Social Isolation in Ants : Evidence of its Impact on Survivorship and Behavior in *Camponotus fellah* (Hymenoptera, Formicidae).

by

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ABSTRACT

We investigated the effect of social isolation on survivorship, body weight, and readiness to engage in allogrooming and trophallaxis in the ant *Camponotus fellah*. Life duration of the workers caged singly with access to food was significantly lower than if they were caged with another nestmate, which implies that the stressful effects of social isolation cannot be reduced to the effects of food deprivation. Three day social isolation and food deprivation led to about 15% weight loss in the ants caged singly, but did not result in significant weight loss in the ants caged by tens. Social isolation also led to significant increase in the readiness to engage in trophallaxis. In the ants isolated with access to food, increased rate of trophallaxis between dyads of workers reunited after the period of social isolation (24 - 480 hours) might have been triggered by possible divergence of their cuticular profiles acting as colony recognition cues: trophallactic exchanges are known to play a crucial role in the exchange of recognition labels among the members of ant colonies.

Key words: Group effect, social isolation, trophallaxis, *Camponotus fellah*

INTRODUCTION

In his classical books on the biology of social insects, W. M. Wheeler (1926, 1928) postulated that social animals possess a "social drive" similar to alimentary or sexual motivations. He put a particular emphasis on the fact that, in social animals, separation from other members of the social group leads to substantial modifications of physiology and behavior of the individual. Further experimental research showed that social insects are unable to survive prolonged social

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isolation (Grassé and Chauvin, 1944 for *Reticulitermes lucifugus*, *Apis mellifera*, *Leptothorax tuberum* and *Formica rufa*). They also demonstrated that the survivorship of individuals isolated from their society depended on the size of the group. This phenomenon was interpreted by the authors in terms of the so called *"group effect"*, a notion introduced by them to denote profound modifications of the physiology of animals caused by their grouping. Grassé (1946) also proposed to distinguish between: (1) mass effect, in which the medium, modified by the population affects the physiology of the individual; and (2) group effect, in which the individual is affected by some stimulation directly emitted by other members of the group. To make more sharp the distinction between the group effect and other forms of animal communication, Wilson (1971) defined group effect as "an alteration in behavior or physiology within a species brought about by signals that are directed in neither space nor time". A similar distinction between "worker-worker interactions" and "worker medium (worker-nest) interactions" has been drawn more recently by Lenoir (1979) and Huang and Robinson (1992).

In the ants, behavioral and physiological consequences of social isolation were investigated in relatively few studies; however, that research already revealed a variety of effects. Thus, among others, it was shown that social isolation slows the ethogenesis in *Ectatomma tuberculatum* (Champalbert, 1986 ; Champalbert and Lachaud, 1990), and negatively influences the number of eggs laid by workers of *Leptothorax nylanderi* (Salzemann 1986 ; Salzemann and Plateaux 1988). In *Leptothorax allardycei*, social isolation also leads to disappearance of periodicity in the activity level (Cole, 1991). One of the strongest effects of social isolation was recorded in army ants : workers of *Eciton burchelli* survive for only hours when they are separated from their nestmates (Francks and Partridge, 1994). However, the influence of access to food on the mortality of isolated individuals has not yet been analyzed in ants. Furthermore, no study has ever combined data concerning mortality and behavioral changes that occur in ant workers after different social isolation periods.

In the ants, nestmate recognition (which assures altruistic behavior is directed only toward members of the same colony) is commonly considered to be mediated by specific cuticular cues (Hölldobler and Wilson, 1990). The colony odor is not fixed but results from a continual blend of individually produced cues. A social contact has to be maintained among all members of the colony to allow the transfer of the recognition labels. During encounters between nestmates, the recognition cues are exchanged principally via trophallaxis and allogrooming

(Soroker *et al.*, 1995b ; Vienne *et al.* 1995 ; Meskali *et al.*, 1995 ; Lenoir *et al.*, in press).

Considering these new data, we revisited the old problem of social motivation in a new light. As the colony odor is dynamic, we predicted that after a period of social isolation, workers' cue profiles could diverge. Consequently, we also predicted that nestmates reunited after a period of social isolation should show enhanced readiness to display trophallaxis and allogrooming behavior, so as to restore recognition discriminators.

