Group effect on fertility, survival and silk production in the web spinner *Tetranychus urticae* (Acari: Tetranychidae) during colony foundation

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Summary

In many vertebrates and invertebrates, individuals reared in isolation show biological modifications compared with those reared in groups of two of more. The spider mite *Tetranychus urticae* is characterised by a communal organization and displays some forms of cooperative behaviour (aggregation and common web spinning). To evaluate the potential fitness cost or gain of group living, we investigated the effect of being in group on life history parameters (silk production, fecundity, death rate, feeding rate). In this respect, virgin single females and grouped females (two to six individuals) were compared every day for 5 days. Grouped mites produced significantly more web/mite per day (since the second day of experiment) and more eggs/mite per day (since the fourth day of experiment) than single mites. Moreover, single mites had a higher death rate than mites living in groups. However, no difference was found concerning feeding rate. We assume that mites could benefit from the web production of other individuals and invested resources in other activities such as egg production. We showed that these group effects already exist in small groups. In natural conditions with a higher group size, the impact of group living might be stronger for the dynamics of *T. urticae* populations and the colony foundation.

Keywords: *Tetranychus urticae*, group effect, Allee effect, fitness indicators.

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Introduction

The social environment of an individual may have a great impact on its behaviour (Wilson, 1975; Prokopy & Duan, 1998; Prokopy & Reynolds, 1998; Krams et al., 2009) or on its physiology (Chauvin, 1946, 1958; Grassé, 1946; Long, 1953; Wharton et al., 1967, 1968; Yoder & Grojean, 1997; Holbrook et al., 2000; Rotem & Agrawal, 2003; Lihoreau & Rivault, 2008), for both vertebrates and invertebrates. Such alterations of individuals living in a group have been termed 'group effects' (Grassé, 1946; Holbrook & Schal, 1998; Boulay et al., 1999; Holbrook et al., 2000; Lihoreau & Rivault, 2008) and imply the costs and benefits of so living (Barbault, 1977). These group effects might be derived from simple numerical effects and/or synergistic inter-individual effects. For example, in vertebrates, Krams et al. (2009) showed the importance of group size for communal defence against predators in the pied flycatchers *Ficedula hypoleuca.* In invertebrates, Lihoreau & Rivault (2008) showed that the presence of conspecifics increased rates of both nymphal development and oothecae production in *Blatella germanica*. Furthermore, Avilés & Tufiño (1998) and Salomon & Lubin (2007) observed that in social spiders, the average number of eggs per female and the probability of offspring survival to maturity increased with colony size.

Tetranychus urticae is considered as a major pest of many cultivated plants (more than 900 listed host-plants; Van Impe, 1985). Consequently, research has mainly focused on the management and control of this species whereas its behaviour, especially its social behaviour, has often been disregarded. *T. urticae* was chosen as a biological model for studying group effects for several reasons. Firstly, the individuals of this species can survive on their own and/or in groups of two or more. Indeed, thanks to its arrhenotokous parthenogenetic reproductive system, *T. urticae* females can disperse on their own and found colonies on a host plant by mating with her own sons (Yano, 2008). This feature enables experimentation with a continuum in the group sizes. Secondly, *T. urticae* exhibit various forms of social behaviours such as aggregation (Le Goff et al., 2009) or construction of a common web (Saito, 1983; Clotuche et al., 2009). These studies suggest that there is a higher level of sociality than just being gregarious. However, according to Costa (2006), the next level of sociality corresponds to subsocial with parental care behaviours. Parental care behaviours have never been described for *T. urticae*, but if we consider the web as a common living space for individuals of the same generation, *T. urticae* could be so a communal species.

From an evolutionary point of view, group living has many advantages for both individuals and groups because it helps access to food and mates and protects against predators (Ranta et al., 1993; Dyer, 2000; Wertheim, 2005; Costa, 2006; Mori & Saito, 2006; Sato & Saito, 2006). Indeed group formation confers on individuals a net benefit from prédation (Wertheim et al., 2005). However, it also presents disadvantages such as having to share food, mates and living space and can result in inter-individual conflicts (Ranta et al., 1993). The construction of a common web also confers a selective advantage over the group. A group of spider mites produce a denser web than an single individual. The resulting web offers better protection from the rain (Davis, 1952), pesticides (Ashley, 2003) and predator attacks (McMurtry et al., 1970). One group effect has already been evidenced in *T. urticae*. Van Impe (1984, 1985) found that male development times decreased when the density of individuals increased. However, besides this work and despite indicators of a social organization (aggregation and common web), group effects in *T. urticae* have been poorly investigated.

