

How does group interaction and its severance affect life expectancy?

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Abstract The phenomenon of apoptosis observed in cell cultures consists in the fact that unless cells permanently receive a “Stay alive” signal from their neighbors, they are bound to die. A natural question is whether manifestations of this apoptosis paradigm can also be observed in other organizations of living organisms. In this paper we report results from a two-year long campaign of experiments on three species of ants and one species of (tephritid) fruit flies. In these experiments individuals were separated from their colony and kept in isolation either alone or in groups of 10 individuals. The overall conclusion is that “singles” have a shorter life expectancy than individuals in the groups of 10. This observation holds for ants as well as for fruit flies. The paper also provides compelling evidence of a similar effect in married versus unmarried (i.e. single, widowed or divorced) people. A natural question concerns the dynamic of the transition between the two regimes. Observation suggests an abrupt (rather than smooth) transition and this conclusion seems to hold for ants, fruit flies and humans as well. We call it a shock transition. In addition, for red fire ants *Solenopsis invicta*, it was observed that individuals in groups of 10 that also comprise one queen, die much faster than those in similar groups without queens.

The paper also examines the corresponding survivorship curves from the perspective of the standard classification into 3 types. The survivorship curves of ants (whether single or in groups of 10) are found to be of type II whereas those of the fruit fly *Bactrocera dorsalis* are rather of type III. In this connection it is recalled that the survivorship curve of the fruit fly *Drosophila melanogaster* is of type I, i.e. of same type as for humans.

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To many readers this paper will appear somewhat unconventional. There is a simple reason for that. It results from a collaboration between physicists and entomologists. Physicists always try to find fairly general rules. Of course, all rules and laws have limitations, but the broader the better¹. This is why this paper does not limit itself to just one specific species but rather offers a comparative approach involving several species. This comparative perspective is one of the unconventional features we were referring to.

A second characteristic of this paper can be explained as follows. Physics experiments are more than just careful observations; they always ask Nature specific questions. If an experiment is well designed² Nature will provide a clear answer. The present study was set up in a similar way. The question that we submit to Nature is the following.

Is the lifespan of living organisms affected by changes in group interaction?

This is not a new question. As a matter of fact, we will see that an attempt to get an answer was made as early as 1944. Yet, to our best knowledge, in the past decades there have been few investigations focusing on this question from a broad comparative perspective.

There is a third noteworthy characteristics of our experimental methodology but we will postpone its discussion until the end of the paper.

The paper is organized as follows. First, we discuss relevant results published in former decades and at the same time we explain how we came to study this question. Secondly, we present our experiments. Their methodology will be discussed and detailed results will be given mostly in graphical form. In the following part, we try to make some sense of our results by considering them in a broad systems science perspective. Finally, in the conclusion, we summarize our results and we discuss a possible agenda for further investigations.

How interaction-changes affect survival: former studies

The present questioning started in September 2005 when we came across a paper describing an experiment done in 1944 by two eminent French entomologists, Pierre-Paul Grassé and Rémy Chauvin³. They separated small groups of social insects (of

¹As an illustration one can recall that the law of free fall discovered by Galileo four centuries ago applies to balls of metal as well as to apples, nuts or hailstones and many other objects falling in air. Yet, it does *not* apply to falls occurring in water instead of air. Even in air the law of free fall no longer holds for small objects of a size under one micrometer.

²Which in particular means that by choosing appropriate experimental conditions the ratio signal/noise should be made as high as possible.

³Whereas Grassé was already well-known, Chauvin who was almost 20 years younger became famous only in subsequent decades. He gave a great impulse to the study of the collective behavior of insects. Unfortunately, due to the invasive development of genetics and molecular biology, this field was progressively deserted which explains that after

1 to 10 individuals) from their colony in order to measure their respective life span. The groups of 10 individuals turned out to have a longer life expectancy than the groups of 1 or 2. The corresponding graphs are given below in Fig. 1.

Of the 3 types of survivorship curves shown in Fig. 1, the simplest one is Type II because it corresponds to a mortality rate that is constant over time and independent of age. Type III corresponds to a very high “infant” mortality (e.g. when thousands of seeds are released of which only a few will grow). In contrast, Type I corresponds to low infant mortality and a mortality rate that becomes substantial only in old age.

Apart from the 3 types of survivorship curves shown in Fig. 1, there is a 4th type namely the so-called bathtub curve. In this case, both the infant mortality and the old age mortality are high and are separated by a range in which the mortality is low and fairly constant (the “bathtub” label originates from this shape). The resultant survivorship curve looks very much like Type III with the addition of a downward section in old age. The bathtub curve applies mainly to technical devices such as ball bearings, electronic components, relays or hard drives.

Of course, the idea that the lifespan of individuals may be affected by their interaction with the group to which they belong was not completely new. Surprisingly, however, very little reliable experimental data seemed to be available on this issue. The results obtained by Grassé and Chauvin were a good starting point because they were clear, straightforward and covered different species.

Then, in 2008 we discovered similar experiments done for cells by Prof. Martin Raff and his collaborators (Ishizaki 1993,1994).

For two different types of cells, they showed that their *in vitro* lifespans increased with their density (see the graphs in Fig. 2). Prof. Raff summarized this result (along with similar ones) by saying that the cells will die unless they get from their neighbors repeated signals saying “Stay alive, stay alive”. These experiments were done in 1993 and 1994. Yet, according to Prof. Raff (in an email of 4 August 2008) few (if any) similar investigations were conducted in the following years. This means that we still do not know what is the field of validity of this mechanism. Is it common to most cells? Is it also shared by bacteria?

Mortality according to marital status

Around the same time, thanks to 19th century data and data from US yearbooks, we became aware of the fact that the death rates of non-married persons (i.e. persons who are single, widowed or divorced) are on average about two times higher

his retirement Chauvin had no followers whatsoever.

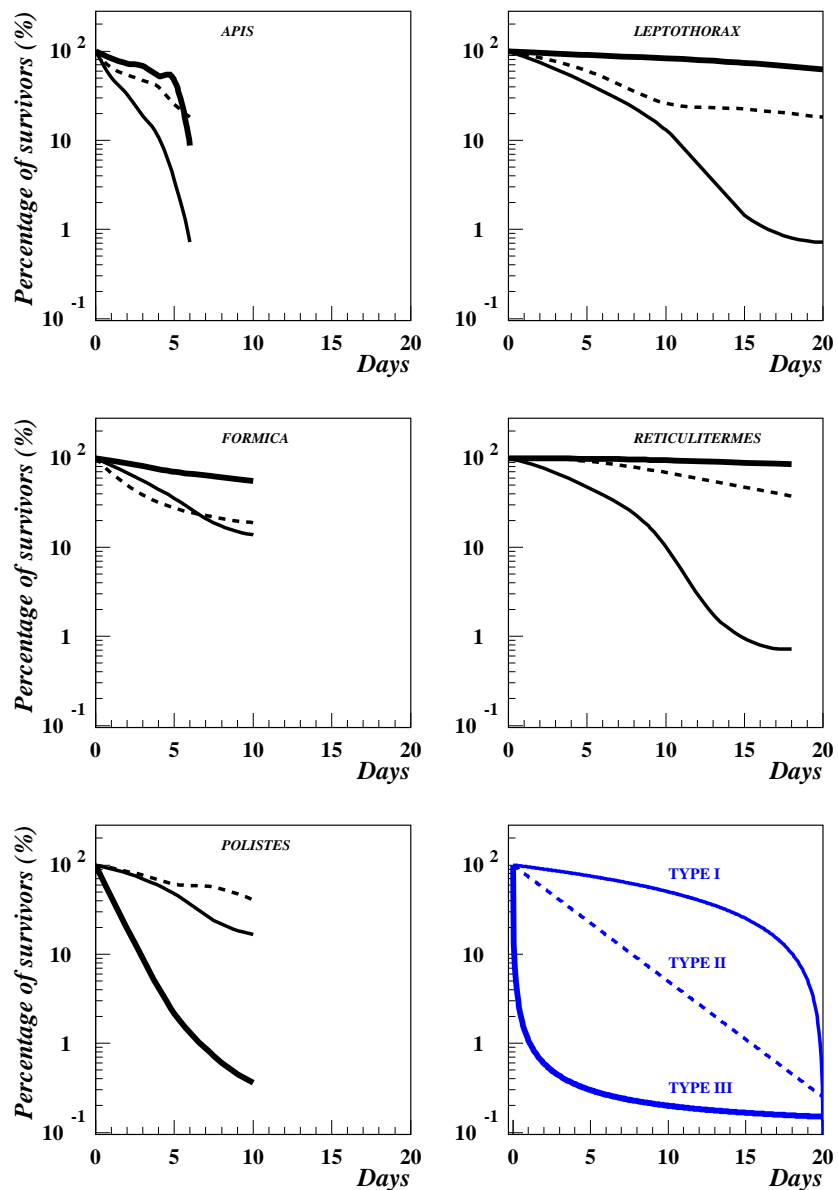


Fig.1 Survivorship curves of social insects removed from their colony. Several groups of 1, 2 and 10 insects were removed from their nest and kept in isolation. They received plenty of food and were kept in conditions which matched as closely as possible those in the nest. The vertical scale shows the cumulative percentage of survivors in each group. The thin solid lines represent single insects, the broken lines represent groups of two insects and the thick solid line represents groups of 10 insects. Initiated in 1944 by P.-P. Grassé and R. Chauvin this kind of experiment may provide a methodology for gauging the strength of the interactions in the colony. *Apis* designates a species of bees, *Leptothorax* and *Formica* are two species of ants, *Reticulitermes* are termites and *Polistes* are wasps. It can be seen that all these survivorship curves are (approximately) of type II, except those for bees which are rather of type I although in this later case the bees die so quickly that the curve is not well defined. The last graph shows the three standard survivorship curves. Type I corresponds to the case of humans (and also drosophila); it is characterized by low death rate for most of the life until an age around 70. Source: Grassé and Chauvin (1944); Roehner (2007, p. 236); see also Arnold (1978).

