

Phase transitions in insect swarms

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Abstract In contrast with laboratory insect swarms, wild insect swarms display significant coordinated behaviour. It has been hypothesised that the presence of a fluctuating environment drives the formation of transient, local order (synchronized subgroups), and that this local order pushes the swarm into a new state that is robust to environmental perturbations. The hypothesis is supported by observations of swarming mosquitoes. Here I provide numerical evidence that the formation of transient, local order is an accidental by-product of the strengthening of short-range repulsion which is expected in the presence of environmental fluctuations. The results of the numerical simulations reveal that this strengthening of the short-range can drive swarms into a crystalline phase containing subgroups that participate in cooperative ring exchanges – a new putative form of collective animal movement lacking velocity correlation. I thereby demonstrate that the swarm state and structure may be tuneable with environmental noise as a control parameter. Predicted properties of the collective modes are consistent with observations of transient synchronized subgroups in wild mosquito swarms that contend with environmental disturbances. When mutual repulsion becomes sufficiently strong, swarms are, in accordance with observations, predicted to form near stationary crystalline states. The analysis suggests that the many different forms of swarming motions observed across insect species are not distinctly different phenomena but are instead different phases of a single phenomenon.

Introduction

In contrast with bird flocks, fish schools and animal herds, mating swarms of flying insects are a form of collective motion lacking global order [1-15]. Their behavior is also context dependent. Insect swarms observed in the wild exhibit long-range correlations [10-12] and can contain synchronized subgroups whose size and membership change rapidly over time [13], while those observed in a controlled laboratory environment do not display any form of local ordering [14] unless they are perturbed [15]. Reynolds [16] hypothesised that the presence of a fluctuating environment drives the formation of transient, local order (synchronized subgroups), and that this local order pushes the swarm into a new state that is robust to environmental perturbations. The hypothesis is supported by a theoretical analysis and by analysis of observations of swarming mosquitoes [16]. Here the formation of transient, local order of the kind observed in wild mosquito swarms is shown to be a by-product of short-range repulsion [3,14] which is expected to increase in the presence of environmental perturbations that can disrupt normal flight behaviours, enhancing the likelihood of collisions. Indeed, if individuals were responding to the same (swarm wide) environmental noise and if these fluctuations dominate then irrespective of initial conditions, all individuals will, in the absence mutual repulsion converge onto a common trajectory [17]. The results of the numerical simulations reveal that strengthening of short-range repulsion can, when sufficiently strong, drive swarms into a crystalline phase containing subgroups that participate in cooperative ring exchanges – a new form of collective animal behaviour. The emergence of these ordered states is perhaps not surprising given that crystal-like structures are known to emerge from the competition between attraction and repulsion in the physics of solids. Nonetheless, as shown later, the newly identified collective modes are quite unlike the collective elastic modes that spontaneously emerge in crystalline solids, in which individuals oscillate back-and-forth past a fixed position. The fact that the predicted properties of the crystalline phase have similitude with the transient, local order found in wild mosquito swarms suggest that these swarms are close to an order-disordered phase transition. Finding such putative evidence for order-disordered phase transitions in insect swarms is significant because a substantial body of influential literature pertaining to swarming [10-12] presupposes that swarms are poised at the cusps of order-disorder phase transitions. Evidence for ordered phases has, until now, remained elusive. The new results complement the growing realization that perturbations can drive swarms into different kinds of disordered states with distinct mechanical and thermodynamical properties [4,5,7-9]. And may be of interest to engineers and scientists working on self-organising geometric pattern formation in mobile multi-robot (or swarm robotic) systems [18].

Model formulation and results

Stochastic models for the trajectories of swarming insects predict accurately many of the properties of laboratory swarms [1,7,15,19-23], including phase coexistence the occurrence of solid-like properties such as tensile strength and a finite Young's modulus and the emergence of viscoelastic properties and thermodynamic-like properties in perturbed swarms. The models also reconciled disparate observations made in the laboratory (wherein correlations are absent [14]) and in the wild [10-12] by showing how environmental perturbations induce correlations, of the kind reported on by Cavagna and co-workers. In these model interactions between the individuals are not explicitly modeled; rather, their net effect is subsumed in a restoring force term, since observations have suggested that to leading order insects appear to be tightly bound to the swarm itself but weakly coupled to each other inside it with no local alignment between individuals [3,14]. When this restoring force is taken to be harmonic, and so consistent with observations [1,2], the positions of each simulated individual are Gaussian distributed. Here stochastic models for the x-components of the trajectories of insects in wild swarms are founded on the joint distribution for the positions, x_1, \dots, x_n , of n individuals

