

How individual interactions control aggregation patterns in gregarious arthropods*

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Aggregation is one of the most widespread phenomena in animal groups and often represents a collective dynamic response to environmental conditions. In social species the underlying mechanisms mostly obey self-organized principles. This phenomenon constitutes a powerful model to decouple purely social components from ecological factors. Here we used a model of cockroach aggregation to address the problems of sensitivity of collective patterns and control of aggregation dynamics. The individual behavioural rules (as a function of neighbour density) and the emergent collective patterns were previously quantified and modelled by Jeanson et al. (2003, 2004). We first present the diverse spatio-temporal patterns of a derived model in response to parameter changes, either involving social or non-social interactions. This sensitivity analysis is then extended to evaluate the evolution of these patterns in mixed societies of sub-populations with different behavioural parameters. Simple linear or highly non-linear collective responses emerge. We discuss their potential application to control animal populations by infiltration of biomimetic autonomous robots that mimic cockroach behaviour. We suggest that detailed behavioural models are a prerequisite to do so.

Keywords: aggregation, *Blattella germanica*, self-organization, distributed control, autonomous lure

Introduction

Aggregation of animals has been the subject of scientific study for a long time (Allee, 1931; see Parrish & Hamner 1997; Krause & Ruxton, 2002 for recent

surveys) and there now exist many examples where the underlying (behavioural or ecological) mechanisms have been identified qualitatively as well as quantitatively (e.g. Deneubourg et al., 1990; Boi et al., 2000; Jeanson et al., 2004).

Aggregation can occur for different reasons. One is the presence of environmental heterogeneities with particularly “attractive” living conditions at a well-defined spot (Camazine et al., 2001). Cockroaches, for example, spend the diurnal phase preferentially in dark, warm and humid places (Rust et al., 1995). The environment creates in this case a template and the gathering of individuals at the same place will be mainly governed by the template.

This template-based form of aggregation does not require any social interactions. However, a template is not mandatory for the occurrence of aggregation. It can also be the result of behavioural responses of organisms to conspecifics (i.e., congregation (Turchin, 1998)). The most striking examples come from studies of fish schooling (Parrish & Hamner, 1997) in homogeneous large water bodies. These fish form aggregates to increase the chances of survival (anti-predator behaviour), find mates, decrease individual displacement energy costs or for collective foraging (Parrish & Edelstein-Keshet, 1999). This co-operative aspect often gives simple aggregates in social insects a functional importance on the colony level (e.g. chains and nest building in *Oecophylla* weaver ants (Ledoux, 1950; Hölldobler & Wilson, 1990), bivouac formation in army ants (Schneirla, 1971; Gotwald, 1995), defence of food sources (Beckers et al., 1990, 1993).)

The development of models to study these self-organized spatio-temporal patterns often aims at explaining the observed dynamic efficiency of animal groups to adapt to environmental variation (see for instance adaptive foraging patterns in army ants (Deneubourg et al., 1989; Franks et al. 1991)). The current core methodology to disentangle the underlying mechanisms of structures relies on the controlled variation of some environmental parameter. An important complementary question is the robustness of these self-organised structures to high interindividual variability. Here we suggest the introduction of artificially modified individuals as a complementary tool.

We address this question with the basic phenomenon of aggregation in the presocial German cockroach *Blattella germanica*. The underlying behavioural mechanisms and their parameters have been quantified and modelled in a previous study in controlled experimental setups (Jeanson et al., 2003, 2004).

The german cockroach forms aggregates when not foraging and if environmental conditions (temperature, humidity) are not favourable (Dambach & Goehlen, 1999; Rivault & Cloarec, 1998). This behaviour has been studied with

cockroach larvae in controlled homogeneous environments to concentrate on the contribution of social interactions to aggregation (that is, its congregative part). These social interactions are strong enough to foster aggregation in absence of environmental heterogeneities. The self-organized nature of this process is confirmed by the unpredictability of spatial positions of the aggregates (thus no environmental template) and the effect of animal density on mean aggregate size and numbers (identifying density as a bifurcation parameter). Jeanson et al., (2003, 2004) developed from these experiments a Lagrangian model of cockroach aggregation. The decisive mechanism that was identified to lead to congregation can be summarised in the following way: cockroaches do not rest for a long time in places with few cockroaches, and once moving they stop preferentially in places of high cockroach density. All behavioural parameters to “implement” this behaviour in the cockroach were quantified in Jeanson et al. (2004) and the resulting individual based model (IBM) was validated in novel experimental conditions (varying cockroach density).

In this paper we will explore how the introduction of “modified” animals (that is, animals or autonomous insect-like robots where the behaviour underlying the aggregative response has been changed in a quantitative way) can change the dynamical and statistical aspects of this aggregation process. The underlying question is whether our knowledge of the individual mechanisms can enable us to change congregation patterns by the introduction of “modified” animals, and whether this would be of any use for the management of such animals (for further information see <http://leurre.ulb.ac.be/>).

While it has been shown that the dynamically rich behaviour of a self-organized process adapts well to external variation (Seeley, 1996; Camazine et al., 2001), to what extent are these systems robust to internal changes such as an expanding heterogeneity amongst individuals (through mutation or invasion) that affects the individual quantitative parameters at the base of the emergent structures? Understanding the thus induced alteration in the emergent structures would be of great theoretical interest and may potentially lead to new ways to control such systems (De Schutter et al., 2001).

Based on a more generic version of the IBM developed in Jeanson et al. (2004) we will first characterise the collective cockroach behaviour (spatio-temporal dynamics) by size and number of aggregates over time and by their stability or longevity. We will then explore its sensitivity to individual (or ‘non-social’) parameters (speed, spontaneous stopping rate) and to interaction (or ‘social’) parameters (that are modulated through local cockroach density: probabilities to stop or to start moving). We will then explore the dynamics of

mixed societies where one or more individuals are “modified” to test whether there is only a gradual change on the collective level or whether non-linear changes arise.

The behavioural model and its characterisation

Individual behaviour is modelled in terms of propensity to perform some action in response to the environment. This propensity may depend on local animal density. The collective behaviour will emerge from numerous local perception/action loops.

