *t* = 0.85, p = 0.42).

Third, there was evidence for different scalings of soldier number between species. In *N. braziliensis*, there was no support for an interaction between worker number and breeding status (*F* = 2.09, p = 0.17), nor for an independent effect of the latter (*F* = 0.01, p = 0.89); rather, soldier number was proportional to worker number (*t* = 4.93, p < 0.001) (Table 2, Fig 4a). In *L. labralis*, breeding status had no effect on soldier number as well (interaction model: *F* = 1.33, p = 0.26; independent effect model: *F* = 1.66, p = 0.21), but soldier number scaled with worker number with an exponent significantly lower than 1 (*t* = 2.30, p = 0.03) (Table 2, Fig 4b).

The mean number of immatures per worker was highest in *A. banksi* (1.60 ± 9.34, mean ± SE) and lowest in *N. braziliensis* (0.15 ± 0.05), with *L. labralis* in the middle (0.66 ± 7.52); all pairwise differences were statistically significant (*z* > 3.0 and p < 0.01 in all cases). Fewer colonies were breeding in *N. braziliensis* (five colonies out of 16, or 31%) than in *L. labralis* (nine colonies out of 18, or 50%) and *A. banksi* (nine colonies out of 17, or 52%). Moreover, imagoes only occurred in *L. labralis* and *A. banksi*; breeding colonies of *N. braziliensis* contained winged nymphs only. Still, considering only breeding colonies, there was no difference in mean number of alates per worker among species (|z| > 0.96 and *P* > 0.26 for all comparisons), with colonies averaging 0.03 ± 0.05 alates per worker. Likewise, there was no difference in mean number of soldiers per worker between *N. braziliensis* and *L. labralis* (*t* = -0.55, *P* = 0.58), with both species averaging 0.05 ± 0.38 soldiers per worker.

Table 2. Summary of GLM results on the scaling of caste numbers with worker number in three Amazonian termite species. Numbers of immatures, alates and soldiers were modeled assuming Poisson-distributed errors (corrected for overdispersion) and log link. Prob(alate), or the probability of producing alates, was modeled using alate presence-absence and assuming binomial errors and logit link. Worker number was log-transformed in all analyzes. Numbers in parentheses are 95% confidence limits; numbers in bold are slopes significantly different from zero. *N. braziliensis*: *Neocarpitermes braziliensis*; *L. labralis*: *Labiotermes labralis*; *A. banksi*: *Anoplotermes banksi*.

Response	Species	Intercept	Slope	r^2
Number of immatures	*N. braziliensis*	-5.58 (-19.9 – 4.87)	**1.32 (0.41 – 2.52)**	0.40
	L. labralis	1.12 (-2.23 – 4.22)	**0.86 (0.60 – 1.14)**	0.74
	A. banksi	2.24 (-1.25 – 5.38)	**0.79 (0.44 – 1.17)**	0.60
Number of alates	*N. braziliensis*	5.1 (2.31 – 6.83)	0.00 (0.00 – 0.00)	0.00
	L. labralis	-3.49 (-36.03 – 15.75)	0.78 (-0.93 – 3.48)	0.00
	A. banksi	-0.77 (-22.64 – 11.94)	0.43 (-0.75 – 3.05)	0.00
Prob(alate)	*N. braziliensis*	-9.58 (-29.36 – 5.62)	0.78 (-0.57 – 2.50)	0.00
	L. labralis	-9.12 (-24.66 – 3.73)	0.81 (-0.32 – 2.18)	0.00
	A. banksi	-2.12 (-11.99 – 6.77)	0.23 (-0.80 – 1.37)	0.00
Number of soldiers	*N. braziliensis*	-2.32 (-6.97 – 1.85)	**0.94 (0.58 – 1.34)**	0.70
	L. labralis	2.75 (-2.20 – 7.25)	**0.47 (0.08 – 0.90)**	0.27

