

# Transitioning from unstable to stable colony growth in the desert leafcutter ant *Acromyrmex versicolor*

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**Abstract** Like organisms, cohesive social groups such as insect colonies grow from a few individuals to large and complex integrated systems. Growth is driven by the interplay between intrinsic growth rates and environmental factors, particularly nutritional input. Ecologically inspired population growth models assume that this relationship remains constant until maturity, but more recent models suggest that it should be less stable at small colony sizes. To test this empirically, we monitored worker population growth and fungal development in the desert leafcutter ant, *Acromyrmex versicolor*, over the first 6 months of colony development. As a multitrophic, symbiotic system, leafcutter colonies must balance efforts to manage both fungus production and the growth of the ants consuming it. Both ants and fungus populations grew exponentially, but the shape of this relationship transitioned at a size threshold of  $89 \pm 9$  workers. Above this size, colony mortality plummeted and colonies shifted from hypometric to hypermetric growth, with a distinct stabilization of the relationship between the worker population and fungus. Our findings suggest that developing colonies undergo key changes in organizational structure and stability as they grow, with a resulting positive transition in efficiency and robustness.

**Keywords** Development · *Acromyrmex* · Division of labor · Colony growth · Leafcutter ant · Social allometry

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## Introduction

Growth is a defining process for individuals at all levels of biological organization, whether in cells in an organism or individuals in a population or social group. For organisms to grow successfully, they must respond robustly to environmental challenges while following an intrinsically based growth trajectory (Salazar-Ciudad and Jernvall 2004). The interactions between environmental constraints such as nutrient intake and the intrinsic developmental program collectively shape an organism's ontogenetic phenotype (Glazier 2005; Doi et al. 2010). A similar interplay between environmental influences and growth shapes the ontogeny of insect societies, as they grow from a few individuals to a size of thousands or millions (Oster and Wilson 1978; Nonacs 1991; Kay 2004; Kay et al. 2006; Hou et al. 2010).

Despite recognition that development constrains social phenotype, surprisingly few studies have characterized how complex social groups such as insect colonies navigate developmental challenges as they move from foundation through maturity (Wilson 1983; Porter and Tschinkel 1985, 1986; Tschinkel 1988, 1991, 2011). Such characterization is critical for understanding how natural selection shapes growth and phenotypic expression. Social groups, like individual organisms, must balance between allocation to growth and allocation to physiological maintenance; the mechanisms used to achieve this balance are based on organizational properties specific to the system and subject to selection.

Here, we study the growth dynamics of newly initiated colonies of the desert leafcutter ant *Acromyrmex versicolor* to understand how the fungus garden/worker ant relationship unfolds as colonies develop over the first 6 months of life. Leafcutter and related fungus-growing ant colonies provide a unique opportunity to track nutrient balancing and colony growth within an enclosed trophic system because the ants directly regulate the growth of their immediate food source, the fungus garden (Weber 1972; Hölldobler and Wilson 1990; Wirth et al. 2003; Seal and Tschinkel 2008; Mehdiabadi and

Schultz 2010). Colony growth is thus dependent on a feedback system between the nutritional state of the fungus and the colony's work allocation across tasks (Bass and Cherrett 1994; Burd and Howard 2005; Camargo et al. 2008). This balance may be particularly important during early growth, when colonies are more vulnerable to perturbation and/or stochastic effects (i.e., they possess lower robustness; Kitano 2004). Indeed, mortality rates generally are highest in small, young colonies, suggesting that this is a critical period in colony life history (Autuori 1950; Fowler 1992; Cole 2009; Adams et al. 2012). Previous studies with this species and the fungus gardener *Trachymyrmex septentrionalis* suggest unstable or variable ant–fungus relationships during early colony development, but it is unclear how this occurs or at what point it is resolved by successful colonies (Julian and Cahan 1999; Seal and Tschinkel 2007; Kang et al. 2011).

