Extending physical chemistry to populations of living organisms.
First step: measuring coupling strength

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Abstract For any system, whether physical or non-physical, knowledge of the form and strength of inter-individual interactions is a key-information. In an approach based on statistical physics one needs to know the interaction in order to write the Hamiltonian of the system: $H = H_{\text{free}} + H_{\text{interaction}}$. For non-physical systems, based on qualitative arguments similar to those used in physical chemistry, interaction strength gives useful clues about the macroscopic properties of the system (e.g. for an institution the dropout rate is expected to be smaller when the inter-individual attraction is stronger).

Even though our ultimate objective is the understanding of social phenomena, we found that systems composed of insects (or other living organisms) are of great convenience for investigating group effects. In this paper we show how to design experiments that enable us to estimate the strength of interaction in groups of insects. By repeating the same experiments with increasing numbers of insects, ranging from less than 10 to several hundreds, one is able to explore key-properties of the interaction. The data turn out to be consistent with a global correlation that is independent of distance (at least within a range of a few centimeters). Estimates of this average cross-correlation will be given for ants, beetles and fruit flies. The experimental results clearly exclude an Ising-like interaction, that is to say one that would be restricted to nearest neighbors. In the case of fruit flies the average cross-correlation appears to be negative which means that instead of an inter-individual attraction there is a (weak) repulsive effect.

In our conclusion we insist on the fact that such “physics-like experiments” on insect populations provide a valuable alternative to computer simulations. When testable group effects are predicted by a model, the required experiments can be set up within a short time, thus permitting to confirm or disprove the model. This marks a significant progress with respect to modeling of social systems where, all too often, the requested statistical data just do not exist, thus obstructing any fruitful dialogue between theory and observation.

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In a first version of the paper the title made reference to “statistical physics” rather than to “physical chemistry”. Although chemistry itself plays no role in our investigation, we think it is important to emphasize that at this point it relies rather on the approach of “physical chemistry” than on that of statistical mechanics. The reasons for that will be explained later on.

**Rationale and motivations**

By using the theoretical framework of statistical mechanics one can derive the macroscopic properties of a system from the characteristics of its microscopic elements. This is a major achievement and so it is hardly surprising that researchers from other disciplines (e.g. biology, demography, sociology or economics) have been tempted to adapt such a powerful tool to their own field. In light of the successful record of statistical mechanics in physics there is little doubt that such extensions appear highly desirable. Yet, to our best knowledge, in spite of many attempts in this direction such attempts have not been highly successful so far.

**Obstacles**

As a matter of fact this is hardly surprising for there are indeed many obstacles.

- Statistical physics is fundamentally a theory of systems in equilibrium. For systems which are (strongly) out of equilibrium the very concept of temperature becomes meaningless.
- Statistical physics relies on the identification of ensemble averages (which are predicted theoretically) and time-averages (which are measured in experiments). This so-called ergodic hypothesis may be valid for physical systems which move from one state to another every picosecond so that there are trillions of transitions during an observation time of a few seconds. Yet, it is not obvious that such an assumption can still be accepted for socio-economic systems for which the transition rates are much slower.
- Last but not least, one should not forget that in order to use the theoretical framework of statistical mechanics one needs to know the Hamiltonian $H$ of the system which indicates how energy is distributed in the system. Generally $H$ includes three parts:

$$H = H_0 + H_{\text{inter}} + H_{\text{exo}}$$

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1 A preliminary but extended version (some 100 pages) of the present paper is available on the following website: [http://www.lpthe.jussieu.fr/~roehner/effusion.pdf](http://www.lpthe.jussieu.fr/~roehner/effusion.pdf)

2 Recently, some promising breakthroughs were made in this direction by Japanese economists; see Aoki and Yoshikawa (2007), Iyetomi et al. (2011), Iyetomi (2012).

3 The highest transition rates are probably those in currency exchange markets with hundreds of orders (worldwide) every second. Recently so-called high speed trading, that is to say transaction orders passed by computers, has reduced transition times to a few micro-seconds at least for a number of actively traded securities.
where $H_0$ stands for the free particles, $H_{\text{inter}}$ for the interaction energy between them and $H_{\text{exo}}$ for the energy of the particles when an exogenous field is involved. For instance $H_0 \sim \sum p_i^2/m$ for a system containing the molecules of a gas, $H_{\text{inter}} \sim \sum \frac{1}{(r_i - r_j)^6}$ when one wants to take into account the van der Waals forces between the molecules, and $H_{\text{exo}} \sim \sum S_i H(i)$ for the energy of a set of spins in an external magnetic field.