We investigated the effects of social isolation in the ant *Camponotus fellah* in three experiments. The first experiment dealt with the influence of social isolation on survivorship, in conditions of presence/absence of food. The second experiment explored the influence of social deprivation on body weight. The third experiment examined congruent changes in social behavior (readiness to engage in trophallaxis and to display allogrooming) occurring after a period of social isolation.

MATERIALS AND METHODS

Ants

In the ants, the readiness to engage in trophallaxis is related to the importance of liquids in the diet (in particular nectar and homopteran honeydew) (Gösswald and Kloft, 1960). In preliminary tests, we investigated the frequency and duration of trophallactic behavior in dyads of four species of Formicinae (*Formica polyctena* Först., *F. fusca* Latr., *Camponotus aethiops* L., and *C. fellah* Dalla Torre). Each dyad consisted of two nestmates reunited after a 72 hour period of social isolation. The highest readiness to engage in trophallaxis was recorded in the ants of the genus *Camponotus*. For our further research, we choose specifically *C. fellah* because the colonies of that species are easier to collect and because the large size of the workers facilitated the experiments.

Camponotus fellah Dalla Torre 1893 live in large scattered colonies with only one queen. Measurements of inter-ocular distance (ID) of 235 workers from three queenless colony fragments, revealed the existence of a continual morphological polymorphism with two clear-cut morphological sub-castes: minor workers (mean ID=0.8 ± 0.17 mm) and soldiers (mean ID=2.3 ± 0.29 mm). This type of polymorphism has been commonly identified in many *Camponotus* species (Oster and Wilson, 1978 ; Passera, 1984). Only minor workers were used as subjects in our experiments.

The ants used in our experiments were taken from two young queenright colonies composed of approximately 200 workers. Foundresses of

these colonies were collected near Tel Aviv and Beer Sheva (Israel) in February 1996. Workers of the two source colonies were always equally distributed among the treatments. The ants were reared in the laboratory under controlled conditions (12:12 LD, $26°C \pm 2°C$, 25% RH $\pm$ 5%). Because the maximum activity occurs in the middle of the scotophase, experiments were conducted during the four hours after the beginning of the dark phase.

The ants were reared in artificial nests made of plaster. The nests were composed of 6 chambers, each of them covered by a separate glass plate. Thus, we could collect ants without sedated them with CO_2. In the honeybee, this gas decreases significantly the survival of isolated individuals (Chauvin, 1972) and alters recognition (Breed, 1981). The nests were connected via a plastic tube with a large enclosure (30x30x10 cm) acting as a foraging area and where the ants had an *ad libitum* access to food (mealworms and honey supplemented nectar for humming birds, supplied 3 times a week).

Experiment 1: Effects of isolation on survivorship

The aim of this experiment was to analyze the effect of social isolation on survivorship of workers of *C. fellah* in relation to access to food.

In a preliminary test, we used as subjects 90 minor workers of *C. fellah* captured in the field less than 15 days earlier. Each of these ants was placed inside isolation tubes closed with a cork. Ants had no access to food but each tube contained a water reservoir held in by means of a tightly fitting cotton plug at the bottom of the tube. Almost half of these ants (41 out 90) died after only three days of social isolation. This experiment demonstrated an important variability in the survivorship of isolated workers of *C. fellah* that incited us to control the age of the workers used in our tests.

In the principal tests, we used workers aged 2 to 3 weeks, born in the laboratory. To control the age of the ants, pupae were collected in the two mother colonies every week. They were placed into little test tubes with 4 or 5 workers until the emergence. Callows were marked with a spot of paint on their thorax and replaced into the nest. Various colors were used for various weeks on which the ants emerged, to allow us to determine their age.

Two to three week old workers were collected and placed inside test tubes, (16 mm in diameter, 160 mm long or 18 mm in diameter, 180 mm long) closed with a cork. Each tube was filled to about one-third with water held in by means of a cotton plug.