Most models of societal growth have been based on ecological models of population growth with the assumption that societies retain similar organizational structure from small initial sizes to maturity (Oster and Wilson 1978). While such models may effectively predict growth patterns for larger colonies, they are less useful for predicting events in small colonies, where internal organizational and demographic factors play an important role in determining growth rates (Porter and Tschinkel 1986; Jeanne and Nordheim 1996; Jeanne 1999; Gautrais et al. 2002; Tenhumberg et al. 2009). As an example, small colonies have to complete much of the same task repertoire as larger colonies, but with a limited workforce (Wilson 1983; Karsai and Wenzel 1998; Augustin and Santos 2008). This has consequences for colony-level division of labor and colony growth efficiency, both of which may increase with colony size (Gautrais et al. 2002; Jeanson et al. 2007; Waters et al. 2010; Kang et al. 2011).

In this study, we used noninvasive methods to correlate the growth trajectories of the worker population and fungus garden biomass in leafcutter ant colonies from foundation through the first 6 months of development. *A. versicolor* colonies are relatively long-lived and can grow over the course of several years to a size of around 10,000 workers prior to reproducing, making it possible to study growth processes without confounding effects from the onset of reproduction (Julian and Cahan 1999). We focus on the critical early phase of colony growth, from colony initiation through sizes of 100+ workers. We show that, in colonies at this scale, the worker–fungus relationship undergoes a qualitative shift from negative, variable allometry (a hypometric relationship with fewer workers produced per unit of fungus present) to hypermetry, where more workers are produced per unit of fungus as colony size increases. This transition occurs at a critical worker population size threshold, above which colonies achieve a more stable relationship between worker and fungus populations. Together, these patterns suggest that colonies undergo a phase transition in efficiency during early colony development.

## Methods

### Study species

*A. versicolor* colonies are found along washes (arroyos) in low desert areas throughout the southwestern USA and northern Mexico (Weber 1972; Wetterer et al. 2001; Johnson and Ward 2002; Ward 2005). The ants function as generalist herbivores, collecting both fresh and dry leaves and flowers from trees and shrubs, including mesquite (*Prosopis juliflora*), ironwood (*Olneya tesota*), acacia (*Acacia* spp.), palo verde (*Cercidium* spp.), creosote (*Larrea tridentata*), and ocotillo (*Fouquieria splendens*; R. Clark, personal observation; Gamboa 1975; Wetterer et al. 2001). Mating swarms are triggered by summer monsoon rains with >2.5 cm of precipitation (Johnson and Rissing 1993), which causes queens to fly from their natal nests to aggregates, where they mate multiply and then shed their wings and excavate new nests, typically at the canopy edge of palo verde or mesquite trees (R. Clark, personal observation; Reichardt and Wheeler 1996). In some areas, multiple queens form pleometrotic foundress groups, and mature colonies are thought to remain polygynous (Rissing et al. 1986, 1989, 2000; Cahan and Julian 1999). This is supported by the observation that all queens remain reproductively active in polygynous nests maintained in the laboratory (R. Clark, unpublished data).

Many attine ants, including *A. versicolor*, possess semi-claustral queens, which leave their newly excavated nests occasionally to forage for leaves as substrate for the fungus garden, which in turn provides food for the developing brood (Rissing et al. 1989; Fowler 1992; Fernández-Marín et al. 2004). When workers emerge, queens gradually reduce their behavioral repertoire and remain inside the nest to lay eggs, while workers assume the tasks of collecting and preparing leaves for the fungus garden, raising brood, tending the fungus garden, and removing waste materials from the nest (Cahan and Julian 1999). In laboratory nests, queens start the fungus garden on the bottom of the nest chamber, allowing full visibility of workers and developing brood, but mature gardens are typically hung in patches on the chamber ceiling that grow downward, forming “curtains” that increase in density with the age of the garden, and gardens in field colonies also hang from the ceiling (U. Mueller, personal communication).