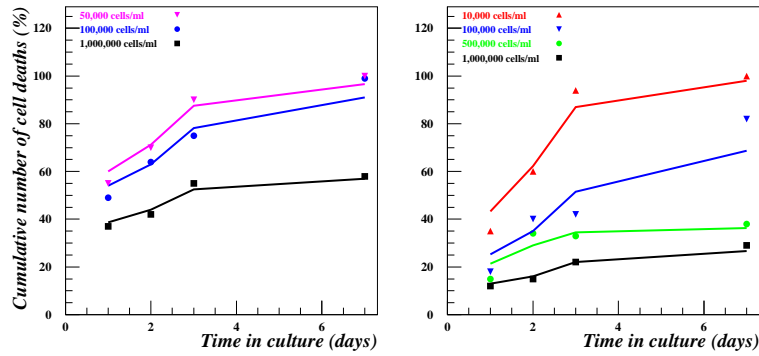


Fig. 2 Relationship between cell-density in culture and their death rate. Left-hand side: cells from the surface (epithelium) of the crystalline lens of rat. Right-hand side: cells from the cartilage of rat. It can be seen that the higher the density, the lower is the death rate. In both cases the culture was made on a gel of agarose which means that the cells were disjoint and could not communicate by contact. *Source: Adapted from Ishizaki et al. (1993 p. 904, 1994 p. 1072).*

than the death rates of married persons. (see Fig. 3a,b).

Bonds between husbands and wives

Before giving fairly recent data we first provide evidence from the 19th century and for different countries. Our purpose is to show that the rule holds not just for one country in a specific times but under a fairly broad range of conditions. Fig. 3a shows the ratios of mortality rates of non-married to married people in France, Belgium and the Netherlands.

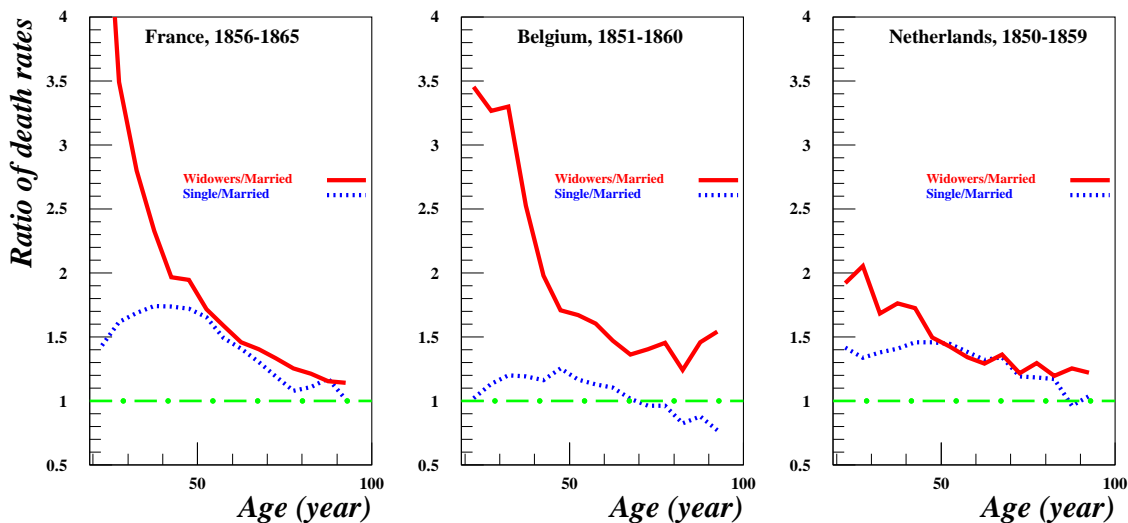


Fig. 3a Ratio of mortality rates according to marital status. The graph is based on mortality rates for 5-year age groups; altogether, from 20 to 95 there are 15 age groups. As a rule, the death rate of married persons appears to be lower than the death rate of non-married persons. The ratio is larger for widowers than for bachelors. The results for females are similar but the effect is weaker. The primary data compiled by Bertillon give death rates of Belgian bachelors above the age of 80 that are on average 1.7 times smaller than corresponding rates in France and the Netherlands; this makes one suspect a possible statistical bias in the Belgian data for this late age interval. *Source: Bertillon (1872)*

The fact that the ratio widowers/married is higher for young people than in old age may at first sight seem surprising. Indeed, one can argue that the bond due to a marriage that has lasted many years should be stronger than the link between young people who got married just a few years ago. If the bond is stronger, then its severance should have a more dramatic effect, a prediction that comes in contradiction with the evidence shown in Fig. 3a. However, to say that the strength of a bond increases in the course of time is just wishful thinking. In fact, the attraction between men and women becomes weaker for old ages; this is not wishful thinking for it is attested by the observation that the marriage rate of single people (for both males and females) decreases steadily after reaching a maximum around the age of 25⁴. Hence, if the attraction is stronger for young people it is natural that the severance of the bond should be more detrimental.

Perhaps some readers may think that attributing the lower death rate of married people to the existence of a bond between them is a conclusion that is drawn too quickly. After all, there could be other explanations. For instance one could argue that the economic situation of married people is on average better than the situation of non-married people. In order to answer this kind of objections we provide two other pieces of evidence.

Bonds between parents and children

It seems plausible to expect the bond between parents and their children to be almost as strong as the bond between husbands and wives. This conjecture is confirmed by the data in Table 1.

Death rate by marital status and by cause of death

The graphs in Fig. 3b give detailed data by marital status and by age for 6 different causes of deaths. The age-group correspond to 10-year intervals. Needless to say, such statistics make sense only for a country with a large population, otherwise there would be too few cases in each cell of the table. Just as an illustration, for widowed men in the 25-34 year age group there were only 54 suicides and 7 deaths due to cancer.

Quite surprisingly, the excess mortality due to the marital status is broadly the same for various causes of mortality ranging from heart attack to suicide or accident. So, once again, reduced ties result in higher mortality. As a matter of fact, these data raise more questions than they provide answers. Unfortunately, as far as statistical data are concerned, one can hardly expect more detailed statistics. Hence, if one wishes to get a better understanding, one needs an alternative approach that would allow us to perform more focused experiments.

⁴The rate is of course computed with respect to the population of bachelors present at each age; it shrinks quickly after the age of 25.

Table 1: Effect on suicide rates of husband-wife bonds and parents-children bonds

Situation	M	F	M	F
Married with children	20	4.5	1	1
Married without children	47	16	2.4	3.6
Widowed with children	52	10	2.6	2.2
Widowed without children	100	23	5.0	5.1

Notes: The table gives suicide rates (per 100,000 people) in France in the 8 years between 1861 and 1868. “M” means male, “F” means female. The two columns on the right-hand side repeat the same data with a different normalization. If one accepts the hypothesis (made by Emile Durkheim and other sociologists of the late 19th century) that it is the severance of bonds and especially of family bonds which is the main social factor in the phenomenon of suicide, then these data allow us to compare the respective strengths of the bonds between husband and wife on the one hand and between parents and children on the other hand. The fact that the increase in the suicide rate is almost the same through widowhood or through lack of children suggests that these bonds have almost same strength.

Source: Bertillon (1879, p. 474)

Alternative approach

That is how the present collaboration between entomologists and physicists emerged. The active phase of this investigation started in September 2010. Within the past two years a broad but well focused set of experiments were performed. Each of them lasted about one month and many were repeated several times. Our major objective was to establish with high reliability whether or not the effect really exists. As will be seen the answer is “yes”. Moreover, the experiments show that the effect is not limited to social insects but occurs also for such non-social insects such as fruit flies⁵.

We realize very well that the present results are only the beginning of this interesting story and that more experiments are needed in order to identify basic mechanisms. Our hope in writing this paper is that it can encourage further investigations in this direction.

Objectives of the present paper

In this paper we will try to answer the three following questions.

- It is customary to distinguish 3 types of survivorship curves. Such a classification is based on curves that give the logarithm of the proportion of surviving elements as a function of age. Type 1 curves are flat for most of the life-time and fall off rapidly in old age. Human survivorship curves are of this type. Type 2 curves fall off linearly; examples will be given below. Type 3 curves drop sharply in early life and then level off in later life. To what type belong the survivorship curves of the ants investigated in this paper?

⁵For the *Bactrocera dorsalis* species that we tested, “tephritid fruit flies” would be the more correct term but, for the sake of simplicity, this precision will be omitted thereafter.

