

Non-Asymptotic Trends in the Social Facilitated Survival of Termites (Isoptera)

by

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ABSTRACT

Survival of grouped termites is known to be socially facilitated, since individual times to death correlate positively with the number of termites confined per unit volume (= group density). Intuitively, this should attain an asymptote, but here we report on experimental evidence that survival as a function of group density in confined *Cornitermes cumulans* (Kollar) termites does not increase asymptotically. Rather, it peaks at a density range at which individual survival is maximal. Interestingly, this same pattern was noted more than fifty years ago for some social insects, but it was regarded as “aberrant” due to the intuitive notion that individual survival should increase asymptotically with the number of individuals in the group. We also provide evidence that individual activity –measured as mobility– is maximal at approximately the same group density range as the observed survival. We argue that a biological link exists between survival and individual mobility of termites confined in groups.

Keywords: optimal density, group size, self-organized survival

INTRODUCTION

Grassé and Chauvin (1944) reported a number of experiments to check the effects of group size on the survival of *Apis* sp., *Polistes* sp, *Leptotrax* sp., *Formica* sp. (Insecta: Hymenoptera) and *Reticulitermes* sp.(Insecta: Isoptera). In all of them, but in *Polistes*, survival increased with increasing group size. In *Polistes*, survival in both large and small groups was smaller than in the middle sized ones. The authors regarded this last result as “aberrant” and attributed it to bad experimental procedures or to a very particular physiological trait of the species. The experiment was hence repeated several times –even by independent observers– but the “aberrant” result was always found. On a survey experiment performed in the summer of 1994, we tested grouped individuals of *Syntermes* sp., *Nasutitermes* sp., and *Cornitermes* sp.

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(Insecta, Isoptera). Preliminary results showed the same nonasymptotical trend on the survival of grouped *Cornitermes cumulans* (Kollar).

Such a convergence of results led us to suspect that Grassé & Chauvin (1944) had spotted a biologically sound pattern, rather than an idiosyncratic result. We based our suspicion on previous experimental works which show that (i) individual survivorship of termites, while affected by group density, may be related to individual mobility of group components (Miramontes and DeSouza, 1996), and (ii) survival of individual termites seems to obey a hump-shaped curve, clearly dependent on some (yet) unknown attribute of the number of individuals confined per unit volume (= "group density") (DeSouza *et al.* 2001). In addition, there is theoretical evidence that cooperation could either stabilize or destabilize the dynamics of a social group, leading to maximal individual fitness at intermediate colony sizes (Avilés 1999).

This paper aims to present experimental evidence linking individual mobility, survivorship, and group density (=number of individuals per volume) for *C. cumulans* termites. To achieve this we show that both individual mobility and survival are humped functions peaking at similar group-density range. We argue, on experimental and theoretical grounds, that survival of starving grouped termite workers –at least in *C. cumulans*– obeys a humped-shape curve which present a biologically sound relationship to individual mobility.

MATERIAL & METHODS

To confirm the trend observed in survey experiments, two further experiments were performed in 1996 and 1997 with grouped termites of this species collected from wild colonies in Viçosa in the state of Minas Gerais, Southeastern Brazil. The first experiment, spanning several days, was designed to measure survival while the second was intended to measure individual activity. Both experiments involved termite workers from third instar and beyond.

In the survival experiment, termites collected from a wild colony were placed in groups of 1, 2, 4, 8, 12, 16, 20, and 24 (each group replicated eight times). Collection took place on 04 April 1996. The groups were confined in test tubes made of transparent glass (9.5 cm long \times 1.4 cm diameter) with hermetically sealing rubber caps. Diameter of these test tubes resembles closely the dimension of tunnels built by field colonies of *C. cumulans* in this region. Densities (=number of individuals per volume) provided by experimental groups are, therefore, in accordance with the natural range of uncrowding-crowding situations faced by such termites.