### Growth study

To establish colonies, we collected newly mated queens from the field before they began excavating new nests. Queens were collected on 8 August 2005 underneath a mating flight along North Swan Road just north of North Plaza del Baron, in Tucson, AZ (32.31° N, –110.89° W). Queens were housed in groups of four; this is within the range of queen group sizes commonly found in field nests (Rissing et al. 1986), and queens in groups have higher survival than queens kept by

themselves (Julian and Cahan 1999). Nests consisted of two circular plastic dishes (internal dimensions, 8.4 cm diameter  $\times$  3.3 cm high) connected with vinyl tubing ( $\sim$ 3 cm long  $\times$  0.64 cm inner diameter). The bottom of one chamber was lined with  $\sim$ 1 cm of plaster of Paris and was used by colonies to house the fungus; the other chamber served as a foraging arena. Throughout the study, colonies were provided with an ad libitum mixture of palo brea leaves (*Cercidium praecox*), polenta (coarsely ground cornmeal), and oatmeal, refreshed once a week. Humidity levels were maintained in the fungus chamber by watering the plaster weekly with 2–4 mL of water. Ambient temperature was maintained at 30–32 °C from August through October and at 25 °C from November through March, with natural lighting from windows along one wall.

Colony worker population and fungus size were estimated once a week using noninvasive methods to minimize disturbance to nests, with the exception of weeks 17–22, when no measurements were made. Weeks 17–22 occurred during the early winter (December–January), a period with lower temperatures and shorter day length, so slow/little growth was expected. Fungus area was measured from overhead photographs of the fungus chamber taken from a set distance to standardize size and was calculated using ImageJ (<http://rsbweb.nih.gov/ij/>). We visually estimated worker numbers by scanning the nest and counting individuals with a hand counter. By week 30 (210 days), surviving colonies reached an average size of 182 workers, and population sizes appeared to be consistently increasing from week to week (on average, 17 new workers added per week for the last 4 weeks). The study was, therefore, ended at week 30, in March 2006.

We validated the worker and fungus estimation methods by repeating them on a separate set of 21 nests because direct assessment of fungus mass requires destructive sampling, which we could not perform on our focal nests. These nests were started at the same time as the focal colonies, but their fungus gardens died at different points during development. After fungus garden death, these colonies were reduced in size to approximately 10–20 workers plus surviving queens (between one and four queens), and fungus gardens were replaced by transplant material from other laboratory colonies. Colonies were then left to grow for 6 months (26 weeks) before measurement validation. We repeated the estimation methods described previously, and then separated workers and removed pupae from the fungus gardens so the pupal mass did not influence the fungus garden measurements. We counted the total number of workers and weighed the entire worker population and the fungus garden (still including eggs and larvae, which are a small fraction of the total fungus garden mass) and used the data to assess the accuracy of our estimation methods. At small colony sizes ( $<$ 50 workers), all workers are easily visible and can be accurately counted. For larger colony sizes ( $>$ 100 workers), the nondestructive sampling method tends to underestimate total worker numbers, but estimates remain

strongly positively correlated with actual worker numbers ( $r^2=0.983$ ,  $n=21$  colonies;  $\text{number}_{\text{workers}}=1.483 \times \text{estimate}_{\text{workers}}$ ; Electronic supplementary material 1 [ESM 1] Fig. 1), as well as total worker wet mass (in grams;  $r^2=0.9728$ ,  $n=21$ ,  $\text{mass}_{\text{workers}}=0.00375 \times \text{estimate}_{\text{workers}}$ ). Fungus area was also strongly and positively correlated with the total wet mass (in grams) of the fungus garden ( $r^2=0.9765$ ,  $n=21$  colonies,  $\text{mass}_{\text{fungus}}=0.0997 \times \text{area}_{\text{fungus}}$ ; ESM 1 Fig. 1).