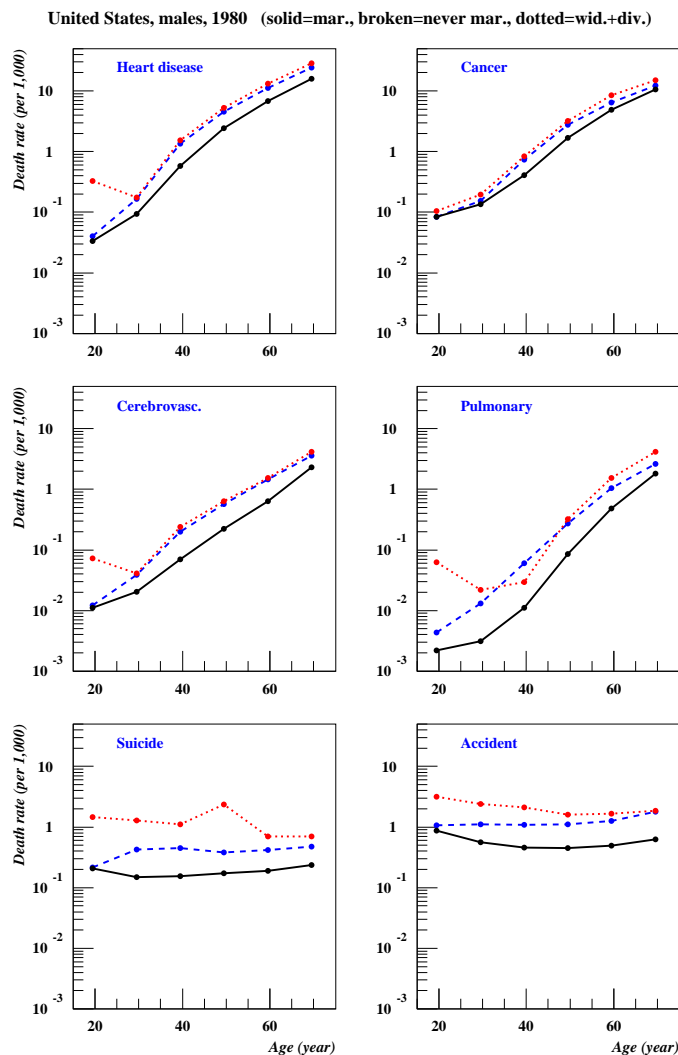


Fig. 3b Mortality rates by cause of death according to marital status. On average the death rate of non-married persons is about twice the rate of married persons. For cancer the ratio is somewhat smaller but for the suicide of widowers and divorced males it is a factor of about 5. There is a similar but somewhat weaker effect for females. Similar data are available also for 1979 and show very much the same effect. In terms of life expectancy the higher mortality rate results in a reduction of about 4-5 years. This fairly small reduction is due to the fact that doubling a death rate that is very low (as is the case until the age of 60-65) does not produce much difference in life expectancy. *Source: Vital Statistics of the United States, 1980.*

- Do our experimental results show evidence of a group effect? More specifically, are the survival rates of 10-ant groups higher than those of single ants?
- If the answer to the previous question is “yes”, does observation suggest a mechanism for this effect. At this point it would be too early to propose a detailed mechanism. Instead, we will consider more closely two types of effects: (i) a “shock effect” that occurs shortly after the ants are separated from their colony. (ii) A long-term effect that slowly erodes the survival likelihood of the ants. While the existence of the second effect seems fairly expected and unsurprising, the role of the first one is less obvious. Yet, as will be seen, it plays a significant role.

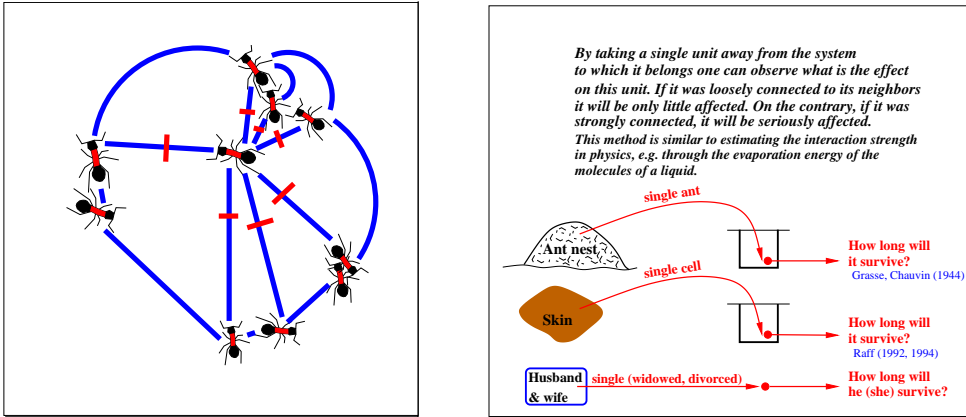


Fig. 4a (left): Schematic representation of the links within a group of ants. If (within a range of a few centimeters) the interaction between pairs is not distance dependent, then the interaction within a group of size n will increase approximately as the number of ties, that is to say as $\binom{n}{2} \sim n^2/2$. Fig. 4b (right) summarizes the severing of the ties that link an unit to its neighbors in different situations.

Experiments

In the first part we describe the experiments with various species of ants. The experiments with fruit flies are described in the second part. Then we discuss our procedure in the light of other possible methods.

Ants

The ants used in the experiments were taken from artificial colonies kept in the laboratory. They were placed in plastic bowls which had a lower diameter of 4.3cm and an upper diameter of 10.5cm. To prevent the ants from escaping the upper sides of the bowls were painted with Fluon⁶.

With only one ant per bowl the density will be 7 ants per square decimeter on the bottom of the bowl. With 10 ants per bowl the density will naturally be 10 times higher that is to say 70 ants per square decimeter. In other words, this means that each ant will have an area of 1.4 square centimeter. When ants form clusters their density can easily be of the order of 20 to 30 per square centimeter that is to say some 35 times higher.

The different replicas (30 were used in the first experiment but in subsequent experiments there were usually about 10) were placed on tables with a distance of 60cm

⁶It is important to understand how Fluon works for otherwise one might be tempted to think that it is through the toxicity of its chemicals that it repulses ants. Needless to say, such a toxicity could affect the experiments.

Fluon is a white liquid containing small (less than one micrometer in diameter) particles of a solid substance called polytetrafluorethylene, a non-stick material better known under its brand name of Teflon. It has been used to control the movements of ants as early as 1956 (see Merton 1956). It works by preventing ants from using the adhesive pads that they have at the end of their legs. The role of this pads becomes clear by observing that ants which have been made to walk on French chalk can no longer climb up a vertical glass tube (Merton 1956, p. 219). In short, toxicity does not seem to play any role.

between adjacent bowls. Thus, altogether the 60 bowls occupied a surface of 21 square meters. Each contained a tampon with sugar water which was changed every week.

Average death rate of ants in their colony

What is the lifespan of the ants in normal conditions that is to say in their nest? In the case of the red fire ants (*Solenopsis invicta*) one can distinguish three subgroups of workers according to their size: minor, medium and major ranging from 1.5mm to 3mm. For each kind estimates of their average lifespan are 45 days, 75 days and 135 days respectively⁷. In order to get an overall average life span for the whole population we need to estimate the proportion of each subgroup in our colonies. To this end several samples containing between one and two hundred ants were taken, photographed and counted. This lead to the following percentages (the coefficient of variation for the various samples was of the order of 30%):

minor: 62%, medium: 28%, major: 10%

which in turn gave the following weighted average for the lifespan:

Average lifespan of red fire ants $L \simeq 62$ days

What is the average mortality rate corresponding to this life expectancy? L gives a daily death probability of $1/L$; consequently, the death rate per day and per 1,000 ants will be $1000/L = 16$. We will see later that the average death rate of isolated ants is about 2 or 3 times higher.

Fruit flies

The fruit flies *Bactrocera dorsalis* were reared in the laboratory. As they are about 3 to 4 times bigger than the ants, they needed larger containers. Moreover, in order to prevent them from flying away the cages had to be closed. The cages were (30cm, 30cm, 30cm) cubes with wooden frames and sides consisting of gauze except for the top side which had Plexiglass to allow easy inspection. The fruit flies were adult unmated females. They were given water, yeast and sugar. There were 30 replicas with a spacing of 60cm between the cages.

The bowls and cages were inspected every 12 hours.

Experimental procedures

In what will be called the main experiment there were two kinds of cells: those containing just one worker, and those with 10 workers. It must be observed that in addition to this experiment, different variants were carried out which involved the following changes.

- (1) In variant (1), a queen was added to the *Solenopsis invicta* workers. Thus,

⁷Website of the University of Florida Institute of Food and Agricultural Sciences.

there were two kinds of cells: those containing 1 worker + 1 queen and those with 10 workers + 1 queen.

(2a) In variant (2a) the ants received water but no sugar.

(2b) In variant (2b) the ants received neither water nor sugar.

Starvation procedure

The main purpose of experiments (2a) and (2b) was to make the experiment faster. Whereas from the start to the death of all ants the main experiment lasted almost 30 days⁸, variant (2a) lasted only 8 days for *Solenopsis* and 2.5 days for *Bactrocera*. Not surprisingly, variant (2b) was even shorter: 2 days for *Solenopsis* and 2 days for *Bactrocera*. These experiments were inspired by those done in December 1972 - January 1973 by Rémy Chauvin on bees (Chauvin 1973). Chauvin observed that for single bees death rates were some 2 to 3 times higher than in groups of 10, a result which was consistent with those obtained previously by Grassé and Chauvin in 1944 (Fig. 1). This supported the hope that meaningful results could be obtained in a much shorter time than in the main experiment.