Four experimental groups were created. In the first group, the ants (n=25 individuals) were isolated singly with *ad libitum* access to food (supplied 3 times a week). In the second group, workers (n=36) were

isolated in dyads (n=18) with access to food. In both cases, food consisted of a liquid mixture of honey and nectar. In the third group, workers (n=20) were isolated and food deprived. In the fourth group, workers (n=38) were isolated in dyads (n=19) without access to food. The number of dead ants was recorded every morning. In the second and fourth group we only counted the first dead ant of each couple.

Experiment 2: Effects of isolation on body weight

The aim of this experiment was to investigate the influence of social isolation on body weight of workers of *C. fellah*. To that purpose, we tested 4 groups of young (about 2 to 3 week-old) individually marked workers (in total, n=74 ants).

In the first group (n=16), the ants were isolated singly without access to food. In the second group (n=18), they were isolated singly with *ad libitum* access to food. In the third and fourth group the ants were caged by tens (in two different test tubes ; n=20 in each case), with and without access to food respectively. Each of these four treatments was maintained for a 72 hour period. The same isolation tubes and food were used as in the first experiment. Each ant was individually weighed using a Sartorius® scale, just before and after the isolation time.

Experiment 3: Effect of isolation on behavior

The aim of this experiment was to test the effect of various social isolation periods on behavior of minor workers of *C. fellah* during a reunion with a nestmate which also had been subjected to the same period of social deprivation.

Two to three week old ants were placed singly in isolation tubes as described in the first experiment. They were subjected to social isolation for 24, 72, 120, 240, 480 hours. During the isolation period, the ants were either food-deprived or fed every day with honey supplemented with nectar. Thus, in total, 10 experimental groups were created. In each group, we tested 10 dyads.

Each behavioral test consisted of two encounters between the same dyad of nestmates of the same age. The first encounters (control encounters) were carried out 20 minutes after the workers were taken away from the mother colony (this time was required to allow individuals to calm down). The second encounters (test encounters) occurred after a period of social isolation, identical in the case of both tested nestmates. During the isolation period, the two ants were either starved or fed every day.

At the start of each encounter, the open ends of the tubes in which the ants have been isolated were put together, one against the other. Then, we recorded the total duration of trophallaxis and allogrooming

(licking the other ant). Each encounter lasted 15 minutes.

Statistical analysis

Experiment 1: The average lifetime of ants placed in the four conditions (isolated or grouped, fed or starved) was compared by means of two-way ANOVA.

Experiment 2: For each of the four treatments, the weight of ants before and after the social isolation period was compared by means of a two-tailed matched-pairs signed-ranks Wilcoxon test. The homogeneity of the control values (weight before treatment) of the four groups was checked by means of one-way ANOVA.

Experiment 3 : We tested jointly the effect of duration of social isolation period and of food deprivation. In that analysis, the total duration of trophallaxis and allogrooming recorded during the control encounters were subtracted from the values of these variables recorded in the respective test encounters. The values of these new variables, independent of the values recorded before isolation, were then compared by means of two-way ANOVA.

RESULTS

Experiment 1 : Influence of social isolation on survivorship

In contrast to the workers of *C. fellah* collected in the field shortly before the isolation period where we observed a high mortality after only 3 days of social isolation (preliminary tests), workers born in the laboratory proved to be less sensitive to social isolation (46% vs 4%).

The ants that had access to food survived longer than food-deprived ones, irrespectively of being isolated or not. The average life duration of the food-deprived ants was reduced by 53% relative to that of ants which received food regularly (respectively 30 ± 13 and 67 ± 22 days two-way ANOVA, $P<0.001$).

Nevertheless, being isolated or kept by twos has an important effect on their survivorship: on the average, isolated individuals died more quickly than individuals kept in dyads (respectively, 43 ± 25 and 54 ± 25 days, two-way ANOVA, $P<0.01$).

