

The role of per-capita productivity in the evolution of small colony sizes in ants

Boris H. Kramer · Inon Scharf · Susanne Foitzik

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Abstract The evolution of colony size in social insects is influenced by both extrinsic and colony-intrinsic factors. An important intrinsic trait, per-capita productivity, often declines in larger colonies. This pattern, known as *Michener's paradox*, can limit the growth of insect societies. In this study, we first describe this problem, survey its occurrence across different ant species, and present a case study of eight cavity-dwelling ants with very small colony sizes. In these species, colonies might never reach sizes at which per-capita productivity decreases. However, in six out of the eight focal species, per-capita productivity did decline with increasing size, in accordance with other studies on per-capita productivity in ants. Several mechanisms, such as resource availability or nest-site limitation, may explain the decrease in per-capita productivity with increases in colony size in our focal species. In these central-place foragers, the individual foraging mode is expected to lead to an increase in travel time as colonies grow. We suggest that polydomy, the concomitant occupation of several nest sites, could serve as a potential strategy to overcome this limitation. Indeed, for one species, we show that polydomy can help to circumvent the reduction in productivity with increasing colony size, suggesting that limited resource availability causes the observed decrease in per-capita productivity. Finally, we discuss the influence of other factors,

such as the nesting ecology and colony homeostasis, on the evolution of colony size in these cavity-dwelling ants.

Keywords Colony size · *Leptothorax* · Social insects · Productivity · Per-capita productivity · Michener effect · *Temnothorax*

Introduction

Evolution shapes growth, reproduction, and aging in animals (Stearns 1992). In social insects, colony size is a characteristic trait that forms the basis for various life-history trade-offs (Bourke 1999; Dornhaus et al. 2009; Kramer and Schaible 2013). Colony size varies among populations and species: Some species reach enormous colony sizes of several million individuals (Beckers et al. 1989), whereas the mature colonies of other species (e.g., our focal species) contain only a few dozen individuals. Species-specific colony sizes are determined by factors both extrinsic (e.g., predation) and intrinsic (e.g., foraging mode) to the colony (Jeanne and Nordheim 1996). The advantages of large colony size include better fighting abilities and defense, higher annual survival, and increased production of sexuals (Wilson 1974; Cole 1984; Kaspari and Vargo 1995; Bourke 1999; Palmer 2004; Sorvari and Hakkarainen 2007). On the other hand, colony growth can be restricted by the limited availability of construction materials or nesting sites, by a limited egg laying rate of the queen or due to resource limitation caused for example by the specific foraging mode of the species (Beckers et al. 1989; Wenzel and Pickering 1991; Foitzik and Heinze 1998).

An important intrinsic measure of colony fitness is the biomass production, which has been used to quantify the benefits of group living (Weislo and Tierney 2009). Two common fitness measures in social insects, colony productivity and per-capita productivity, are defined as the total number

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B. H. Kramer (✉)
Max Planck Institute for Demographic Research, Konrad-Zuse-Str. 1,
18057 Rostock, Germany
e-mail: kramer@demogr.mpg.de

I. Scharf
Department of Zoology, Faculty of Life Sciences,
Tel Aviv University, Tel Aviv, Israel

S. Foitzik
Institute of Zoology, Johannes Gutenberg University of Mainz,
Mainz, Germany

of new workers and sexuals produced by a colony, divided by the total number of adult workers (Clouse 2001; Scharf et al. 2011a). It was suggested that colonies should only grow larger if each additional group member leads to a per-capita fitness increase and, therefore, per-capita productivity could be used to study the evolution of colony size (Naug and Wenzel 2006). However, many eusocial insect species display a decline in per-capita productivity with increasing colony size or after exceeding a certain colony size (Michener 1964; Litte 1981; Cassill 2002). Within the Formicidae, studies on changes in per-capita productivity with colony size revealed both decreasing (Brian 1953, 1956; Wilson 1974; Cole 1984; Porter and Tschinkel 1985; Tschinkel 1993, 1999; Hee et al. 2000; Cassill 2002; Franks et al. 2006) and constant (Cole 1984; Kaspari and Byrne 1995; Hee et al. 2000; Billick 2001) patterns, whereas increasing patterns were never detected. Species with large colonies such as *Myrmica rubra*, *Solenopsis invicta*, and *Pogonomyrmex badius* display a peak in per-capita productivity, which is then followed by a decline in per-capita productivity at colony sizes much smaller than the species-specific average (Brian 1953, 1956; Tschinkel 1999; Cassill 2002). These decreasing patterns of per-capita productivity have been linked to logistic population growth caused by resource limitation and increasing forager density or increasing numbers of inactive workers (Porter and Tschinkel 1985; Naug and Wenzel 2006; Dornhaus et al. 2009). Additionally, increasing colony size, at the cost of per-capita productivity, may lead to improved colony homeostasis, accompanied by a decreasing variance in per-capita productivity, and improved annual survival (Cole 1984; Naug and Wenzel 2006; Tindo et al. 2008).

In this study, we investigated whether colony-size-related changes in per-capita and colony productivity may have selected for the small colony sizes found in cavity-dwelling ants. Two mechanisms were hypothesized to be responsible for the small colony sizes of the focal species. First, if per-capita productivity decreases continuously with increasing colony size, small colonies should be selected for (Michener 1964; Oster and Wilson 1978). Second, if per-capita productivity increases with colony size or if it increases up to a certain optimal size and then decreases at sizes above that, colony size might be kept below this optimum by disturbances that lead to worker and brood loss (Kaspari and Byrne 1995). Here, we focus on the productivity of eight cavity-dwelling ant species from temperate forests with small colony sizes, of the genus *Temnothorax*, *Myrmica*, and *Leptothorax* and related slavemaking species. We test two alternative hypotheses that may explain the small colony sizes of our focal species: (1) Due to economy of scale, per-capita productivity should tend to increase with colony size up to a maximum, but disturbances may keep colonies below the optimal size, as suggested by Kaspari and Byrne (1995). Disturbances should lead to worker and brood loss and consequently affect both

productivity and colony size. Alternatively, (2) rising costs of central-place foraging with increasing colony size will lead to a decline in per-capita productivity caused by resource limitation. In contrast to the effect of disturbances, resource limitation should mainly affect resource availability and consequently the productivity of the colony, but only secondarily its size.