However, the experiments that we have done for *Solenopsis* and *Bactrocera* did not lead to any clear results. Altogether 5 graphs were drawn:

Solenopsis: (water, no sugar) + (no water, no sugar)

Bactrocera: (water, no food) + (no water, food) + (no water, no food)

In all cases except one the death rates of the two sorts of groups were almost the same. The only case which showed a difference was *Solenopsis*, (water, no sugar). In this case, after 8 days the cumulative deaths in the 10-ant groups was 2.3 times *higher* than the deaths in the 1-ant group. These mostly meaningless results lead us to drop this methodology⁹.

Before we close this discussion about starvation experiments, it can be of interest to mention that this procedure was also used by another group, as documented in Miramontes et al. (1996) and in DeSouza et al. (2001). This team conducted survival experiments on groups of termites of various sizes, namely 1,2,4,8,16 in the paper of 1996 and 1,2,4,8,12,16,20 in the paper of 2001. All in all, their results were more orderly than our starvation results. In the experiment of 1996 for the groups of 16 (there were 4 replicas) 64% of the termites were still alive after 3 days when the experiment was stopped whereas all isolated termites had died within the first two days. In the experiment of 2001 the longest survival occurred for the groups of 4,

⁸For *Bactrocera* the duration was even much longer. After 40 days, 30% of the single flies and 12% of those in groups of 10 had died. Then, between day 40 and day 70 for some unknown reason there was a rapid increase of the mortality in the 10-fly groups. On day 70 when the experiment was stopped one half of the single flies and one fourth of flies in the 10-fly groups were still alive.

⁹It can be added that the necessity of making the insects starve was fairly unpleasant which explains that we were rather glad to forget this method.

8 and 12 whereas the average life durations in the groups of 1, 2 and also (more surprisingly) 16 and 20 were about 40% lower.

Possible procedures with respect to dead insects

Whereas the 1-ant cells were just removed after the death of the ant, for the 10-ant cells several experimental procedures were possible.

- Each dead insect could be replaced by a new living insect so as to maintain the same number of 10 throughout the experiment.
- The dead ants could be left in the bowls.
- The dead ants could be removed at time of inspection which means that their corpses may remain in the container for a maximum of 12 hours.

It is the last option which was selected. Of course, it would be interesting to see whether or not the two other options lead to similar results. This is a point which may be investigated in the future.

The main features of the different experiments are summarized in table 2.

Experimental results for groups with 1 versus 10 workers

The figures 5 and 6 give detailed results for each separate experiment. Why did we choose to give separate results rather than just global averages? The reason is very simple. For most experiments the groups of 10 had a lower mortality than the singles, yet there were a few exceptions. We do not wish to hide such exceptions behind global averages (which will be given later). Needless to say, the fact that a replication gives a result which contradicts the initial experiment is quite intriguing and one would like to know the reason for that. This is not easy, however, because there are many possible explanations and in order to determine which one is correct one needs to perform numerous control experiments.

Just to give an idea of the kind of effects that may be involved, we recall a similar problem which arose in survival experiments done by Rémy Chauvin (1952). In 1952 he tried to replicate his experiment of 1944 (summarized in Fig. 1). In this second experiment the bees received exclusively sugar water with 20% sugar. Chauvin was very surprised to see that the results were opposite to what he had observed in 1944 in the sense that the mortality was higher in the groups with many individuals than in those with only a few¹⁰.

Eventually, Chauvin came up with the following explanation. The bees in large groups were more active and therefore absorbed more sugar water. However, for

¹⁰Actually, Chauvin should not have been so surprised. Indeed, what is very clear from Fig. 1 is that the bees die *quickly*; however, the difference between groups of 1,2 or 10 is fairly small. In other words, the shock of being cut off from their colony is so strong that even a few neighbors make no difference.

Table 2: Summary of the experiments

Date	Insect	Species	Average size [mm]	Replic.	Replic.	Mortality ratio
				1 W	10 W	(1)/(10)
1 25 Sep 2010	ant	Solenopsis inv.	2	30	30	2.25
2 18 Dec 2010	ant	Solenopsis inv.	2	9	9	1.10
3 12 Jan 2011	ant	Solenopsis inv.	2	10	10	0.93
4 6 Sep 2012	ant	Solenopsis inv.	2	10	10	1.95
Average (1-4)						1.80±0.3
				1 W	10 W	(1)/(10)
5 18 Dec 2010	ant	Pheidole pall.	2	13	10	2.12
6 18 Dec 2010	ant	Tapinoma mela.	1.5	23	11	0.70
Average (1-6)						1.62±0.2
				1 fly	10 flies	(1)/(10)
7 15 Nov 2010	fruit fly	Bactrocera dors.	8	20	8	2.12
				1W+Q	1W	(1W,Q)/(1W)
8 18 Dec 2010	ant	Solenopsis inv.	2	9	9	2.00
9 12 Jan 2011	ant	Solenopsis inv.	2	10	10	1.43
10 6 Sep 2012	ant	Solenopsis inv.	2	10	10	1.00
Average (8-10)						1.48±0.3
				10W+Q	10W	(10W,Q)/(10W)
11 18 Dec 2010	ant	Solenopsis inv.	2	9	9	6.00
12 12 Jan 2011	ant	Solenopsis inv.	2	10	10	1.30
13 6 Sep 2012	ant	Solenopsis inv.	2	10	10	2.00
Average (11-13)						3.10±1.5

Notes: All mortality ratios were computed 20 days after the experiments started even when the experiment lasted longer; this ensured that the number of ants in the groups of 10 did not fall off too much. The error bar indicated after \pm is the standard deviation (which corresponds to a confidence level of 0.68). Each experiment lasted about one month. The dates refer to the end of the experiments. The replication columns refer to the number of groups of each kind that were observed in parallel. W means worker, Q means queen. The size of the insects was indicated because it is well known that bigger insects survive longer but one does not expect size to play a role in the mortality ratio.

Source: *Experiments done at South China Agricultural University.*

some reason, it seems that the sugar syrup made them ill. Their abdomen was inflated and eventually they died. It is possible that some kind of bacteria had developed in the syrup. It was changed only every 5 days. So the more active the bees, the more of the deadly syrup they absorbed and the quicker they died.

This story also shows the limit of control experiments. If no bacteria develop during the control experiment the result will be different once again.

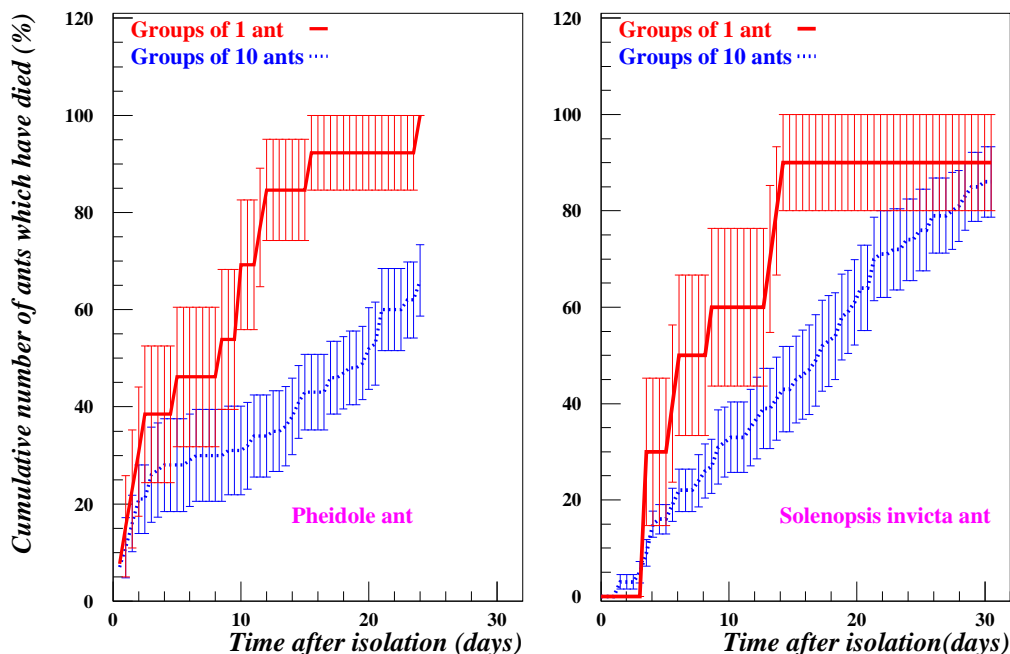


Fig. 5 Two examples of graphs with error bars. For the left-hand side experiment (which corresponds to number 5 of Table 2) there were 13 groups of 1 ant and 10 groups of 10 ants. For the experiment on the right-hand side (which corresponds to number 4 of Table 2) there were 10 groups of 1 ant and 10 groups of 10 ants. At each time step the standard deviation σ of the cumulative number of deaths in each box was computed. The error bars show $\pm\sigma$. Under the (standard) assumption of a Gaussian distribution this corresponds to a probability confidence level of 0.68. It is customary to say that one curve (the red one) is *significantly* higher than another (the blue one) when their error bars do not overlap. Of course, such a statement is confidence level dependent. For a confidence level of 0.99 the error bars would be 2.58 times wider which would make them overlap. Thus, it can be said that our conclusion holds with probability 0.68 but to confirm it with probability 0.99 would necessitate additional observations. *Source: The experiments were performed at the South China Agricultural University in November 2010 and September 2012 respectively.*

Experimental results for groups with/without queen

The experiments considered in this section are similar to the fire ant experiments done in the previous section except that a queen was added to each of the groups. What was our purpose in adding queens?