Table 1. Life duration of minor workers of *C. fellah*, isolated or kept by twos, and with or without access to food. Values represent means $\pm$ S.D. and are compared using two-way ANOVA. Factor 1 (food access): $P<0.001$; Factor 2 (isolation): $P=0.004$; Interaction: $P= 0.18$.

	isolated singly	kept by twos	P values
with access to food	59.2 ± 23.1	74.3 ± 13.1	< 0.001
without access to food	27.1 ± 12.9	33.1 ± 11.7	0.26
P values	< 0.001	< 0.001	

Isolation did not affect the survivorship of individuals isolated without access to food (Table 1, 27.1 vs 33.1, two-way ANOVA, *P*=0.26). However, the ants that had access to food during the social isolation period survived significantly longer if they were kept in dyads than if they were kept singly (table 1, 59.2 vs 74.3, two-way ANOVA, *P*<0.01).

Experiment 2: Effects of social isolation on body weight

Before the social isolation period, all young ants showed some degree of gaster distension. The four groups were homogenous with respect to the body weight (one-way ANOVA, *P*=0.33), and the mean weight for a minor worker was 8.85 ± 2.25 mg.

The body weight measured before and after the three days isolation period showed highly significant differences solely in the case the ants isolated singly without access to food (Table 2, two-tailed matched-pairs signed-ranks Wilcoxon test, *P*<0.001). During the isolation period, the ants of that group lose approximately 15 % of their weight. In all

Table 2. Influence of social isolation and access to food on live body weight of young minor workers of *Camponotus fellah*. Values represent means ± S.D. just before and after the social isolation period of three days and are compared using two-tailed matched-pairs signed-ranks Wilcoxon test (weights before the experiment are homogenous among the four groups, two-way ANOVA, *P*–0.33).

weight [mg]	isolated singly		kept by groups of ten	
	with access to food (n=16)	food-deprived (n= 18)	with access to food (n=20)	food-deprived (n=20)
weight before the experiment (mean ± S.D.)	8.78 ± 2.64	9.06 ± 2.01	8.59 ± 1.97	8.95 ± 2.23
weight after the experiment (mean ± S.D.)	8.52 ± 2.95	7.94 ± 2.06	7.95 ± 2.32	8.46 ± 3.04
percentage of variation	4.96 %	15.01 %	8.45 %	9.31 %
P-values (Wilcoxon)	0.54	<0.001	0.06	0.33

remaining groups, the weight measured before and after the isolation period did not show significant differences (Table 2).

Experiment 3: Effect of social isolation on behavior

When the tubes containing workers of *C. fellah* were joined together, the ants as a rule encountered their nestmate in few seconds.

During the control encounters, carried out before the social isolation period, the total duration of allogrooming and trophallaxis was usually very low (82.2 ± 72.4 and 12.4 ± 17.2 respectively), and did not differ

significantly among the ten groups (ANOVA, $P=0.338$, and $P=0.118$ respectively).

During the test encounter, carried out after the period of social isolation, the total duration of trophallaxis depended both on the duration of the isolation period and on presence/absence of food access. In the ants which had access to food during the isolation period, the total duration of trophallaxis increase between the control and the test encounters as the isolation period augment (indicated on table 3 by the difference between the control and the test encounters). This augmentation reached its maximum after 480 hours of social isolation, the longest of the social isolation periods used (Table 3a, in lines). The dyads of ants reunited after 480 hours of social isolation displayed

Table 3 : Influence of access to food and duration of social isolation on (a) variation of the total duration of trophallaxis [secondes] and (b) on variation of the total duration of allogrooming [secondes]. For each dyad of ants, this variation corresponds to the difference between the total duration of trophallaxis (allogrooming) during the control encounter (carried out just before the isolation period) and the test encounter (carried out just after the isolation period). Values are means ± S.D.. Letters (a,b,c,) indicate significant differences (ANOVA; $P<0.05$) related to the duration of social isolation (in lines). For each duration (columns), differences between workers which had and had not access to food are indicated by the values of P(ANOVA) given below. In all cases, sample size is n–10 dyads.