If we find decreasing per-capita productivity with increasing colony size, we can hypothesize that the rising costs of central-place foraging could lead to decreasing per-capita productivity in these solitary foraging species (Naug and Wenzel 2006). In order to overcome the costs of increased travel time, large colonies may split to occupy several nesting sites concurrently and thereby increase their foraging range. Polydomy could restore high per-capita productivity in large colonies, indicating a link between per-capita productivity, foraging mode, and resource limitation. To test this, we conducted a case study on the facultative polydomous and polygynous ant *Temnothorax longispinosus*, employing genetic data to identify nests that might constitute a polydomous colony. We then compared colony-size-related changes in per-capita productivity between polydomous and monodomous colonies. Finally, we examined whether the lack of availability of large nesting sites could limit colony growth in the focal population, by testing for an association between colony size and nesting site size.

Methods

Study systems

Cavity-dwelling ants of the genera *Temnothorax*, *Leptothorax*, and *Myrmica* are characterized by a small body size and colony size (a few dozen ants). They inhabit the leaf litter layer of temperate forests and reside in acorns or any wooden structures providing protection (Möglich 1978; Foitzik and Heinze 1998; Herbers and Johnson 2007). Nest sites are a limiting factor, as they quickly decompose and therefore colonies often relocate their nests (Herbers 1986; Hölldobler and Wilson 1990; Byrne 1994; Foitzik and Heinze 1998). Larger colonies usually occupy larger nest sites (Herbers 1986; Foitzik and Heinze 1998; Pratt and Pierce 2001; Scharf et al. 2011b), and the size of the nest site is probably the most important limiting factor for colony size (Byrne 1994; Kaspari 1996). Space limitation can be overcome by polydomy, i.e., the occupation of multiple nest sites per colony. In addition, cavity-dwelling ants are often polygynous and the occurrence of several queens in the nest allows them to permanently split their colonies (Alloway 1979; Herbers 1986). These ants are food generalists and forage individually without using chemical or mass recruitment. However, during nest movement, they employ a slow recruitment behavior called

“tandem running” (Möglich 1978; Beckers et al. 1989; Herbers and Choiniere 1996).

Data collection and analyses

We analyzed 12 datasets on cavity-dwelling ants from four genera and eight species across six localities (see Table 1), incorporating colony size (counting the number of workers in each colony; mean values in Table 1), worker production (worker pupae and newly emerged workers), and sexual production (males, male pupae, new queens, and queen pupae). Two slavemaking species are included in the dataset: *Protomognathus americanus* parasitizes *Temnothorax* species in North America and *Harpagoxenus sublaevis* parasitizes the Eurasian *Leptothorax* species. The habitat of the different localities, temperate forest, has already been described in detail elsewhere: Abensberg (Abe.) (Scharf et al. 2011b), Sommerhausen South & West (So. W, So. S) (Foitzik et al. 2003), and New York (NY) and West Virginia (WV) (Foitzik et al. 2009). Since the sampling was destructive, colony development could not be monitored over several seasons.

Colony productivity and per-capita productivity

We sought to determine how colony productivity and per-capita productivity are related to colony size. For the analysis, we calculated the biomass (in milligrams) of the annual production by multiplying the number of produced males, queens, and workers (including pupae) by the species-specific average biomass values for workers, queens, and males (Table 1). The data for *H. sublaevis* differ from the other datasets because we had data only on the number of newly produced individuals but no data on their caste. Hence, we based our analyses for this species on the number of produced individuals.

First, we used colony productivity and linear regressions to determine the effect of colony size on productivity. We then log-transformed both total production and colony size, which resulted in normally distributed residuals. The log transformation allowed for easier interpretation of the relationship between size and productivity: a slope of 1 represents a constant increase in productivity with each added individual, a slope smaller than 1 represents decreasing marginal returns, and a slope larger than 1 represents increasing marginal returns.

To analyze whether developmental stage (immature colonies: only worker production; mature colonies: sexual and worker production) was associated with productivity, beyond the effects of colony size, we conducted an analysis of covariance (ANCOVA) with colony size as the covariate, mature/immature colonies as the explanatory variable, and productivity as the response variable. A significant interaction term (colony size \times mature/immature colonies) would indicate different slopes in the pattern of per-capita productivity for

mature and immature colonies. As noted, this analysis was not performed for *H. sublaevis*.

To analyze the per-capita productivity, we divided colony productivity by the number of workers present in the colony. In the case of the slavemaking species (*P. americanus* and *H. sublaevis*), we divided colony productivity by the number of slaves because the slaves conduct the workers' routine tasks and thus we expect these species to show patterns similar to those observed in the parasitized species (Alloway 1979; Pamminer et al. 2011). The variance of the dependent variable was not homogenous, but decreased with increasing colony size. The Breusch-Pagan test (Breusch and Pagan 1979) showed heteroscedasticity for most datasets (Table 3). To overcome this, we used quantile regressions (Koenker and Hallock 2001). This enabled an examination of the relationship between per-capita productivity and colony size. Quantile regression estimates multiple rates of change (slopes) from the minimum to the maximum response, providing a more complete picture of the relationships between variables (Koenker and Bassett 1978; Cade and Noon 2003). Quantile regressions are semi-parametric, in the sense that no parametric distributional form is assumed for the error distribution (Cade 2003). From the quantile regression, we obtained data on the best and worst performing colonies. The quantiles used (0.1, 0.25, 0.5, 0.75, and 0.9) represent the bottom 10 and 25 %, the top 25 and 10 %, and the median (0.5) of the colonies in terms of per-capita productivity. The differences in the quantile regression show the changes in variance over all colony sizes.