Each test tube is a 'replicate'. Test tubes have been previously washed and rinsed, soaked in sodium **hypochlorin** for 24h, rinsed again, and sterilized **at high temperature for** one hour. Tubes with termites were kept horizontally, separated by plastic foam to prevent stridulation or other mechanically transmitted signals to propagate between the tubes. The workers were incubated in the dark at a constant temperature chamber ($25^{\circ}\text{C} \pm 0.5$) and were allowed to acclimatize for 12h. No food or water was provided, but tubes were opened each 24h, to allow air exchange. Tubes were exposed to light during the counting of survivors only (no more than 5 min). Observations were made each eight hours intervals, until all individuals were dead (153h; 20 observations). Termite groups in which dead individuals presented any sign of cannibalism were excluded from data analysis.

In the activity experiment, termites collected from another wild colony were placed in groups of 2, 4, 6, 8, 16, 20, and 30 individuals (each group replicated four times). Collection took place on 12 October 1997. The experiment was setup as above, using a controlled temperature room ($24^{\circ}\text{C} \pm 0.5$) rather than a chamber. Termites were allowed to acclimatize in such a room, for three hours before the observations began. Two observers took notes of the number of termites moving in each group, at five minute intervals, during ten continuous hours. Each observer managed two replicates of the experiment (two tubes of each group density). Light intensity in the room was the lowest possible to allow the work of the observers.

Statistical analyses aimed to check whether group density (= number of individuals per volume) would affect (i) survival and (ii) mobility of termites. Either quantities were treated as the y -variable in separate regression analyses, always with group density as the x -variable. Prior to regression analyses, each y -variable was estimated as follows. Survival was estimated as the average number of hours spent until individual termites die in a given group, which was calculated for each replicate (a given test tube containing termites), using Weibull frequency distribution (Crawley 1993). Each of the means thereby calculated represent the number of hours spent to die averaged across all individuals belonging to a given replicate, and are referred to as "mean time to death". Mean times to death for each replicate were then collapsed into a single arithmetic mean for each group density, a valid procedure to avoid pseudoreplication effects (Crawley 1993). Such a procedure produces eight means (each one represented by a dot in Fig. 1), one for each group density. This set of eight means was then used to check whether termite survival (y -var) would be affected by group

density (x-var). To do so, models were fitted to the data, starting from a null model ($y=b$, where b is the grand mean), and adding new terms until achieving the best trade-off between percent of variance explained (r^2), and P -values obtained (Table 1)

Mobility of termites in a given replicate (a test tube containing termites) was estimated by fitting a simple regression line of the form $y=b+ax$, through the data points formed by plotting the number of moving termites (y-var) against time in minutes (x-var). The slope a of each line was used as an estimate of the general pattern of mobility for termites belonging to that replicate. If the number of moving termites increases as times goes by, the curve fitted to the data would show a positive slope. Conversely, a negative slope would indicate a decay in group mobility. When no clear trend is to be observed for a given replicate, its "mobility curve" would show a null slope. For each group density we obtained four slopes, since there were four replicates (i.e., four test tubes containing termites). The slope values thereby obtained were collapsed into a single arithmetic mean for each group density aiming, as above, to avoid pseudoreplication effects. Such a procedure produces seven means (each one represented by a dot in Fig.2), one for each group density. Such means are referred to as the "general pattern of mobility" for that group density.

Means thereby produced were used to check whether the general pattern of mobility (slope a of mobility lines, see above) would depend on the density of the group where termites have been confined. Models were fitted and selected as above (Table 2).

All statistical analyses were performed using R (Ihaka and Gentleman 1996).

RESULTS

Only four out of the 64 replicates presented signs of cannibalism: one replicate of group 12, one replicate of group 16, and two of group 20. These replicates were excluded from any analyses reported below.