We considered two actions for our individuals: (1) to stop or rest in place, and (2) to start or keep moving (Figure 1). The individual behavioural state has thus two values: moving or resting. It has been shown experimentally (Jeanson et al., 2004) that the transition probabilities for an individual to switch from one state to the other is continuously modulated by its local environment within its perception radius, namely the number of stopped neighbours. From earlier studies it is also known that the German cockroach can distinguish conspecifics from simple environmental heterogeneities (Rivault & Cloarec, 1998; Rivault et al., 1998). In the case of isolated individuals we will talk of

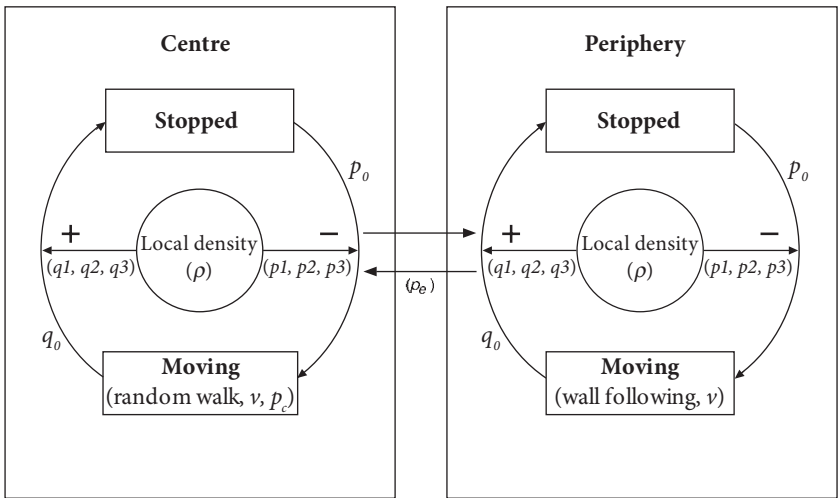


Figure 1. The behavioural model with its parameters. The signs + and — indicate positive and negative feedback respectively. For parameters and their values see Table 1.

spontaneous stopping and starting rates. This process can be described in terms of a Local Activation — Long range Inhibition (LALI (Gierer & Meinhardt, 1972)) system: the probability to stop in an aggregate is enhanced as this aggregate grows, so that aggregate growth is locally self-enhancing (local positive feed-back). As more and more individuals join aggregates, aggregate growth is inhibited by the depletion of still moving individuals (long-range inhibition). Since the probability to leave an aggregate is inhibited by the aggregate size but is not zero, a competition arises amongst aggregates to “trap” moving cockroaches. As a result, aggregates can disappear or grow as time goes. The individuals moving around, and spontaneously stopping or restarting moving, represent the diffusion component in the system. It is noteworthy that the absence of environmental heterogeneities implies that aggregates cannot but originate from individuals that stopped spontaneously at some random place.

Movement parameters

Diffusion pertains to the speed v of animals, their path geometry and their probabilities to spontaneously stop or start moving. The path geometry depends on the animal's location in the arena. It performs a diffusive random walk in the centre of the arena (isotropic phase function, exponentially distributed free paths with mean free transport path $l^* = 2.3\text{cm}$ ($=v/p_c$), (see Jeanson et al., 2003)), but switches to wall following behaviour when approaching an arena wall closer than 0.5 cm (thigmotaxis). It will decide to follow the wall in clockwise or counter-clockwise orientation such that the directional change necessary to align along the wall is minimal. While being in wall following movement the animal has a fixed rate p_e to quit the peripheral zone and to re-enter the central zone in an angle that is drawn from a log-normal distribution α (Table 1). Diffusion is thus two-dimensional in the arena centre and one-dimensional when animals follow the circular wall. See Table 1 for standard parameter values and further details.

Aggregation parameters

Local environment is defined by the individual's circular perception area (radius 3 mm, given by their antenna length and their cercae, they can thus detect a cockroach as far as 6 mm away by mutual antennal contact) and we assume that cockroaches can discriminate between stopped and moving neighbours. Jeanson et al. (2004) had shown that propensity is strongly modulated

Table 1. Model parameters for a single individual (called ‘non-social’ parameters in the text) and interaction parameters (called ‘social’ parameters). The log-normal angle α is given in Limpert et al.’s (2001) notation as the median, times or divided by (*) its shape parameter. Technically it is created as the exponential of a normally distributed random variate with mean log (36.6) and standard deviation log (2.14).

Parameter	sign	value	
Spontaneous stopping rate	q_0	0.08	s^{-1}
Start rate (isolated cockroach)	p_0	0.17	s^{-1}
Cockroach speed	v	0.011	$m\ s^{-1}$
Exiting rate from periphery	p_e	0.12	s^{-1}
Direction change rate (in centre)	p_c	0.47	s^{-1}
Angle when re-entering centre (log-normally distributed)	α	36.6*/ 2.14	°
Perception radius	ρ	0.003	m
Start rate (1 neighbouring cockroach)	p_1	0.00625	s^{-1}
Start rate (2 neighbouring cockroaches)	p_2	0.0015	s^{-1}
Start rate (31 neighbouring cockroaches)	p_3	0.0006	s^{-1}
Stopping rate (1 neighbouring cockroach)	q_1	0.49	s^{-1}
Stopping rate (2 neighbouring cockroaches)	q_2	0.63	s^{-1}
Stopping rate (3 neighbouring cockroaches)	q_3	0.65	s^{-1}

by local densities up to three individuals but becomes constant above this level. It is thus sufficient to implement different stopping and starting rates for local densities of 1, 2 and 3 (or more) individuals. Jeanson et al. (2004) also found that cockroaches can be in two stopping states, a short one (with a short mean stopping time) or a long one (see Figure 2 in Jeanson et al. (2004)). This latter property is probably very specific to the larval stage of the German cockroach. Since the current study focuses on the generic robustness of aggregation patterns with respect to mixing with modified animals, the model was slightly cleared up and cockroaches are here simulated with intermediate stopping times. As will be seen below, this apparently major modification of intra-individual variability has little effect on model dynamics and almost none on the final pattern. Naturally one should be cautious before making specific predictions for other species and/or later life stages. The parameter values are given in Table 1, q_x for the rates to stop and p_x for the rates to start moving (x is the number of stopped neighbours within the animal’s perception radius: $x = 1, 2$ or ≥ 3). See Figure 1 and the profile P-Q+ in Figure 6.

Numerical implementation

This IBM, with the individuals represented by their location, their orientation and their perception radius, was implemented in a C++ program that computes individual displacement on a continuous scale and approximates continuous time by discrete time steps Δt . The time step was coerced by the animal speed in order to be small enough to ensure an accurate perception of the neighbourhood ($\Delta t = 0.2$ s for the standard parameter set in Table 1). The rates p (and q) to switch between states were implemented during run-time by drawing at each time step a random uniform number $r \in [0,1)$ and switch state whenever $r < (1 - \exp(-\Delta t p))$. We used the “maximally equidistributed combined Tausworthe random generator” provided by the GNU Scientific Library (see <http://www.gsl.org> and <http://www.iro.umontreal.ca/~lecuyer/myftp/papers/tausme.ps>).

Simulations were done over 1 h when illustrating the relation to the experimental data and over 12 h when exploring the sensitivity to ‘non-social’ or ‘social’ parameters and the ‘mixed’ society.

Dynamic characterisation of the behavioural model

We chose to characterise these dynamic patterns with three dynamic indices:

1. the fraction of cockroaches that are aggregated,
2. the number of aggregates,
3. the cumulative distribution of aggregate lifetimes.

As in Jeanson et al. (2004) we consider two cockroaches to be aggregated if their body centres are less than 1 cm distant from each other. An aggregate consists therefore of all individuals that have at least one neighbour within this distance and that are “connected” to all other aggregate members indirectly via other individuals. These aggregates were determined to compute the number and sizes of aggregates and the fraction of aggregated cockroaches as time elapses.