The effect of polydomy on per-capita productivity

In a case study on *T. longispinosus* (NY), we examined whether polydomy could be used to overcome Michener's paradox. We had data on the relatedness of *T. longispinosus* colonies from mapped 6 \times 6 m plots in NY (Foitzik et al. 2009). Up to three workers per colony (565 workers in 195 colonies) were genotyped at four microsatellite loci: LXA GT1, L-18, L-5, and Myrt3. The pair-wise relatedness value among all individuals in a plot was calculated using the Queller and Goodnight estimator of pair-wise relatedness (Queller and Goodnight 1989) within the program COANCESTRY (Wang 2011). To calculate the relatedness between two colonies, we used the average relatedness of all possible combinations between the individuals of the two colonies (e.g., if two ants of each colony are genotyped, then there are four possible combinations). Merging colonies based on genetic data is always problematic (Pedersen and Boomsma 1999) because it is unclear which cut-off point reflects real colony boundaries. In our study, the median of the within-nest relatedness values was $r=0.55$. Between-nest relatedness values had a median of 0.03, and only 3 % of pair-wise nest comparisons had a higher relatedness value than 0.40. We then decided to merge colonies that were more

Table 1 Study species information, sample sizes, mean colony size, and weight data

Dataset/ location	Density (nests/m ²)	Monogynous (M)/polygynous (P)	Monodominous (M)/polydomous (P)	Reference species	Sampled colonies (N)	Colony size (mean, SD)	Dry mass		
							Individual ^a	mg	Reference dry mass
<i>L. acer.</i> (Abe.) ^b	0.06	Facult. P	M	Chan et al. (1999)	237	44.1±45.3	Q M W	0.412 0.432 0.401	^c
<i>L. musc.</i> (Abe.) ^b	0.05	Facult. P	M	Stuart and Alloway (1988)	204	40.3±31.0	Q M W	0.276 0.302 0.206	^c
<i>T. cras.</i> (Abe.)	0.02	M	P	Strätz and Heinze (2004)	83	58.6±53.3	Q ^d M ^d	0.921 0.19	Strätz and Heinze (2004)
<i>T. cras.</i> (Reg.)	No data	M	P		198	43.5±38.2	W ^d	0.203	
<i>T. nyla.</i> (So. S)	7	M	P	Foitzik and Heinze (1998); Foitzik et al. (2003)	730	51.4±47.5	Q M	0.921 0.19	Foitzik and Heinze (2000)
<i>T. nyla.</i> (So. W)	3	M	P		273	60.5±50.1	W ^e	0.203	
<i>T. long.</i> (NY)	0.8	Facult. P	P	Herbers (1986)	498	18.2±14.3	Q	0.873	Foitzik et al. (2004)
<i>T. long.</i> (WV)	0.4	M	P	Herbers and Stuart (1996)	295	15.1±11.6	M W	0.231 0.217	
<i>M. punc.</i> (NY)	0.2	Facult. P	M	DeHeer et al. (2001) ^f	134	12.7±8.24	Q M W	1.16 0.63 0.55	Herbers and Bansbach (1999)
<i>P. amer.</i> (NY)	0.1	M	P	Foitzik and Herbers (2001)	83	3.06±5.61	Q M	0.58 0.19	Herbers and Stuart (1998), this study
<i>P. amer.</i> (WV)	No data	M	P		49	5.95±7.42	W ^f	0.231	
<i>H. subl.</i> (Abe.)	0.01	M	M ^c	Scharf et al. (2011a)	59	11.9±17.96			

^a W=worker, Q=queen, M=male^b Parasitized by slavemaking ants^c Personal observations (B. Fischer-Blass and S. Foitzik)^d *T. crassispinus* dry mass is very similar to its relative *T. nylanderii*, and the dry mass of the latter has been already used in *T. crassispinus* studies (Strätz and Heinze 2004)^e *P. americanus* workers were weighted for this study (mean of 10 workers)^f Differences among localities and years are evident and documented

closely related than $r=0.40$, a value lower than the median relatedness within colonies but rarely reached in between-colony comparisons. We only merged colonies that were less than 5 m apart, a distance that is far greater than the travel distance of the foragers (Heinze et al. 1996). We also eliminated colonies with either no productivity or no workers before the analysis.

In addition to the general rules mentioned above, we applied two different schemes for merging. First, we merged all related nests independent of the number of queens (AR, *all related*). *T. longispinosus* is facultatively polygynous in the NY population (Foitzik et al. 2009). We then followed the rule that each added nest must be related by >0.4 to 2/3 of the other merged nests. For the analysis, we merged 89 nests to 38 colonies leaving 104 nests unmerged. We merged on average 2.3 (range 2–4) nests.

Because sub-nests are often used periodically and often contain no queen (Foitzik et al. 2009), we decided upon a

second approach (hereafter called OTM, or *one to many*), merging one queenright to several queenless nests if relatedness was >0.4 . The more nests were merged, the more likely that the between-nest relatedness of the queenless nests would show a lower relatedness than 0.4. Therefore, we relaxed our relatedness criteria somewhat for in-between queenless nests, which now had to show a relatedness value above $r>0.3$. We merged 87 colonies from the original dataset to create 35 merged colonies, leaving 110 colonies unmerged. The mean number of merged nests was 2.5 ranging from 2–6 nests.

We then compared the change in per-capita productivity as a response to colony size between the single and merged colonies. We used an ANCOVA, with colony size as the covariate, single/merged colonies as the explanatory variable, and per-capita productivity as the response variable. A significant interaction term (colony size \times single/merged colonies) would indicate different slopes in the pattern of per-capita productivity for merged and unmerged colonies.

To test for nest-site limitation, which might force bigger colonies to split, we used the colonies from the same *T. longispinosus* dataset inhabiting acorns ($N=146$). For acorns, as compared to sticks or other nesting cavities, a proportional relation between diameter and volume exists. We used linear regressions to test for a relationship between nest and acorn size, measured as the acorn diameter.