First of all, it must be recalled that fire ant colonies have several queens. For species whose colonies contain only one queen it is a common idea that the queen is a crucial node in the global colony network (although we do not know precisely how this node is integrated in the rest of the network). Even for species whose colonies have several queens it is natural to assume that in the colony's organization the queens play a more important role than ordinary workers. In adding a queen to the isolated groups one may expect them to become mini-colonies in their own right. This idea was particularly plausible for groups of 10 ants, which is why our analysis will mainly focus on this case. Under the assumption that groups of 10 ants plus one queen

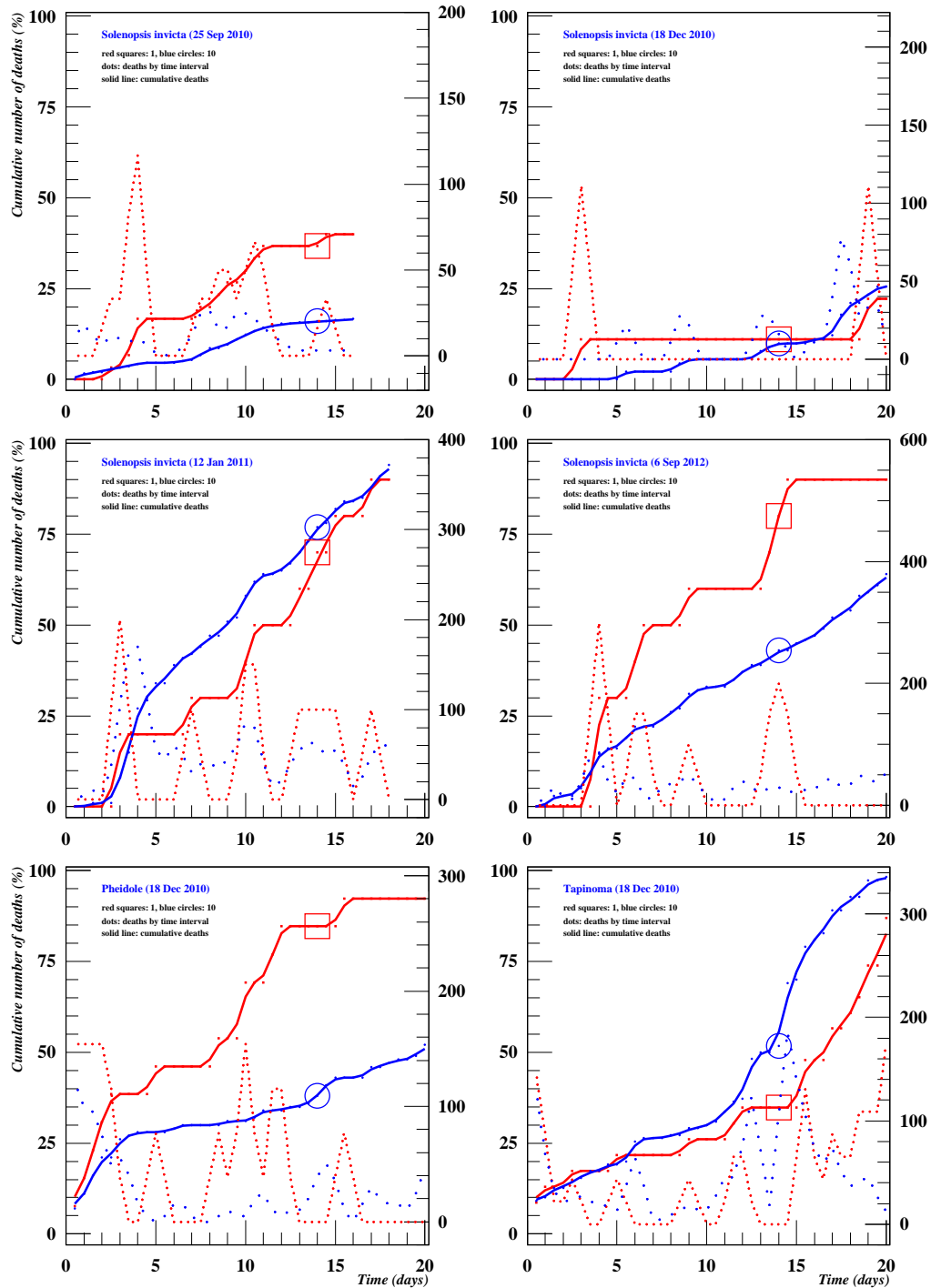


Fig. 6 Survival experiments with 1 or 10 workers per group. The solid line curves give the cumulative numbers of deaths whereas the dotted curves give the death rates per 1,000 individuals in successive 24-hour intervals that is to say the number of deaths during such intervals divided by the living population at the beginning of the interval. Graphs 1,2,3 and 4 are replications of the fire ant experiment, while graphs 5 and 6 concern two different species of ants. It can be observed that there is often a big surge of deaths at the beginning of the experiment especially for single ant groups. *Source: These experiments were done at the South China Agricultural University at various times between September 2010 and September 2012.*

become mini-colonies one expect them to survive longer than groups of 10 without

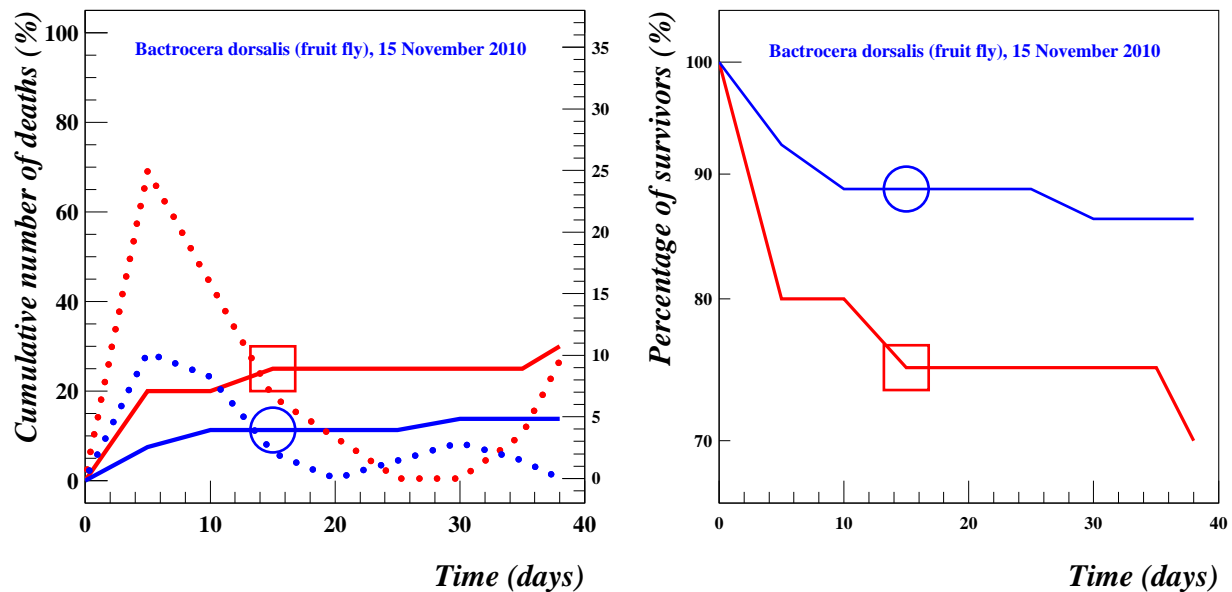


Fig. 7 Survival experiment for fruit flies. As in the previous graphs, the red solid line with the square represents single-individuals (20 groups) while the blue solid line with the circle represents the 10-flies groups (8 groups). The dotted curves represent the daily death rates per 1,000 individuals. Compared with the ant experiments, the mortality is much lower. The dotted-line curves show the daily mortality rate (expressed in number of deaths per insect). It can be seen that there is a big mortality burst at the beginning of the experiment. After that the mortality is very low.

The graph on the right-hand side shows the survivorship curve. It belongs to type 3. In fact, the experiment was continued until day 70. After day 45, for some unknown reason, the mortality in the groups of 10 started to grow and eventually their cumulative number of deaths crossed and surpassed the curve of singles. *Source: This experiment was done at the South China Agricultural University in October-December 2010.*

queens.

However, as seen in the graphs that are on the right-hand side of Fig. 8, the experiments showed exactly the opposite. That was a big surprise. How can one interpret this result?

