

**Research article**

## **Latency time and absence of group effect**

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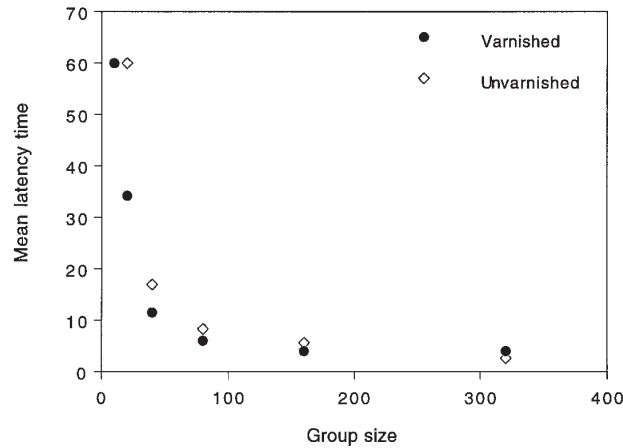
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### **Summary**

We suggest that group effect need not be invoked to explain the differences in latency times exhibited by groups of different sizes in the initiation of building in the termite *Macrotermes subhyalinus* (Rambur). A simple, alternative, model is presented, that is fully consistent with experimental data.

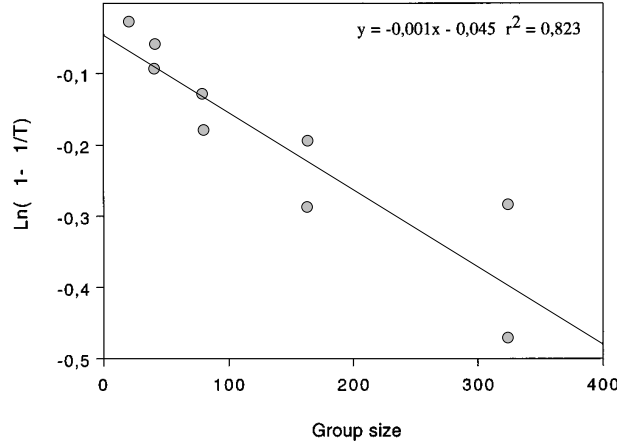
In a remarkable series of laboratory experiments Bruinsma (1979) studied the building behavior of the fungus-growing termite *Macrotermes subhyalinus*, in particular the construction of the royal chamber in the presence of a live physogastric queen. Among his observations is the fact that the time it takes for a group of termites to initiate the building of the royal chamber (which, following Bruinsma, we shall call building “latency time”) is a nonlinearly decreasing function of groups size. Such an observation could be interpreted as resulting from a group effect (Grassé, 1946), or socially facilitated behavior (Clayton, 1978). However, a simple model that does not invoke group effect, fully consistent with the data of Bruinsma (1979), can very satisfactorily account for this observation. The behavior of individual workers during building seems to be made up of relatively few and relatively simple activities: a worker picks up a piece of soil close to or underneath the queen, transports the pellet to a site of deposition (a narrow band around the queen at 2–5 cm from her and determined by a pheromonal template that she emits), where it deposits and cement it. This behavior, combined with an attraction towards sites where pellets have already been deposited, leads to the formation of pillars or columns a few centimeters away from the queen. Pillars are lengthened until they reach a height of between 0.5–0.8 cm; workers then start to build horizontal lamellae that grow from the pillars to form a roof over the queen; finally, the interpillar space is filled with pellets to form walls. The building latency time, that is, more precisely, the time elapsed between the introduction of workers in the arena with



**Figure 1.** Latency time as a function of group size found by Bruinsma (1979; p39) for varnished and unvarnished workers of *Macrotermes subhyalinus*. The value for the 10 workers group and the group of 20 unvarnished workers is at least 60 minutes – at this stage no building had been observed. For each condition (varnished or unvarnished and different value of N), the number of replications is between 3 and 5

the queen and the first observed grasping of a soil pellet within 0.5 cm of the queen, is the focus of the present note. Figure 1 shows the decrease of latency time with group size, for varnished and unvarnished workers. Varnished workers were unable to lay trail. It can be seen in Figure 1 that there is no significant difference between varnished and unvarnished workers with respect to the latency time (whereas subsequent stages of the building process are affected by the inability of varnished workers to lay trail: for example, such workers were unable to start pillars): this indicates that trail is not involved in the determination of the latency time. It could be that increased direct communications among termites when group size (and hence density) increases accelerate the process by stimulating workers to start building. More generally, a group effect, or socially facilitated behavior, could be invoked: individuals may modulate their behavior in response to the presence of other group members through omnipresent signals or cues (by omnipresent signals, we mean signals that do not result from specific events in space or time (Grassé, 1946; Wilson, 1971)). Let us consider the following alternative answer, that relies on the idea that the decrease in latency time is simply a numerical effect: let us assume that each individual has a fixed probability  $p$ , independent of group size ( $N$ ), and uncorrelated to the behavior of other workers, of picking up a pellet per unit time. When  $p$  has not been measured, a relation can, however, be established between the average latency time  $\langle t \rangle$ , this probability  $p$  and the group size.