The mean time to death of starved termites obeyed a humped function of group density, presenting a peak at a characteristic group density and decreasing at both smaller and larger densities (Polynomial model, order four: $F[4;3] = 20.22$; $r^2_{adj} = 0.916$; $P = 0.02$; Fig. 1; Table 1) Accordingly, group activity presented a similar dependency on group density, showing a peak at an intermediate density and decreasing at both smaller and larger values (Quadratic model: $F[2;4] = 9.095$; $r^2_{adj} = 0.730$; $P = 0.03$; Fig. 2; Table 2). This quadratic model explained the data better than the simple linear one: adding a quadratic term to the linear model, increased the percentage of variance explained by 18.7%

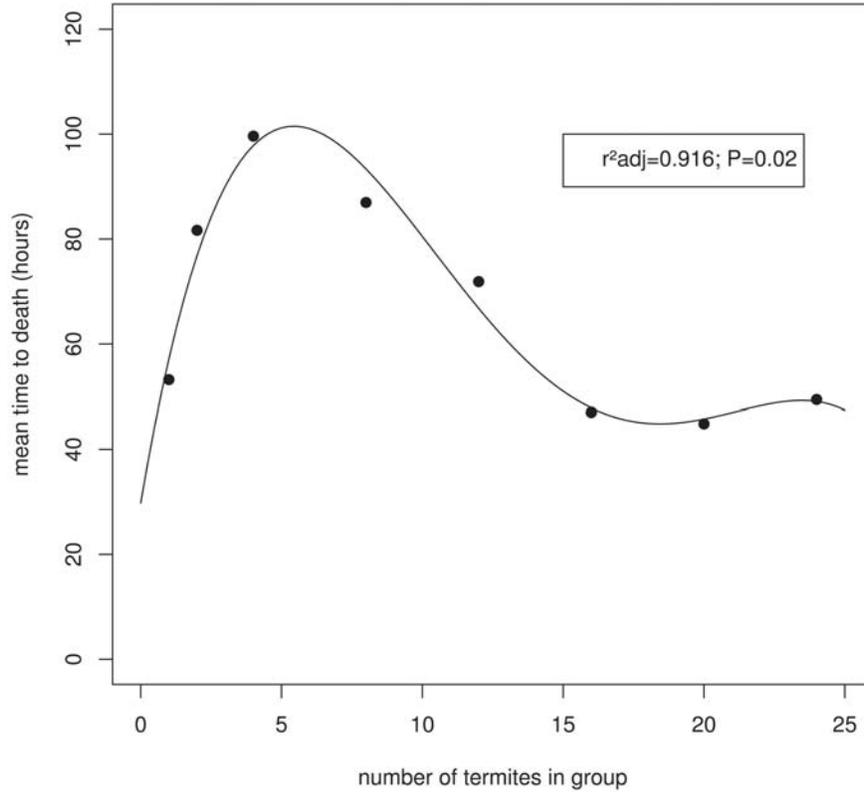


Fig. 1. Average number of hours termite workers spent to die when confined with conspecifics in test tubes, in the absence of food. Each dot represents an arithmetic mean across eight replicates (eight different test tubes). Average number of hours for each replicate was calculated by censored survival analysis, with Weibull distribution.

Table 1. Models explaining the effect of group density (x-var) on the mean time to death (y-var) of starved termites confined in test tubes. Models provided here are intended to be illustrative of the general shape of the curves described by the data, rather than a statement on its specific position when plotted. Models were calculated on the datapoints of Fig.1. Polynomial model of order 5 is not significant.

Model	r ² adj	P
y=68.829	0.00	1.00
y=88.8355-15638x	0.31	0.09
y=75.8990+0.8722x-0.1016x ²	0.26	0.20
y=47.94922+1677077x-1.74097x ² +0.04376x ³	0.80	0.02
y=29.783398+31.56777x-4.431666x ² +0.211764x ³ -0.003355x ⁴	0.92	0.02