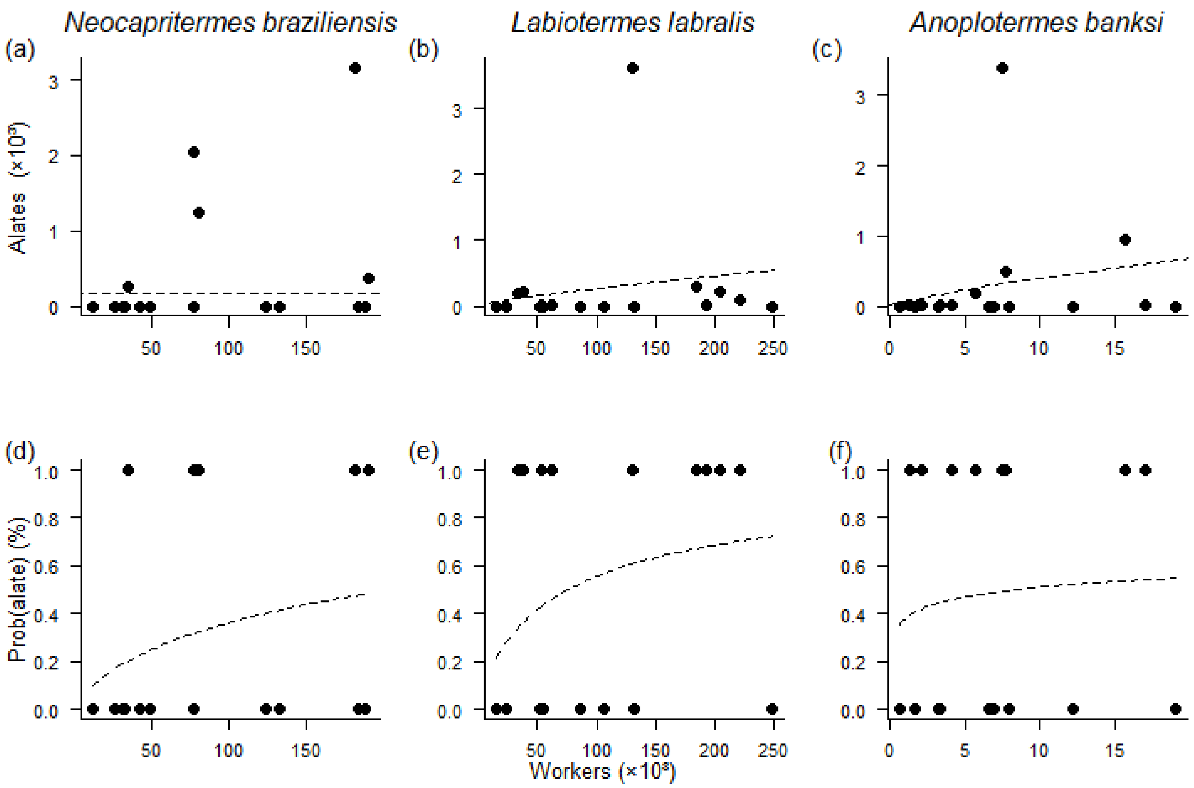

Fig 3. Whole-colony scalings of reproduction in three Amazonian termite species. Points represent colonies. Dashed lines represent statistically non-significant GLM fits at the 0.05 level, as indicated in Table 2. Prob(alate): probability of producing alates.

Discussion

Optimal caste ratio theory (Oster & Wilson, 1978) and termite caste allocation theory (Higashi et al., 2000) make several predictions about how eusocial colonies should allocate resources to growth, reproduction and defense as their workforce increases (Fig 1). Using data on three common Amazonian termite species, we found that most such predictions were not supported, suggesting that neither theory provides a generally valid explanation for life-history allocation strategies in termites.