In order to compute the distribution of lifetimes and mean size of aggregates we had to track the aggregates individually with the following procedure: after each time step the barycentre of each aggregate is compared to the aggregate barycentres at the previous time step. If it has moved less than one perception radius then the lifetime of this aggregate is increased by Δt , otherwise one of the three following events has happened: (1) it represents a newly formed aggregate that starts its lifetime, (2) it is the result of a fission (an

aggregate breaking in two) in which case it inherits the lifetime of the original aggregate if it is larger than the other resulting aggregate or starts as a new aggregate otherwise, (3) it is the result of a fusion (two aggregates melt into one) in which case it inherits the lifetime of the larger aggregate while the smaller aggregate ends its lifetime. All preceding barycentres that belong neither to a surviving aggregate nor have participated in a fission or fusion have ended their lifetime. These lifetimes, cumulated over one hundred 12 h simulations, are used to construct the cumulative distributions of lifetimes, including the ones that are still “alive” when the simulation stops (leading to a “saturation” effect at 12 h).

In the experimental conditions (Jeanson et al. 2004) as well as in the simulations we observed that within few minutes over 90% of the cockroaches moved along the arena walls (thigmotactic behaviour). The spatio-temporal dynamics can thus be visualized by the animal's position in the peripheral zone (normalized to the interval $(0, 2\pi)$) as a function of time. Figure 2 shows four examples of the experimental dynamics in a 11-cm diameter arena at two densities, 10 (a,b) and 20 (d,e) cockroach larvae (a total of 20 experiments were done for each density (see Jeanson et al. 2004)). After some transient dynamics in the first minutes (where the cockroaches recover from anesthesia for transportation) we can see that even at low density aggregates can form and persist for a certain time, a tendency that is stronger at high density. These aggregates are not always stable, they can split in two, merge with another aggregate (what Flierl et al. (1999) called fissions and fusions) or dissolve completely and reassemble elsewhere. Figure 2 also shows examples of simulated spatio-temporal dynamics (1h as in the experiments) with 10 cockroaches (c) or 20 cockroaches (f): we can identify the same qualitative features as in the experimental dynamics (though the transient phase is much shorter, which does not surprise since our ‘in silico’ cockroaches didn't need any anesthesia).

Figure 3 shows the dynamics of these indices for the experimental data and the 1 h simulations. We observe that reaching stationary levels takes more time for the number of aggregates than for the fraction of aggregated cockroaches; the “true” stationary state is thus reached only after ≈ 1 h. In experiments, the number of aggregates peak at 1.0 (density 10) and 2.0 (density 20) before levelling off at 1.0 and 1.7 respectively. In simulations, the number of aggregates reach a peak of 1.5 (density 10) and 3.0 (density 20) to decrease then to a constant level of 1.1 and 1.7 respectively. Figure 4 shows the mean (\pm standard deviation) size of the largest aggregate (a) and of the fraction of cockroaches aggregated (b) in stationary state (60 min). We see that these statistics are very similar.

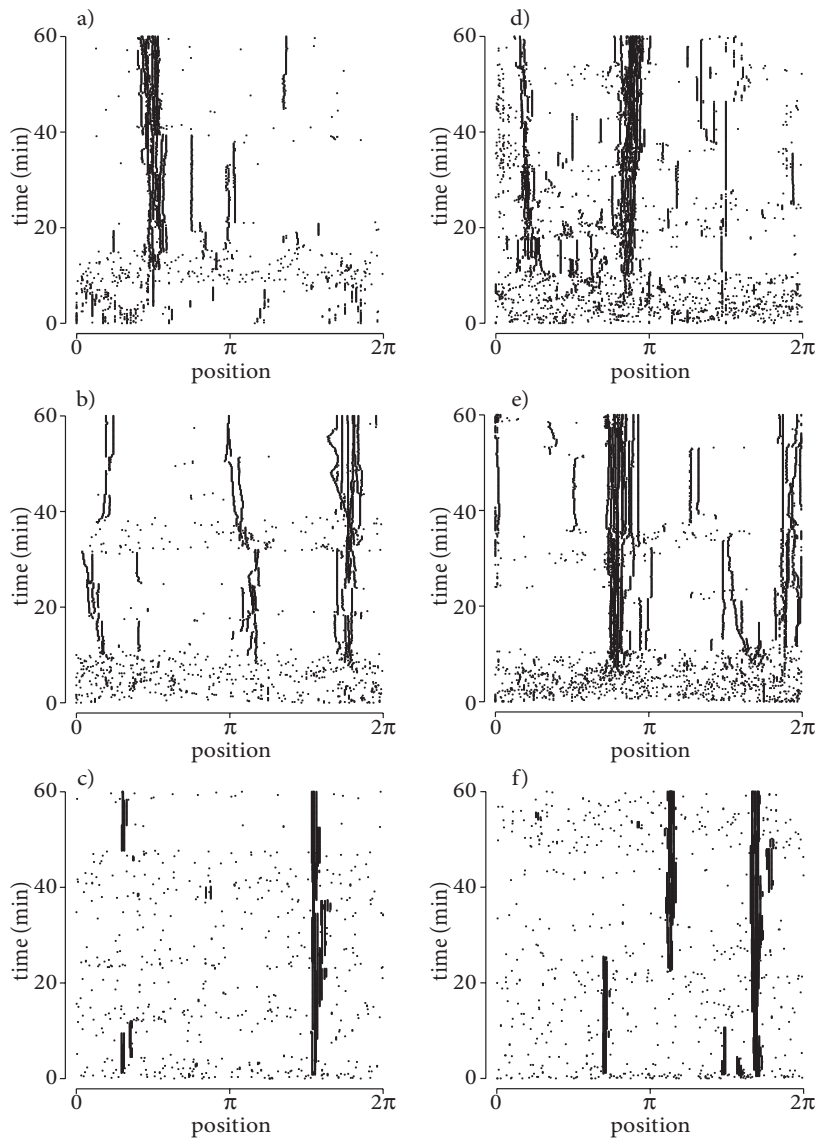


Figure 2. Spatio-temporal dynamics of two experiments with 10 cockroaches ((a) and (b)), another two with 20 cockroaches ((d) and (e)) and two simulations with the parameters in Table 1 and density 10 (c) and 20 (f). Each horizontal line shows the radial position (radian) of each cockroach when present in the peripheral zone at the time (min) indicated on the y -axis.