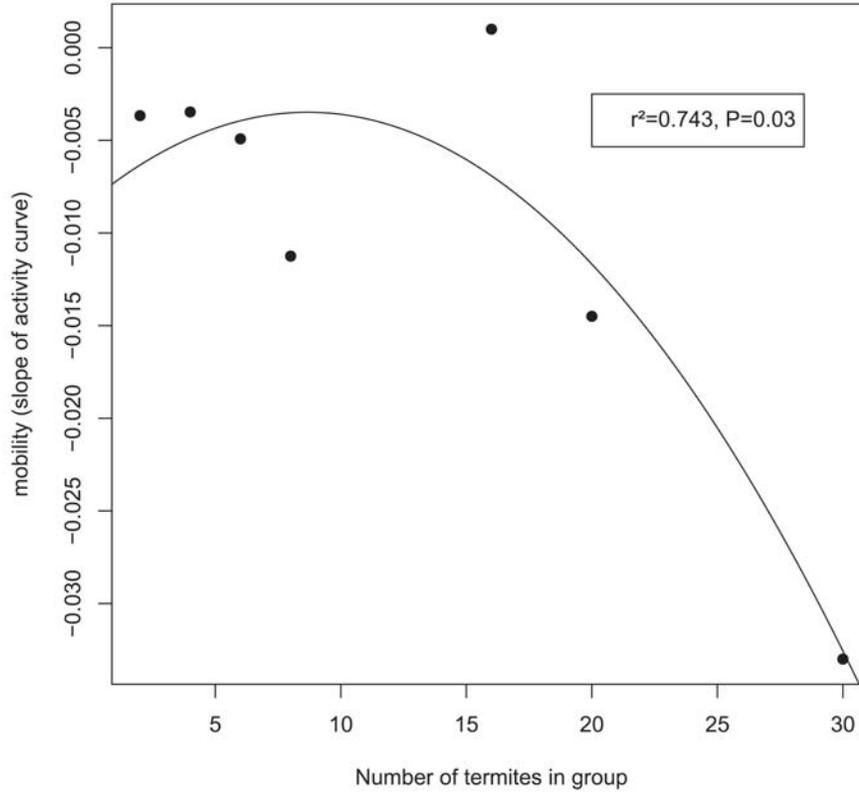


Fig. 2. General pattern of mobility of termites confined with conspecifics in test tubes, in the absence of food. Mobility patterns are characterized here using the slope of a line fitted across a scatterplot of the number of moving termites (y-var) versus time (x-var), four each of the group densities tested. Positive slopes denote that the number of moving termites increases with time, negative slopes denote the opposite. Null slopes denote a constant number of moving termites across the time range when observations were done. Each dot represents the average of the slopes presented by each of four replicates (four different test tubes)

Table 2. Models explaining the effect of group density (x-var) on the mobility (y-var) of starved termites confined in test tubes. Models provided here are intended to be illustrative of the general shape of the curves described by the data, rather than a statement on its specific position when plotted. Models were calculated on datapoints of Fig.2. Polynomial model of order 3 is not significant.

Model	r^2 adj	P
$y = -0.009973$	-	1.00
$y = 0.0008778 - 0.0008832x$	0.54	0.04
$y = -0.008299 + 0.00111x - 0.00006396x^2$	0.73	0.03

and improved the P -value (Table 2).

Such results showed consistency across different procedures of data analysis. As specified above, each dot in Figs.1 and 2 represents an arithmetic mean taken across the respective replicates. If, however, we plot the raw data (i.e., splitting the arithmetic means into their components), we observe the same general shape in both curves (Figs.3 and 4).

DISCUSSION

Across the Isoptera, a range of different socially facilitated behaviors has been extensively reported, although survival is the one that has