*A. versicolor* workers vary in size (and, therefore, mass), and leafcutter colonies' worker size distributions are thought to increase as colonies grow (Wilson 1983). If this were to occur across the colony size range studied here, the conversion coefficients could overestimate total worker wet mass, particularly for small colonies. However, worker mass distributions were constant across the reference colonies used to validate the colony size estimation methods (ESM 1 Figs. 2 and 3). Further, while average worker mass ranged from 1.92 to 3.47 mg, for colonies ranging between 21 and 594 workers, a colony's average worker mass was not related to its total worker mass (methods and data in ESM 1 Figs. 4 and 5).

We assessed queen and colony survival throughout the study. The obligate mutualistic relationship between leafcutter ants and their fungus means that neither the fungus nor the ants can survive and reproduce in the absence of the other and loss of the fungus garden is frequent in young colonies (Cahan and Julian 1999). Therefore, death of a colony was defined by death of the fungus garden, although in the wild, it is possible that colonies could revive fungus gardens by stealing garden material from other colonies (Adams et al. 2000; Green et al. 2002). Subsequent analyses of ant–fungus dynamics and mass relation analyses included only those colonies for which both the original fungus garden and at least one queen survived the entire study period.

#### Data analysis

Data were analyzed using R, version 2.11.1 (R Development Core Team 2010); the R script and associated data used for the analysis are available as Electronic Supplements 2 and 3. To allow direct biomass comparisons between the fungus and workers in the same units, data for fungus area and worker population size were converted to wet mass units (in grams) based on the correlations described previously, then linearized and normalized by log transformation. To assess whether all colonies followed the same or different growth patterns, we first constructed an overall simple linear model for each given size measure (fungus and ants) over time, using data for all surviving colonies (11 colonies; see the succeeding section). The simple linear model was compared to a linear mixed-effects model, where colony identity was included as a random factor in the model. In the case of a significant difference between models, we selected the most parsimonious

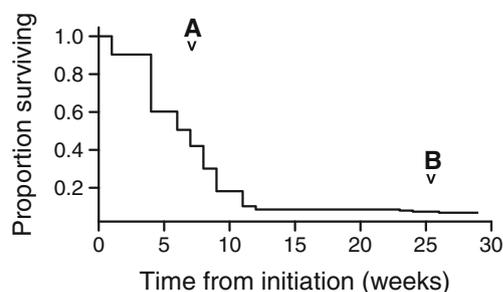
model with higher explanatory value, based on lower Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) indices (likelihood ratio test; Sakamoto et al. 1986; Schwarz 1978). In the event that the linear mixed-effects model was selected, post hoc comparisons between colonies were conducted by constructing separate simple linear models for each individual colony.

Preliminary analyses of the overall mass relationship between fungus and workers suggested that the relationship might not necessarily follow a simple linear trend, but instead consists of two separate linear trends with a breakpoint. To determine the location of a general size breakpoint, we created a combined plot of all of the (log) worker mass and (log) fungus mass data from the surviving colonies and used the R package “segmented” to estimate the value of a common breakpoint (Muggeo 2003, 2009). We then compared the AIC and BIC indices of two separate linear models to indices for an overall linear model with no breakpoint and selected the model with lower values as most appropriate. This may underestimate or overestimate breakpoints for individual colonies, but allows the identification of a general trend across colonies.

## Results

### Colony survival and worker emergence

A total of 176 colonies were initially established and monitored, as there was an expectation of high mortality during colony foundation. Survival was monitored across two periods: from initiation to first worker emergence (weeks 1 through 9) and from first worker emergence until the end of the study at week 30. The first period had high colony mortality rates (Fig. 1; ESM 1 Table 1). By week 9, 132 of the colonies (75 %) had lost their fungus gardens and were, therefore, considered dead. An additional 32 colonies (18 % of



**Fig. 1** Colony survival during early development, from foundation through week 29. A total of 176 colonies were initially established, with four foundress queens each, and monitored. Marker *A* indicates the average week of first worker emergence. Marker *B* indicates where the mean number of workers in each colony was >89. A summary table with confidence intervals is in ESM 1 Table 1

the original 176) died from fungus loss between weeks 9 and 30. Only 12 colonies (7 %) survived the entire study, although in one colony, the fungus garden collapsed and partially died over the final 6 weeks of the study, so this colony was excluded from subsequent analyses.