Table 3a: trophallaxis

social isolation period	24 hours	72 hours	120 hours	240 hours	480 hours
(1) ants isolated with access to food	43.3 + 103.7 a	234.3 ± 192.2 b	334.0 ± 175.4 bc	307.2 ± 112.3 bc	495.0 ± 212.2 c
(2) food-deprived ants	37.4 ± 168.5 a	362.8 ± 136.5 b	190.7 ± 145.4 ab	236.8 ± 248.6 ab	165.1 ± 107.1 ab
comparison (1) vs (2)	N.S.	N.S.	N.S.	N.S.	$P<0.001$

Table 3b: allogrooming

social isolation period	24 hours	72 hours	120 hours	240 hours	480 hours
(1) ants isolated with access to food	25.7 ± 35.0 a	72.6 ± 135.3 a	78.4 ± 221.3 a	24.5 ± 95.7 a	-24.3 ± 46.9 a
(2) food-deprived ants	-7.6 ± 125.0 a	-44.5 ± 127.1 a	-132.1 ± 96.5 a	-82.3 ± 117.4 a	-129.2 ± 46.9 a
comparison (1) vs (2)	N.S.	N.S.	$P<0.05$	N.S.	N.S.

trophallactic behavior during, on average, 495s ± 155s, which represented 55 % of the total test time. The total duration of allogrooming did not vary with the augmentation of the social isolation period (Table 3b, in lines).

In the ants which did not have access to food during the social isolation period, the total duration of trophallaxis increase with the augmentation of the social isolation period. This augmentation reached its maximum after 72 hours (Table 3a, in lines). The duration of allogrooming did not change globally as a function of the duration of the social isolation period (Table 3b, in lines ; ANOVA, P=0.21).

The comparison of the variation of the total duration of trophallaxis recorded in the groups of ants which have been subjected to the same duration of social isolation but differed in respect to presence/absence of access to food revealed significant differences solely in the case of the ants isolated during 480 hours (Table 3a, in columns ; ANOVA, P<0.001). Concerning allogrooming, this variable revealed differences solely in the case of ants isolated during 120 hours (Table 3b, in columns ; ANOVA, P<0.05).

DISCUSSION

The results of the experiment 1 demonstrated that social isolation has an important effect on the survivorship of minor workers of *Camponotus fellah*. As expected, ants which had access to food during their social isolation period survived longer than food-deprived ones. However, even if the ants received food regularly, life duration of workers caged singly was drastically reduced (by about 20%) in comparison to that of workers caged together with one nestmate. These findings imply that stressful effects of social isolation cannot be reduced to the effects of food deprivation. They also confirm earlier data demonstrating that in social insects, group effect may sometimes appear even if only two individuals are put together (Chen, 1937a, b ; Grassé and Chauvin, 1944 ; Grassé, 1946 ; North, 1987).

The effects of social isolation and access to food on survivorship of social insect workers have been investigated relatively rarely. In the honeybees, increased mortality in response to social isolation was reported by Grassé and Chauvin (1944). Causal factors of the phenomenon were then studied extensively, but no result provide an unequivocal explanation of increased mortality of isolated honeybees (see review in Arnold, 1976 and 1978). In the ants, Grassé and Chauvin (1944) reported that isolated workers of *Formica rufa* and *Leptothorax tuberum* captured in the field died very quickly in spite of unlimited access to food: in both cases, about 50% of the isolated ants were dead after 5

days. In our experiment 1, we used as subjects young workers (2-3 week old), born in the laboratory. When they received food, these workers lived on average 60 days if they were isolated and 75 days if they were caged with another nestmate. However, in our preliminary tests with workers of *C. fellah* captured in the field, we obtained a result similar to that of Grassé and Chauvin (1944): 46% of these ants died after only 3 days. The differences in survivorship observed by us between these two classes of workers could be due to the breeding conditions of the laboratory colonies. A second explanation could be that young ants may be more sensitive to social isolation than older ones : for instance, Hölldobler (1966) demonstrated that life-span of isolated males of *Camponotus herculeanus* is shortened, but only if they are isolated at a relatively young age. Different survivorship of workers captured in the field and born in the laboratory might also be related to a difference in nutrient stores depletion. This variable is known to be a general limiting factor for the survivorship of ants (Fowler, 1986 ; Lachaud *et al.*, 1992).