Whereas the third term can possibly be omitted when the experimental device can be shielded from external fields, the interaction term must always be taken into account. Needless to say, there are almost no biological or social systems for which one has a clear knowledge of their interactions. It is precisely the main purpose of the present paper to explain how such interactions can be measured.

**Reasons for optimism**

The previous list of obstacles could appear discouraging especially if one realizes that there are many other problems in non-physical systems just for defining key-variables such as velocity or energy. However, there are also good reasons for optimism as we will see now.

First it can be observed that the theory of phase transitions has been used to describe the transition between ordinary hadronic matter and quark-gluon plasma. As such states are characterized by temperature of the order of $10^{12}$K and life-times of the order of $10^{-20}$s, it means that this theory is applied well beyond the limits of the phenomena for which it was originally developed. Does the ergodic assumption hold for such extremely short time intervals? Nobody knows and probably nobody cares. The strategy of physicists is to use this framework without giving too much concern to underlying assumptions. If sensible results emerge this will provide so to say ex post justification.

Secondly, it can be observed that the title of this paper does not refer to statistical physics but to physical chemistry. Why?

- Although the objective of physical chemistry is also to explain the properties of macroscopic systems in terms of molecular interactions, there are two main differences with the approach of statistical mechanics. First, physical chemistry considers a broad range of molecules rather than just the simplest ones as is done in physics. Thus, because many cases are being considered, it becomes indispensable to adopt a comparative perspective. Why is the melting point of argon lower than the melting point of water? Why is the equilibrium vapor pressure higher for ethanol than for water? And so on and so forth.

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4 Even in order to use a mean field approximation one must know the form of $H_{\text{inter}}$.

5 E.g. second order phase transitions such as the paramagnetic-ferromagnetic transition in iron.
Because it would be an almost impossible task to propose (and solve) full-fledged models for all these cases, physical chemistry will rather resort to qualitative arguments. For instance, a standard argument is to observe that the stronger are molecular interactions in a liquid, the fewer molecules will be able to escape which in turn will lead to a low equilibrium vapor pressure above the liquid. Whereas this argument relies on a specific mechanism describing how molecules leave the liquid, it does not require any of the assumptions that we listed in previously. Even equilibrium is not strictly required. Indeed, if the container is left open, no equilibrium will take place and no equilibrium vapor pressure can be defined, but the same argument can nevertheless be used for explaining differences in the evaporation rate.

Such kind of argument can be used with success to explain many physical properties. For instance, the boiling temperature of alkanes (C\textsubscript{n}H\textsubscript{2n+2}) is expected to increase with \(n\) because the so-called London attraction forces (due to induced polarization which create short-lived dipoles that attract one another) exist between all atoms and therefore, in the absence of any other force, attraction will be stronger for big molecules than for small ones. Through a similar argument one would also expect the heat of vaporization to increase with \(n\). These predictions are indeed confirmed by experimental data; two graphs displaying such data can be found in Roehner (2004, p. 663).

In short, once one knows the strength of interaction in a system, one should be able to derive several of its macroscopic properties. Thus, we are again confronted to the same key-question: how can we measure interaction strengths? To answer this question we will make yet another simplification.

(3) The simplifications that we have already made consisted firstly in saying that we do not need to care too much about the underlying hypotheses of statistical physics, secondly that (at least in a first stage) there is no need to use the mathematical framework of statistical mechanics. Now our objective has become less ambitious and the only question on which one needs to focus is to develop experimental ways for measuring coupling strength between the elements of the system. The word experimental leads us to a third simplification.

It is often said that for socio-economic systems one cannot make experiments. However, this is only partially true. In fact, social sciences researchers are in the same position as astrophysicists. While they cannot perform any observation that they

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6In the discussion which follows we leave apart so-called class-room experiments that are performed with small groups of students. Such experiments can be useful to study how people will react in specific circumstances such as in response to auction rules for instance. However, one does not see how collective behavior can truly be studied in such a way because the experiment will only reflect genuine behavior if the people are not told that they are involved in an experiment. In the 1970s and 1980s the psycho-sociologist Stanley Milgram has performed experiments of this kind. However, such an approach raises major ethical problems and should rather be avoided.
would like to do, nevertheless they can use such statistical data that are available to make a limited number of observations. Yet, one must recognize that in many investigations the very data that one would need turn out to be unavailable. This is a serious obstacle. The task of designing appropriate measurement methods is difficult enough in itself; it would become altogether impossible if at each step progress is hindered by a lack of data.

There is a simple solution. Instead of studying people we can study populations of living organisms such as bacteria, insects or small fishes. For all these populations there exists a broad range of species. Different species will have different inter-individual interactions. Thus, one is very much in the same position as in physical chemistry. In what follows we will limit ourselves to populations of insects.