In this study, we wanted to explore the importance of group living in this species without any important selective pressure like predation. In this respect, we continued the work of Van Impe (1984, 1985) one step further as we focused on the individual consequences of being associated to conspecifics in *T. urticae*. In this respect, we studied the impact of group living on some major biological features by assessing the variations of different indicators, i.e., white faecal pellet production as a web production indicator (Hazan et al., 1971), fecundity, cumulative death rate and the necrotic area of the leaf as a feeding indicator (Candolfi et al., 1991).

Material and methods

The mites used in this study belonged to the red form of *T. urticae* (also called *T. cinnabarinus*) and were provided by the Institut National Agronomique, Tunisia (Tunis, Dr K. Lebdi-Grissa). The breeding stocks were maintained at 26°C, 50–60% relative humidity, 16:8 (L/D). The experiments were undertaken in the same environmental conditions as breeding. Only virgin females less than 24 h old were used to standardize the experiments as mated and virgin females have different ovipostition rates (Van Impe, 1985) and furthermore, mated females have a greater variable ovoposition behaviour than virgin females (Van Impe, 1985).

At the beginning of each experiment, females (single or in groups of 2, 4 or 6) were put onto one new bean leaf disc (*Phaseolus vulgaris*) and this disc was placed onto damp cotton in a Petri dish (92 mm diameter). Thirty replications were done for each group size.

For experiments with one, 2, 4 and 6 individuals, the diameters of the leaf discs were 7.5 mm, 10 mm, 15 mm and 18 mm, respectively, to insure the same density of mites (0.02 individuals/mm^2). Indeed, the aim was to test the influence of conspecific presence independently of any density effect (different amount of food and living space per individual). The following parameters were measured every day for five days (before the first eggs hatched) per live individual:

(1) The silk production indicator, which was the mean number of white faecal pellets on the web per live individual per day (Hazan et al., 1971) for 5 days. We also measured the volume (μm^3) of white faecal pellets as a function of the number of individuals. According to Wiesmann (1968), the pellets were roughly spherical. This approximation was supported by preliminary experiments. White faecal pellets produced by single individuals and individuals in groups of 2, 4 and 6 were chosen at random ($N = 30$). The areas were photographed from the top and side points of view (Mailleux et al., 2000) and measured with the ImageJ software (Rasband, W.S., ImageJ, US National Institutes of Health, Bethesda, MD, USA, http://rsb.info.nih.gov/ij/, 1997–2008). The side and top areas were correlated when pellets were laid by single individuals ($N = 30$) and groups of 2 ($N = 30$), 4 ($N = 30$) and 6 ($N = 30$) individuals using the Spearman's rank correlation (R_s) coefficient (1: $R_s = 0.71$, $p < 0.001$, 2: $R_s = 0.80$, $p < 0.001$, 4: $R_s = 0.57$, $p < 0.001$, 6: $R_s = 0.86$, $p < 0.001$). The average top:side ratio was 1.01 ± 0.01 (mean±95% confidence interval (CI)), with ratios of 1.13 ± 0.09, 1.16 ± 0.01 and 1.14 ± 0.09 for single individuals and individuals in groups of 2, 4 and 6, respectively. This confirmed that the pellets were spherical and we only measured the top area of the pellets to calculate and compare their volumes for single individuals and individuals in groups of 2, 4 and 6. The focal distance between the white faecal pellets and the lens was carefully kept constant.

(2) The mean number of eggs laid per live individual per day for 5 days. We also measured the volume (μm^3) of 30 eggs of less than 24 h old, chosen at random in each group size. Eggs of *T. urticae* are spherical (Crooker, 1985). The eggs were photographed (the focal distance between the eggs and

the lens was carefully kept constant) and measured with the ImageJ software (Rasband, W.S., ImageJ, US National Institutes of Health, Bethesda, MD, USA, http://rsb.info.nih.gov/ij/, 1997–2008).