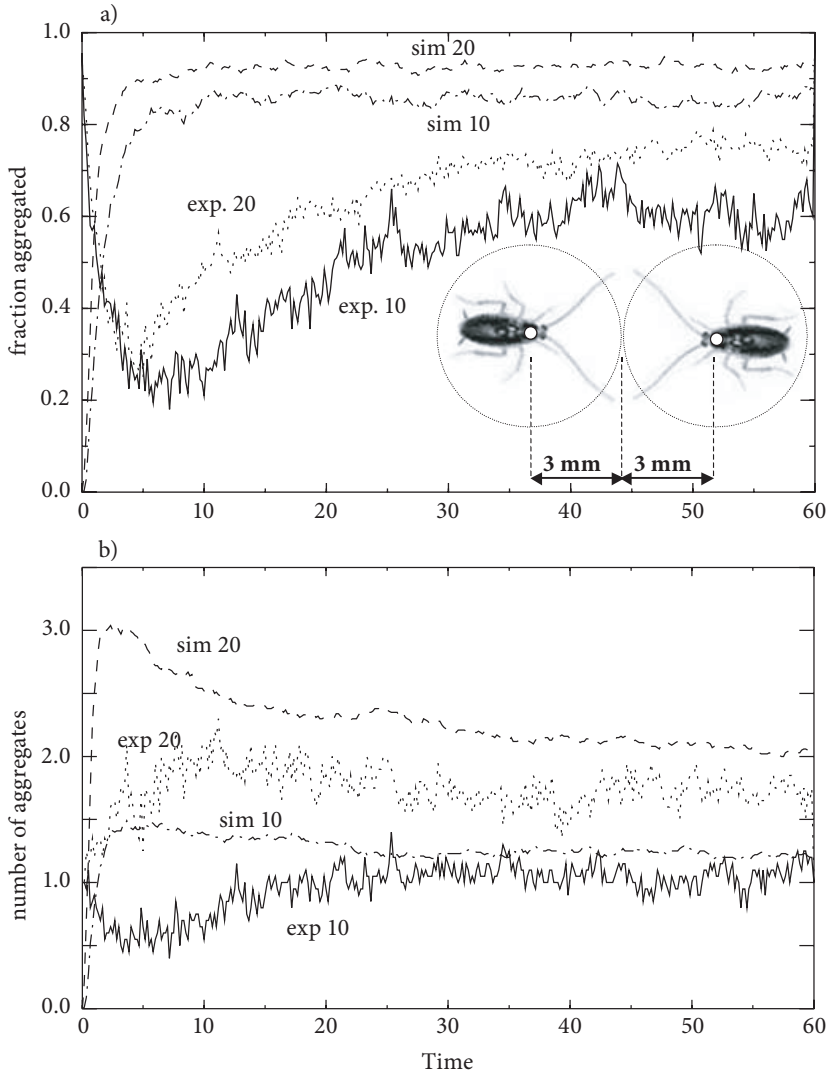


Figure 3. Temporal dynamics of the fraction of cockroaches that are aggregated (a) and the number of aggregates (b) for the experiments with 10 cockroaches (mean over 20 replicates, exp10) and 20 cockroaches (mean over 20 replicates, exp20) and corresponding simulations (averaged over 100 Monte Carlo simulations, sim10 and sim20). The x-axis is time (in min) and the y-axis the fraction of cockroaches aggregated and the number of aggregates respectively. The inset shows two cockroaches with their perception circle (covered either by their highly mobile antennae or by their cercae). In the model they are represented by their centre (white dot) and their perception radius (3 mm).

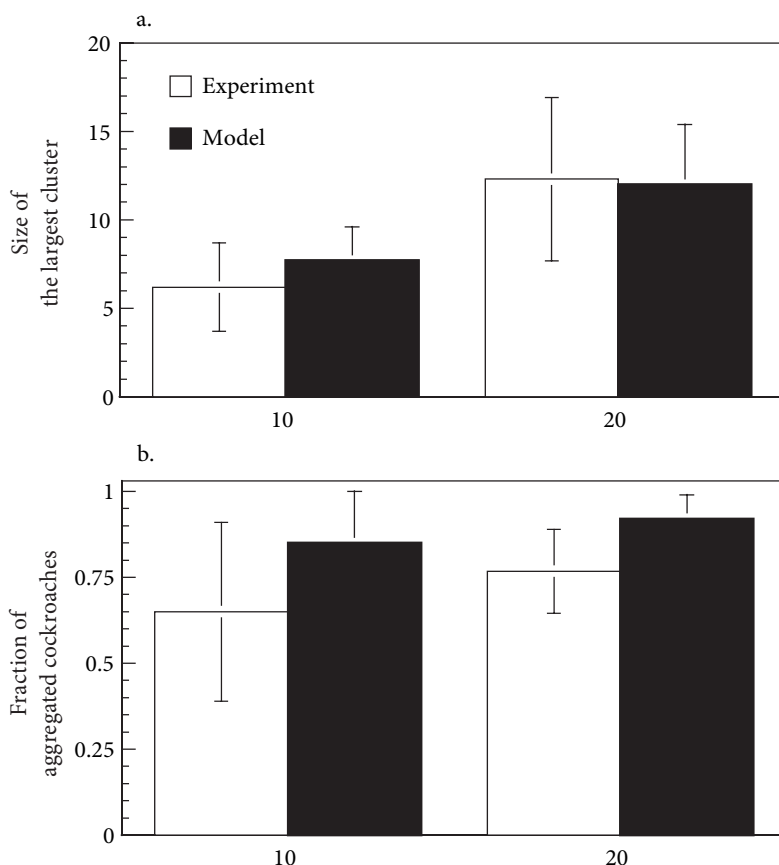


Figure 4. Size of the largest aggregate and fraction of aggregated cockroaches (at 60 min, mean \pm standard deviation) for experiments and simulations at the two conditions (10 individuals and 20 individuals).

In conclusion, the experiments and the model exhibit striking features of LALI systems: (1) the maximal number of aggregates is proportional to density and it is reached earlier at high density (from a mean number of 1.5 aggregates for 10 individuals to a mean number of 3.0 slightly earlier for 20 individuals) and (2) the number of aggregates then decreases slowly to its stationary value due to competition to attract and trap moving cockroaches. For further comparisons see Jeanson et al. (2004).