Our goal is to study groups of insects not at all as an entomologist would do but from the perspective of physical chemistry. In this respect living organisms have another important advantage over social or economic systems. Energy is a key notion in physics. While it is not obvious how to define the “energy” of a set of stocks or a sample of companies, it is easy to define the velocity and kinetic energy of a group of ants. In other words, systems of living organisms are much closer to physical systems than are socio-economic systems.

In the next section we explain how we designed and implemented our experiments. In the last section we propose some consistency tests of our results.

**Design of the experiments**

The experiment will be described for ants but their design is fairly similar for other insects such as fruit flies or beetles.

A number $n$ of ants are contained in a rectangular box (15cm long and 5cm wide, 4mm high) (see Fig. 1a). In this box one defines two part: an area $A$ and the part $B$ of the box which does not belong to $A$. For the sake of simplicity we can think of $A$ as being the left-hand side of the box as is the case in Fig. 1a. However, one should keep in mind that $A$ can also be much smaller than one half of the box. This allows to explore the behavior of the ants at smaller scale.

The ants can choose the compartment in which they wish to go or to stay. We record the number $n_A(t)$ of ants which are in compartment $A$ at time $t$.

The idea of the experiment is the following.

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*Researchers who have appropriate funding can even organize surveys in order to collect data that would not be available otherwise.*
• Suppose for a moment that the movements of the ants are completely correlated. This means that if one ant goes from $A$ to $B$ (or from $B$ to $A$) all the others will follow. Thus at each time step $n_A(t)$ may experience huge jumps, either from $N$ to 0 or vice versa.

• Suppose now that there is a zero correlation between the movements of the ants. This means that if one ant goes from $A$ to $B$ it will not be imitated by others. Of course, other ants may make the same move but they will do so independently from one another. As a result their moves will follow a binomial process. A move of all the ants together is not completely excluded but it will occur with a probability of $(1/2)^N$ and decrease exponentially when $N$ increases.

This argument suggests that there is a connection between the standard deviation of $n_A(t)$ and the average correlation between the movements of the ants. Needless to say, we wish to know the mathematical form of this relationship. Then, by recording the fluctuations of $n_A(t)$ we will be able to compute its variance and to derive the average correlation between ants. This average correlation can be considered as a measure of their interaction strength.

**Formalization**

To each ant $i$ we associate a random variable $X_i$ which takes the value 1 when $i$ is in compartment $A$ and 0 otherwise. Thus, at any moment $t$, the number of ants in compartment $A$ will be given by: $S_n = \sum_1^n X_1$. If $n_A(t)$ is a stationary random function, it is reasonable to assume that the variance computed from the time series $n_A(t)$ coincides with the probabilistic (i.e. ensemble) variance of the random variable $S_n$.

Various assumptions can be made regarding inter-individual interaction. Each as-

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8While of course necessary, the stationarity condition is not sufficient to guaranty ergodicity of the standard deviation. The specific mathematical condition that $n_A(t)$ must satisfy is given in Papoulis (1965, p. 330).
assumption leads to different correlations between the $X_i$. We will examine two specific cases: uniform correlation which means that $r_{ij} = r(X_i, X_j)$ is basically the same for all pairs $(i, j)$ and correlations which decrease exponentially when the difference $i - j$ increases: $r_{ij} \sim \eta^{|i-j|}$

**Uniform correlation**

In this case, $\sigma^2(S_n) = \sigma^2(nA)$ is given by the following proposition.

**Variance of a sum of uniformly correlated variables.** We consider a sum $S_n$ of $n$ identically distributed random variables $X_i$ of variance $\sigma^2$. We assume that between $X_i, X_j, i \neq j$ there are cross-correlations $r_{ij}$, the average of which is is denoted by $\tau$: $\tau = \frac{1}{n(n-1)/2} \sum_{i<j}^n r_{ij}$. Then, the variance of $S_n = X_1 + \ldots + X_n$ is given by:

$$\frac{\sigma^2(S_n)}{n\sigma^2} = (n - 1)\tau + 1 \quad (1)$$

The proof is fairly straightforward and is given in Appendix A.

Four observations are of interest in relation with formula (1).

1. The factor $n\sigma^2$ represents the variance of $S_n$ when the variables are uncorrelated. Therefore the ratio on the left-hand side represents the variance of $S_n$ divided by what it would be if the correlations are switched off. Subsequently this ratio will be denoted by $g^2$.