(3) The mortality indicator, which was the cumulative death rate after 5 days.

(4) The feeding indicator, which was the cumulative necrotic area of the leaf per live individual (Candolfi et al., 1991) after 5 days. It was measured with the software ImageJ. This area was measured only for single females and females in groups of six individuals at the fifth day.

Statistical tests

As all data were normally distributed, parametric statistics were used. Repeated measures ANOVA, one-way ANOVA, t-tests and linear regressions were performed using GraphPad Prism version 5.01 for Mac OS (GraphPad Software, San Diego, CA, USA, www.graphpad.com). Linear regressions, which are represented on all graph were calculated on 120 points (4 group sizes and 30 replicates) and analysed using an F test to understand the influence of group size on these parameters and whether the slope was significantly non-zero. All tests were applied under two-tailed hypotheses and the significance level p was set at 0.05.

Results

Silk production

Repeated measures ANOVA showed that whether a female was kept single or in group had a significant effect ($F = 22.20$, $\mathrm{df_n} = 3$, $\mathrm{df_d} = 435$, $p < 0.001$, Figure 1) on silk production per individual. This finding was, however, rendered ambiguous by a significant interaction ($F = 2.10$, $\mathrm{df_n} = 12$, $\mathrm{df_d} = 435$, $p < 0.05$) between the day of experiment and the group size. We, therefore, used the Bonferroni procedure to detect differences in silk production for similarly aged single and grouped females (Table 1). Grouped females did not produced more silk than single ones on the first day (Table 1). For each of the next four days of experiments, significant differences were observed between grouped females and isolated ones (Table 1). At the fifth day, single individuals produced 2.94 ± 1.24 pellets/live individuals per day,

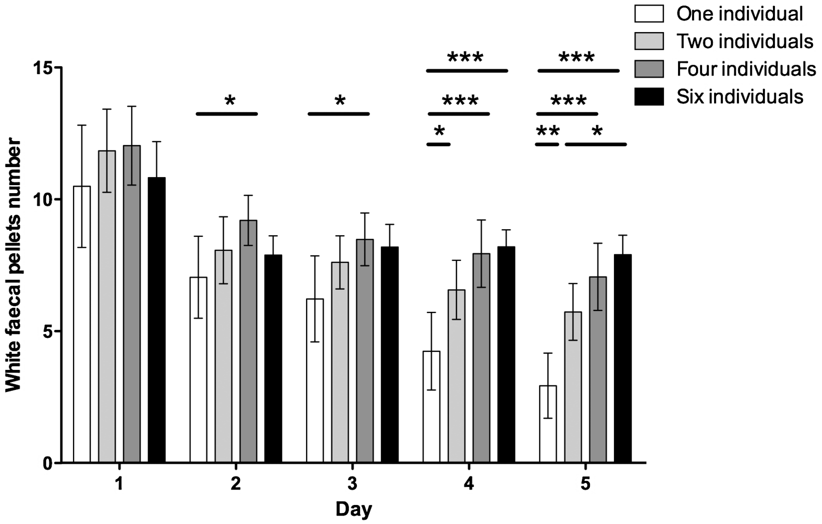

Figure 1. Mean daily white faecal pellet production production per live individual for five days of experiment and each group size ($N = 30$). Error bars indicate 95% CI.

Table 1. Student's t-values of the Bonferroni's multiple comparison test between each group sizes for the silk production, the egg production and the cumulative death rate (CDR).

	Silk production					Egg production					CDR
	Day 1	Day 2	Day 3	Day 4	Day 5	Day 1	Day 2	Day 3	Day 4	Day 5	Day 5
1 vs 2	1.64	1.25	1.68	2.83*	3.40**	0.49	1.34	1.04	1.56	2.10	2.58
1 vs 4	1.87	2.62*	2.75*	4.49***	5.01***	0.64	0.56	1.62	3.75***	3.61**	2.58
1 vs 6	0.40	1.02	2.39	4.80***	6.03***	0.29	0.44	1.46	2.83*	4.00***	3.19*
2 vs 4	0.23	1.38	1.06	1.67	1.61	0.15	0.78	0.58	2.20	1.50	0.00
2 vs 6	1.24	0.22	0.70	1.98	2.64*	0.20	0.89	0.41	1.28	1.90	0.61
4 vs 6	1.47	1.60	0.36	0.31	1.02	0.34	0.12	0.16	1.67	0.39	0.61

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, significantly different from control.

whereas individuals in groups of 2, 4 and 6 produced 5.74 ± 108, 7.06 ± 1.28 and 7.91 ± 0.74 pellets/live individual per day, respectively.