The fact that immature number did not level off as worker number increased suggests that colonies were not resource-limited in the studied species (Kaspari, 1996; Kramer et al., 2014). In line with this, the nest density of the three termite species was unrelated to the density of their respective food sources across the landscape (Pequeno et al., 2015). It is also possible that extrinsic mortality rates are so high that colonies die before their growth saturates, as suggested for litter ants (Kaspari, 1996). There are few data on termite colony demography, but Bourguignon et al. (2011) estimated that around a third (and up to a half) of the nests of *A. banksi* within 1 ha of rainforest in French Guiana died each year. Whether this is high enough to prevent colonies from reaching their limiting size is unclear. Yet, a non-saturating increase in colony productivity with colony size has also been reported for many ants and other hymenopterans (Kaspari & Byrne, 1995; Kaspari, 1996; Billick, 2001; Bouwma et al., 2006; McGlynn, 2006; Smith et al., 2007). Taken together, these results suggest that, under natural conditions, colony growth is less constrained than usually assumed.

The independence between reproduction (either measured as number of alates or as probability of producing alates) and worker number contradicts both optimal caste ratio theory and termite caste allocation theory (Higashi et al., 2000; Oster & Wilson, 1978; Poitrineau *et al.*, 2009). This result also contrasts with the suggestion of a colony size threshold for reproduction in termites, albeit this is based on very few species (Lepage & Darlington, 2000). In the better studied Hymenoptera, the uncoupling between reproduction and colony size seems to be at least as common as size-dependent reproduction within species (Kaspari & Byrne, 1995; Beekman et al., 1998; Cole, 2009). Importantly, we found that alate number was independent of worker number even when considering breeding colonies only, so that variation in breeding status among colonies cannot account for this result. This may reflect the finding that, contrary to theory assumption, colonies did not appear to be resource-limited. If resources are abundant enough to allow production of alates early in the colony life cycle, there may be no fitness advantage in postponing reproduction until some threshold colony size.

Optimal caste ratio theory was also refuted by the observed patterns of soldier allocation in *N. braziliensis* and *L. labralis*, as soldier number was independent of colony breeding status. In parallel, termite caste allocation theory was only partially supported: while soldier number was predicted to be proportional to worker number in both species, this was

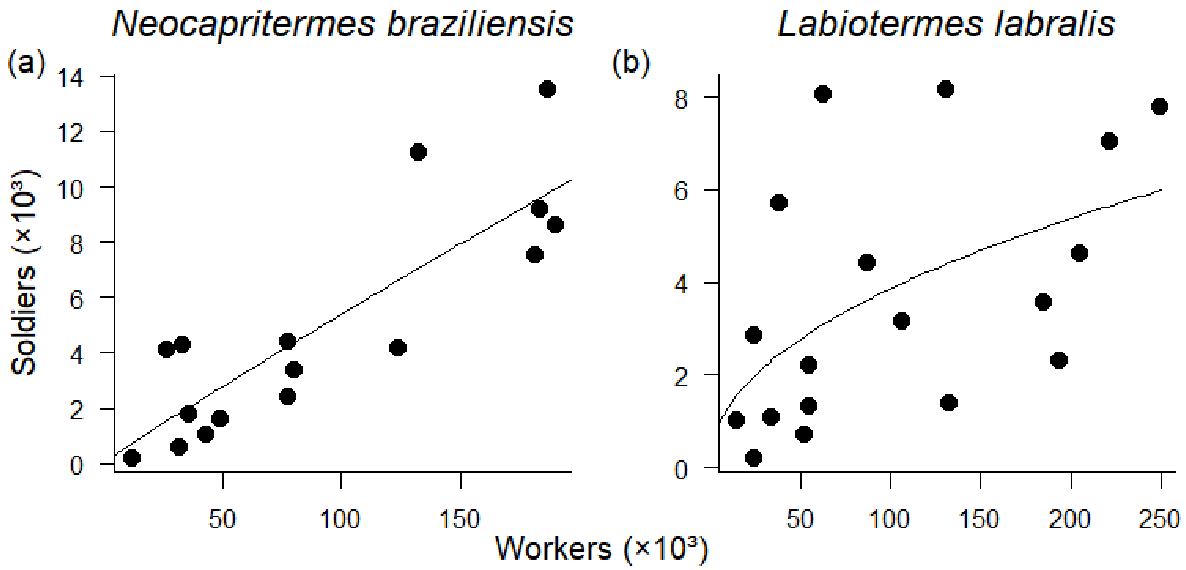

Fig 4. Whole-colony scalings of defense in two Amazonian termite species. Points represent colonies. Solid lines represent statistically significant GLM fits at the 0.05 level, as indicated in Table 2.