2. In the special case where $\tau = 1$, formula (1) gives: $\sigma^2(S_n) = n^2\sigma^2$. This result can be confirmed by observing that $\tau = 1$ means that all variables $X_i$ are identical that is to say take the same values (with probability 1). Thus, $S_n = nX_1 \Rightarrow \sigma^2(S_n) = \sigma^2(nX_1) = n^2\sigma^2$

3. A negative average correlation reduces the variance instead of increasing it. This would correspond to a repulsive force between the individuals. It is of interest to observe that $\tau$ cannot become smaller than $-1/(n - 1)$. In this case the variance is reduced to zero. Intuitively, this corresponds to a situation where the move of any individual is countered by the moves of the others in a way which leaves $S_n$ unchanged.

4. Formula (1) applies to any random variables $X_i$. For the problem in which we are interested, the $X_i$ have a special meaning from which results that:

$$\sigma^2(X_i) = E(X_i^2) - E^2(X_i) = P\{X_i = 1\}1 - (P\{X_i = 1\}1)^2 = p(1 - p)$$

where $p$ is the fraction of $A$ with respect to the total area.

**Ising-like correlations**

When the interaction is restricted to nearest neighbors as in the one-dimensional Ising model for spins, the correlation between the $X_i$ decreases exponentially when
the “distance” between the spins increases (Glauber 1963 p. 300). In this case the variance of \( S_n \) is given by the following proposition.

**Variance of a sum of Ising-like correlated variables.** We consider a sum \( S_n \) of \( n \) identically distributed random variables \( X_i \) of variance \( \sigma^2 \). We assume that between \( X_i, X_j, i \neq j \) there is a cross-correlation \( r_{ij} = \eta^{||i-j||}, \ 0 < \eta < 1 \). Then, the variance of \( S_n = X_1 + \ldots + X_n \) is given by:

\[
\frac{\sigma^2(S_n)}{n\sigma^2} = \frac{1 + \eta}{1 - \eta} - \frac{2\eta}{n(1 - \eta)^2}
\]  

(2)

The proof is fairly similar to the proof of the first proposition and it is outlined in Appendix A. According to this result, the ratio \( g^2(n) = \frac{\sigma^2(S_n)}{n\sigma^2} \) is slightly increasing when \( n \) increases (see Appendix A). However, when \( n \) becomes large the term involving \( n \) becomes negligible with respect to the first term. Thus, it is legitimate to say that for large \( n \), \( g^2(n) \) is almost constant.

Can one explain the difference between case 1 and 2 intuitively? We have already observed that if \( \tau \) is close to 1, almost all insects will cross from one side to the other at the same time which will result in big fluctuations of \( n_A(t) \) between 0 and \( n \). In the second model the parallel of such a high correlation would be \( \eta \) close to 1, e.g. \( \eta = 0.9 \). Yet, even with such a value of \( \eta \) the correlation between \( i \) and its neighbors will fall off rapidly when the distance increases. This means that when \( i \) will change side, only a small number (\( f \)) of neighbors will follow. As \( f \) depends only upon \( \eta \) (and not upon \( n \)) one sees that \( g^2(n) \) does not increase with \( n \).

In short, for the models that we considered the ratio \( g^2(n) \) can behave in three different ways as a function of \( n \).

1. It decreases linearly when \( \tau < 0 \)
2. It is almost constant when \( r_{ij} \) decreases exponentially with respect to \( ||i - j|| \).
3. It increases linearly when \( \tau > 0 \).

We will see that only cases 1 and 3 occur in our observations.

**Experimental results**

**Procedure**

The experimental procedure involves the following steps.

- First one must spread \( n \) ants fairly uniformly in the whole container. Then pictures will be taken every \( \delta \) seconds\(^9\).

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\(^9\)An “appropriate” time interval is important for the accuracy of the measurement. Of course, it is useless to take pictures when nothing happens that is to say when \( n_A(t) \) does not change. On the other hand, simulations show that one
• These pictures will allow us to record the numbers \( n_A(t) \). Once the variance of this time series has been computed one gets the ratio \( g^2(n) \).

• By repeating this procedure for different number of ants one gets results which can be represented as a set of points \((n - 1, g^2(n))\) (see Fig. 2).

• A linear regression performed on this set of points gives an estimate of the slope \( \tau \).

**Results**

See the graphs in Fig. 2a,b,c.

An important observation is in order regarding the magnitude of the estimated average correlation. First, it must be emphasized that \( \tau \) is very different from the correlation estimated from a scatter-plot. In the latter case a correlation as low as 0.01 would be non-significant (in the sense that the confidence interval would contain 0) except if the scatter-plot contains several thousand data points. Here, however, the correlation was obtained as the slope of a regression line and its estimate is quite significant as can be seen from the size of the error bars.

