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Effect of isolation on life expectancy of red imported fire ant *Solenopsis invicta* and tephritid fruit fly *Bactrocera dorsalis*

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ABSTRACT

The influence of conspecific interactions on behavior of individuals is an interesting topic, but with elusive proof. Here, we studied one species of ants *Solenopsis invicta* (social insects) and one species of tephritid fruit fly *Bactrocera dorsalis* (non-social insect) to determine whether lifespan of organisms could be affected by changes in the number of individuals interacting. In our experiments, isolated individuals, and the individuals that were grouped every 10 insects, were compared. We found that "singles" had a shorter life expectancy than grouped individuals. We also observed the upsurge of death in 3–4 days after isolation in *S. invicta* and *B. dorsalis*. This observation suggests an abrupt transition, which affects *S. invicta* and *B. dorsalis*. Our study showed that lifespan of individuals can be affected by group effect, and the effect was not limited to eusocial insects. A hypothesis of initial shock effect, which occurred within 4 to 5 days after isolation, was suggested and need further research to prove it.

1. Introduction

Aggregations have been found in many animals, and the group structure ranges from loose aggregates to sophisticated eusocial colonies [1]. In social animals, the sociality can be classified into three categorizations, communal, cooperatively breeding, and eusocial depend on the degree of their cenospecies interaction [2]. A study on lifespan of five social insects including *Apis* sp., *Leptothorax* sp., *Formica* sp., *Reticulitermes* sp., and *Polistes* sp. showed that individuals living in larger groups had a longer life expectancy than those living in smaller groups [3]. Consequently Grassé [4] introduced a "group effect" which is caused by the perception of social stimuli emanating from conspecifics and can be observed even only two individuals are grouped [4, 5]. Studies on other insect species also that showed life expectancy is affected by conspecific interaction [6–9].

Although some researchers suggest interactions between close individuals can have an influence, some questions are still unclear. The first one is whether or not the group effect exists in common. Lihoreau et al. [10] predicted that social cohesion of species and characterize their sociality level are related to their inter-individual dependence. Therefore, this is also an interesting topic whether the level of group effect would vary among social and non-social animals because of different degree of their cenospecies interactions?

The red imported fire ant, *Solenopsis invicta*, is an invasive ant species which has negative effects on economy, ecology and human health in introduced areas [11]. The tephritid fruit fly, *Bactrocera dorsalis* is an important pest of tropical and subtropical fruits and vegetables, which lays eggs in their hosts wherein their larvae will live until pupation [12]. According to the definition of eusociality, which is defined by the presence of distinct sterile workers and specialized reproductive castes [13], *S. invicta* and *B. dorsalis* are regarded as eusocial and non-eusocial species, respectively. We hypothesized the existence of group effects in eusocial species *S. invicta* and the non-eusocial species *B. dorsalis*, and expected the level of group effect to vary according with social complexity. Based on Grassé's [4] experiment, we investigated the lifespan between the isolated individuals and group-reared individuals of *S. invicta* and *B. dorsalis* to test for the existence of a group effect.

2. Materials and methods

2.1. Test insects

A eusocial insect, red imported fire ant *S. invicta*, and a non-eusocial insect species, tephritid fruity fly *B. dorsalis*, were chosen for the test. All the experiments were conducted at South China Agricultural University, Guangzhou, China. *S. invicta* colonies were collected from campus of the

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university and brought to the laboratory. These ants were separated from the soil and reared in open plastic boxes (23.5 cm × 15.5 cm × 9.0 cm) which were coated with Fluon to prevent workers from escaping. These colonies were fed with water, 10% w/w sugar water and larvae of flour weevil *Tenebrio molitor* in laboratory under 26 ± 1 °C and 40–60% relative humidity. A laboratory strain of tephritid fruit fly *B. dorsalis* was reared on water, yeast and sugar inside in cages (30 cm × 30 cm × 30 cm) under conditions of a constant temperature of 25 ± 1 °C and a 16:8 light–dark photoperiod and 70–80% relative humidity [12]. Unmated female adults of same age were chosen for the experiment.