All statistical analyses were performed using R-Statistical software (R Core Development Team 2010) and the package quantreg (Koenker 2011).

Results

Log-linear models

The log-linear models of colony productivity revealed that for most datasets and species (seven of 12 datasets and five of eight species) additional workers led to decreasing marginal returns (slope \pm confidence interval <1 ; Table 2, Fig. 1). The change in productivity with colony size (measured as the slope \pm confidence interval of the linear regressions) for *Temnothorax crassispinus* in both datasets included the slope of 1, indicating independence of production from colony size. *T. crassispinus* was the only species for which the slope estimate was >1 . For the two populations of *P. americanus*, the confidence intervals around the slope estimate included 1, but due to the small number of sampled colonies ($N=50$ and $N=36$) the confidence intervals are large compared to the other datasets (Table 2). We cannot rule out that colony productivity increased linearly for *P. americanus*, with increasing size leading to constant per-capita productivity (Fig. 1). The confidence intervals around the slope for a single

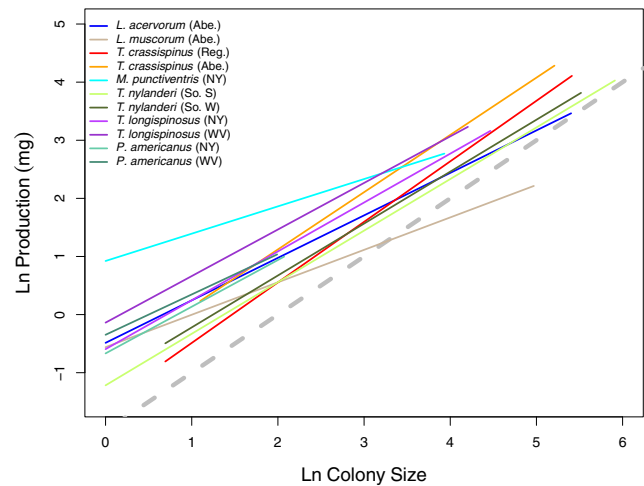


Fig. 1 Results of log-linear models showing the relationship between colony productivity and colony size (see Table 2 for the regression results). The dashed line indicates a slope of 1

Temnothorax nylander population (So. W) also included the slope of 1, while the other population (So. S) showed significant decreasing marginal returns (Table 2, Fig. 1). For all other datasets and species (*Leptothorax acervorum*, *Leptothorax muscorum*, *Myrmica punctiventris*, *T. longispinosus*, and *H. sublaevis*) colony productivity showed decreasing marginal returns, which can be interpreted as decreasing per-capita productivity (Table 2, Fig. 1).

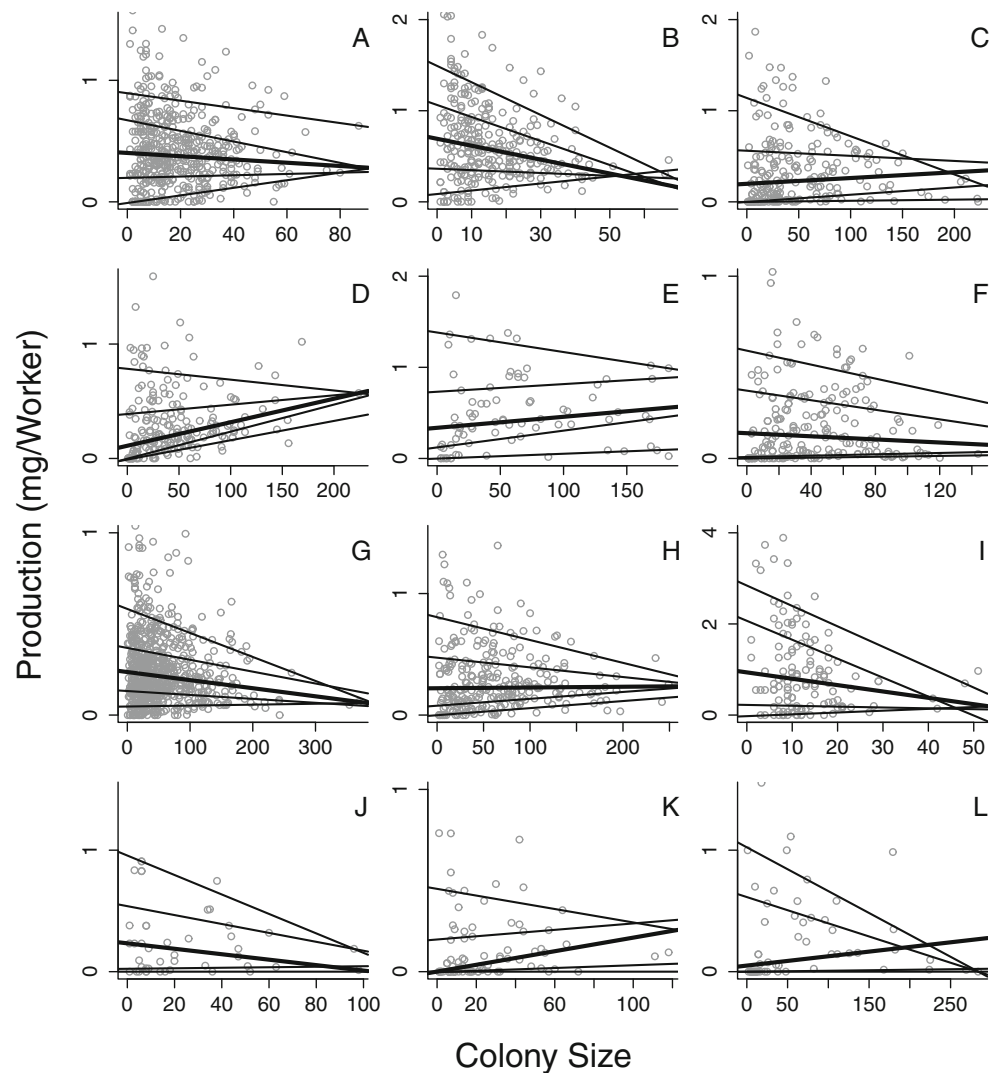
The effect of sexual reproduction

Sexual production occurred across all colony sizes in all datasets and species. When colony size was taken into account, 3 of the 11 populations showed a significant relationship between developmental stage and productivity. Mature