In order to get an intuitive understanding of \( \tau \), one should compare the actual trajectories of the insects to those shown in the simulation of Fig. 1b. Broadly speaking, the comparison will reveal that at individual level the actual trajectories of the insects are even more random than those in Fig. 1b. In spite of this high degree of randomness there is an observable effect at the macro level. The situation is somewhat the same as for a gas or a liquid. In spite of the randomness of the movements of individual molecules there are nevertheless well defined macroscopic properties.

**Problems**

Although the procedure may appear fairly straightforward there are a number of hurdles; while some are purely technical others are of more fundamental importance. Let us begin with the latter.

Ideally, in order to remain in a stationary equilibrium situation one would like \( n_A(t) \) to fluctuate around \( 1/2 \). Actually, for ants as well as for beetles, \( n_A(t) \) can become very different from \( 1/2 \). This is due to the fact that in such cases the individuals will form a big cluster in one part of the container. Thus, if the cluster is in \( A \), the ratio \( n_A(t)/n \) will become close to 1, whereas it will decrease toward 0 if the cluster is in part \( B \).

In a sense, this clustering behavior is good news because it is a direct proof of the existence of an inter-individual attraction. On the other hand, however, it introduces a bias in the measurement of \( \tau \). A correction procedure was introduced to take this
Fig. 2a,b,c: Relation between the variance of the number of individuals in a compartment \( A \) and the size of the group. We suppose that the whole domain which contains the ants has been divided into two parts and we observe the fluctuations \( n_A(t) \) of the number of individuals in part \( A \). The slope of the regression line gives an estimate of the mean correlation between the moves of individual elements. The negative correlation observed for drosophila can be interpreted as the result of repulsive forces between individuals. The ability to form clusters can be seen as revealing the existence of attractive inter-individual forces. Thus, this characteristic comes as a confirmation of the sign of the correlation.

The confidence intervals (at a probability level of 0.90) are as follows: ants: \( 100\tau = 3.37 \pm 0.9 \), drosophila: \( 100\tau = -1.29 \pm 1.16 \), for the beetle graph there are too few points to compute the confidence interval.

These experiments were performed between June and October 2012 in three different places, first in Paris (ants and drosophila), then in Beijing (drosophila) and finally in Kunming, Yunnan Province, China (beetles).

effect into account.

There is a problem which arises especially for drosophila, namely the fact that once introduced in the observation device only a few of the insects will move. In the case of drosophila this may take the following form: in a group of some 50 only about
5 to 10 will move at one moment and they will do so with great speed going from one end of the container to the other without seemingly caring about the 45 others. Another circumstance which will prevent the insects from moving is when they form a cluster. Although a correction can be introduced in the analysis to take into account such “frozen” elements, it is clear that the analysis eventually becomes meaningless when the proportion of frozen elements is too high.

The formation of clusters also leads to a more practical difficulty namely the fact that once ants are part of a cluster their spatial density becomes so high that it is difficult to count them. As they form several layers, counting becomes nearly impossible even on high resolution pictures. Recently, we have tried an alternative method which consists in weighing rather than counting. This method is well suited for small beetles whose unit weight is of the order of 15mg (see Fig 3). It is more difficult for ants whose typical weight (e.g. workers of “Formica japonica”) is about 3mg. It is altogether impossible for drosophila whose typical weight is around 0.2mg.

**Fig. 3: Container with weighing device on one side.** The compartments A and B are slightly (0.5mm) disjoined along the blue and red lines respectively so that the weight measured by the scale corresponds only to the beetles contained in the left-hand side part but that the beetles can nevertheless cross from A to B and vice-versa. Here most of the beetles have formed a cluster in a corner. The weight is 357 mg which, when divided by 15 mg, gives a total of 24 beetles.

**Consistency tests**

For a liquid inter-molecular attraction can be estimated through various means and variables: evaporation rate, equilibrium pressure of vapor, boiling temperature, heat of vaporization. It is the fact that such estimates are (at least most often) consistent with one another which gives us confidence in them. One would like to do the same here.

A simple qualitative consistency test is provided by the following “evaporation” experiment. One takes a test tube containing some 50 drosophila and one makes them all move to the bottom of the tube by hitting the tube on a table. Then, very quickly one puts the tube on the table in horizontal position. Let us assume that the bottom of the tube is on the left. After a few seconds, some 5 flies will have reached the right-hand side, and may be 10 others will be in the middle of the tube. If one waits 5mn, the flies will be distributed fairly uniformly throughout the tube. If one repeats the same experiment with “Tenebrio molitor” beetles it will be seen that after 5mn almost all insects are still together on the left-hand side of the tube.

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10 Whereas ants will tend to slow down or stop every time they come close to another ant.
11 This movement must be fast because drosophila have a natural tendency to go upward.
This experiment can be repeated in a more precise way by using the following procedure.