Before the experiment, we estimated the average lifespan of *S. invicta* workers in laboratory colonies. *S. invicta* workers were allocated to one of three subgroups according to their head widths: minor (0.7 ± 0.03 mm), medium (0.9 ± 0.04 mm) and major (1.3 ± 0.04 mm) [14], and the average lifespan of minor, medium and major workers were estimated at 45 days, 75 days and 135 days respectively, after the setup of colonies [14]. To obtain an average life span for the population of *Solenopsis invicta* colonies in our experiment, we estimated the proportion of each subgroup in our colonies because the rate of minor, medium, and major workers in fire ant colonies may vary in different areas. Fifteen samples from five *Solenopsis invicta* colonies containing between one and 200 ants were obtained, photographed and counted. We then obtained the workers of colonies is composed of 62 ± 10% minor, 28 ± 8% medium, and 10 ± 2% major workers (the coefficient of variation for the various samples was of the order of 30%). These percentages resulted in the weighted average lifespan of *S. invicta* of $L \approx 62 \pm 4$ days. L gives a daily death probability of 1/L. Consequently, the death rate per day and per 1000 ants is $1000/L = 16$. Results show that the average death rate of isolated ants was approximately two or three times higher than individuals in colony.

2.2. Isolated individual versus group with 10

Groups of one and ten ant workers from same colonies selected randomly were placed in plastic bowls of lower diameter of 4.3 cm, upper diameter of 10.5 cm, and 8 cm high. To prevent ants from escaping, bowls were coated with Fluon. Ants in bowls were fed on water and 10% w/w sugar water. The food in bowls was replenished every week. The bowls were placed on a table with a distance of 60 cm between adjacent bowls, and were inspected every 12 h. The number of dead workers were recorded and removed at each inspection. This experiment was run four times. In the first time, isolated individual treatment and treatment of group of ten was replicated 30 times. In the second time, each of the two treatments was replicated 9 times. In the third and fourth time, each of the two treatments was replicated 10 times, respectively.

One and ten fruit flies were put in cages which were cubic cages of wooden frames (30 cm × 30 cm × 30 cm). The sides of the cage consisted of gauze, except for the top side, which had Plexiglass to allow easy inspection, because they are about 3 to 4 times bigger than ant workers. *B. dorsalis* in cages were given water, yeast and sugar. The food in cages was replenished every week. The distance between cages was 60 cm. The cages were inspected every 12 h. The number of dead fruit flies were recorded and removed at the time of inspection. This experiment was run four times. Isolated individual treatment was replicated 20 times while treatment of group of ten was replicated 8 times.

2.3. Data analysis

We used generalized linear model (GLM) to test the mortality of *S. invicta*. We used repeated measures ANOVA to test the mortality of *B. dorsalis* in different groups, because these data did not fit generalized linear model (GLM). All data in percentages distributed binomially and thus arcsine-square-root transformed prior to analysis. All statistical methods were conducted using SAS 9.2 (SAS Institute Inc., Cary, NC, US).

3. Results

3.1. Experimental results for isolated individual and group of 10 S. invicta workers and B. dorsalis

The average mortality of workers differed significantly between isolated individual and 10-ant groups ($F = 10.39$, $df = 1$, $P = 0.0015$, Fig. 1A), as well as among different time steps ($F = 4.81$, $df = 31$, $P < 0.0001$).

Fig. 1B showed the cumulative number of deaths with isolated individual or group with 10 *B. dorsalis*. The average mortality of *B. dorsalis* showed significant difference between isolated individual and group with 10 *B. dorsalis* ($F = 10.573$, $df = 1$, $P = 0.003$), as well as among different time steps ($F = 4.442$, $df = 37$, $P < 0.0001$). A marked upsurge in mortality was observed at the start of the experiment, followed by a low mortality.