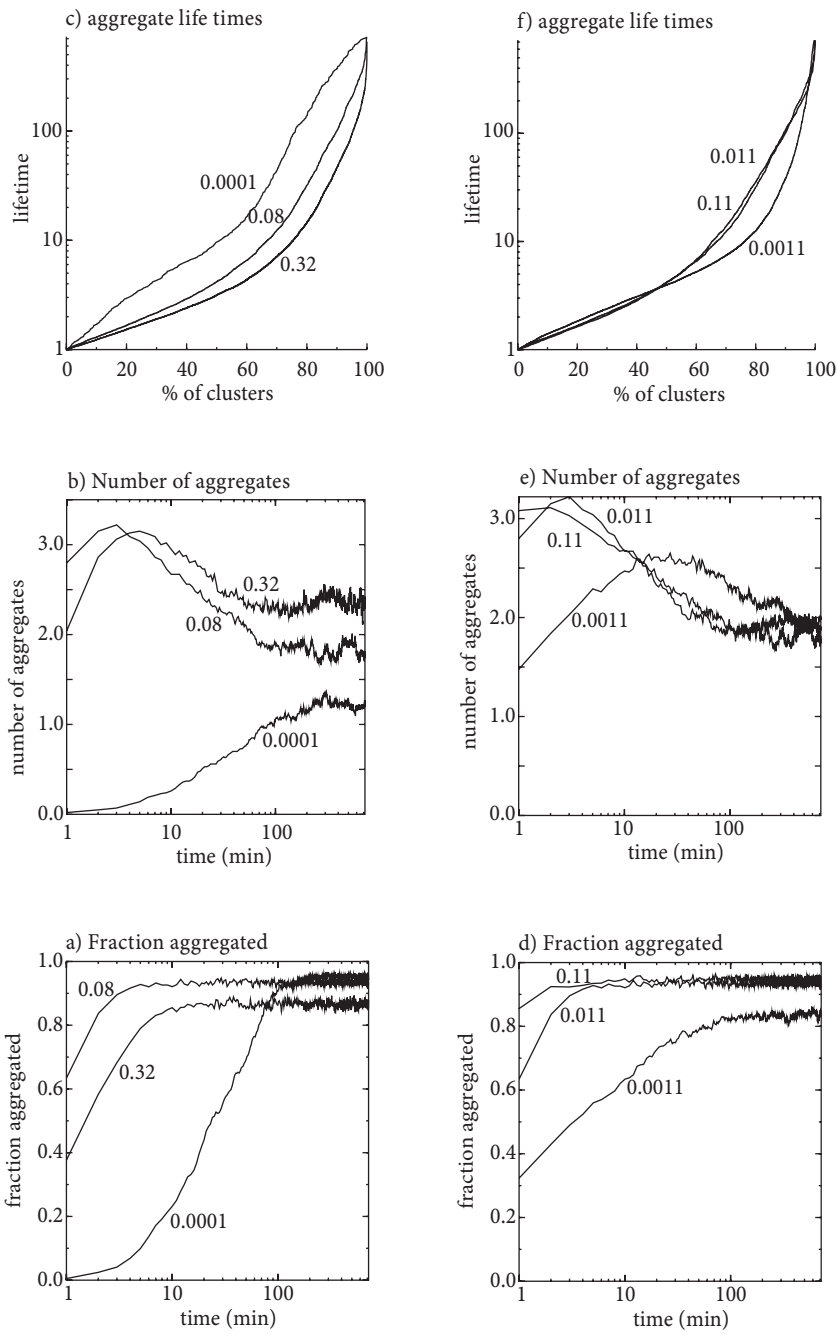
Sensitivity to model parameters

In the following we will study the sensitivity of our dynamic indices to changes in model parameters (using the constant density of 20 individuals). We will first study the influence of ‘non-social’ diffusion-related parameters that are independent of the presence of other individuals (speed v and spontaneous stopping rate q_0), switching then to ‘social’ parameters that are modulated by the local animal density. Indices will be averaged over 100 Monte-Carlo simulations, and to increase the accuracy of the aggregate lifetime estimates we extend the simulation time to 12 h (extending thus the stationary dynamics phase of the simulated system).

Sensitivity to ‘non-social’ parameters

Figure 5 summarises the sensitivity to the ‘non-social’ parameters v and q_0 . q_0 is the probability of stopping spontaneously, i.e. without any resting neighbours. The rates of stopping and restarting moving control two features of the system: they have an indirect effect on the dispersion when considered over a large period of time (i.e. the diffusion rate), and they drive the mean rate at which new potential sites for aggregation (“seeds”) occur. Increasing q_0 from the standard value of 0.08 s^{-1} to 0.32 s^{-1} slows down the mean dispersion but it enhances the rate of seed occurrences. In the transient phase, we observe a slowdown of the aggregation dynamics (which means that the effect on the mean dispersion more than compensates the higher rate of seeds occurrence). The system then converges to a lower fraction of aggregated cockroaches: a higher stopping rate combined with the same probability to leave existing aggregates gives a higher fraction of the population that is trapped into isolated resting states outside of the aggregates.

Figure 5. Sensitivity of temporal dynamics to ‘non-social’ parameters: the fraction of cockroaches that are aggregated ((a) and (d)), the number of aggregates ((b) and (e)) and the cumulative distribution of aggregate lifetimes ((c) and (f)). For the left three graphs we varied the spontaneous stopping rates $q_0=0.0001, 0.08$ and 0.32 . For the right three graphs we varied speed $v=0.0011, 0.011$ and 0.11 . Note that the simulations were done for 12h in order to have more aggregates that end their lifetime. The time axis in (a), (b), (d) and (e) are on log scale to better visualise the transient dynamics and to condense the stable stationary states. The curves of (a), (b), (d) and (e) represent the mean over 100 Monte Carlo simulations.



If on the contrary q_0 is decreased to 0.0001 s^{-1} then the cockroaches nominal dispersion is affected little, but the rate of seed occurrence dramatically decreases. Hence, it takes a long time for a first aggregate to appear. While the larger q_0 always formed a peak number of aggregates before decreasing to their stationary values (which are positively correlated to q_0), here the mean number of aggregates remains below 1.0 for a long time (representing the probability that at least one aggregate already formed) and increases in a sigmoid way to ≈ 1.0 : once the first aggregation site appears, it tends to attract more cockroaches than in the standard condition since only very few other isolated stopped cockroaches (and hence seeds of aggregates) can be found. Accordingly, decreasing q_0 also has a tendency to increase aggregate lifetime (Figure 5c) because competition between concurrent aggregation sites almost vanishes.

Speed v as the nominal value of the speed of individuals when they are in a moving state has a direct effect on the mean dispersion (diffusion) but no effect on the rate of seed occurrence. Of course, only modifying speed v in the system alters the duration of the transient dynamics because the frequency of encounters with stopped cockroaches heavily depends on the speed. In the stationary phase, competition between aggregates is still the major process and the sensitivity of aggregate numbers to the diffusion rate disappears. The fraction of aggregated cockroaches is lower for slow animals: while moving between aggregates they have more time to get trapped in the isolated resting state (since the probability to stop per unit of time remains the same). Speed has little influence on aggregate lifetime (see Figure 5(f)).

Sensitivity to ‘social’ parameters

To study the sensitivity to social parameters we modified the propensities to stop or restart as a function of the number of neighbours: we will name “starting profile” the vector P of the starting rates p_0 to p_3 when 0 to 3 neighbours are present respectively, and accordingly Q for “stopping profile”. A minus sign (–) indicates less sensitivity to local neighbour density, while a plus sign (+) indicates a high sensitivity. The measured parameter profiles (Table 1) are $P-$ and $Q+$. We chose to study the collective response when (1) starting rates are more sensitive to neighbourhood ($P+$) or (2) stopping rates are less sensitive ($Q-$) to neighbourhood. Figure 6 summarises these two starting and two stopping profiles. The standard parameter values $P-Q+$ are represented by bold curves. The parameter values for profiles $P+$ and $Q-$ are given in the Figure legend. The spatio-temporal examples in Figure 7 demonstrate clearly