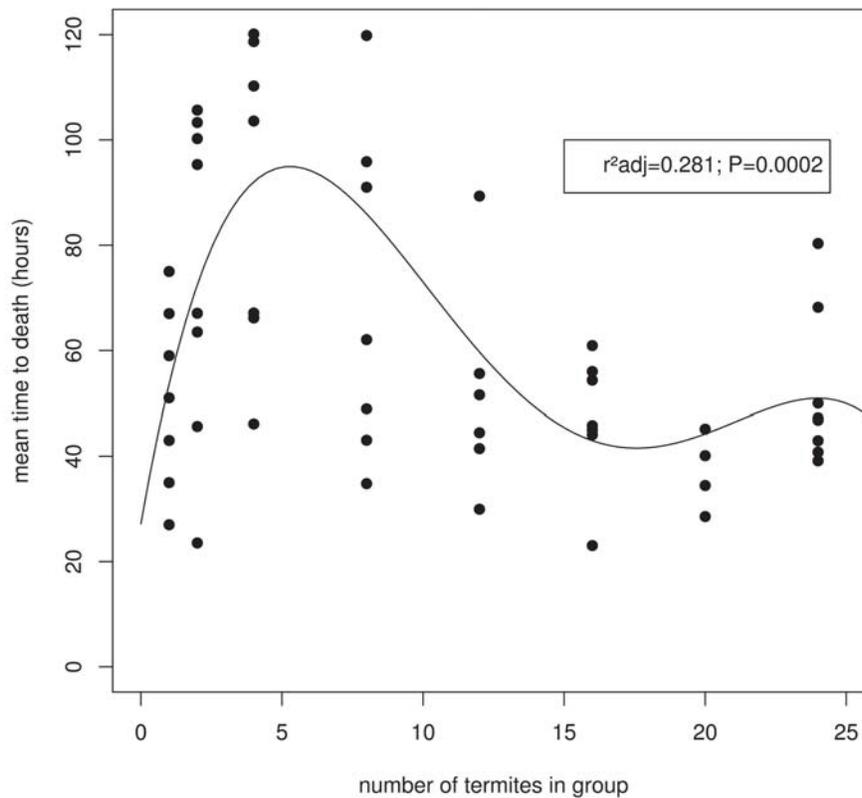


Fig. 3. Average number of hours termite workers spent to die when confined with conspecifics in test tubes, in the absence of food. Each dot represents the average number of hours termites survived in a single replicate (a test tube), as estimated by censored survival analysis, with Weibull distribution. Within each group density, datapoints of this figure were collapsed into a single arithmetic mean in order to produce Fig.1.

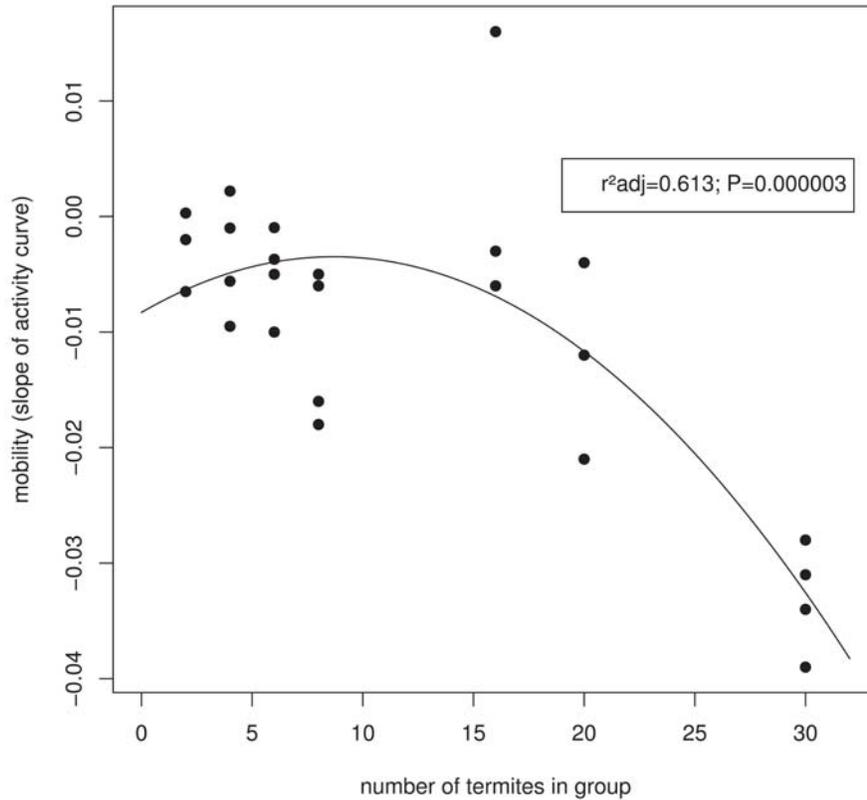


Fig. 4. General pattern of mobility of termites confined with conspecifics in test tubes, in the absence of food. Mobility patterns are characterized here using the slope of a line fitted across a scatterplot of the number of moving termites (y-var) versus time (x-var), four each of the group densities tested. Each dot represents the slope presented by a single of four replicates (four different test tubes). Within each group density, datapoints of this figure were collapsed into a single arithmetic mean in order to produce Fig.2.

