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Research article

Social facilitation affecting tolerance to poisoning in termites (Insecta, Isoptera)

O. DeSouza[1], O. Miramontes[2], C.A. Santos[1] and D.L. Bernardo[1]

[1] *Departamento de Biologia Animal, Universidade Federal de Viçosa, 36571-000 Viçosa MG, Brazil, e-mail: og.souza@mail.ufv.br*
[2] *Departamento de Sistemas Complejos, Instituto de Física, Universidad Nacional Autónoma de México, Apdo. Postal 20-364, México 01000 DF, México, e-mail: octavio@fenix.ifisicacu.unam.mx*

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Summary. Previous works have shown that social interactions may enhance termite ability to overcome physiological stresses such as starvation and disease. We evaluated the effects of group size on termite tolerance to poisoning, by submitting groups of *Cornitermes cumulans* workers to an organophosphorus insecticide (chlorpyrifos). Survival of both, poisoned and non-poisoned termites, depended on the number of individuals in the group, presenting a peak at an density around 8 individuals/test tube. Survival of poisoned termites, however, showed a peak much lower than that of non- poisoned termites. We conclude, therefore, that socially induced ability to overcome physiological stresses in termites may be expressed even under "non-natural" stresses, such as poisoning by insecticides. The mechanisms leading to such a result remain to be investigated. It seems, however, that social facilitation may enhance (or trigger) biochemical and/or neurophysiological mechanisms that collaterally may help in the detoxification of insecticides in termites. In addition, we warn that laboratory experiments with termites/insecticides may be severely affected by the group size being tested.

Key words: Termites, social facilitation, physiological stress, insecticide, group effects.

Introduction

Interindividual contact is known to modify behaviours in both social and nonsocial animals. Examples range from humans who consume more food when in groups than when alone (DeCastro, 1995), to non-crossbreeding hermaphrodite snails whose reproductive output is larger when in groups than when isolated (Vernon, 1995). Such a phenomenon has been refereed to as "social facilitation", and can be shortly defined as the ordinary patterns of behaviour that are initiated or increased in pace or frequency by the presence or actions of other animals (Zajonc, 1965; Wilson, 1980; DeCastro, 1995).

Social facilitation is a common phenomenon among termites (e.g. Grassé and Chauvin, 1944; Springhetti, 1990). Social interactions affect survival in such insects (e.g. Mishra and Singh, 1978; Lenz and Williams, 1980), but many authors explicitly or implicitly regard survivorship as a consequence of enhanced food intake, rather than directly emerging from social facilitation (see Miramontes and DeSouza, 1996 and references therein). Collins (1969: p. 453), while commenting on the positive effect of group size on the tolerance of termites to dry conditions, states that "Grassé and Chauvin have suggested that sensory stimuli are of importance, while other investigators have emphasized trophallactic exchange". Recent studies suggest that social facilitation affect survival through mechanisms other than enhanced food intake. Resistance to starvation in *Nasutitermes* cf. *aquilinus* (Holmgren) (Isoptera, Termitidae), for instance, is greatly improved by social contact: starving workers survived longer in groups than when kept isolated (Miramontes and DeSouza, 1996). Accordingly, resistance to fungal infections in *Zootermopsis angusticollis* (Hagen) (Isoptera, Termopsidae), was shown to increase with group size (Rosengaus et al., 1998).

If, in fact, social interactions are so effective in minimizing deleterious actions of strong stresses such as starvation and disease, one could hypothesize that they would also impact survivorship of termites imposed to insecticides. This work tests such a hypothesis, comparing the survivorship of poisoned and non-poisoned termites which have been confined in groups of different sizes.

Materials and methods

The experiment was performed using workers (third instar and beyond) collected from five field colonies of *Cornitermes cumulans* (Kollar) (Isoptera, Termitidae), in Viçosa, state of Minas Gerais, in southeastern

Brazil. *Cornitermes* spp are Neotropical termite species occurring in several habitats, including forests, "cerrados" (Brazilian savannas) and man-modified habitats, such as pastures or even gardens within cities, where they feed on living and dead grass and herbs (Cancello, 1989). Several species of this genus (among them *C. cumulans*) build large epigeous nests which are simultaneously inhabited by inquilines, such as other termite genera, ants, beetles, birds, snakes, etc (Redford, 1984).