For each value of \( n \) the experiment was repeated 10 times, which means that 80 experiments were performed altogether. For the 10 repetitions the coefficient of variation \( \sigma/m \) was around 50%. The slopes of the regression lines (with the numbers of beetles expressed in thousands) are as follows (the error bars correspond to a probability level of 0.90):

- evaporation: \(-2.8 \pm 0.5\); 1 to 2, 10mn: \(-1.10 \pm 0.7\); 1 to 2, 30mn: \(-2.2 \pm 1.8\); not in cluster: \(-1.3 \pm 0.8\). The average slope is \( a = -2.0 \).

The experiments were done in November 2012 by Ms. Mengying Feng and Shuying Lai from Beijing Normal University, Department of Systems Science.

The experiment starts after a number \( n \) of beetles has been introduced into a container that we will call part 1. In the “evaporation rate” version of the experiment, the beetles can just walk out into open space. In the equilibrium version of the experiment the opening of part 1 leads to a container of same size. In this case, most often, the beetles formed a cluster both in part 1 and in part 2. However not all the beetles were in the clusters. This leads to the definition of two different variables: \( n_2(t) \), the number of beetles in part 2 at time \( t \), and \( n_3(t) \), the number of beetles which are not in a cluster. It is this latter variable which is the analog of the molecules in the vapor
Fig. 4b: “Not in cluster” experiment with bees. After formation of a bee cluster, the number of those outside of the cluster were counted. The duration of each experiment was comprised between one hour and one hour and a half. The three different colors correspond to slightly different experimental conditions. For instance, for the black data points there was a single cluster whereas for the red points two clusters formed. In the latter case we divided all numbers by 2. The slope of the regression line (also expressed per 1,000 bees) for the 7 experiments, namely $a = -0.55 \pm 0.68$, is 2.3 times smaller than the “not in cluster” slope in the beetles experiment. The experiments were done in June and July 2012 by Mrs. J. Darley and B. Roehner in Val Fleury (western suburb of Paris). The bees were Appis Mellifera mellifera.

phase over a liquid. The observations summarized in the figure show that whether in the non-equilibrium case of evaporation or in the quasi-equilibrium case, the escape rate decreases when the number of beetles increases. A natural interpretation is that the combined attraction of $n$ beetles on one of them increases with $n^{12}$.

## Conclusion

In physics real progress occurs when there is a fruitful dialogue between theory and observation. This is currently one of the problems faced by string theory. There is a similar problem with computer simulations of social phenomena because of the fact that they rarely lead to testable predictions and when they do, most often, the requested statistical data turn out to be unavailable. Thus, there is almost no dialogue between theory and observation. This greatly hampers real progress.

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12More precisely, one can say that the experiment displays two competing forces: (i) attraction and (ii) increased volatility. The increased volatility likely comes with the beetles’ new environment. Indeed, when they are left alone for a long time they cluster together instead of occupying the whole available area, a typical liquid-like behavior.
For experiments on groups of insects the situation is completely different. Usually a model set up to account for a given phenomenon also leads to predictions for other phenomena. The nice feature is that most often the experiments required for exploring those phenomena can be designed and implemented within a few days. In terms of speed and convenience such experiments are very much alike computer simulations. In addition they allow a real dialogue between theory and observation.

What kind of experiments should be tried by physicists? Clearly, it would be useless to repeat the experiments already done by entomologists. So far however, entomologists have given only scant attention to the exploration of group effects. The experiments which come closest to those that we advocate are probably those conducted by the teams of Jean-Louis Deneubourg (a former physicist) in Brussels and Deborah Gordon at Stanford. However, because they confined themselves to the study of ants both Deneubourg and Gordon could not draw on the benefits and broader perspective that might come from comparative studies.

Appendix B gives some practical hints for performing experiments with living organisms. We hope that this information will enable a number of other groups to carry out such experiments. This is a field where there is much to explore. For instance, some preliminary observations convinced us that the temperature plays a role in this kind of experiments which is fairly similar to what can be seen in chemistry and statistical physics. However, this must be confirmed and documented by a set of systematic experiments.

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One of the experiments reported above was done in Kunming at the Eastern Bee Institute of Yunnan Agricultural University, China; we wish to express our appreciation to Prof. He and Tan for their hospitality and to Dr. Chen and Wang for their help.

We also want to express our gratitude to Ms. Mengying Feng and Shuying Lai from the Department of Systems Science of Beijing Normal University whose results were mentioned in our discussion of the “evaporation” rate of beetles.

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13 A few centuries ago when physicists studied the phenomenon of “free” fall they did not confine themselves to falling apples. Indeed, comparative observation was the only way to demonstrate that, at least in air, the law is fairly independent of the shape and density of the falling object. This was a milestone in the development of classical mechanics.