The transition from high to low colony mortality corresponded with first worker emergence. The average time of first worker emergence in the 12 surviving colonies was week 7; at least one worker had emerged in all 12 of these colonies by week 10 (Fig. 2).

Queen mortality across the study was extremely low. All queens were alive in the majority of colonies surviving to the end of the study (9 of 12 colonies). In the three colonies that survived with fewer than four queens, queen deaths occurred before any workers emerged and were nonviolent (most likely due to pathogen exposure), occurring during weeks 1, 3, and 7. Across both the surviving and the non-surviving colonies (initial  $n=176$ ), the week-by-week average queen number was 3.5, with a median queen number of 4, and no aggressive interactions were observed among queens (ESM 1 Fig. 6).

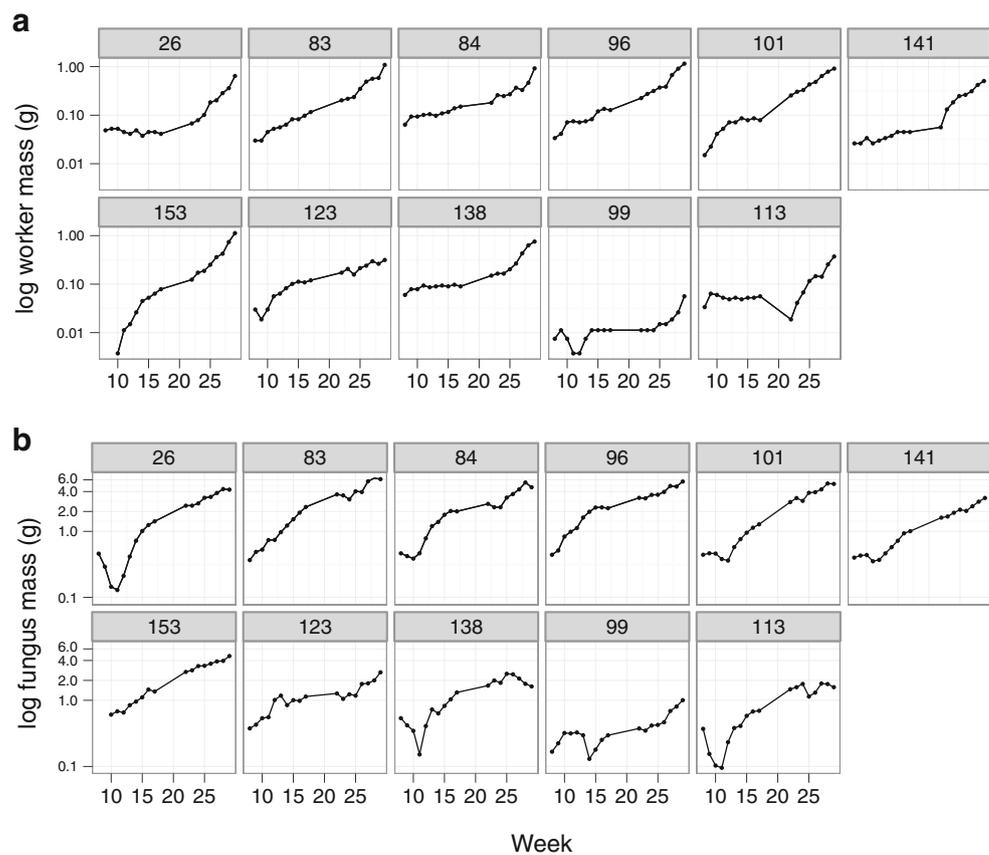
### Worker population growth

In the 11 colonies surviving through week 30, worker populations grew exponentially, with an overall growth mass exponent of 0.12 ( $t=8.53$ ,  $p<0.0001$ ; Fig. 2). Although all 11 colonies followed an exponential growth pattern, colonies varied considerably in worker production rates (likelihood ratio=280.7,  $p<0.0001$ ). Individual colony growth exponents varied threefold, over a range from 0.07 to 0.21. In the mixed-effects model, colony identity translated into a weighted effect of 0.05 on the worker population growth exponent.