The volume of white faecal pellets increased with the size of the group ($R^2 = 0.06$, $p < 0.01$, $N = 120$, slope ± CI = 16 270 ± 11 613, y-intercept ± CI = 222 800 ± 43 800) ($F = 7.54$, $p < 0.01$) (Figure 2). The volume of pellets laid by single individuals was 253 505 ± 48 585 μm^3,

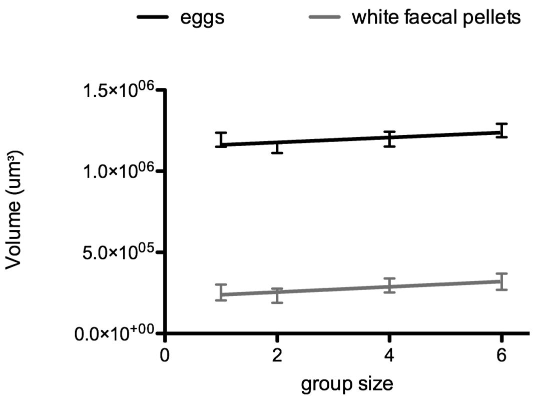

Figure 2. Linear regression of eggs and white faecal pellets of less than 24 h versus group size ($N = 30$). Error bars indicate 95% CI.

an area similar (232 923±43 667 $\mu\mathrm{m}^3$) to that of the pellets laid by groups of 2 mites. For white faecal pellets laid by groups of 4 and 6 mites, the volumes were 296 645 ± 43 252 $\mu\mathrm{m}^3$ and 319 644 ± 50 094 $\mu\mathrm{m}^3$ respectively.

Fecundity

Repeated measures ANOVA showed that being in group did not significantly influence the fecundity/female per day ($F = 2.64$, $\mathrm{df_n} = 3$, $\mathrm{df_n} = 464$, $p > 0.05$, Figure 3). However, the significant interaction between the day of experiment and the group size rendered difficult to interpret this result ($F = 2.91$, $\mathrm{df_n} = 12$, $\mathrm{df_d} = 464$, $p < 0.001$). We, therefore, used the Bonferroni procedure to detect differences in fecundity for similarly aged single and grouped females (Table 1). Grouped females did not lay more eggs than single ones on the three first days (Table 1). For the fourth and the fifth day of experiments, significant differences were observed between grouped females and isolated ones (Table 1). At the fifth day, a single individual produced 0.97 ± 0.41 eggs/live individual per day, whereas individuals in groups of 2, 4 and 6 produced 1.33 ± 0.38, 1.58 ± 0.25 and 1.65 ± 0.21 eggs/live individual per day, respectively.

The volume of eggs laid also increased with the size of the group ($R^2 = 0.07$, $p < 0.01$, $N = 120$, slope ± CI = 15 150 ± 10 385, y-intercept ± CI = 1 147 000 ± 39 000) ($F = 8.35$, $p < 0.01$) (Figure 2). Regarding individuals in groups of 2 mites, the egg volume was 1 143 000±31 000 $\mu\mathrm{m}^3$. Larger egg volumes were measured for single individuals (1 194 000±43 000

