Unexpected trends in the social facilitated survival of termites

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Running head: Unexpected trends in termite survival

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Abstract

Survival in groups of termites is known to be socially facilitated since individual longevity is increased together with the size of the group. Here we report on experimental evidence that survival as a function of group size in Cornitermes cumulans (Kollar) does not increase asymptotically but it peaks in a group size range at which individual longevity is maximal. Strikingly, this same effect in other social insects was noted more than fifty years ago, but it was regarded as “aberrant” since it has been generally assumed that individual survival should increase with the size of the group. We also provide evidence that individual activity – measured as mobility – is maximal at approximately the same group-size range as the observed survival.
1 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, *Leptotorax* 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* they reported an “aberrant” result in which survival in both large and small groups was smaller than in the middle ones. The authors attributed these observations 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 on the summer 1994, we test grouped individuals of *Syntermes* sp., *Nasutitermes* sp., and *Cornitermes* sp. (Insecta, Isoptera). Preliminary results showed the same unexpected behaviour on the survival of grouped *Cornitermes cumulans* (Kollar).

Such a convergence of results allow us to suspect that Grassé & Chauvin (1944) have in fact unwarrantly spotted a pattern that is biologically sound. We base our suspicion on previous experimental works which show that (i) individual survivorship of termites, while affected by group size, may be related to individual mobility of group components (Miramontes and DeSouza, 1996), and (ii) longevity of individual termites seems to obey a hump-shaped curve, clearly dependent on some (yet) unknown attribute of group size (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 size in termites. To achieve this we show that both individual mobility and survival are humped functions peaking at similar group-size range. We argue, on experimental and theoretical grounds, that survival of starving grouped termite workers –at least in *Coptitermes* sp– obeys a humped-shape curve which present a biologically sound, not fortuitous, relationship to individual mobility.

2 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, South-eastern Brazil. The first experiment, spanning several days, was designed to measure longevity while the second was intended to measure individual activity. Both experiments involved termite workers (third instar and beyond) of different group sizes.

In the longevity experiment, termites from a wild colony were randomly placed in groups of 1, 2, 4, 8, 12, 16, 20, and 24 (each group replicated eight times). Collection took place in 04 April 1996. The groups were confined in test tubes made of transparent glass (9.5 × 1.4cm) with hermetically sealing rubber caps. Each test tube is a ‘replicate’. Test tubes have been previously washed and rinsed, soaked in sodium hypochlorin for 24h, rinsed again, and
sterilised at 180 °C 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 °C ± 0.5) and were allowed to acclimatise 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 from another wild colony were randomly placed in groups of 2, 4, 6, 8, 16, 20, and 30 individuals (each group replicated four times). Collection took place in 12 October 1997. The experiment was setup as above, using a controlled temperature room (24 °C ± 0.5) rather than a chamber. Termites were allowed to acclimatise 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 minutes intervals, during ten continuous hours. Each observer managed two replicates of the experiment (two tubes of each group size). Light intensity in the room was the lowest possible to allow the work of the observers.

Statistical analyses aimed to check whether group size would affect (i) survival and (ii) mobility of termites. Either quantities were treated as the y-variable in separate regression analyses, always with group size as the x-variable. Survival was measured as the average number of hours spent until individual termites die in a given group, which was calculated for each repli-
cate (a given test tube containing termites), using Weibull frequency distribution (Crawley, 1993; Pinder III et al., 1978). Survival functions obey the general form:

$$\ln S(t) = \mu^{-\alpha} t^\alpha$$

(1)

where $S(t)$ is the proportion of individuals from the initial cohort (the initial group of termites) still alive at time $t$, $\alpha$ is the shape parameter, $\mu$ is the mean number of hours until death by the termites from a given replicate. The first step in the survival analysis was to establish the value of the shape parameter $\alpha$, thereby defining whether or not the proportion of individuals dying was constant through time ($\alpha = 1$, $dN/dt = 1/\mu$, exponential fit). To do so, survival curves were tentatively fit to the data, simulating different shape parameters, one at a time, until the error deviance reached an asymptote. The model obtained was then compared with a model assuming $\alpha = 1$ (exponential fit), on the basis of their contribution to the error deviance. Parsimony requires to choose the exponential fit (simplest model) if it does not differ significantly ($P > 0.05$; $\chi^2$ tables; 1 df) from an alternative, more complete, model.

After defining the shape parameter, the next step was to calculate the mean number of hours termites spent to die when confined in each group size ($\mu$ in equation 1 above). Each of such means 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 size, 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 size.

Means thereby produced were used to check whether termite survival (y-var) would be affected by group size (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 (see Table 1).

The general pattern of mobility of termites in a given replicate (a test tube containing termites) was measured 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 a measurement 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 size 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 size 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 size. Such means are refereed to as the “general pattern of mobility” for that group size.