### Fungal growth

Fungus gardens also grew exponentially, with an overall growth mass exponent of 0.098 ( $n=11$ ,  $t=12.03$ ,  $p<0.0001$ ; Fig. 2). As with worker populations, garden growth varied across a threefold range among colonies, from an exponent of 0.05 to 0.14 (likelihood ratio=241.5,  $p<0.0001$ ). In the mixed-effects model, colony identity represented a weighted effect of 0.03 on the fungus growth exponent. Despite high variation in growth rates, colonies with faster fungal growth did *not* have correspondingly faster ant population growth rates ( $F_{1,9}=3.171$ ,  $p=0.11$ ). Also, interestingly, many fungus gardens experienced a period with no growth or a transient decline shortly after workers began to emerge, subsequently resuming a size increase (Fig. 2). This contributed to higher variance in fungal garden masses when colonies contained small fungus gardens (under 2.4 g; see the succeeding section)

**Fig. 2** Growth patterns of workers and fungus during early colony development across a set of 11 colonies, from first worker emergence (on average, week 8) through week 29, with the exception of weeks 17–22, during which no measurements were made. **a** Changes in the total worker population mass. **b** Changes in the total fungus garden mass. *Title boxes* indicate colony identity



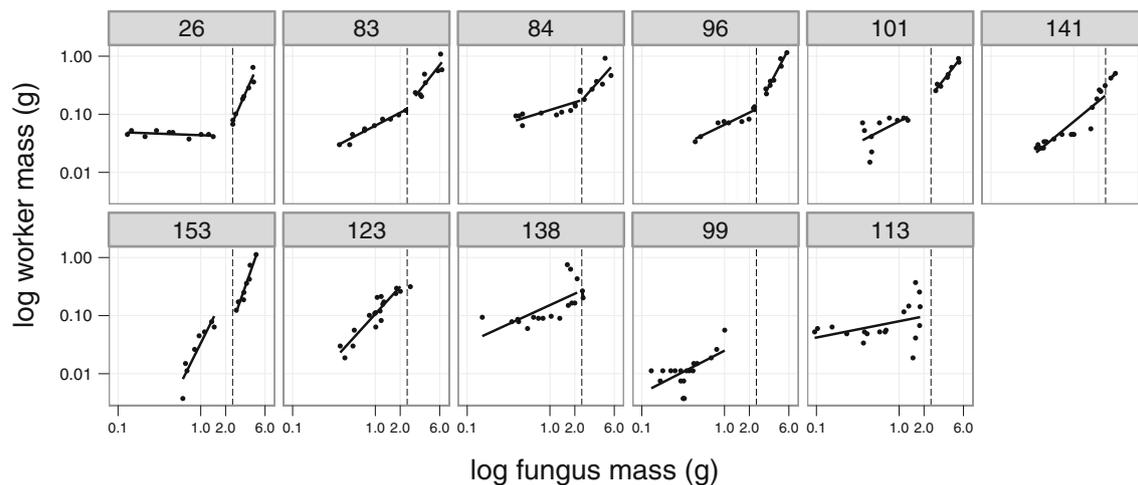
as compared to larger gardens (Levene's test,  $W=18.7$ ,  $p<0.0001$ ).