Table 2 Relationship between colony size and colony productivity. Linear model on log-transformed values

Dataset	Intercept estimate	Pr($> t $)	Slope estimate	Pr($> t $)	R^2	df	Slope confidence intervals	
							0.025	0.975
<i>L. acervorum</i> (Abe.)	−0.486	0.187	0.731	<0.001	0.233	181	0.537	0.926
<i>L. muscorum</i> (Abe.)	−0.561	0.190	0.558	<0.001	0.119	169	0.328	0.789
<i>T. crassispinus</i> (Reg.)	−1.529	<0.001	1.042	<0.001	0.549	168	0.898	1.185
<i>T. crassispinus</i> (Abe.)	−0.849	0.083	0.985	<0.001	0.468	72	0.738	1.232
<i>M. punctiventris</i> (NY)	0.922	0.013	0.470	0.002	0.080	117	0.178	0.762
<i>T. nylander</i> (So.S)	−1.218	<0.001	0.887	<0.001	0.494	697	0.821	0.954
<i>T. nylander</i> (So.W)	−1.114	<0.001	0.893	<0.001	0.435	247	0.766	1.021
<i>T. longispinosus</i> (NY)	−0.595	<0.001	0.841	<0.001	0.430	450	0.751	0.931
<i>T. longispinosus</i> (WV)	−0.139	0.333	0.801	<0.001	0.433	278	0.693	0.909
<i>P. americanus</i> (NY)	−1.538	0.006	0.804	<0.001	0.312	49	0.461	1.147
<i>P. americanus</i> (WV)	−0.8	0.135	0.694	<0.001	0.297	35	0.327	1.061
<i>H. sublaevis</i> (Abe.)	0.31	0.688	0.567	0.004	0.213	35	0.193	0.940

Fig. 2 Quantile regressions. The lines represent the results of the quantile regressions using different percentiles of the datasets (0.1, 0.25, 0.5, 0.75, 0.9). The 0.5 percentile is represented by the wider line. **a** *T. longispinosus* (NY), **b** *T. longispinosus* (WV), **c** *L. acervorum* (Abe.), **d** *T. crassispinus* (Reg.), **e** *T. crassispinus* (Abe.), **f** *L. muscorum* (Abe.), **g** *T. nylanderii* (So. S.), **h** *T. nylanderii* (So. W.), **i** *M. punctiventris* (NY), **j** *P. americanus* (WV), **k** *P. americanus* (NY), **l** *H. sublaevis* (Abe.). For *H. sublaevis*, the y-axis represents individuals not milligrams per worker



colonies of *L. acervorum* of the Abe. population (ANCOVA: $F_{4,156}=324.9$, $P=0.005$), *T. nylanderii* of the WV population (ANCOVA: $F_{4,230}=723.5$, $P=0.009$), and *P. americanus* of the NY population (ANCOVA: $F_{4,31}=71.66$, $P=0.008$) showed higher productivity in colonies producing sexuals.

Quantile regressions and per-capita productivity

The quantile regression showed the potential effect of a decreasing variance in per-capita productivity. At small sizes, the expected productivity of the colony varies strongly while at larger sizes colonies are homogenous in their productivity. All datasets showed a switch from positive to negative slopes with increasing quantiles used for the regression analysis (Fig. 2, Table 3). When focusing on highly productive colonies (quantiles, 0.9 and 0.75), per-capita productivity decreased with colony size, while the opposite was true for the low performing colonies (quantiles, 0.1 and 0.25), resulting in

similar per-capita productivity among larger colonies. Further, there was a decreasing variance in per-capita productivity with increasing colony size, as indicated by the quantile regressions and the Breusch-Pagan test (Table 3). In all datasets, decreasing variance can be seen in the different intercepts and the convergence of the quantile regressions (Fig. 2, Table 3). For some species, the quantile regressions overlapped at large colony sizes: *T. nylanderii* in both populations, *T. longispinosus* in both populations, and *M. punctiventris* and *T. crassispinus* in the Regensburg (Reg.) population. The other populations showed the same trend, but convergence of the regression lies outside of the size range of the population (Fig. 2). As in the linear models on log transformed data, *T. crassispinus* did not show a decrease in per-capita productivity with increasing colony size. Per-capita productivity was either constant (Abe. population) or increasing (Reg. population). Only the 0.9 quantiles showed a

Table 3 Results of the quantile regressions on per-capita productivity and the Breusch-Pagan test for heteroscedasticity