The results of our experiment 2 demonstrated that minor workers of *C. fellah* subjected to 72 hours of social isolation and food deprivation lose 15% of their weight. In food-deprived ants kept in groups of ten workers, such weight loss was not observed. One can hypothesize that the overall activity level of the ants isolated singly was higher than in the case of ants kept in groups of ten, which resulted in a more important energy consumption by these ants, and, consequently, led to their weight loss. This assumption is supported by the fact that in *Camponotus vagus* and in various species of *Formica*, social isolation may strongly increase oxygen consumption (Gallé, 1978). Moreover, Cole (1991) indicated that the spontaneous activity depends on the size of the group, in *L. allardycei*. However, in *Myrmica rubra*, Brian (1973) failed to find a significant difference in the rate of oxygen consumption between isolated workers and individuals caged by tens, but the experiment was only conducted for 5 hours. In the case of *Dolichoderus quadripunctatus*, Torossian (1977) obtained different results according to the season.

The experiment 1 and 2 showed jointly that in young minor workers of *C. fellah*, social isolation is an important physiological stress which reduces survivorship and induces body weight loss.

The experiment 3 demonstrated that minor workers subjected to social isolation and then reunited with a nestmate subjected to the same treatment show increased readiness to engage in trophallaxis. The frequency of trophallactic exchanges is already known to depend on the state of satiety of the colony (Markin, 1970 ; Howard and Tschinkel, 1980 and 1981). However, in our experiment, increased readiness to

engage in trophallaxis was observed not only in food-deprived ants, but also in the ants which had access to food during their social isolation period. This result suggests strongly that trophallactic behavior observed in our tests was not related solely to the motivational context of food exchange. We rather suppose that it might have involved the exchange of compounds acting as colony recognition cues. In species that lived in big scattered societies, the colony odor is dynamic and has to be continually homogenized (Vienne *et al.*, 1995). Temporal changes of the colony odor have even been demonstrated in the case of *Solenopsis invicta* (VanderMeer *et al.* 1989), in *Leptothorax curvispinosus* (Stuart, 1987) and in *L. lichtensteini* (Provost *et al.* 1993). More recently, Dahbi *et al.* (1997) showed that in the polydomous and monogynous ant *Cataglyphis iberica*, the hibernation represents a period of separation between all satellite nests of one society. In spring, when the activity starts again, the colony odor has to be homogenized via mutual transports of callows, trophallaxis and allogrooming. In *Cataglyphis niger*, chemicals acting as recognition labels are stocked in the postpharyngeal gland which plays the role of a 'Gestalt organ' (Soroker *et al.*, 1994). The occurrence of special sets of muscles controlling the opening of this gland in the oesophagus indicates that the exchange of these compounds is independent of food flow (Soroker *et al.*, 1995a). Thus, it appears that trophallaxis is not only a simple way of exchanging food, but it allows a continuous flow of recognition cues between all members of the colony as well. In our experiment, social isolation could lead to a divergence between social and individual odor. Trophallactic exchanges between nestmates reunited after a period of social isolation could permit them to reestablish a social link with their nestmates, mainly by exchanging chemicals that constitute the colony recognition cues. Soroker *et al.* (1995b) also indicated that trophallaxis constituted a preferential way for exchanging recognition cues, in comparison with allogrooming and cuticle contact. This observation could explain why, in our experiments, there is no significant increase of the duration of allogrooming, related to the length of the isolation period.

The role of trophallactic exchange in the behavior of social insects is not limited to distribution of food and compounds acting as colony recognition cues. The so called "trophallactic appeasement" (regurgitation of liquid food followed by its offering to an attacking conspecific or allospecific ant) is widely documented in many ant species (Bhatkar, 1979a and 1979b ; Liebig et al., 1997). Detailed analysis of behavior of workers of ants of the genus *Camponotus* revealed that food exchanges may be cooperative or aggressive, although the distinction between these two subcategories of trophallactic behavior may be ambiguous

(Carlin and Hölldobler, 1986).

To conclude, trophallactic behavior observed by us in the ants reunited after a period of social isolation might have involved (1) food sharing between the nestmates, (2) exchange of compounds acting as recognition cues, and (3) appeasement of aggression of another ant. Further research is needed to determine to what degree each of these types of trophallactic behavior contributes to the duration of trophallaxis recorded in dyads of workers reunited after a period of separation.

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