When an element has very few interactions with its neighbors, its isolation will make little difference; hence, one expects little or no reduction in life expectancy. On the contrary, for an element which interacts strongly with its neighbors isolation will be a great shock; therefore one would not be surprised to see a sharp reduction in life expectancy. This is schematized in Fig 4a,b. The conclusion which derives from this argument is that the groups of 10 ants plus one queen have a stronger interaction with the rest of the colony than the groups of 10 ants without queen. This is a natural conclusion in spite of the fact that, so far, we do not understand the mechanism of this interaction.

Systems science perspective about survivorship

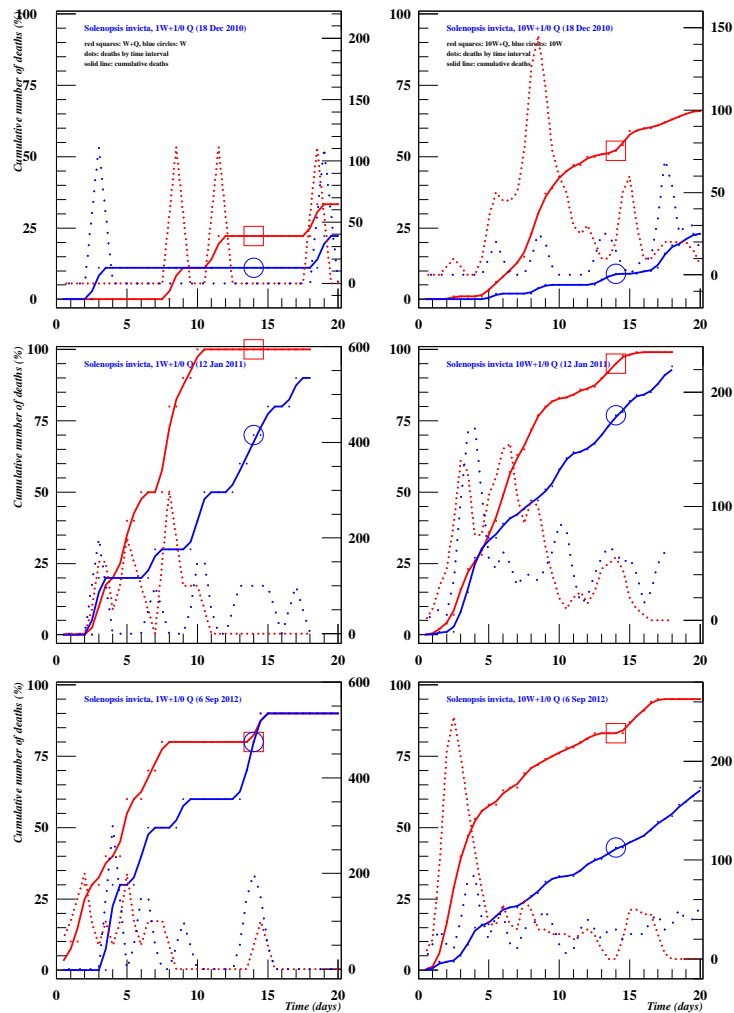


Fig. 8 Survival experiments with or without queen in the groups of workers. The graphs in the first column give a comparison of groups of 1 worker with or without queen. The second column compares groups of 10 workers with or without queen. It should be noted that only the deaths of the workers were recorded, so the proportions refer to the ratios: (deaths of workers)/(Initial number of workers). the dotted curves represent daily death rates per 1,000 individuals. *Source: The experiments were performed at the South China Agricultural University in November-December 2010 and in September 2012.*

In the following sections we will draw parallels between systems which, at first sight, seem to be very different. We realize very well that in current conceptions such comparisons may appear questionable and far-fetched. However, we believe that such reservations more due to our own peculiar position in the observation process rather than to objective factors. The key-point is that systems of living organisms are of macroscopic dimension which means that we can easily observe them. In physics we easily accept that the same rules applies to very different objects because we do not realize how dramatically different they are. This results from our inability to observe them directly. Before we discuss survivorship curves for ants and other organisms we wish to explain and illustrate this important point through a specific case.

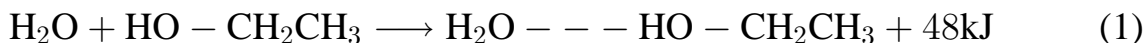
Binding energy in systems science perspective

What makes the strength of physics is the fact that its laws have a broad range of validity. An obvious example is the law of free fall that we already mentioned at the beginning. A hazelnut or an apple have little in common with the Moon, yet their movements are governed by the same law.

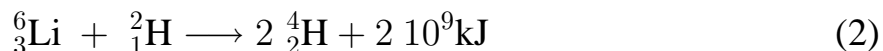
Here is another illustration that is not so well known but is more germane to the topic of this paper. There is a basic rule which says that the creation of links is an exothermic process whereas breaking existing links requires heat to be applied to the system and is therefore an endothermic process.

Water molecules versus protons and neutrons in nuclei

A well-known illustration is the boiling of water in which the links between water molecules are severed. A less-trivial example is the mixing of water and ethanol. If the mixing is done with same volumes of water and ethanol it evolves about 200 calories (48 kJ) per mole of mixture (Bose 1907). This release of heat is the consequence of the fact that the mixing results in strong hydrogen bonds being established between water and ethanol molecules¹¹:



Yet another completely different case where the same rule applies is the “mixing” of lithium and deuterium nuclei¹²:



Writing these reactions in the same form as in (1) and (2) conveys the impression that the two cases are fairly similar. In fact, there are huge qualitative differences between them as we will see now.

- First, we can see that the amount of energy that is released is tremendously higher for reaction (2). In fact, even for a nuclear reaction the energy produced in (2) is particularly high. This is due to the fact that the α particles that are created have a very high binding energy per nucleon. In this sense (2) provides a good illustration of the general rule.

- One should realize that in (2) the energy is released in completely different ways than in (1). Whereas in (1) the energy is released as heat, in (2) it is produced

¹¹Actually, the heat that is released is the difference between the energy that it takes to push the water and ethanol molecules apart and the energy that is produced by the creation of the water and ethanol molecules. The fact that heat is released rather than absorbed shows that the latter is larger than the former.

¹²Li designates lithium, the second nucleus is deuterium. The upper figure is the number of protons and neutrons, the lower figure is the number of protons. The two nuclei which are produced are so-called α particles. More details can be found in the following Wikipedia article:

http://en.wikipedia.org/wiki/Nuclear_reaction

in the form of (i) high energy light rays called gamma rays (ii) kinetic energy of the α particles. It is because we *now* know that these effects are just different forms of energy that we can establish a parallel between (1) and (2).

- Needless to say, the lithium, deuterium and α nuclei are very different from the water and ethanol molecules. First, there is a huge difference in size. The diameters of water and ethanol molecules are 200 picometer ($1\text{pm}=10^{-12}\text{m}$) and 500pm respectively¹³, whereas the diameter of an α particle is $4 \cdot 10^{-3}$ pm. In other words, the difference in size is much larger than between ants and humans.

- In terms of interaction, the nuclei of reaction (2) are also much different from the molecules of reaction (1). The intermolecular attraction is an electrostatic force that depends on the spatial distribution of electrical charge of the molecules whereas the protons and neutrons of the nuclei are held together by the so-called nuclear force which is independent of electric charge.

Before we close this discussion we must devote a few words to an apparent paradox that will certainly come to the mind of the reader. It is the fact that *some* fission reactions can release huge amounts of energy as seen in the atomic bomb.

Explanation of the paradox of fission reactions.

At first sight, the rule stated above seems to be contradicted by nuclear fission reactions. As one knows, by breaking up a heavy nucleus such as uranium-235 or plutonium-239 into two smaller nuclei one can obtain the release of a substantial amount of energy. Such energy is used in nuclear bombs and reactors.

However, this effect is due to what can be called an “anomaly”. It results from a competition between two forces: on the one hand there is the nuclear force which binds together the protons and neutrons but has a very short range and on the other hand there is the electrostatic force which is a repelling force (at least for the protons) of much larger range and which therefore tends to dominate for large nuclei. This explains why most of the large nuclei are in fact unstable.

This explanation can equivalently be presented in terms of binding energy. By convention a bound state such as a nucleus has a *negative* energy¹⁴ whose absolute value is the binding energy, i.e. the energy that must be applied to separate all components. The higher the binding energy per nucleon the more stable is the nucleus. As a function of nucleus size this maximum occurs in the vicinity of iron. Most nuclei which are bigger than iron nuclei are unstable and that instability increases as the nuclei become bigger. It is because of this anomaly that a fission reaction can release

¹³In ethanol, the average distance between two molecules is about 700pm (by dividing the volume of one mole by Avogadro's number one get the volume of the space allowed to each molecule from which the previous value derives easily).

¹⁴This is because of the convention which attributes a zero potential energy to the state in which all constituents are far apart from one another.

energy.

In contrast, the phenomenon of fusion of two light nuclei is a more “normal” nuclear process because in this case the electrostatic force is negligible.

In the early 20th century when physicists started to study nuclear reactions they were altogether ignorant about nuclei and nuclear forces and almost as ignorant about intermolecular forces. In a sense that is what allowed them to make bold assumptions. Nobody was shocked because nobody had a clear understanding of the qualitative differences between molecules and nuclei. On the contrary, the organization of ant colonies has been known for at least three centuries (e.g. see the work of the French naturalist Réaumur¹⁵). Needless to say, our knowledge of human societies is even much older. However, knowledge does not necessarily imply understanding. Our point is that too detailed knowledge may be an obstacle to overall understanding.