Species and location	Quantile	Intercept	P value	Slope	P value
<i>L. acervorum</i> (Abe.)	0.1	−0.001	<0.005	0	0.089
	0.25	−0.002	0.929	0.001	0.053
	0.5	0.198	<0.005	0.001	0.321
	0.75	0.561	<0.005	−0.001	0.598
	0.9	1.14	<0.005	−0.004	<0.005
	Breusch-Pagan test			<0.005	
<i>L. muscorum</i> (Abe.)	0.1	−0.001	0.327	0	0.004
	0.25	0.008	0.379	0	0.063
	0.5	0.139	<0.005	0	0.504
	0.75	0.372	<0.005	−0.001	0.121
	0.9	0.592	<0.005	−0.002	0.154
	Breusch-Pagan test			<0.005	
<i>T. crassispinus</i> (Reg.)	0.1	−0.01	0.086	0.002	<0.005
	0.25	−0.002	0.842	0.002	<0.005
	0.5	0.111	<0.005	0.002	<0.005
	0.75	0.388	<0.005	0.001	0.397
	0.9	0.784	<0.005	−0.001	0.638
	Breusch-Pagan test			<0.005	
<i>T. crassispinus</i> (Abe.)	0.1	−0.002	0.914	0.001	0.096
	0.25	0.121	0.107	0.002	0.081
	0.5	0.336	<0.005	0.001	0.256
	0.75	0.732	<0.005	0.001	0.55
	0.9	1.382	0.009	−0.002	0.51
	Breusch-Pagan test			0.01	
<i>H. sublaevis</i> (Abe.)	0.1	—	—	—	—
	0.25	−0.001	0.875	0	0.778
	0.5	0.05	0.568	0.001	0.036
	0.75	0.614	<0.005	−0.002	0.25
	0.9	1.023	0.088	−0.004	0.383
	Breusch-Pagan test			0.02	
<i>M. punctiventris</i> (NY)	0.1	−0.002	0.914	0.001	0.096
	0.25	0.121	0.107	0.002	0.081
	0.5	0.336	<0.005	0.001	0.256
	0.75	0.732	<0.005	0.001	0.55
	0.9	1.382	0.009	−0.002	0.51
	Breusch-Pagan test			<0.005	
<i>P. americanus</i> (NY)	0.1	—	—	—	—
	0.25	−0.003	<0.005	0	0.068
	0.5	0.001	0.985	0.002	<0.005
	0.75	0.177	0.014	0.001	0.293
	0.9	0.454	<0.005	−0.002	0.669
	Breusch-Pagan test			0.1	
<i>P. americanus</i> (WV)	0.1	—	—	—	—
	0.25	0.024	0.459	0	0.598
	0.5	0.233	0.038	−0.002	0.071
	0.75	0.539	0.001	−0.004	0.031
	0.9	0.956	0	−0.008	0.032
	Breusch-Pagan test			0.02	
<i>T. nylanderi</i> (So.W.)	0.1	−0.001	0.913	0.001	0.005

Table 3 (continued)

Species and location	Quantile	Intercept	<i>P</i> value	Slope	<i>P</i> value
<i>T. longispinosus</i> (NY)	0.25	0.077	0	0.001	0.008
	0.5	0.221	<0.005	0	0.672
	0.75	0.472	<0.005	−0.001	0.014
	0.9	0.806	<0.005	−0.002	<0.005
	Breusch-Pagan test			<0.005	
	0.1	−0.009	0.586	0.003	<0.005
	0.25	0.197	<0.005	0.001	0.279
	0.5	0.402	<0.005	−0.001	0.144
	0.75	0.672	<0.005	−0.004	<0.005
	0.9	0.894	<0.005	−0.003	0.21
<i>T. longispinosus</i> (WV)	Breusch-Pagan test			<0.005	
	0.1	0.086	0.042	0.004	0
	0.25	0.363	<0.005	−0.002	0.404
	0.5	0.692	<0.005	−0.008	<0.005
	0.75	1.063	<0.005	−0.013	<0.005
	0.9	1.492	<0.005	−0.018	<0.005
	Breusch-Pagan test			<0.005	
	0.1	0.047	<0.005	0	0.634
	0.25	0.132	<0.005	0	<0.005
	0.5	0.236	<0.005	0	<0.005
<i>T. nylanderi</i> (So.S.)	0.75	0.368	<0.005	−0.001	0.014
	0.9	0.582	<0.005	−0.001	<0.005
	Breusch-Pagan test			<0.005	

negative slope. Interestingly, the two *P. americanus* populations showed opposite trends (Table 3, Fig. 2). For the NY population, the median quantile (0.5) estimate showed increasing per-capita productivity, while for the WV population a decrease in per-capita productivity was found. *L. acervorum*, *H. sublaevis*, *M. punctiventris*, and one of the *T. nylanderi* populations (So. W) showed slightly positive per-capita productivity in the median (0.5) quantile (Table 3). Decreasing per-capita productivity was found for *T. nylanderi* (So. S), *T. longispinosus* (both populations), *P. americanus* (WV), and *L. muscorum* (Table 3, Fig. 2).

A possible solution: the effect of polydomy on productivity

T. longispinosus colonies from the NY dataset inhabiting acorns showed a significant relation between colony size and the diameter of the acorn housing those colonies. The slope of the linear regression (intercept=14.55, $P<0.001$; slope=0.03, $P=0.006$; $R^2=0.04$; $F=7.77$; $df=145$) is close to 0, pointing to a weak relationship between colony size and acorn diameter (Fig. 3), in spite of the significant correlation. Because volume increases as the cube of the diameter of the

acorns, we would expect a cubic relationship between diameter and colony size, if cavity volume were the main factor limiting colony size.

The association of per-capita productivity and colony size differed between merged vs. unmerged colonies, as indicated by the significant interaction term (colony size \times merged/unmerged colonies). The OTM method (ANCOVA: $F_{1,110}=6.450$, $P=0.012$) led to different slopes for both groups (merged/unmerged), meaning that the decline in productivity with colony size was attenuated in polydomous colonies. This interaction was not significant for the AR approach (ANCOVA: $F_{1,110}=1.853$, $P=0.176$; Fig. 4).

Discussion

A decrease in per-capita productivity with colony size is prevalent in ant societies (Brian 1953, 1956; Cole 1984; Porter and Tschinkel 1985; Tschinkel 1993, 1999; Hee et al. 2000; Cassill 2002; Franks et al. 2006) (see Table 4 in the Appendix). The suggested mechanism behind this decline is that the increasing number of foragers leads to a depletion of resources and consequently to logistic population growth