#### Worker–fungus population dynamics

Total per-colony worker population mass was positively related to fungus garden mass. However, the relationship between worker population mass and fungus garden mass showed a transition point at a distinct size threshold, corresponding to a fungus garden mass exponent of  $0.386 (\pm 0.074 \text{ SEM})$ ; Fig. 3). Specific transition points varied between colonies (see, e.g., colony 141; Fig. 3). This fungus mass exponent translated to a worker population size of  $89 \pm 9$  workers, achieved on average by week 27 for colonies that grew above this size (9 of the 11 colonies). The relationship transitioned from hypometric to hypermetric: below the threshold, garden biomass and worker population mass scaled with an overall slope significantly  $<1$  ( $0.776 \pm 0.145$ ,  $t=5.36$ ,  $n=11$ ,  $p<0.0001$ ). For colonies that grew above the size threshold for at least six measurements (6 of 11 colonies), fungus and worker masses scaled with an overall slope significantly  $>1$  ( $1.841 \pm 0.276$ ,  $t=6.68$ ,  $p<0.0001$ ). The worker–fungus relationship differed across colonies at both size ranges (likelihood ratio<sub>small</sub> = 100.6,  $p<0.0001$ ; likelihood ratio<sub>large</sub> = 24.2,  $p<0.0001$ ).

#### Discussion

A long held expectation of growth in complex social groups is that they should move to increased efficiency as they become larger (Michener 1964; Oster and Wilson 1978; Karsai and Wenzel 1998; Anderson and McShea 2001). However, most models of colony growth portray this transition as a gradual process, as per expectations of simple ecological population growth models (Oster and Wilson 1978). By tracking growth during the first 6 months of colony development, we found that young leafcutter ant colonies undergo a distinct phase transition, in which the correlation between growth in fungus and worker population size becomes significantly tighter and positive. The transition to stable growth relationships occurred at a colony size of approximately 89 workers, two orders of magnitude beyond initial worker emergence. Comparable threshold shifts had previously been found in other behavioral contexts, such as in quorum sensing during nest site selection in *Temnothorax* ants, nest site signaling in honey bees, and in honey bee pollen foraging effort relative to colony need (Fewell and Bertram 1999; Pratt et al. 2002; Seeley and Visscher 2004); here, we expand them to a fundamental colony attribute, growth, in a species that maintains an obligate mutualism with its food source.



**Fig. 3** Log–log plots of the relationship between fungus garden mass and total worker mass, fit to segmented linear regression models. The critical size threshold marking a transition point in the fungus–worker mass

relationship is indicated by the *vertical dashed line* (see the text for details). *Title boxes* indicate colony identity

Phase transitions of this nature—from a hypometric and highly variable growth relationship to more stable hypermetric growth—are not usually captured by population growth models of consumer–resource dynamics (Murdoch et al. 2003; Holland and DeAngelis 2010). These models do not address how behavioral complexity influences growth. However, such transitions fit reasonably with newer models of growth relationships that uses a Michaelis–Menten approach to factor in the allocation of resources between self-growth and growth of the mutualist partner (Holland and DeAngelis 2010; Kang et al. 2011). For growth models of leafcutter ant colonies, consideration of how worker effort is allocated to foraging (fungus growth) versus brood care (worker growth) produces the observed threshold shift in growth at small colony sizes (as was shown for the colonies studied here in Kang et al. 2011).

#### Biological mechanisms influencing growth efficiency

Biologically, the observed growth transition could reflect changes in colony priorities and in the organization of work as colonies grow. These expectations are not usually incorporated into population growth models because they do not consider the population as a complex system with structured differentiation in individual behavior (although, see Tenhumberg et al. 2009). In small colonies, however, individual worker actions assume greater importance with respect to colony function, especially when the number of individuals is low relative to critical tasks that must be performed (Jeanne and Nordheim 1996; Jeanne 1999; Gautrais et al. 2002; Jeanson et al. 2007). Once a certain level of redundancy is achieved, colonies may expand task repertoires to include noncritical tasks that contribute to overall stability and may be able to subdivide task sequences to minimize costs of transitioning between tasks (Karsai and Wenzel 1998; Holbrook et al. 2011). Workers in