3.2. Survivorship curves

Fig. 2A shows the survivorship curve of *S. invicta*. The graphs indicate that: (i) the survivorship curves are of Type II (almost constant mortality rate) and (ii) an upsurge in mortality, which was significantly higher than subsequent fluctuations, was observed at 4 days after isolation.

Fig. 2B shows the survivorship curve of *B. dorsalis* belongs to Type III. A marked upsurge in mortality was observed at the start of the experiment, followed by a low mortality.

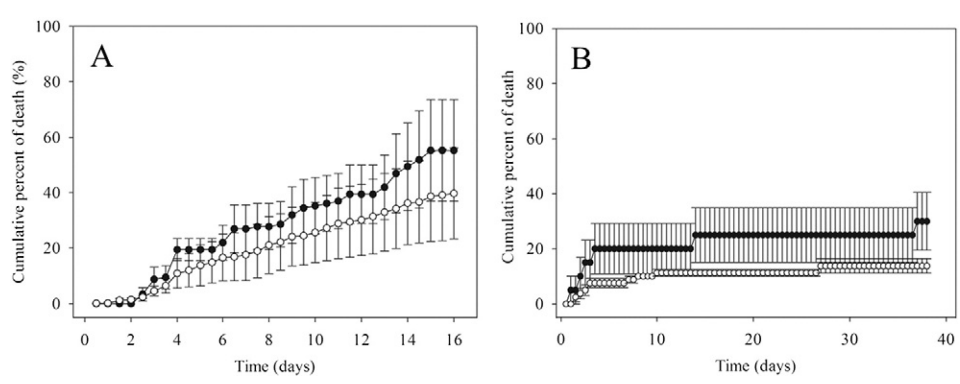

Fig. 1. Mortality of *Solenopsis invicta* (A) and *Bactrocera dorsalis* (B) when maintained as isolated individual or 10-insects group in the laboratory. Black and open circles stand for the individual and group, respectively.

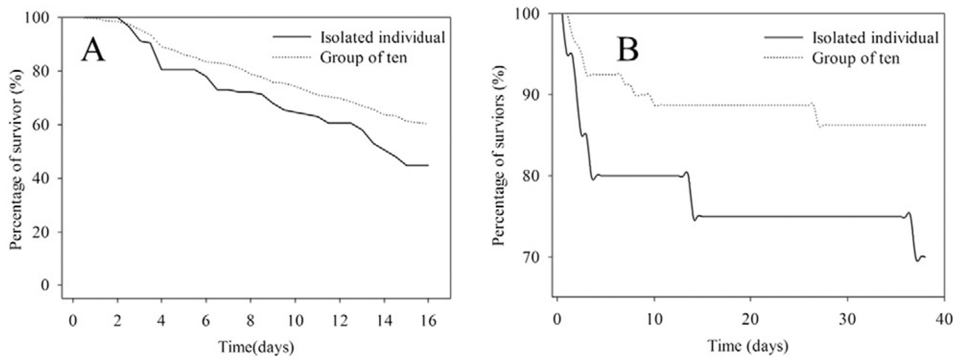

Fig. 2. Averaged survivorship curves. Graph A is an average over *Solenopsis invicta* experiment whereas graph B is an average over *Bactrocera dorsalis* experiment.

4. Discussion

Our study showed that individuals in groups of 10 insects generally had a lower mortality than isolated individuals. The results provide clear evidence for the existence of a group effect among the insects, and the group effect not only exists in eusocial insect, but also in non-social insect. It is very interesting that survival of solitary insect *B. dorsalis* was also affected by interaction-changes. *B. dorsalis* have its mating system, via which males aggregate and produce a pheromone that is attractive to females [15]. Meanwhile, *B. dorsalis* aggregations are always formed by food [16]. Lihoreau and Rivault [5] found such a group effect was present in aggregating cockroach species, but absent in cockroach species that will not form aggregations. Thus, we suspect that *B. dorsalis* is not a highly solitary species and that social interactions occurring upon aggregation on food may have had impact on survival.