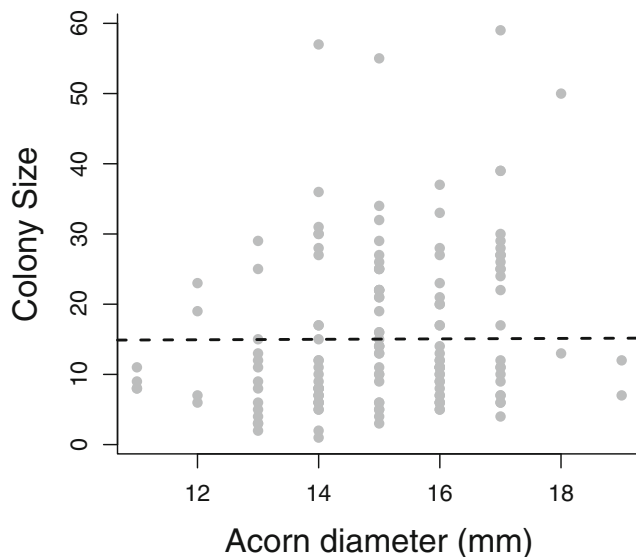


Fig. 3 Relationship between colony size and acorn diameter. The dashed line indicates the result of the linear model (intercept=14.55, $P<0.001$; slope=0.03, $P=0.006$; $R^2=0.04$; $F=7.77$; $df=145$)

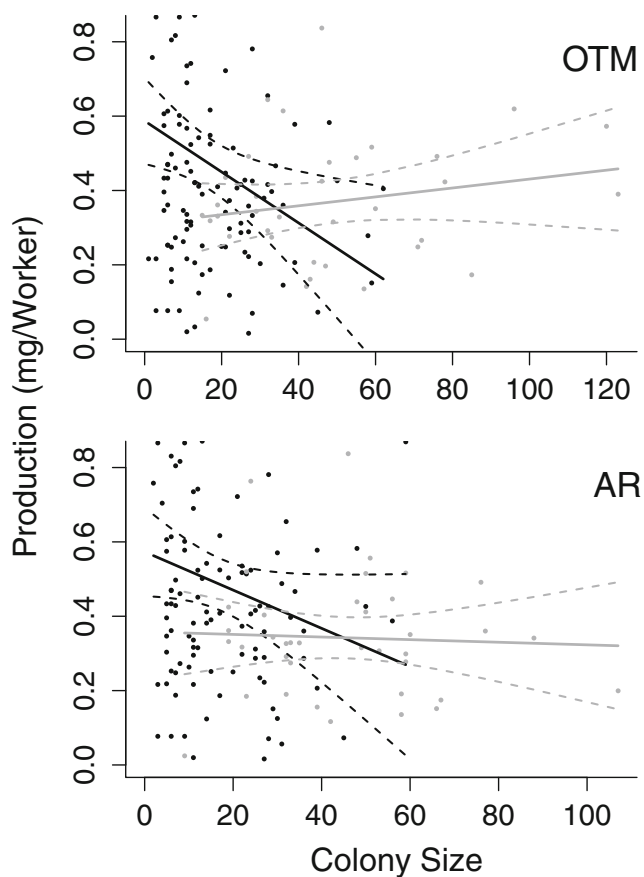


Fig. 4 Per-capita productivity (in milligrams per worker) of *T. longispinosus* colonies in relation to colony size for the different merging strategies (OTM: one queenright nest and several queenless nests, AR: all related colonies). Single colonies are shown in black and merged colonies in gray. Solid line linear regression, broken line 95 % confidence intervals

(Naug and Wenzel 2006). Our *Temnothorax* and related genera case studies demonstrated that this decrease in per-capita productivity is common even in species with small colonies. We suggest that these ants overcome this problem of a limited foraging area through polydomy. Comparison of per-capita productivity of single and polydomous colonies partially supports this suggestion.

The findings of this study do not support the hypothesis that disturbances prevent species with small colony sizes from reaching optimal per-capita productivity. If disturbances did prevent the cavity-dwelling species from reaching colony sizes at which per-capita productivity is optimal, we would have expected constant or increasing patterns of per-capita productivity. However, log-linear models revealed that none of our study species showed increasing per-capita productivity, and only one of our focal species (*T. crassispinus*) showed a constant pattern of per-capita productivity. For two species, *P. americanus* (both populations) and *T. nylanderii* (So. W. population), the confidence intervals of the log-linear model included constant per-capita productivity. It is therefore possible that the constant patterns result from the small colony size of these species, as shown for *Pheidole* ants (Kaspari and Byrne 1995) and *Temnothorax allardyei* (Cole 1984). Colonies of these ants may never reach sizes at which the local resources are overexploited (Cole 1984; Kaspari and Byrne 1995). It remains unclear, however, why *T. crassispinus* showed a constant pattern, whereas the closely related sister species *T. nylanderii* did not.

For none of the focal cavity-dwelling species, a peak in productivity occurred which could point to an optimal colony size with respect to productivity (Brian 1953; Porter and Tschinkel 1985; Tschinkel 1999). Instead, the study species reached the highest levels of productivity at very small colony sizes. Sexual reproduction occurred at all colony sizes, starting in nests with less than ten workers for all datasets, and more productive colonies had a higher chance of producing sexuals.

Larger colonies may be labor-saturated and retain a larger reserve work force, indicated by increasing numbers of inactive workers (Robinson 1992; Dornhaus et al. 2009; Waters et al. 2010). However, it remains unclear whether the reserve work force is a response to the decrease in per-capita productivity caused by decreasing foraging returns or whether the productivity decline is caused by the increase in the number of inactive workers. We suggest that if additional workers add negligible productivity to the colony due to resource limitation, it may be beneficial for the colony to keep these workers inside the protected colony. These reserve workers represent redundancy and ensure the system reliability of the colony by allowing it to replace missing workers without losing any

function essential to the colony (Oster and Wilson 1978; Porter and Tschinkel 1985).

As the colony grows, the increasing forager density leads to longer individual foraging trips as resources become depleted (Jorgensen and Porter 1982; Jun et al. 2003) and, hence, to a reduction in individual foraging returns. Indeed, a theoretical approach using foraging economics demonstrated that, under certain conditions, additional workers do not result in a further increase in productivity (Naug and Wenzel 2006) because density-dependent effects lead to logistic population growth and may place an ultimate limit on colony productivity (Michener 1964; Oster and Wilson 1978; Sudd and Franks 1987).