mature leafcutter ant colonies have been observed to perform up to 30 different task-related behaviors associated with fungus garden cultivation, garden maintenance, brood care, grooming, and waste management (Wilson 1980; Camargo et al. 2007). Colonies shift worker allocations across these task groups as they grow, away from behaviors focused on brood rearing toward tasks promoting nest maintenance, such as refuse removal and fungus garden maintenance (Clark and Fewell, unpublished data).

The worker population's age and size structure also expand as colonies grow, with consequences for flexibility of task performance and repercussions for the division of labor and overall efficiency (Wilson 1983; Gautrais et al. 2002; Jeanson et al. 2007; Fewell et al. 2009). For example, Seid and Traniello (2006) found that older *Pheidole dentata* workers exhibit larger task repertoires and are able to quickly respond to colony needs by upregulating specific behaviors. In leafcutter colonies, expansion of the worker age and size distribution is also expected to generate specialist groups with possibly higher individual behavioral efficiency. Larger workers in large colonies tend to specialize on leaf cutting, whereas smaller workers specialize on fungus care, including weeding confined spaces in the fungus garden to remove parasites and pathogens (Oster and Wilson 1978; Wetterer 1994; Bass and Cherrett 1994, 1996). It would be especially useful to pinpoint when and how the *A. versicolor* size and age distributions develop relative to the stabilization of the worker–fungus relationship.

Recent theoretical and empirical work have shown that division of labor increases as colonies grow, but have not revealed how such increases translate into changes in overall colony efficiency (Gordon 1989; Karsai and Wenzel 1998; Thomas and Elgar 2003; Holbrook et al. 2011). In harvester ants (*Pogonomyrmex californicus*), the intensity of division of labor (i.e., levels of individual specialization) increases

linearly with colony size (Holbrook et al. 2011). Leafcutter colonies additionally shift task allocation in association with changing task demand, and the overall task repertoire expands as colonies grow (Clark and Fewell, unpublished data); the interaction effects across these aspects of work could produce nonlinear efficiency gains, such as were observed here.

Increased size also has repercussions for the colony's communication structure, as additional contact between individuals and enhanced information flow within the colony network could be required for a stable and tightly regulated system. Network connectivity tends to increase nonlinearly with size (Shapiro and Varian 1999), and higher connectivity should generate more stability and greater robustness in response to environmental inputs. Both stability and robustness contribute to a colony's ability to withstand environmental perturbation and regulate nutrient intake and growth.

Overall, then, expansion of the worker size distribution and of colony age structure, in conjunction with increased numbers of workers relative to tasks and improved network connectivity, could increase both efficiency and robustness as colonies grow. While some of these factors have been individually manipulated in previous studies (e.g., in ants: Wilson 1983; Brown and Traniello 1998; in honey bees: Huang and Robinson 1996; in wasps: Naug and Gadagkar 1998), it has proven difficult to map the effects of such manipulations back onto dynamic, functional measures of colony performance (Jeanne and Nordheim 1996; Karsai and Wenzel 1998). The phase transition found here, and potentially present in other fungus-growing species (e.g., Seal and Tschinkel 2007), provides a valuable starting point for dissecting the components and interaction effects contributing to stability and robustness as social systems scale in size. It would be useful to use the growth dynamics shown here to model the relative influence of age structure, size structure, and division of labor on development, as well as to compare across a range of social groups that vary in organization, to pinpoint which factors exert strong selective pressure on social development and, thus, social evolution (Dornhaus et al. 2012). An understanding of how these organizational forces interact to produce changes in colony-level efficiency and phenotype should improve and inform our understanding of how developmental processes unfold across levels of biological complexity (Yang 2007; Salazar-Ciudad 2010).

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