14 In a general way observation shows that the “temperature” of the living organisms (in the sense of statistical physics) is determined by the temperature of the environment.
Appendix A: Variance of a sum of correlated variables

We proceed in several steps.

For the sake of simplicity we first consider the average of a sum of three correlated random variables $X_1, X_2, X_3$ of mean $m$ and identical standard deviation $\sigma$. Our objective is to compute the variance of $S_3 = X_1 + X_2 + X_3$.

By definition of the variance $\sigma^2(S_3) = E[(S_3 - E(S_3))^2]$. One knows that the expectation of a sum of random variables is always equal to the sum of the expectations, whether the variables are correlated or not. Thus: $E(S_3) = E(X_1) + E(X_2) + E(X_3)$.

Consequently:

$$\sigma^2(S_3) = E\left(\sum_{i=1}^{3} \hat{X}_i^2\right)$$

where: $\hat{X}_i = X_i - E(X_i)$

Thus,

$$\sigma^2(S_3) = \sum_{i=1}^{3} E(\hat{X}_i^2) + 2\left[E(\hat{X}_2\hat{X}_3) + E(\hat{X}_3\hat{X}_1) + E(\hat{X}_1\hat{X}_2)\right]$$

We express the expectations of the products by introducing the coefficient of correlation of the $X_i$: $r_{ij} = E(\hat{X}_i\hat{X}_j)/\sigma^2$. Thus: $\sigma^2(S_3) = 3\sigma^2 + 2\sigma^2(r_{23} + r_{31} + r_{12})$

From that point on, we will consider two cases.

**Uniform correlations**

Introducing the mean of the $r_{ij}$, $\tau = (r_{23} + r_{31} + r_{12})/3$, we obtain:

$$\sigma^2(S_3) = 3\sigma^2[1 + 2\tau]$$

This formula has an obvious generalization to an arbitrary number $n$ of random variables:

$$\sigma^2(S_n) = n\sigma^2g^2, \quad g^2 = (n - 1)\tau + 1$$

where:

$$\tau = \frac{1}{n(n - 1)/2} \sum_{i\neq j}^n r_{ij}$$

**Ising-like correlations**

For a one dimensional Ising spin system the correlation between spins $i$ and $j$ is: $r_{ij} = \eta^{|i-j|}$ where $\eta$ can be expressed (if one wish) as a function of the parameters which define the interaction between the spins (see Glauber 1963 p. 299, formulas (56) and (57)).

Introducing this expression of $r_{ij}$ gives: $\sigma^2(S_3) = \sigma^2(3 + 2\eta + \eta^2)$

In extending this formula to any $n$, one needs to express the finite sum $f(\eta) = \sum_{i=0}^{n-2} \eta^i$ (as well as its derivative $f'(\eta)$). Instead of using the exact expression $f(\eta) = (1 - \eta^{n-1})/(1 - \eta)$ we will consider that the term $\eta^{n-1}$ is negligible with respect to 1, which means that we approximate the finite sum by the corresponding infinite series. This approximation is acceptable for our experiments because most of the time $n > 20$. Of course the approximation is no longer valid when $\eta \rightarrow 1$ but $\eta = 1$ is the case of uniform correlation already considered above.

Under this assumption one obtains finally:

$$\sigma^2(S_n) = n\sigma^2\left[1 + \frac{2\eta}{1-\eta}\left(1 - \frac{1}{n(1-\eta)}\right)\right]$$
$$g^2(n) = \frac{\sigma^2(S_n)}{n\sigma^2} = \frac{1 + \eta}{1 - \eta} - \frac{2\eta}{n(1 - \eta)^2}$$

Due to the approximation made in the derivation, this formula is not valid when \( n \) is close to 1. We have seen above that for \( n = 2, 3 \) one gets:

$$g^2(2) = 1 + \eta, \quad g^2(3) = 1 + \frac{4}{3}\eta + \frac{2}{3}\eta^2$$

which shows that the function \( g^2(n) \) increases toward its asymptotic limit \((1 + \eta)/(1 - \eta)\).

**Remark** Can the Ising case be seen as a special instance of the uniform case? Formally, it may seem so. However, the real picture emerges when we consider large values of \( n \). In the Ising case, due to the exponential decrease, all elements in the correlation matrix are almost equal to zero except for a zone around the first diagonal whose width depends only upon \( \eta \). Consequently, for such a matrix the average correlation goes to zero when \( n \) becomes larger.