The individual foraging mode without recruitment, as displayed by our focal species, limits the foraging range, the number of foragers needed to efficiently exploit resources, and the possibility of retrieving distant food items, leading to a density-dependent reduction of foraging returns. The optimal number of foragers should thus be smaller compared to species with more complex foraging strategies (Beckers et al. 1989). A switch in foraging strategy, or the ability to overcome larger prey items by means of increasing numbers of foragers, as shown for social spiders (Pasquet and Krafft 1992; Yip et al. 2008), might circumvent the resource limitation and attenuate the decrease in per-capita productivity.

For species that have not evolved effective recruitment mechanisms, an alternative solution by which to circumvent the decrease in per-capita productivity may be to expand the colony's foraging range by splitting into several nests in order to reduce both travel time and worker density. Our analysis of the effect of polydomy on per-capita productivity indicated that a polydomous *T. longispinosus* colony with a certain number of workers may be more productive compared to a monodomous colony with the same number of workers. We therefore suggest that an increase in per-capita productivity, achieved by the splitting of the colony, could be selected for. We note that sample sizes, especially for the merged colonies, were low (35 and 38 colonies) and regression lines had large confidence intervals (Fig. 4).

Selection on ant colony size may be driven by colony homeostasis and predictability of production because ecological conditions (e.g., disturbances, predators) do not moderate the productivity of large colonies as strongly as in smaller colonies (Naug and Wenzel 2006; Tindo et al. 2008). The quantile regression approach suggests a trade-off between colony homeostasis and per-capita productivity (Fig. 2). The lesser productivity variance at larger colony sizes points to a smaller deviation from the expected amount of food collected or to increased foraging success predictability for the colony and potentially selects for larger colony sizes

(Wenzel and Pickering 1991; Kaspari and Byrne 1995; Stevens et al. 2007).

In addition to improving colony homeostasis, increased colony size improves colony survival and thus potential future reproduction (Cole 1984; Kaspari and Vargo 1995; Bourke 1999; Hou et al. 2010). Since larger colony sizes may have increased survival (Wilson 1974; Cole 1984), increased colony size may improve the colony's lifetime reproductive success even if it leads to a decrease of per-capita productivity.

Ultimately, the small colony sizes of the cavity-dwelling ants in this study may be explained by nest-site limitation and frequent nest relocations. One strategy to overcome nest-site limitation is that of polydomy, a trait displayed by four of our study species (Table 1). Selection for polydomy would serve two functions: to reduce the dependency on large naturally occurring nesting sites and to improve resource availability which might otherwise have been achieved by evolving more complex foraging modes. Seasonal polydomy could be a strategy to increase colony efficiency and decrease the chance of being parasitized in summer, as larger colonies are more prone to an attack by slavemaking species (Pohl and Foitzik 2011), while increased colony size in winter could improve survival (Kaspari and Vargo 1995).

In conclusion, all our focal ant species show either declining or constant colony-size-related changes in per-capita productivity. In contrast to predictions of earlier hypotheses, we demonstrate that even for species that form small-sized colonies per-capita productivity may decline. Our study has shown that species-specific colony size is not predicted by optimal per-capita productivity. Rather, we suggest that several other parameters influence the evolution of colony size in opposite directions. Ecological (nest-site) limitations and social limitations (e.g., foraging mode; Beckers et al. 1989), which lead to declining per-capita productivity, may limit colony size, whereas colony homeostasis and increased survival probabilities of larger colonies should promote the evolution of larger colonies. Polydomy, leading to an extension of the foraging area, may be a common mechanism to overcome the decrease in per-capita productivity that accompanies increase in colony size.

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Conflict of interest The authors declare no conflict of interest.

Appendix

Table 4 Per-capita productivity in ants

Species	Study colony size	Decline at size	Productivity measure	Response to colony size	Reference
<i>Formica neorufibarbis</i>	100–21,000	–	p	Constant	Billick (2001)
<i>Harpagoxenus sublaevis</i>	1–250	–	o	Decrease	This study
<i>Leptothorax allardycei</i>	1–100	–	ee	Constant	Cole (1984)
<i>Leptothorax acervorum</i>	1–220	–	bio	Decrease	This study
<i>Leptothorax muscorum</i>	1–140	–	bio	Decrease	This study
<i>Temnothorax crassispinus</i>	1–210	–	bio	Constant	This study
<i>Temnothorax curvispinosus</i>	1–120	1	e+1	Decrease	Wilson (1974); Cole (1984)
<i>Temnothorax longispinosus</i>	1–90	–	bio	Decrease	This study
<i>Temnothorax nylanderi</i>	1–330	–	bio	Constant/ decrease ^a	This study
<i>Linepithema humile</i>	10–1,000	100	b	Decrease	Hee et al. (2000)
<i>Linepithema humile</i>	1000–11,000	–	b	Constant	Hee et al. (2000)
<i>Myrmica punctiventris</i>	1–50	–	bio	Decrease	This study
<i>Myrmica rubra</i>	5–320	10	brc	Decrease	Brian (1953, 1956)
<i>Pheidole</i>	1–250	–	p	Constant	Kaspari and Byrne (1995)
<i>Pogonomyrmex badius</i>	100–10,000	60	ee	Decrease	Tschinkel (1999)
<i>Protomognathus americanus</i>	1–120	–	bio	Constant/decrease	This study
<i>Solenopsis invicta</i>	100–300,000	100, 0.75 g	ee, sl, sp, o, bio	Decrease	Porter and Tschinkel (1985); Tschinkel (1993); Cassill (2002)
<i>Temnothorax albipennis</i>	400	–	b	Decrease	Franks et al. (2006)

ee ergonomic efficiency (brood/worker), *sl* number of larvae (sexual), *sp* number of pupae (sexuals), *b* number of brood items, *sp* sexual production, *p* number of pupae, *bio* biomass, *o* number of offspring, *brc* brood rearing capability, *e* number of eggs, *l* number of larvae

^a Findings from different populations

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