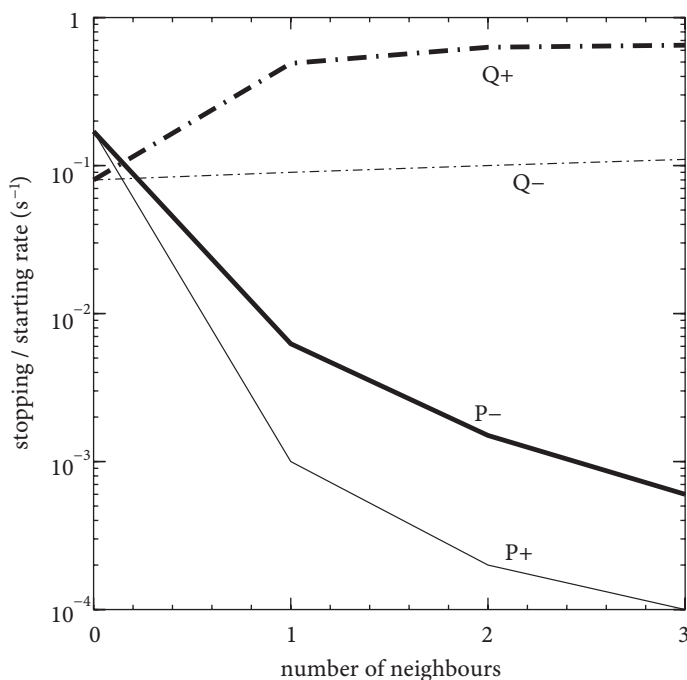


Figure 6. The profiles of individual stopping (Q) and starting (P) rates (our ‘social’ parameters) as a function of the number of resting cockroaches within the perception radius ρ . Profiles Q+ and P+ show a strong (non-linear) influence of local density, while density has less influence in profiles Q– and P–. The standard conditions (Table 1) correspond to profile combination P–Q+. Profile P+ is defined by $p_0=0.17$, $p_1=0.001$, $p_2=0.0002$ and $p_3=0.0001$, while Q– is defined by $q_0=0.08$, $q_1=0.09$, $q_2=0.10$ and $q_3=0.11$. Note the log-scale on the y-axis.

the effects of the different profile combinations. A weak influence of local density (profile combination P–Q– in Figure 7(a)) leads to a weak positive feedback with the formation of numerous short-lived aggregates. A strongly non-linear influence of local density (P+Q+) on the contrary induces a very strong positive feedback with few long-lived aggregates (d). With the standard parameter values (P–Q+) aggregates of an intermediate lifetime are formed (c) while profile P+Q– form stable long-lived aggregates with less isolated or moving cockroaches (b).

Interestingly, the profile combination has little influence on the time to reach stationary dynamics (Figure 8 (a) and (b)) at least for the fraction aggregated (P+ has a slight tendency to prolong them). The asymptotic number

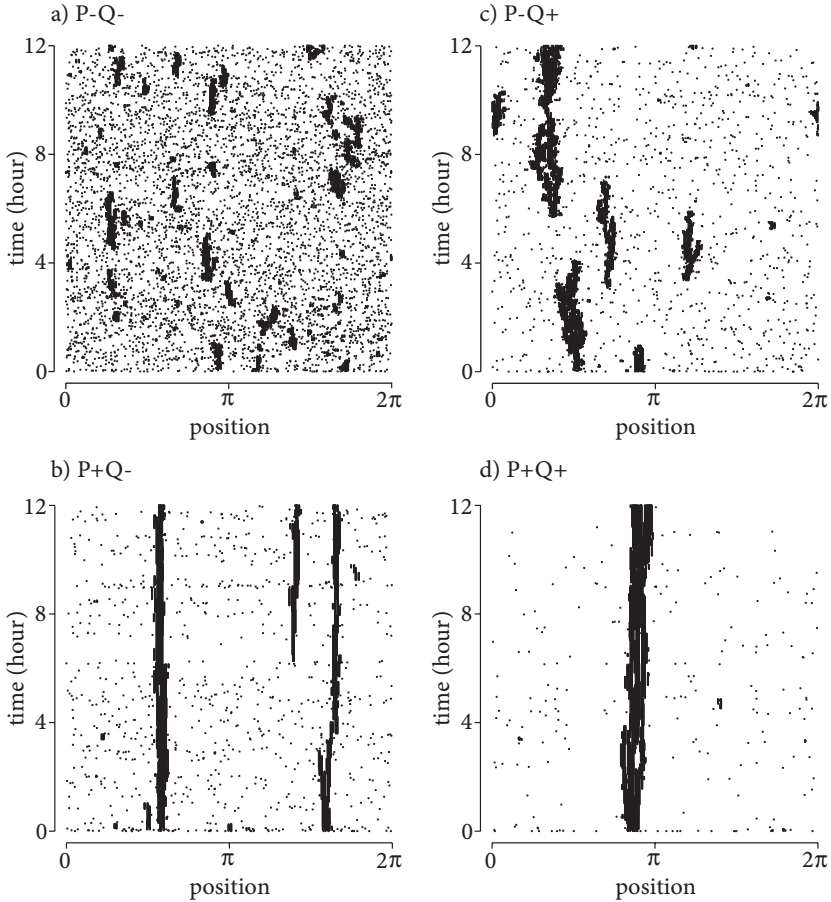


Figure 7. The effects of profiles on spatio-temporal aggregation dynamics. (a) Local density has little effect (P–Q–) thus little positive feedback occurs and aggregation is weak. (b) and (c) show intermediate effects of local density with profiles P+Q– and P–Q+ respectively. The latter (c) corresponds to the standard parameters (Table 1). (d) shows the strongest effect of local density (P+Q+) with strong positive feedback leading to few and stable aggregates.

of aggregates seems also to be independent of profile combinations (≈ 2 aggregates in all cases) while the asymptotic fraction of aggregated cockroaches is nearly 1 with P+Q+, only 0.6 with P–Q– and ≈ 0.93 for both P+Q– and P–Q+ (despite the dynamic differences in Figure 7(b) and (c)).

Other differences emerge in the form of the transient dynamics: Q+ leads in the first minute to 60% cockroaches aggregated with a high number of aggregates

(≈ 2.5), while Q– reaches only 15% aggregated in less than one aggregate.

The strongest differences are seen in the aggregate lifetimes. These are longest for P+Q+ followed by P+Q–, P–Q+ and P–Q– (see Figure 8(c)) and are consistent with the example patterns in Figure 7.

Mixed societies: sensitivity to “modified” individuals

We will now study how the dynamics of a population with 20 standard individuals (P–Q+) change when substituting 1, 2 or more cockroaches with individuals that behave differently. Figure 9 summarises the results when substituting with either P+Q+ individuals (a,b) or individuals with $q_0=0.0001$ (c,d) for the dynamics of the fraction aggregated (a,c) and the aggregate lifetimes (b,d). Increasing proportions of P+Q+ individuals do not change the transient dynamics of the fraction aggregated but only increase gradually their asymptotic value to the levels already observed in Figure 8(a). The change to lifetimes is less gradual: no change is observed for up to 10 (out of 20) P+Q+ individuals, but lifetimes increase drastically when substituting 15 or even 20 individuals.

Substitution with $q_0=0.0001$ individuals shows the inverse sensitivity, aggregate lifetimes are rather unaffected while the time to reach stationarity of the fraction aggregated jumps drastically when substituting more than 15 individuals. This means that as long as there are some individuals with a high spontaneous stopping rate aggregates are founded early on, setting off the positive feedback effect that leads to rapid aggregation.

In Figure 10 we characterised aggregate stability by the longest aggregate lifetime for each simulation (expressed as the fraction of the longest possible lifetime 12 h). This index can be interpreted as some “percolation length” in the spatio-temporal dynamics (Figure 2). While substitution with $q_0=0.0001$ individuals changes the mean longest aggregate lifetime gradually in a linear way, there is a non-linear increase when substituting with P+Q+ individuals. Already as few as 5 individuals bring this percolation index very close to the value of a population consisting entirely of P+Q+ individuals. This observation contrasts with the cumulative distributions of the aggregate lifetimes in Figure 9(b) where there was barely any change when substituting less than 15 individuals.