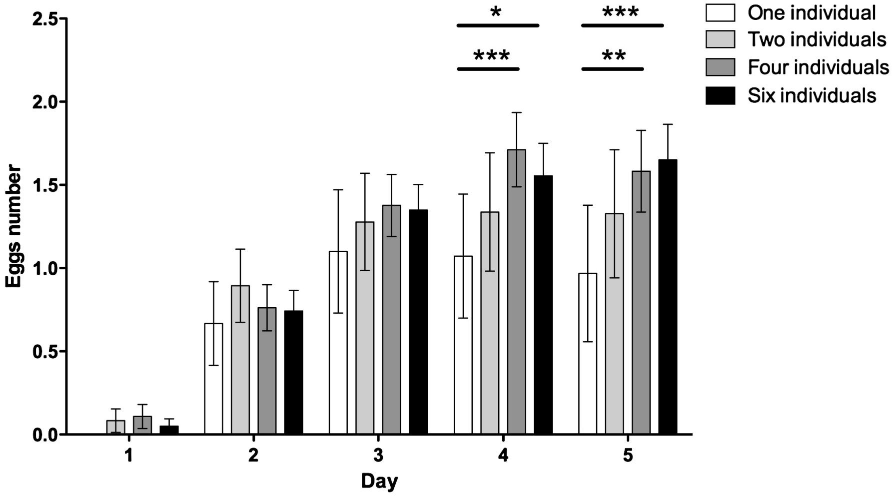

Figure 3. Mean daily egg production per live individual for 5 days of experiment and each group size ($N = 30$). Error bars indicate 95% CI.

μm^3) and individuals in groups of 4 (1 197 000 ± 45 000 μm^3) and 6 mites (1 251 000 ± 41 000 μm^3).

Cumulative death rate

In all treatments, a percentage of individuals died at the beginning of the experiment (death rate approx. 15%), probably because of possible injuries during mite transfers. However, because the same mortality bias was observed on day one for each tested condition, the comparison of our data remained valid (ANOVA $F = 0.04$; df $= 3$; residual error $= 116$; $p > 0.05$). A one-way ANOVA followed by a Bonferroni's multiple comparison test showed a decrease in cumulative death rate as the size of the group increased. We observed a large decrease of the cumulative death rate between single individuals and individuals in groups of 6 (ANOVA $F = 4.05$; df $= 3$; residual error $= 116$; $p < 0.001$, Bonferroni; Table 1) (Figure 4). With single individuals, on the fifth day the cumulative death rate reached 56.67 ± 18.82%, whereas it decreased to approx. 30% in the other groups.

Feeding

The leaf necrotic area/individual did not change with the size of the group ($t = 0.07$, df $= 58$, $p > 0.5$). On the fifth day, the leaf necrotic area of the

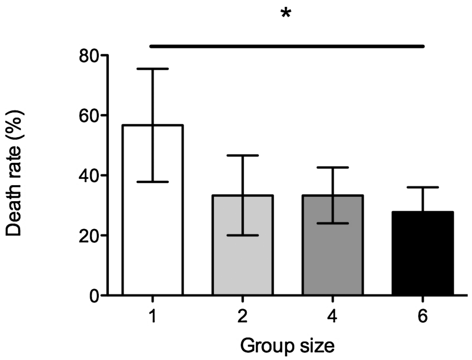

Figure 4. Percentage of death rate after 5 days of experiment and each group size ($N = 30$). Error bars indicate 95% CI.

leaf eaten by single individuals was 0.92 ± 0.28 mm^2. A similar surface of leaf necrotic area/individual (0.93 ± 0.14 mm^2) was eaten by groups of 6 mites.

Discussion

In nature, single individuals of *T. urticae* can disperse to found a colony, or they can disperse in groups of two or more (Yano, 2008). The presence of conspecifics in this species can induce life history traits modifications in individuals compared to single individuals.

Our results showed that in this species (under experimental conditions) living in groups increased silk production, fecundity and survival. This implies that individuals can perceive the presence of their conspecifics through direct and/or indirect interactions. (In)direct perception through chemicals (pheromones) or tactile perception of conspecifics might constitute indicators of group size (Prokopy & Duan, 1998; Prokopy & Reynolds, 1998). Chemical or tactile perception of eggs, faecal pellets, the web, necrotic leaf areas and compounds emitted by the leaf could also play indirect roles in other individuals' presence perception.