However, the death rate of isolated *B. dorsalis* was at least 10 times lower than that of ants except for the upsurge of deaths after isolation. How could this result be interpreted? When an element has very few interactions with its neighbors, its isolation will not lead to much difference. Thus, little or no reduction in life expectancy is expected. However, for an element with strong interaction with its neighbors isolation may be a great shock. This may have caused a sharp reduction in life expectancy. Studies in rodents suggest that effect of isolation is more pronounced in species living in closed social units than in species living in looser structure [17,18]. So, ants may display more interaction networks than *B. dorsalis*. And isolation has more influence in ants' life span changes than in *B. dorsalis*'. Our conclusions support the hypothesis by Lihoreau et al. [10] that isolation syndrome can reveal the strength of social cohesion of species and aid evaluation the level of their sociability.

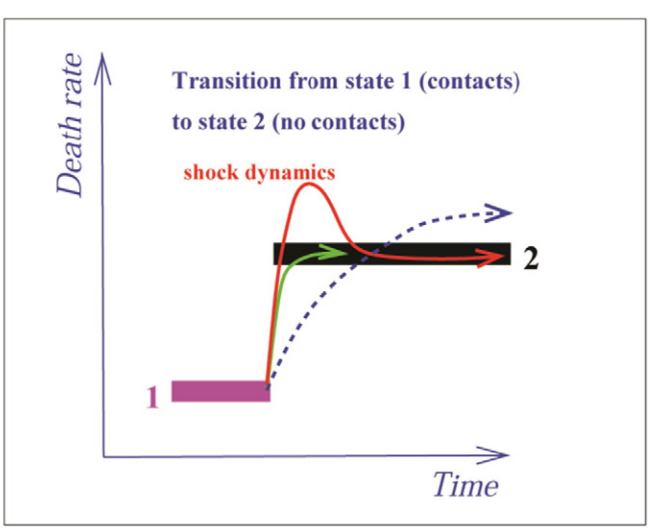

Fig. 3. Three scenarios for the transition to a higher death rate. The shock scenario is characterized by a death rate that becomes temporarily higher than the stationary long-term rate.

Three types of survivorship curves were classified based on the number or proportion of individuals surviving at each age [19]. Type I survivorship curve is characterized by high survival in early and middle life, followed by a rapid decline in survivorship in later life. Type II survivorship curve corresponds to a mortality rate that is constant over time and independent of age. Type III survivorship curve corresponds to the greatest mortality in early life, with relatively low rates of death in old age. In our studies, the survivorship curves of *S. invicta* were classified under Type II. According to data obtained by Dr. Deborah Gordon from experiments involving harvester ants, the survival of newly founded ant colonies is also of Type II (personal communication). By contrast, given the high initial death rate, which was followed by a very low death rate, the survivorship curve of isolated *B. dorsalis* was classified as Type III.

We also observed the upsurge of death in 3–4 days after isolation in *S. invicta* and *B. dorsalis*. Thus we hypothesize the existence of the initial shock effect, which occurred within 4 to 5 days after isolation. Three scenarios are schematically displayed in Fig. 3. In addition to the abrupt change and smooth change scenarios, a third was introduced which we called the shock effect scenario. It is characterized by a sharp increase in death rate shortly after the links are severed. For living organisms without any interactions among one another, separation from their neighbors would not increase their mortality. By contrast, for interconnected organisms, a significant difference is expected upon separation from their neighbors. Lihoreau et al. [10] indicated social deprivation induced gregarious cockroaches (*Blattella germanica*) a decrease activity level. Thus, social deprivation may also cause insects to have an increased mortality in few days after isolation. Further researches and reliability data were need to prove our hypothesis.

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