The experiment aimed to test the effects of group size on the mean time to death of starved termites that were exposed to insecticide. Workers extracted from each of the five colonies were taken to the lab where they were randomly placed in groups of 1, 2, 4, 8, 12, 16, and 20 individuals (one series per colony), confined in test tubes made of transparent glass (9.5 × 1.4 cm) with hermetically sealing rubber caps. Before being confined to the test tubes, termites received a topical dose of 0.5 µl of Chlorpyrifos solution (0.0001 mg/ml a. i., using acetone as a solvent). Such a dose was chosen based on previous tests, in which termites kept alone survived in average 59.9 ± 8.9 h when exposed to 1 µl of this solution. For comparative purposes, other termite workers were extracted from the same five colonies, placed in groups and confined in test tubes as above. These termites did not receive a topical dose of insecticide.

Test tubes had been previously washed and sterilized at 180 °C for two hours, and rubber caps were autoclaved for 15 min. Tubes containing termites were kept horizontally, separated by plastic foam to prevent stridulation, or other mechanically transmitted signals, to propagate between these tubes.

Termites were incubated in the dark in a constant temperature chamber (25 °C ± 0.5) and no food or water was provided. Tubes were exposed to light only during the counting of survivors (no more than 5 min), when tubes were opened to allow air exchange. Observations started 4 h after incubating the termites and proceeded periodically, each 8 h, until most of the individuals were dead. Termite groups in which dead individuals presented any sign of cannibalism, were not included in data analysis. Cannibalism could be readily recognised by examining all termites (i) during each observation period, looking for individuals biting each other and (ii) after finishing the experiment, under a binocular microscope, looking for injuries on their body. The data were subjected to Survival Regression Analysis, based on a censored Weibull model, with two covariates: poisoning status (poisoned vs non-poisoned) and group size (Crawley, 1993). Mean times to death and respective standard errors, as revealed by the Survival Analysis, were then plotted against group size.

Results

Termite survivorship was affect by group size, as expected from previous studies ($P \ll 0.001$, Table 1). Again, as expected, insecticide affected survivorship ($P \ll 0.001$, Table 1). More interestingly, these effects are interdependent, as revealed by the existence of a significant interaction between group size and poisoning status ($P \ll 0.001$; Table 1). Therefore, poisoned and non-poisoned termites profited from social interactions. For poisoned termites survivorship increased for groups of ≥ 4 individuals, reaching a peak at densities around 8 individuals per tube. Above this density survivorship of poisoned termites decreased (Fig. 1). Accordingly, survival of non-poisoned termites also increased with group size, approaching a peak at a similar density (around 8 individuals/tube). Above this density, survivorship decreased. Survival of poisoned termites, however, showed a peak much lower than that of non-poisoned termites (Fig. 1). When kept in starvation, poisoned termites confined in groups of 8 individuals survived, in average, 46.6 h, while non-poisoned termites survived 71.3 h. Interestingly enough, survivorship of poisoned and non-poisoned termites converge to similar values for groups of ≥ 16 individuals. Cannibalism was rare in the experiment: only 4 out of 64 test tubes containing termites in the "non-poisoned" group, and none of the 108 test tubes containing the "poisoned" group, presented cannibalism.

Table 1. Survival Regression Analysis (censored Weibull model) for the effects of group size and poisoning status on the number of hours starved termite workers spent to die, when confined in test tubes in laboratory. Group size (number of termites confined together) is a continuous variable; whereas poisoning status is categorical (poisoned or non-poisoned). Shape parameter taken as 2.4396

Source	Chi-square	df	*P-value*
Model	88.70	3	$\ll 0.0001$
Group size (GS)	31.39	1	$\ll 0.0001$
Poisoning status (PS)	35.21	1	$\ll 0.0001$
Interaction (GS · PS)	22.10	1	$\ll 0.0001$
Error	617.41	478	
Total	706.11	481	

Discussion

Our results support the view that social facilitation enhance termite tolerance to poisoning, since termite survivorship is affected by group size, poisoning status, and their statistical interaction (Table 1). Even when submitted to resource deprivation, workers of *C. cumulans* exposed to insecticide survived longer when in groups than when alone, up to a certain density (= number of individuals per tube), when survival started to decrease with increasing group size (Fig. 1). Notably, non-poisoned termites present a similar survivorship curve, peaking at an equivalent density (≈ 8 individuals per tube) and converging to similar values at higher densities (≥ 16 individuals per tube) (Fig. 1). The mechanisms leading to such a result remain to be investigated. For the specific case of non-poisoned termites, we argued before that survival is intrinsically associated with interindividual physical contacts producing a state of physiological arousal (Miramontes and DeSouza, 1996). For the case of poisoned termites, it seems that socially induced tolerance to insecticides in termites also derives from physiological effects of social interactions other than allogrooming or trophallaxis.