Our work showed that white faecal pellet production increased with the size of the group (more than one pellet more per individual for each added individual). This increase in pellet production per individual indicates an increase in silk production per individual (Hazan et al., 1971), leading to a denser and more protective web against external aggressions (rain, wind and predators). This increase in pellet production can also be explained at the ecological level. We assume that being in a group reduces the ecological stress that mites might face. For instance, being in an aggregate reduce the evaporating surface and avoid desiccation (Joosse, 1970; Wertheim et al., 2005). When confronted with a reduction in ecological stress, individuals can allocate their time differently when they are in groups compared to when they are single. Indeed, the same necrotic surface area does not imply the same necrotic depth and so the same amount of food. Therefore, individuals in groups may spend more time feeding at the same place and, therefore, cause the same necrotic surface with a greater depth and a larger amount of white faecal pellets than when they are alone. Furthermore, there might be one (or more) ecological advantages in producing numerous bigger white faecal pellets when the group size increases. A previous work showed that white faecal pellet volume increases with relative humidity, probably through water absorbency (Hazan et al., 1971). White faecal pellets might buffer variations in relative humidity and stabilise the humidity conditions in the web. It has also been observed that white faecal pellets are frequently the node connecting many silk threads (Figure 5). Hence, we assume that white faecal pellets might also be a component of the web structure; they could be cohesive points or 'tension adjusters' and could affect the web's mechanical properties. White faecal pellets might also have a repellent effect on predators. Oku (2008) showed that white faecal pellets produced by *T. kanzawai* repelled the predator *Neoseiulus womersleyi*. How the predators of *T. urticae* might be influenced by their pellets would be an interesting future study.

Our results showed a positive group effect on the fecundity of *T. urticae.* Living in groups increases egg production by around a third of an egg per individual for each added individual. The next step of this work will be to compare the individuals hatching from eggs laid by single individuals and individuals in groups (hatching rate, fitness of the newly hatched mites). *T. urticae* seems to benefit from the presence of other individuals as this induces life history trait changes which allow an investment in egg production (number and volume). Indeed, as producing a web is likely to entail a cost, mites that arrive on a leaf with a web are expected to refrain from producing it because they will benefit from the protection of the existing web (Oku et al., 2009). Mites that spend less energy producing a web may then allocate resources not spent on web construction to other fitness-enhancing activities, such as laying eggs (Oku et al., 2009). Holbrook et al. (2000) showed

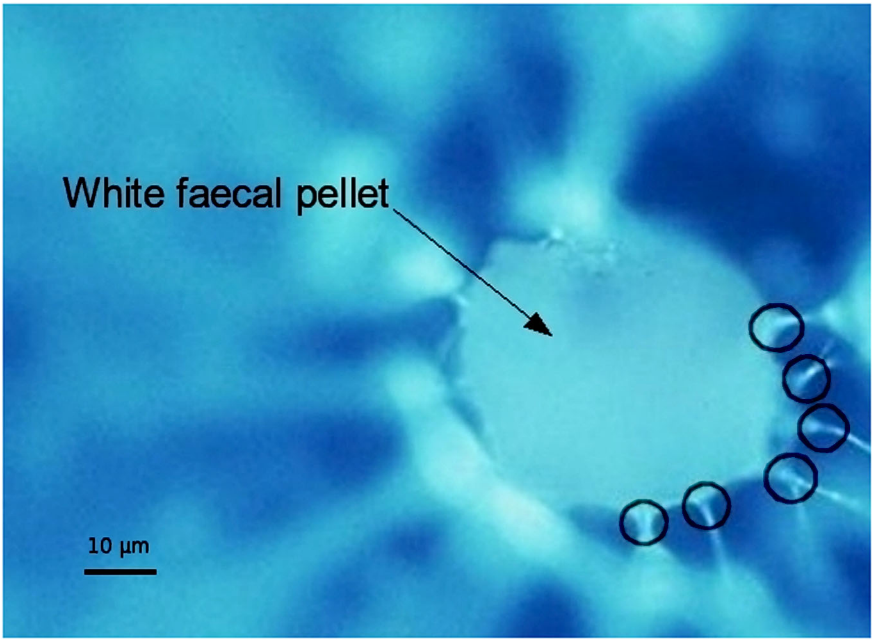

Figure 5. A white faecal pellet penetrated by many silk threads Silk penetrations are encircled by black rings. The pellet was coloured using the technique described in Clotuche et al. (2009). Photo by G. Clotuche. This figure is published in colour in the online edition of this journal, that can be accessed *via* http://www.brill.nl/beh

in *Blatella germanica* that group rearing accelerates oocyte development by diminishing the brain's inhibition of the synthesis of juvenile hormones. In *T. urticae*, such a similar physiological change might also be at work (Regev & Cone, 1976; Thind & Edwards, 1990) and further biochemical measurements can be envisaged, such as the measurement of biochemical messages (hormones, pheromones), as a function of group size. However, it must be noted that our experiments were performed using virgin females and that group effects on egg production could differ with mated females (Van Impe, 1985).