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

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

3 Results

The mean time to death of starved termites obeys a humped function of group size, presenting a peak at a characteristic group size 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 presents a similar dependency on group size, 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 explains the data better than the simple linear one: adding a quadratic term to the linear model, increases by 18.7% the percentage of variance explained and improves the $P$-value (Table 2).

Such results are consistent 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 its components), we observe the same general shape in both curves (Figs. 3 and 4).
4 Discussion

Across the Isoptera, a range of different socially facilitated behaviours has been extensively reported, although survival is the one that has attracted more attention (Table 3). In all survival studies, longevity has been reported to increase as group size increases. This may lead one to intuitively assume an asymptotic behaviour 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 sizes), 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 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 size, but obeys a humped function, in which an optimal density (=number of individuals per unit area) assures maximal survival.

Optimal densities in social insects have already been predicted as a consequence of evolutionary pathways maximising individual fitness (Higashi and Yamamura, 1993). Accordingly, extraordinary lifespan is argued to derive from evolutionary processes in which such insects benefit from sociality (Keller and Genoud, 1977). Proximate mechanisms through which optimal densities would lead to better survival, however, are still poorly understood. Many works deal-
ing with cluster size in group organisms are based on optimality arguments regarding resource usage, territory defence, anti-predatory behaviour and disease resistance (Creel, 1997; Fritz and Garine-Wichatitsky, 1996; Giraldeau and Beauchamp, 1999; Roberts, 1996; Rosengaus et al., 1998). Others, inspired on novel concepts of the sciences of complex systems, would invoke a relationship between group-size, information fluxes and task performance (Adler and Gordon, 1992; Bonabeau et al., 1998; Deneubourg et al., 1986; Gordon, 1996; Pacala et al., 1996). The interconnected nature of such systems is thought to be the basis for the self-organisation of a variety of cluster-related phenomena (Bonabeau et al., 1997; Camazine, 1991; Miramontes et al., 1993; Theraulaz et al., 1995). Specifically for termites, evidences seem to point out that survival is related to mobility (Miramontes and DeSouza, 1996). In addition, studies addressing interindividual interactions and self-organisation predict the existence of group-size effects causing information transfer and behavioural diversity to reach near optimal conditions (Miramontes, 1995; Solé and Miramontes, 1995). Accordingly, termites studied here present maximal values for group activity at intermediate densities (Fig. 2), which lie in the same group-size range as the observed survival (Fig.1). It seems, therefore, that the association between group-size, 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 to those of Avilés (1999), who show an explicit link between cooperation, individual fitness, and group size in social organisms.

These results point out to specific mechanisms present in the dynamics of groups that may act to regulate observables such as density, number of indi-
viduals and rate of social contacts, that in turn have an impact on collective
task performance. Arguably, behaviours 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 under-
standing the life cycles of these organisms, and therefore are worth exploring
further.

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6 Legend to figures

**Figure 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.

**Figure 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 sizes 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).

**Figure 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 calculated by censored survival analysis, with Weibull distribution. Within each group size, datapoints of this figure were collapsed into a single arithmetic mean in order to produce Fig.1.

**Figure 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 sizes tested. Each dot represents the slope presented by a single of four replicates (four different test tubes). Within each group size, datapoints of this figure were collapsed into a single arithmetic mean in order to produce Fig.2.
$r^2_{adj} = 0.916; \ P = 0.02$
Number of termites in group

mobility (slope of activity curve)

$r^2_{\text{adj}} = 0.730; P = 0.03$
$r^2_{adj}=0.281; P=0.0002$
$r^2_{adj} = 0.613; P = 0.000003$
Table 1: Models explaining survival the effect of group size (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    |
|----------------------------------------------------------------------|-------------|------|
| $y = 66.829$                                                         |             | 1.00 |
| $y = 88.8355 - 15638x$                                              | 0.309       | 0.09 |
| $y = 75.8990 + 0.8722x - 0.1016x^2$                                  | 0.262       | 0.20 |
| $y = 47.94922 + 16.77077x - 1.74097x^2 + 0.04376x^3$                  | 0.798       | 0.02 |
| $y = 29.783398 + 31.566777x - 4.431666x^2 + 0.211764x^3 - 0.003355x^4$ | 0.916       | 0.02 |
Table 2: Models explaining survival the effect of group size (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                                      | r²adj | P    |
|--------------------------------------------|-------|------|
| $y = -0.009973$                            | -     | 1.00 |
| $y = 0.0008778 - 0.0008832x$               | 0.543 | 0.04 |
| $y = -8.299 \cdot 10^{-3} + 1.110 \cdot 10^{-3}x - 6.396 \cdot 10^{-5}x^2$ | 0.730 | 0.03 |
Table 3: Some different behavioural traits that are known to be socially facilitated across the Isoptera

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