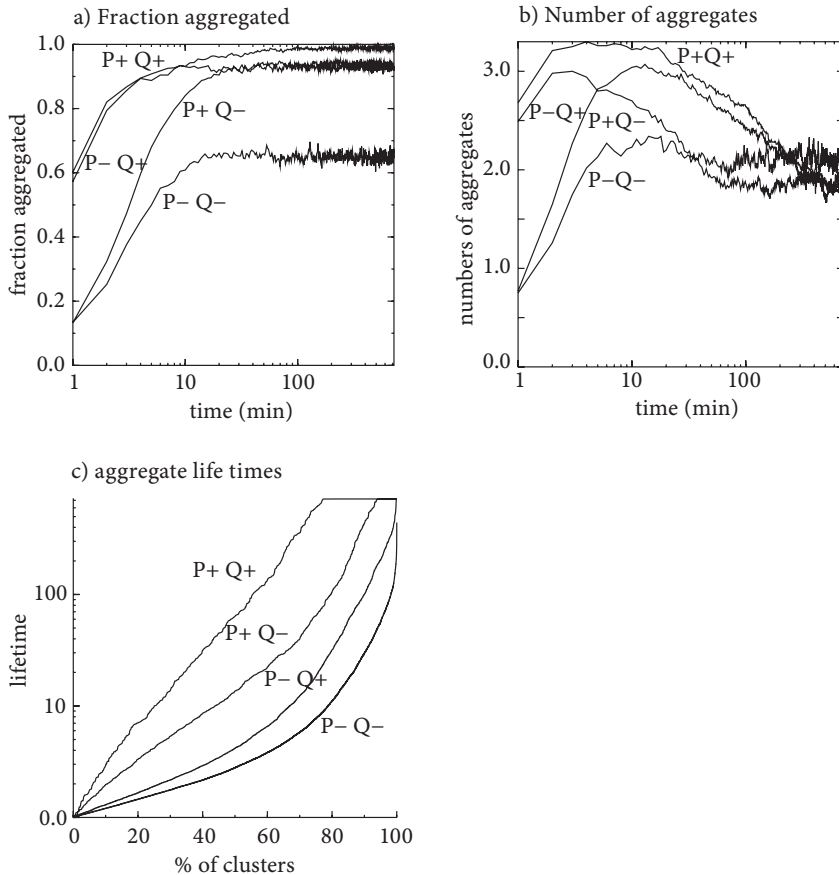


Figure 8. Sensitivity of aggregation dynamics to ‘social parameters’ (profiles) : (a) fraction of cockroaches that are aggregated, (b) the number of aggregates, and (c) the cumulative distribution of aggregate lifetimes. (a) and (b) represent the mean over 100 Monte Carlo simulations.

Discussion and perspectives

In this paper we first analysed the sensitivity of an individual based model of cockroach aggregation to “non-social” and “social” parameters. This classical type of sensitivity analysis was then extended to sensitivity to a “mixed” society where the behavioural parameters of one or more individuals in the population were modified.

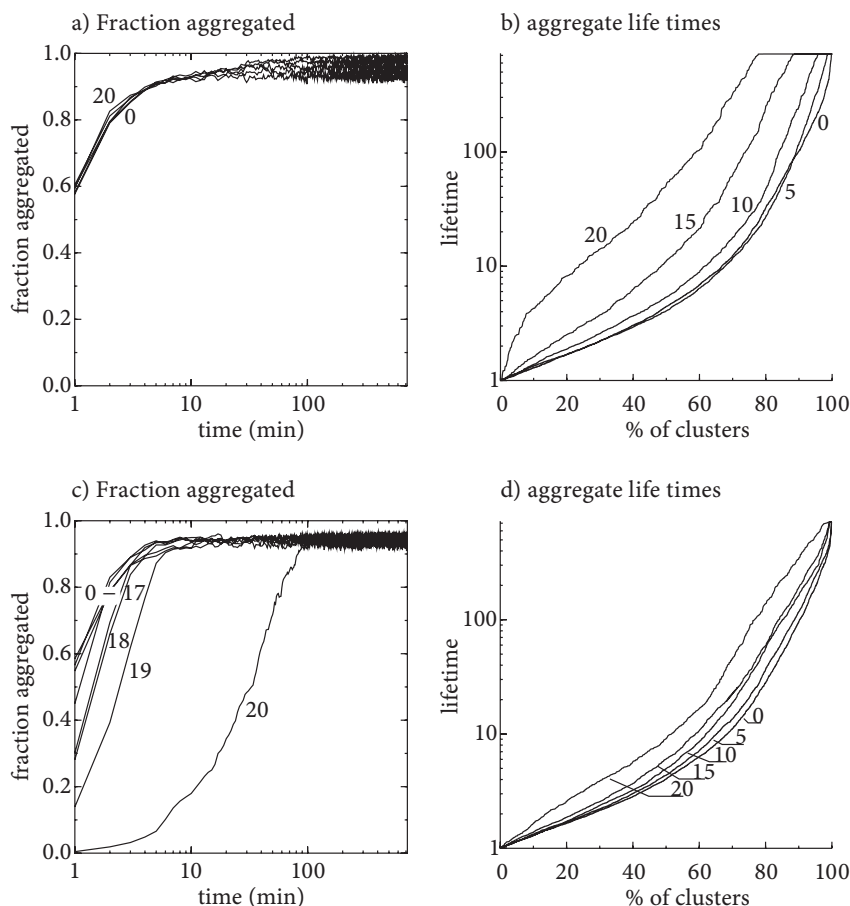


Figure 9. Sensitivity of aggregation dynamics ((a) and (c)) and aggregate lifetimes ((b) and (d)) to substituting standard individuals (with parameters as in Table 1) by either P+Q+ individuals ((a) and (b)) or individuals with a spontaneous stopping rate $q_0=0.0001$ ((c) and (d)). The numbers indicate how many individuals are substituted for the respective curves. (a) and (c) represent the mean over 100 Monte Carlo simulations.