We observed a positive group effect on the survival of *T. urticae.* It has to be noted that this group effect became limited as a plateau of death rate (approx. 30%) was reached, since these individuals were in a group. The death rate of single individuals was higher than for individuals in groups of 6 after the fifth day of the experiment (56.67% versus 27.78%). This supports the view that individuals benefit from environmental modifications created by other individuals, such as increases in web and white faecal pellet production.

T. urticae is a well-known worldwide pest of many agricultural crops, orchards, nurseries, greenhouses and field crops (Margolies & Kennedy, 1985; Eastbrook et al., 2001; Cilli et al., 2005). To control such a pest, a prime necessity is an understanding of the impacts of group living (Myllymäki, 1975). Indeed, social behaviours are behind spatial distribution, dispersal movement and invasions by the pest and, more generally, rule most of their life history traits. Social behaviours usually influence the immediate result of a control measure as individuals living in group may initiate the compensative responses to induced mortality more rapidly. In turn, upsetting normal behavioural mechanisms of a social pest species (e.g., lure with aggregative/dispersal pheromone) might be used as means of control. Therefore, studying social behaviour has great relevance to control a group living pest (Myllymäki, 1975). The control of mites in greenhouses and fields can be complicated. Their nests are covered with dense webs that protect them from acaricides and mites are also difficult to eradicate because of the large number of eggs produced. One proposed technique might be the use of traps or baits loaded with mite pheromones that could attract adults, nymphs and larvae and to hold them in a place without a protecting web. Our study strongly suggests that this method of control would fail because increasing the local density would increase the rate of fecundity, resulting in larger populations which would be much more difficult to control. From a biological control point of view, the use of dispersing pheromones might be more efficient (Dicke et al., 2008). The Allee effect observed in *T. urticae* strongly suggests that regular treatments of the culture in such a way as to prevent its arrival in the cultures, or the maintenance of populations under economically acceptable thresholds might help to control these mites. These might be the next steps of our study.

This paper is a thorough study that opens several doors in an unexplored field of social biology. Indeed, the effects of group size have been poorly studied in species characterised by a communal organization such as spider mites. In this paper, we showed a possible Allee effect in *T. urticae.* Indeed, the Allee effect describes a scenario in which populations at low numbers are affected by a positive relationship between population growth rate and density, which increases their likelihood of extinction (Courchamp et al., 1999). Species in which fitness is enhanced by any type of conspecific facilitation might suffer from reduced density when intraspecific competitive processes are of secondary importance (Courchamp et al., 1999). Despite our experiments was conducted at a constant density, the fact that *T. urticae* is an aggregative species (Le Goff et al., 2009) caused an increase in density at a local scale which increased the encounter rate. The presence of conspecifics seems to facilitate an increase in the fitness of other individuals. In other words, better living conditions created by group living (more web production and humidity buffering), seem to induce a higher investment per mite in eggs and pellets/web production, which also increase the survival rate.

Moreover, we showed that these group effects already exist in small groups (only two to six individuals). We assume that in natural conditions with a higher group size, these Allee effects might have a stronger impact on the dynamics of *T. urticae* populations, especially for colony foundation. Indeed, a positive consequence of this group effect in *T. urticae* concerns the foundation of a new colony. Although a single female is able to found a new colony thanks to its parthenogenetic reproductive system (Yano, 2008), the success of a colony foundation would be much higher in groups than when alone (Ranta et al., 1993; Yano, 2004, 2008) as this would give a passive protection to the individual (Keough, 1983; Rivault et al., 1998; Ame et al., 2004) and also, as we have shown in this study, this would increase an individual's fitness.

However, in overcrowded conditions, the presence of conspecifics could have a negative impact on population dynamics (negative group effect). The physiological and/or behavioural mechanisms involved in these group effects remain unknown and deserve further study (Grassé, 1946; Prokopy & Duan, 1998; Prokopy & Reynolds, 1998; Holbrook et al., 2000).

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