The probability that no worker among  $N$  workers picks up a pellet within a time unit is then given by  $(1-p)^N$ . The probability  $P(t)$  that the latency time be equal to  $t$  time units is the probability that no worker picked up a pellet during the first  $t-1$  time units and that at least one worker picked up a pellet within the  $t^{\text{th}}$  time unit. Therefore, assuming that the process is not correlated in time (that is, the fact that an individual does or does not pick up a pellet within a given unit of time does



**Figure 2.**  $\log(1-\langle t \rangle^{-1})$  as a function of the number of workers (N), where t is the time it takes before a worker of *Macrotermes subhyalinus* first picks up a pellet. The data are combined for varnished and unvarnished termites

not depend on its previous actions), we obtain  $P(t) = (1-p)^{N(t-1)} [1-(1-p)^N]$ . The average latency time under this hypothesis is given by

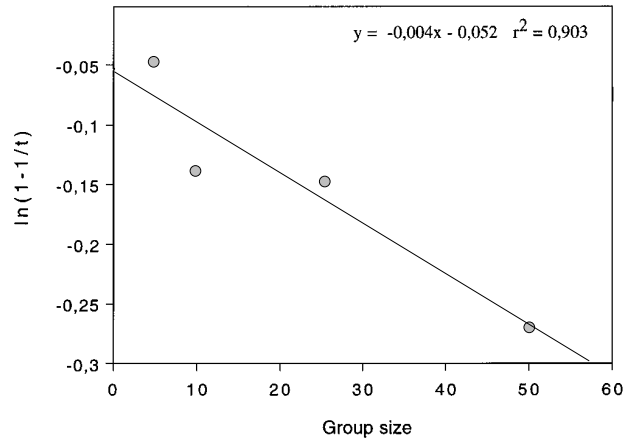
$$\langle t \rangle = \sum_{t=1}^{\infty} tP(t) = [1-(1-p)^N]^{-1}. \tag{1}$$

In order to evaluate the performance of the formula given in equation (1), we can rewrite equation (1) as

$$\log(1-\langle t \rangle^{-1}) = N \log(1-p). \tag{2}$$

A group effect would lead to a dependence of p on N and therefore to a non-linear relationship between  $\log(1-\langle t \rangle^{-1})$  and N. Figure 2 is a good example of linear relationship, suggesting that in this case, there is no significant group effect ( $p = 0.001 \text{ min}^{-1}$ ,  $r = 0.91$ ,  $P < 0.001$ ).

Another example, where the decrease in latency time can be explained as a numerical effect resulting from the increase in group size, can be found in studies of colony defence or aggressiveness in bees. There are many such studies, and we give just a few examples of tests made with various subspecies of *Apis mellifera*. Collins and Rothenbuler (1978) performed laboratory experiments to measure, for different group sizes, the time before the first reaction to a particular chemical, isopentyl acetate, or IPA, the major component of the sting alarm pheromone (Boch et al., 1962). Let N be the number of bees in a cage, and  $\langle t \rangle$  the average time to first reaction. Figure 3 shows  $\log(1-\langle t \rangle^{-1})$  as a function of N: that it can be well fitted by a straight line ( $r = 0.951$ ,  $P < 0.025$ ) suggests that the decrease in  $\langle t \rangle$  when groups size increases is likely to result from a numerical effect, where there is a fixed



**Figure 3.**  $\log(1 - \langle t \rangle^{-1})$  as a function of the number of individuals of *Apis mellifera* guarding the nest entrance, where  $\langle t \rangle$  is the average time (average taken over 75 experiments for all points; error bars not shown) to first reaction to isopentyl acetate (IPA) diluted in paraffin oil (1:10 in volume)

probability  $p$  (given by equation (2)) per individual to respond to the pheromone within a time unit. Here, it appears that  $p = 0.0044 \text{ s}^{-1}$ .

In conclusion, we have presented evidence that the decrease of building latency time in *Macrotermes subhyalinus* and of time of first reaction to a perturbation in *Apis mellifera* can be explained by a simple numerical effect. This result is interesting in that it indicates that a *strongly nonlinear* dependence of some feature (here the building latency time or the time of first sting) on group size may not result from a group effect, involving communication among group members or more generally a modulation of behavior in response to the presence of other group members, but can simply reflect a numerical effect. Although the possibility of group effects or socially facilitated behavior cannot be rejected in many cases, we believe that some other cases where group effects have been invoked, especially to explain the decrease of the time before a first event occurs as a function of group size (latency time), could be reevaluated along the same lines.

Such reevaluations are not limited to the time before the first event. Numerous situations where group effects seem present are described in the literature. The survival of colonies founded by groups of individuals (e.g., pleometrosis in ants, Hölldobler and Wilson, 1990; social spiders, Vollrath, 1982) is a classical example where correlation between survival of the group and its size is well known. Although in most cases, the group effects exist (increase of the individual survival if the group's size increases), numerical effects are also involved. Models similar to (1) are not only useful tools to estimate the contribution of the group effect to this survival but they can also help us to reexamine numerous group effects described in the literature.

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