This observation shows three things. (i) It would be irrelevant to treat the Ising case as a special instance of the uniform case. (ii) The fact that in the Ising case \( \tau \approx 0 \) helps to explain that the ratio \( g^2(n) \) remains basically constant instead of increasing. (iii) It explains why we used the expression “uniform correlations” to designate the first case. The correlations are uniform in the sense that when \( n \to \infty \) the number of elements of the correlation matrix that are “substantially” different from zero must remain of the same order of magnitude as \( n \). For a distance-dependent correlation, this means that the decrease with distance must be slow enough.

**Simulations**

So far we did not need to make the assumption that the \( X_i \) are Bernoulli variables, that is to say variables taking only the values 0 and 1. However, if one wishes to carry out a simulation there is a convenient algorithm which works only for Bernoulli variables (Lunn and Davies 1998). The relevant formulas can be summarized as follows:

**Simulation of uniform correlations between \( n \) Bernoulli variables** \( Z \) and \( Y_i \) are \( \text{Ber}(p) \) random variables while the \( U_i \) are \( \text{Ber}(\sqrt{\tau}) \) random variables. Then, the variables \( X_i \) defined as:

$$X_i = (1 - U_i)Y_i + U_iZ, \quad i = 1, \ldots, n$$

are correlated Bernoulli variables with the following properties:

$$E(X_i) = p, \quad E(X_i^2) = p, \quad \text{Cor}(X_i, X_j) = r, \quad i \neq j$$

It can be noted that this algorithm works only for positive correlations between the variables.

**Simulation of correlated Ising-like Bernoulli variables** \( Y_i \) are \( \text{Ber}(p) \) random variables while the \( U_i \) are \( \text{Ber}(\eta) \) random variables. Then, the variables \( X_i \) defined as:

$$X_1 = Y_1, \quad X_i = (1 - U_i)Y_i + U_iX_{i-1}, \quad 2 \leq i \leq n$$

are correlated Bernoulli variables with the following properties:

$$E(X_i) = p, \quad E(X_i^2) = p, \quad \text{Cor}(X_i, X_j) = \eta^{j - i}, \quad i \neq j$$

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\(^15\)When \( P\{X = 1\} = p \) such a variable will be noted as \( \text{Ber}(p) \).
Fig 1b presents a simulation of the trajectories of ants. Such simulations are useful for testing the estimation procedure. How were they done?

- First of all, in order to introduce a time-continuity which obviously exists in real experiments we generated the $n$ random variables $Z_{i,t}$ through $n$ independent first-order auto-regressive processes.
- Then, the correlations between the variables were introduced following the so-called Cholesky procedure by defining the $X_{i,t}$ as appropriate linear combinations of the $Z_{j,t}$, $j = 1, \ldots n$.

Appendix B: Experimental “toolkit”

Just in order to convince the reader that experiments with insects can be done fairly easily we give some practical hints. It is indeed possible to do this kind of experiments with fairly little sophisticated equipment.

Basically, the needs can be summarized as follows: First one needs to get the living organisms.

- Ants can be easily collected (at least in spring and summer) by putting appropriate food as a bait on a Bristol board just a few centimeters away from the entrance of a colony. Within one hour and depending on the species a few hundred ants may gather on the Bristol board.
- Drosophila can be obtained from biology laboratories.
- Flies and beetles can be bought in the form of larvae (worms) destined to fishermen or for feeding big aquarium-fishes. The waiting time between the larvae stage and the emergence of the adults ranges from less than one week to a few months depending on species, temperature and time of year.

Secondly, in many cases, one needs a small bottle of carbon dioxide to make the insect sleep in order to be able to handle them easily. Carbon dioxide has an almost instantaneous anesthetic effect on all these insects. According to a paper published in the Journal of Experimental biology (Ribbands 1950) anesthesia through carbon dioxide does not infer a memory loss and changes only slightly the behavior of bees. It is probably safe to assume that the effect on the other insects mentioned above is similar.

Next one needs an appropriate container. A simple solution is to cut it into a piece of flexible plastic (such as PVC) of adequate thickness (3mm to 5mm is usually enough). This is illustrated in Fig. 1a.

Finally, one needs a counting device. Taking pictures and counting by hand is a simple solution but not always satisfactory especially for counting the elements in a cluster. For this reason we have developed a weighing method (illustrated in Fig. 3).

Clustering phenomena also occur among bacteria and micro-organisms that are present in so-called biofilms which form at the surface of liquids. Because of the small size and high numbers of such elements one is in a situation fairly similar to physical systems. For instance, it can be mentioned that inter-molecular forces such as van der Waals forces play a significant role in the movements of such micro-organisms.

Studying the collective behavior of such populations from the perspective of physics seems a promising field. However, in contrast to the study of insects, it requires special laboratory devices and equipment.

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