Survivorship curves

Mortality curves are fairly erratic. On the contrary, survivorship curves which are derived from the former by the operation of running summation (which for a continuous variable would correspond to an integral), are much smoother. That is why three standard types could be defined which are shown in Fig. 1.

In this section, we discuss the survivorship curves observed in our experiments. For comparative purpose we also consider survivorship curves for a number of other cases in the hope of throwing some light on our observations.

Survivorship curves for ants are of type II

At the beginning of the paper we mentioned that it is customary to distinguish three types of survivorship curves but we did not yet provide examples nor did we say to which type belong the survival charts given in the previous section. Fig. 9 shows that all ant survivorship curves recorded in our experiments are of type II. On the contrary the curve for *Bactrocera dorsalis* is of type III.

Survivorship curves for ant colonies (type II)

So far we focused on the survival of individuals. What about the survival of *organizations*? From a systems science point of view there is no crucial difference between individuals and organizations for both are a collection of various elements held together by their common interactions. However, it can be argued that individuals are systems that are more integrated than organizations. For instance it is possible to split an organization into two parts (as when one half of a beehive forms a swarm

¹⁵Ren-Antoine Ferchault de Raumur (1683-1757) wrote a “Histoire des Fourmis” [Natural history of ants] which was published only in 1928.

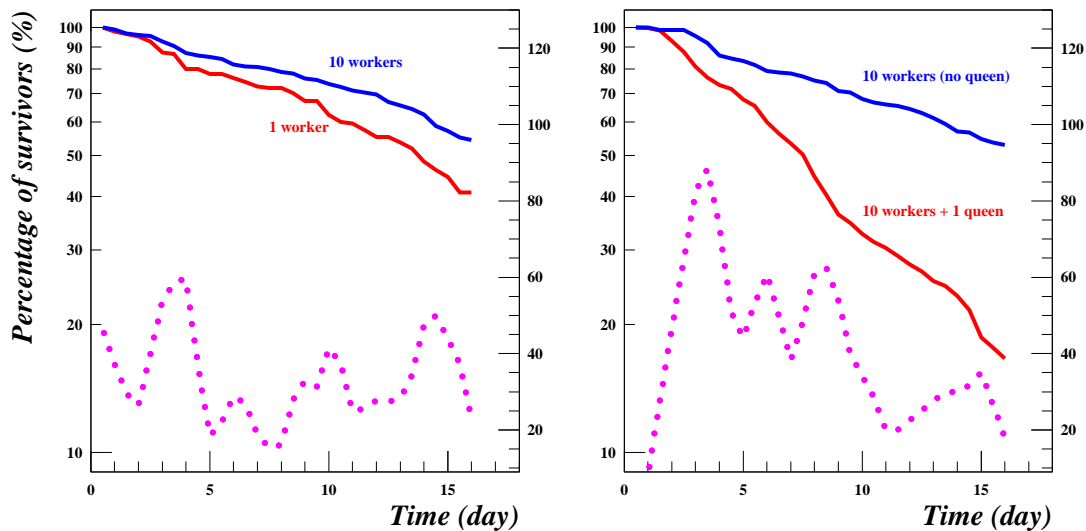


Fig. 9 Averaged survivorship curves for ants. The graph gives averages of results obtained in similar (but separate) experiments. The graph on the left-hand side is an average over 4 experiments in which one compares groups of 1 and 10 whereas the graph on the right-hand side is an average over 2 experiments in which one compares groups of 10 with or without queen. The dotted curves give daily mortality rates expressed in deaths per day and per 1,000 individuals. The graphs suggest two conclusions: (i) the survivorship curves are of type II (almost constant mortality rate) (ii) Nevertheless in the 4 days just after isolation there is an upsurge in mortality that is significantly higher than subsequent fluctuations. *Source: Results of individual experiments given in Fig. 6 and Fig. 8.*

and leaves the colony) whereas individuals cannot be divided into two parts (except fairly rudimentary organisms, e.g. worms).

Fig. 10 shows the survivorship curve for colonies of harvester ants, *Pogonomyrmex barbatus*, in a place near the borderline between the US states of Arizona and New Mexico. The curve is based on an annual census of colonies performed by the team of Prof. Deborah Gordon over a period of 28 years. In an area of about 10 hectares ($250 \times 375\text{m}$) all new or extinct colonies were recorded every summer. The colonies that do not survive until they are 1 year old are not included. The “infant mortality” in the first year can be estimated separately by comparing the numbers of reproductives and the numbers of new 1-year old colonies the following year. In this way, it was found that fewer than 10% of the new colonies survive through the first year.

At first sight, the parallel made in Fig. 10 between the survival of ant colonies on the one hand and high-tech corporations on the other hand may seem surprising. However, from a systems science perspective the two processes are not so different. In both cases, the organization has in principle the potential to develop but its growth can be curtailed by a number of adverse conditions. In that perspective the graph suggests a similarity in the balance between growth factors and growth obstacles, whether exogenous or endogenous.

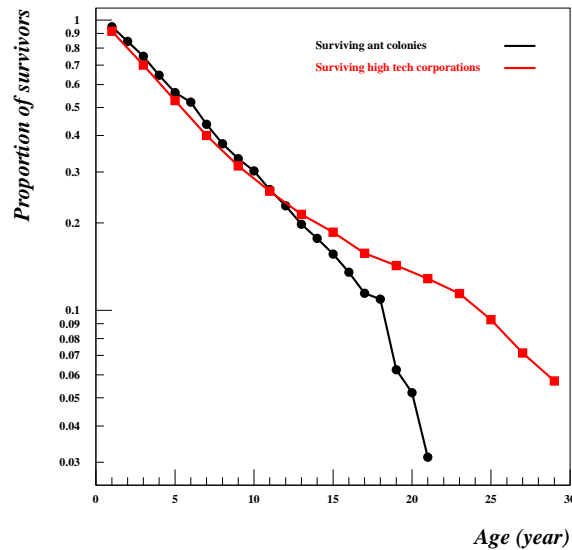


Fig. 10 Survivorship curves for ant colonies and information technology corporations. The curve for ant colonies is based on a sample of 265 colonies. the curve for high-tech businesses (in fact mostly information technology companies) is based on a sample of 23,874 corporations in existence between the years 1998 and 2009. *Sources: Ingram (2013, p. 7, Fig. 4a), Luo and Mann (2011, p. 9, chart 6). The authors would like to thank Prof. Gordon for drawing their attention on the data for ant colonies.*

Survivorship curves for humans and drosophila (type I)

We already alluded to the fact that the human mortality curve has the same shape as the mortality curve of drosophila. If this is true for the mortality curve it is of course even more true for the survivorship curve which is basically the integral of the mortality curve.

It is not clear whether the so-called r/K theory¹⁶ is able to provide a convincing explanation of the parallelism observed in Fig. 11.

Transition dynamics from low to high mortality

When a person becomes widowed does his (or her) mortality rate immediately jump to the higher level which characterizes this new situation or does it increase toward that level progressively with a time constant of a few years? The same question can be asked for ants that are isolated from their colony except that in this case we do not know very well the death rate before isolation that is to say in the colony.

¹⁶The two letters refer to the notation used to write the Verhulst (also called “logistic”) equation namely:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right)$$

r -species have many offsprings while K -species have few offsprings and live in fairly dense habitat. Thus, drosophila would be an r -species while humans would be a K -species.

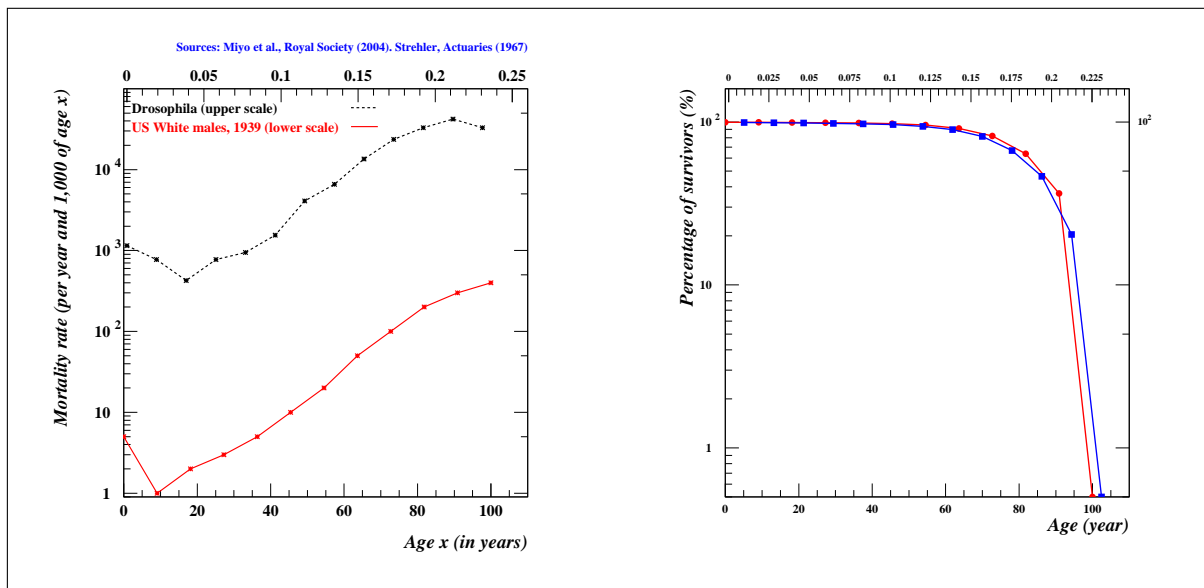


Fig. 11 Age-specific mortality rate for humans versus *drosophila*. The two curves on the left-hand side display three common characteristics: (i) High mortality shortly after birth (ii) exponential growth (Gompertz law) in middle age (iii) leveling off in old age. The graph on the right-hand side shows the corresponding survivorship curves which are the cumulative sums of the mortality data. Sources: Men: Strehler (1967); *drosophila*: Miyo and Charlesworth (2004)

Three scenarios

Three different scenarios are schematically displayed in Fig. 12.