attracted more attention (Table 3). In all such studies, survival has been reported to increase as group density increases. This may lead one to intuitively assume an asymptotic behavior of such a curve, accepting that very large groups would attain the maximal possible survival rates. In this sense, the results reported by Grassé & Chauvin (1944) in which survival of wasps is maximal at moderate densities (rather than at large group densities), could be considered “aberrant”. However, a striking similarity can be observed between such results and those found here for *C. cumulans* termites (Fig. 1). More puzzling, termites from different wild colonies of the same species show a similar humped function, even

Table 3. Some different behavioral traits that are known to be socially facilitated across the Isoptera

Genus	Trait	Reference
<i>Bellicositermes</i>	Ovarium development	Grassé(1939)
<i>Bifiditermes</i>	Food exchange	Afzal(1983)
<i>Cephalotermes</i>	Ovarium development	Grassé(1939)
<i>Coptotermes</i>	Survival and feeding	Lenz & Williams(1980)
<i>Cornitermes</i>	Tolerance to poisoning	DeSouza <i>et al.</i> (2001)
<i>Cryptotermes</i>	Survival	Williams <i>et al.</i> (1982)
<i>Kalotermes</i>	Nest digging	Springhetti(1990)
<i>Macrotermes</i>	Caste differentiation	Okot-Kotber(1983)
<i>Nasutitermes</i>	Survival and feeding	Lenz and Williams(1980)
	Survival under starvation	Miramontes&DeSouza(1996)
<i>Reticulitermes</i>	Survival	Grassé & Chauvin(1944)
<i>Zootermopsis</i>	Survival under infection	Rosengaus <i>et al.</i> (1998)

when they have been poisoned by insecticide (DeSouza *et al.* 2001). Such a convergence of results lead us to suspect that this pattern is, in fact, biologically sound. It seems that survival of starving termite workers –at least in *C.cumulans*– is not asymptotically related to group density, but obeys a humped function, in which an optimal density (=number of individuals per volume) assures maximal survival.

Optimal densities in social insects have already been predicted as a consequence of evolutionary pathways maximizing individual fitness (Higashi & Yamamura 1993). Proximate mechanisms through which optimal densities would lead to better survival, however, are still poorly understood. Many works dealing with cluster size in group organisms are based on optimality arguments regarding, for instance, resource usage, anti-predatory behavior and disease resistance (Fritz & Garine-Wichatitsky 1996; Giraldeau and Beauchamp 1999; Roberts 1996; Rosengaus *et al.* 1998). Others, inspired by concepts of the sciences of complex systems, would invoke a relationship between group-density, information fluxes and task performance (e.g. Adler & Gordon 1992; Pacala *et al.* 1996). The interconnected nature of such systems is thought to be the basis for the self-organization of a variety of cluster-related phenomena (Bonabeau *et al.* 1997; Miramontes *et al.* 1993). Specifically for termites, evidences seem to point out that survival is related to mobility (Miramontes & DeSouza 1996). In addition, studies addressing interindividual interactions and self-organization predict the existence of group-density effects causing information transfer and behavioral diversity to reach near optimal conditions (Miramontes 1995; Miramontes & Solé 1995). Accordingly, termites studied here present maximal values for group activity at intermediate densities (Fig.

2), which lie in the same group-density range as the observed survival (Fig. 1). It seems, therefore, that the association between group-density, non-asymptotic survival and greater individual activity is not fortuitous in *C. cumulans*. Moreover, to the extent that mobility affects the rate of social contacts—and thereby, cooperation—our results seem to agree with those of Avilés (1999), who show an explicit link between cooperation, individual fitness, and group size in social organisms.

These results point to specific mechanisms present in the dynamics of groups that may act to regulate observables such as density, number of individuals and rate of social contacts, that in turn have an impact on collective task performance. Arguably, behaviors such as colony fission, swarming, cannibalism, or resting, may be the natural mechanisms responsible for the regulation of the proportion of individuals in the colony. In other words, the patterns presented here may have unexpected consequences for understanding the life cycles of these organisms, and therefore are worth exploring further.

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