only the case in *N. braziliensis*; in *L. labralis*, soldier number scaled sublinearly with worker number. While the reason for this is unclear, our data hint at an apparent association between the scaling exponents of immatures and soldiers across species: although the scaling of immature number did not differ significantly from isometry in any species, both exponents were lower in *L. labralis* than in *N. braziliensis* (Table 2). Thus, the species seemingly experiencing stronger growth limitation (*L. labralis*) also appeared to invest relatively less in soldiers as colonies grew. As soldiers are generally costly to produce and maintain (Tian & Zhou, 2014), stronger resource limitation might constrain soldier allocation.

While the scalings of growth and reproduction largely coincided among species, relative investment in the former differed markedly: *A. banksi* colonies produced 2.4 and 10.6 times more immatures per worker than *L. labralis* and *N. braziliensis*, respectively. Moreover, although there were no consistent interspecific differences in relative investment in alates, the maximum number of alates per worker was much higher in *A. banksi* (0.45) than in the other species (ca. 0.027). This is consistent with the idea that dispensing with soldiers has allowed greater investment in other colony functions such as growth and reproduction, by freeing energy previously used in soldier production and maintenance. Other species traits may account for this difference, though. For instance, across ant species, mean alate number increases at a decelerating rate with mean worker number, so that species with smaller colonies tend to invest on a relatively larger number of smaller alates (Shik, 2008). If the same applies to termites, *A. banski* may achieve a higher relative reproductive investment simply by having relatively small colonies (Table 1). Discriminating between these alternative hypotheses will require a broad comparative analysis of termite life-history allocation strategies.

Our analysis did not cover one important aspect of termite caste allocation, the number of reproductives. Several termite species are known to produce varying numbers of secondary reproductives (Korb & Thorne, 2017), which may affect caste allocation patterns (Thorne, 1984). However, secondary reproductives were not found in any of the colonies used in this study; whenever reproductives were found, there was always a single pair (Table 1). For *A. banksi* and *L. labralis,* this has been confirmed by experimental orphaning of colonies (Bourguingon et al., 2016) and genetic data (Dupont et al., 2009), respectively. Our data on number of reproductives in *N. braziliensis* and *L. labralis* colonies is not conclusive as nests of these species were subsampled. Yet, for *A. banksi* (whose entire nests were collected), only 2 nests in 17 (ca. 12%) did not had a queen, so that queen number was essentially held constant in the analyses of this species. Therefore, it is unlikely that our results were affected by variation in number of reproductives.

In conclusion, this study showed that optimal caste ratio theory and termite caste allocation theory generally failed to predict life-history allocation patterns of three common Amazonian termite species. Yet, we provide evidence that dispensing with a soldier caste may allow for higher investment in colony growth and reproduction. We propose that the level of resource limitation experienced by colonies (as measured by the scaling between immature and worker number) may partly account for interspecific variation in the scaling of soldier number. In turn, resource limitation may itself depend on other species traits, such as foraging distance, food quality and degree of susceptibility to the effects of competitors and/or predators during foraging (Araújo et al., 2017). Yet, we stress that current theory largely focuses on scaling exponents between caste numbers, and other factors could also influence caste allocation patterns. In fact, r^2 varied between 0.00 a 0.74 in this study, indicating that theoretical relationships may account for small fractions of variance in caste numbers. Moreover, sociobiological theory has largely developed from studies on hymenopterans, even though there is increasing evidence that termite life history evolution has differed from this paradigm in important ways (Pequeno et al., 2017). A broad comparative analysis of termite life-history allocation strategies will likely provide new insights into social evolution and help refine sociobiological theory.

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This study is dedicated to the memory of Joana d'Arc Ribeiro (1953 – 2006), whose work contributed pioneering data on colony life history of Amazonian termites.

Authors' contribution

PACL Pequeno and E Franklin conceived the study and wrote the manuscript; PACL Pequeno assembled and analyzed the data.

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