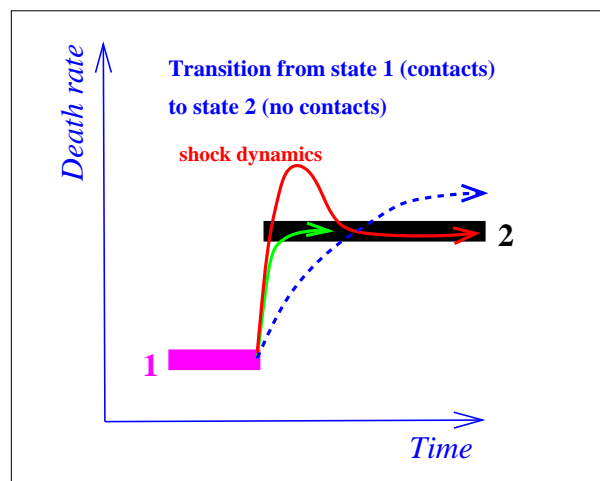


Fig. 12 Three scenarios for the transition to a higher death rate. The shock scenario is characterized by a death rate that becomes temporarily higher than the stationary long-term rate.

In addition to the abrupt change and smooth change scenarios mentioned above there is a third one that we called the shock scenario. It is characterized by a sharp increase in death rate shortly after the links are severed. Below we describe some pieces of evidence which support such a scenario.

Evidence in favor of the shock scenario

First we consider the case of ants. The graphs of average daily death rates show an

upsurge of deaths in the 3-4 days after ants or fruit flies were put in isolation. This effect is not due to the averaging process as can be seen by examining the graphs for separate experiments.

The second piece of evidence comes from statistical data about the transition to widowhood as summarized in Table 3. It can be seen that during the first year after the marriage bond was broken the death rate is higher than in subsequent years. The difference is particularly clear for young widowers.

Table 3: Excess mortality of widows in the years following widowhood.

Length of time after death of partner [years]	35 – 44	35 – 44	45 – 54	45 – 54	55 – 64	55 – 64	65 – 74	65 – 74
	M	F	M	F	M	F	M	F
1	5.3	3.5	3.0	2.0	2.0	1.6	1.7	1.5
3	3.0	2.1	2.1	1.5	1.7	1.3	1.5	1.3
> 3	2.7	1.7	2.0	1.4	1.6	1.3	1.3	1.2

Notes: The table gives the ratio (mortality rate of widowed people)/ (mortality rate of married people of same sex and age); the data are averages over 9 years, namely 1969-1974 and 1989-1991 (the years refer to the years in which the people died). No data were available under the age of 35. The shock effect (that is to say a high excess mortality immediately after the death of the partner) is particularly clear for young men.

Source: *Thierry (1999)*; primary source of the data: *INSEE (French National Statistical Office)*.

Conclusion

First we summarize the main results, then we discuss a possible agenda for further research.

Main results

(1) Although there are a few exceptions for separate experiments, on average the isolated ants in groups of 10 have a lower mortality rate than those isolated alone. A similar group effect is observed for married versus non-married people.

(1) The previous group effect is observed for social insects such as ants as well as for non-social insects such as the *Bactrocera dorsalis* fruit fly.

(3) However a major difference between ants and fruit flies is the fact that if one excepts the burst of deaths just after isolation, the death rate of isolated fruit flies is at least 10 times smaller than the death rates of ants. This conclusion holds for the

groups of 10 as well as for the singles. The experiments done by Grassé and Chauvin show that for isolated bees the death rate is about 3 to 4 times higher than for ants.

(4) For both ants and fruit flies there is a shock effect by which one understands that immediately after isolation the death rate is much higher than during subsequent days. This effect is particularly clear for fruits flies in which case the initial death rate is about 5 times higher than the subsequent death rate. This shock effect is also observed for widowed people and especially for young widowers.

(5) If queens are added to the groups of 10 fire ants their mortality rate is multiplied by 2 or 3. This has been observed repeatedly and without any exception.

(6) In the standard classification of survivorship curves, the curve of humans is of type I. The same conclusion holds for drosophila. In the ant experiments the survivorship curves are of type II. According to data for harvester ants from Deborah Gordon the survival of newly founded ant colonies is also of type II. The same conclusion holds for newly founded information technology corporations in the United States. In contrast, due to high initial death rate followed by a very low death rate, the survivorship curve of isolated *Bactrocera dorsalis* fruit flies is of Type III.

Do standard survivorship types really provide useful clues for a better understanding? It does not seem so, one must recognize.

Inference about the strength of social ties

From the previous results is it possible to infer conclusions regarding the strength of social interactions? For living organisms without any interactions between one another it would not make any difference to be separated from their neighbors. Therefore one would not observe any shock effect nor any death rate increase in groups of “isolated” individuals. As a matter of fact, the very notion of being “isolated” would have no meaning for such organisms. On the contrary, for strongly interconnected organisms it would make a big difference to be separated from their neighbors. This is indeed confirmed by the data in Fig. 2 which show that for low concentrations all cells die within 5-6 days.

From these two extreme cases it is tempting to infer that the increase in the death rate of isolated organisms is an indicator of the strength of their interaction. On this basis one can (tentatively) propose the following ranking from weak to strong interactions.

- (i) Fruit flies (*Bactrocera dorsalis*)
- (ii) Ants without queen
- (iii) Ants with queen
- (iv) Married men over 50
- (v) Young married men under 30
- (vi) Bees

(vii) Cells such as those in Fig. 2.

Needless to say, at this point this ranking is proposed rather as a conjecture. If it can provide an incentive for further research it will not be completely useless.

Agenda for further research

We will consider successively short-term and long-term projects.

One big uncertainty remains the average life duration for ants in the colony. The estimate of 62 days for fire given above was a weighted average taking into account differences in sizes but it was based on fairly imprecise data for each size class. In this connection it would be interesting to see what happens when a big group comprising several hundred ants is isolated from the colony. Will life expectancy in such a group approximate life expectancy in the colony itself? One may get a clue by increasing by steps the number n of ants in the group: for instance, $n = 100, 1000, 10000$.

In the experiments considered in this paper one stumbling-block was the fact that it takes at least one month to complete one of them. It would be a major improvement to be able to reduce this time. One possible method, namely Chauvin's starving technique, was considered above (in the section about experimental procedure) but turned out to be inappropriate for ants or fruit flies.

We have seen that the initial shock which occurs in a 4-5 day time interval after the beginning of isolation is a crucial element of the whole process. Whereas the experimental procedure (whether or not the dead ants are removed/replaced) may affect the results over a period of one month, it seems plausible that the initial shock would be less affected. If so, this would provide a chance to do the main part of the experiments in a shortened time.

The experiments considered so far provide more accurate answers for several issues raised in the present paper. Now, if one wishes to broaden the exploration there is one question which comes to mind immediately which is the following. We have seen that the initial separation shock is observed for social insects such as ants or bees as well as for non-social insects such as fruit flies. However, between social and non-social insects there is an intermediate stage. In many species, e.g. the beetles *Tenebrio molitor*, it is observed that, when put together in a box, they will form a cluster (neither *Bactrocera dorsalis* nor *Drosophila melanogaster* form clusters). This means that Although such beetles apparently do not live in colonies, they are nevertheless strongly attracted to one another (independently of sexual attraction). Preliminary observation showed that a group of about 200 *Tenebrio molitor* does survive several months. It would be interesting to see what happens when subgroups of 1 or 10 individuals are separated from the main group.

Acknowledgements The authors are grateful to Ms. Xin Liu, Yu Guo and Zhaoqing Ding for their help in the experiments. They also wish to thank Pr. Deborah Gordon and Pr. Martin Raff for helpful suggestions.

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[Excerpt (p. D491-D492): “If we plot the log of the probability of death against age we get a Gompertz-type curve for virtually all populations; for smokers the curve is virtually advanced in age so as to approximately double the normal mortality rate. The average cigarette smoker can be considered as an individual who is 7 year older than his chronological age. In like fashion, exposure to ionizing radiation (in doses of 300 to 400 roentgens total exposure) also increases age-specific death rate by a factor of about 2. If we were to eliminate all deaths due to heart diseases and cancer, we would simply move down the Gompertz curve by approximately 10 years.]

Thierry (X.) 1999: Risques de mortalité et de surmortalité au cours des 10 premières années de veuvage. [Excess mortality in the 10-year period subsequently to widowhood.] *Population* 54,2,177-204.