The aggregation mechanism presented here belongs to the class of self-organised processes (Camazine et al. 2001). No explicit cognition of collective features (such as the sizes of aggregates or the number of aggregates) is required on the individual level since only local cues (namely number of neighbours) are used. The collective dynamical patterns that are relevant to biological fitness (short-lived aggregates or persisting and monopolising aggregates) thus result

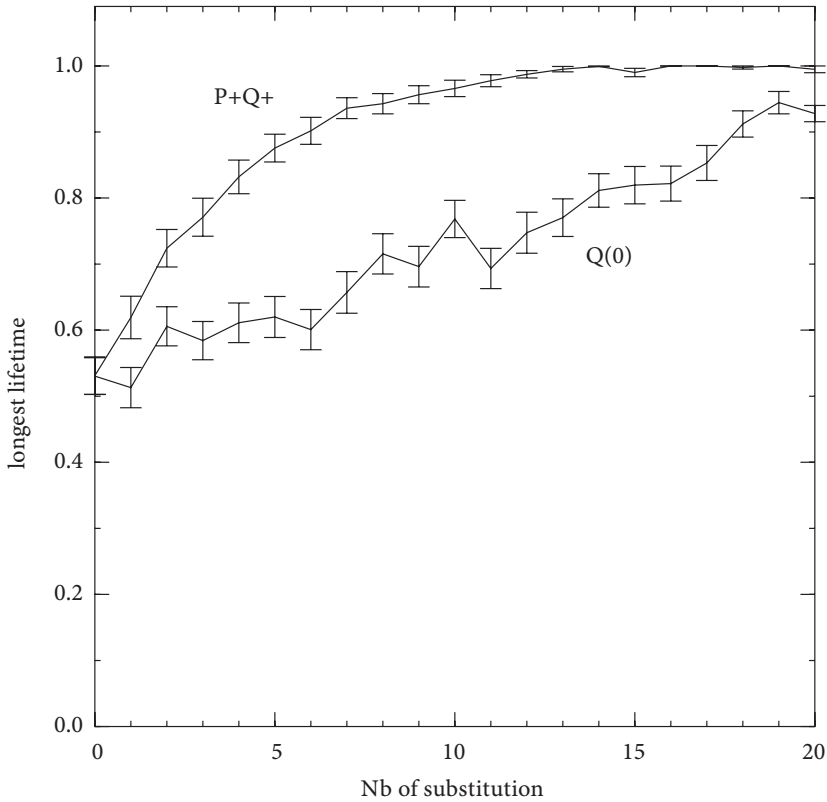


Figure 10. Mean longest lifetime (computed from 100 Monte Carlo simulations) as a function of the number of substituted animals, either with profile P+Q+ or with $q_0=0.0001$.

from a distributed decision. Though they can be described in terms of a LALI process (Gierer & Meinhardt, 1972), the resulting patterns hardly resemble the classical repetitive geometrical patterns found in the literature (Turing, 1952; Gierer & Meinhardt, 1972; Ball, 1998; Meinhardt, 1995). This is probably due to the very low number of individuals in the population (20) and the high tendency to join existing aggregates: the probability to join an isolated stopped individual is as high as 0.5 s^{-1} (the moving cockroach perceives it during $\approx 1 \text{ s}$) and increases even more for larger numbers of neighbours. The historical component (i.e. the ordered chain of individual decisions) is thus very influential on the resulting patterns. Characteristic wave lengths that the corresponding Eulerian model would predict could thus be hard to show up in the experimental

system (contrary to other systems such as ant cemeteries (Theraulaz et al., 2002). This kind of dynamics does not take much time to detect an 'optimal' aggregate location: the very first stopped individual ('seed') rapidly drains the rest of the population from the environment.

The sensitivity analysis shows the variability of spatio-temporal structures when tweaking one parameter for the whole population (e.g. Figure 7). The shift in the resulting structures strongly depends on the involved parameter. For instance, individual speed has little effect in our context (aggregation with few individuals in a small arena) while it may amplify spatial segregation in the case of numerous individuals travelling in schools (Gueron et al., 1996; Couzin et al., 2002; Couzin & Krause, 2003). Inversely, the spontaneous stopping rate strongly affects how long it takes to reach the stationary level of the fraction aggregated. In general, the stopping and starting rates involved in the aggregation process have been identified as bifurcation parameters in numerous insect models (e.g. Deneubourg et al., 2002).

The emergent patterns are most sensitive to the social interaction intensity. This is not surprising with our homogeneous experimental conditions that prevent any facilitation based on an environmental template. Interestingly, the measured biological parameters lead in this case to a balanced situation: stable aggregates rapidly form while there remains sufficient traffic to allow patterns to rearrange. E.g., if the stopping probabilities were less correlated with the perceived stopped conspecifics, aggregation would be tricky to achieve or at least very unstable (see profile P–Q— in Figure 7 and Figure 4 in Jeanson et al. (2004)). On the other hand, a higher negative impact of local density on the probabilities to leave an aggregate would trap the whole population in the earliest aggregates (Figure 7 and Figure 8). In ecological conditions this would decrease the capacity of the system to explore better sites and freeze it in a potentially sub-optimal solution. The chosen site for aggregation should be a function of the interplay between exploration of a heterogeneous environment and rapid gathering at an advantageous spot.

This balanced behaviour was obtained with parameters measured in homogeneous conditions. The model's behaviour in a more realistic heterogeneous ecological environment remains nonetheless to be explored. In such cases parameter values may undergo specific modulations. For instance, the spontaneous stopping rate q_0 (that regulates the emergence of a first aggregation seed) determines the time to reach stationary state (Figure 5a). If there were some very attractive spots they would represent natural seeds and q_0 could lose its importance. Eventually, the interplay between social interactions and environ-

mental heterogeneity should be further explored, in particular in cases where there is an additional feedback of collective behaviour on the environmental conditions (such as locally enhanced humidity by the presence of many individuals).

The examples of mixed societies we gave in this paper illustrate how the relative proportion in behavioural divergence amongst individuals in the population may influence the transition from one pattern to the other in various ways (Figure 9, 10). While the successive introduction of individuals that differ in a particular parameter may change the collective response only gradually (in our case q_0), it is just as possible to obtain highly non-linear shifts where few individuals are sufficient to impose their type of aggregation dynamics on the rest of the population.

In the case of cockroaches it is known that they preferentially gather with their own strain rather than another strain (Rivault & Cloarec, 1998). Despite this preference one can frequently find aggregates containing several strains; mixed societies such as studied in this paper may thus represent a biological reality. Division of labour in eusocial species are an extreme case where the existence of castes (on the morphology and/or behaviour scale) is crucial for an efficient spatio-temporal task allocation.

More interestingly, the 'in silico' study of mixed societies makes sense with the availability of increasingly powerful small autonomous robots (Caprari et al., 2002) that could be programmed to behave like a real animal and that could then infiltrate a natural animal community. The aim of this introduction would be to change the collective animal dynamics in a desired way. This is the declared goal of the currently ongoing European LEURRE project (<http://leurre.ulb.ac.be/>). Such a change can rely on slight modifications of a particular simple behaviour in the insect-like robots (insbots). The non-linear collective responses to such changes that was detected in our study demonstrates that small numbers of insbots can engender drastic shifts in collective responses if only the relevant behavioural trait is correctly identified. In this sense the non-linearity of the collective response represents a valuable asset in the control of animal populations. The main difficulty lies in the identification of the relevant parameters since in such self-organized systems, with their multiple positive and negative feedback, intuition is a poor guide for prediction. Detailed quantitative models at the individual level combined with powerful computations represent a very promising tool to identify these parameters.

In conclusion, this study shows that modulating individual behavioural parameters in a (small) sub-population can change collective dynamics dramat-

ically. Current advances in biomimetic robotics offer new perspectives to apply this result to the control of animal populations. While traditional control concentrates on changing the environment to force population dynamics in a desired direction, a new type of control is to infiltrate the population with insect-like robots that change collective dynamics through their modulated behavioural response. Yet this application is conditional on the intelligent combination of extensive simulation work, a sophisticated experimental methodology and a reliable identification of the underlying behavioural mechanisms.

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