It could be argued that the larger the groups, the more are the tasks such as allogrooming and trophallaxis shared, decreasing each individuals work(stress)load, hence giving it a greater chance to cope with the insecticide effects. Jones (1990), studying termite tunnelling through treated soil, proposed a similar mechanism to explain why larger groups of termites could tunnel deeper than smaller ones, with relative mortality being lower in larger groups. It was claimed that the larger the group, the more could tasks be shared, giving more individuals at any time the chance to loaf, rather than having to be involved in tunnelling and maintenance tasks most of the time, as in small groups.

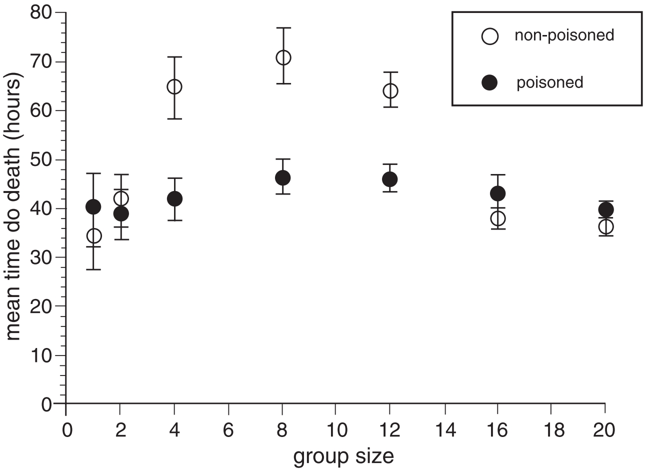

Figure 1. Survival of starving termite workers as a function of the size of the group in which they have been confined. The data is split into two categories: termites which were exposed to insecticides ("poisoned") and termites which were not exposed to insecticides ("non-poisoned"). Survival is measured as the average number of hours group members spent to die. Group size is the number of individuals confined together

Such a mechanism, however, does not seem to take significant part in our results, because it does not explain:

(i) decreasing survival times of individuals in large groups (>8 individuals/tube), which should "have their work(stress)load diminished by sharing tasks, thereby coping better with insecticide effects";

(ii) short survival times of lonely individuals, who have no companion to groom, and therefore should survive longer by not being subjected to "secondary" intoxication through allogrooming and trophallaxis;

(iii) convergence of survival times for poisoned and non-poisoned termites at densities ≥ 16 individuals/tube. Such a convergence could not happen without some physiological route of detoxification, since it is known that tolerance to insecticides is related to the ability of individuals to cope with the physiological stresses imposed by the intoxication (Matsumura, 1985). In fact, while reporting the positive effect of group-induced allogrooming on termite resistance to fungal infections, Rosengaus et al. (1998) also commented that social interactions reduced the prevalence of such infections. These authors present evidence that termites cope with disease through immunological responses (such as induction of new proteins, or enhancement of constitutive proteins, in the hemolymph), thereby suggesting that such mechanisms were enhanced or triggered by social contacts. We, therefore, hypothesize that a similar mechanism would be operating to allow socially induced termite tolerance to insecticide. More generally, social facilitation seems to affect the mechanisms which allow termites to circumvent physiological stresses such as starvation (Miramontes and DeSouza, 1996), disease (Rosengaus et al., 1998), or insecticide intoxication as shown in this work. Such an hypothesis is also based on the fact that social facilitation can affect physiological attributes of individuals. This is known for *Nasutitermes ephratae* (Holmgren) termites, whose energy consumption per capita correlates negatively with colony size (Muradian et al., 1998). Accordingly, in monkeys and rats, hormonal titres are modified by the mere presence of conspecifics (Zajonc, 1965); while in humans, "[…] the presence of others heightens an individual's physiological arousal […]" (Bond and Titus, 1983).

Our results have important practical implications, too. Laboratory experiments with termites/insecticides, for instance, may be severely affected by the group size being tested, providing that social facilitation has a significant impact on the outcome of the termite response to poisoning. Tests performed on groups above/below optimal density may overestimate the effect of the insecticide, restricting the relevance of such studies to the field.

It must be warned that this paper reports on an undescribed phenomenon (or set of phenomena) related to termite tolerance to poisoning. Further studies are needed in order to fully understand all the mechanisms involved.

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