$$p(x_1, x_2, \dots, x_n) \sim \exp \left(-\frac{1}{2} \sum_{i=1}^n x_i^2 - \sum_{\substack{i=1, j=1 \\ i \neq j}}^n \frac{s}{|x_i - x_j|} \right) \quad (1)$$

where s determines the strength of the mutual repulsion between individuals. This distribution ensures that two or more individuals cannot simultaneously occupy the same location. One of the simplest stochastic trajectory simulation models that is consistent with this distribution is given by

$$du_i = -u_i dt - x_i dt + s \sum_{\substack{j=1 \\ j \neq i}}^n \frac{\text{sign}(x_i - x_j)}{(x_i - x_j)^2 + \varepsilon} dt + \sqrt{2} d\xi_i \quad (2)$$

$$dx_i = u_i dt$$

where x_i and u_i are the position and velocity of the i^{th} individual at time t , and where $d\xi(t)$ is an incremental Wiener process with correlation property $\overline{d\xi(t)d\xi(t+\tau)} = \delta(\tau)dt$ [See 19 for details of the model formulation]. The first term on the right-hand side of Eqn. (2) is a memory term that causes velocity fluctuations to relax back to their (zero) mean value. The second term corresponds to a harmonic potential that binds each individual to the swarm center. This is a hallmark of swarming [1,2]. The third term represents the mutual repulsion (acceleration) between individuals, as observed by Puckett et al. [3]. The parameter $\varepsilon=0.01$ is introduced to regularize the divergence. The fourth term, the noise term, represents fluctuations in the resultant internal force that arise partly because of the limited number of individuals in the

grouping and partly because of the nonuniformity in their spatial distribution. By construction velocities are Gaussian distributed and uncorrelated.

As the strength of the repulsion increases, the model predicts that swarms transition from a gas-like state to a crystalline state populated by rings of individuals that sporadically exchange positions (i.e., with individuals switching between quasi stable positions) (Figs.1-3). Cooperative ring exchange is a previously undocumented putative novel form of collective animal behaviour lacking velocity correlations (net displacements made over long times are correlated), although analogous behaviour has been examined in radically different physical systems [24]. Nonetheless, predicted properties of the collective modes are consistent with observations of transient synchronized subgroups in wild mosquito swarms that contend with environmental disturbances [13]. In both cases: the instantaneous probability of an individual belonging to a subgroup (ring) of size n decreases monotonically as n increases (Fig. 3a); the probability of an individual interacting with its n^{th} -nearest neighbour decreases monotonically with n in an exponential-like way (Fig. 3b); the probable duration of a subgroup (ring) decreases monotonically with increasing duration in an exponential-like way (Fig. 3c); and the number of subgroups (rings) increases linearly with swarm size (Fig. 3d). Moreover, as the strength of the repulsion increases, the swarm density profile is predicted to transition from being Gaussian (Eqn. 1 with $S=0$) to having forms that are well represented by q-Gaussians with $q<0$ (Fig. 4). A q-Gaussian has the probability density function, $f(x) = \frac{\sqrt{\beta}}{C_q} e_q(-\beta x^2)$ where $e_q(x) = [1 + (1 - q)x^2]^{\frac{1}{1-q}}$ is the q-exponential, C_q is a normalization constant, and where $q<3$ and β are real-valued parameters. Like the transient order characteristics shown in Fig.3, q-Gaussian density profiles with $q<0$ are hallmarks of wild swarms of mosquitoes [16]. Unlike Gaussians, the q-Gaussians have finite extent. Consequently, wild swarms are predicted to be more tightly bound together than are laboratory swarms which have long-tailed density profiles [2]. Note that q-Gaussians arise in other various theories of swarming [16,22] and in this sense are a robust prediction.

Discussion

The above results complement those of van der Vaart et al. [15] who showed how environmental perturbations induce correlations in midge swarms. The new results show how environmental perturbations can by virtue of strengthening short-range repulsion also induce the formation of sporadic synchronized subgroups that resemble the transient order seen in

135 wild mosquito swarms [13,16] (Figs. 1-4). The results also suggest that mating swarms are
poised at the cusp of a disorder-order phase transition, as anticipated by Attanasi et al. [10,11]
and Cavagna et al. [12], albeit for reasons which now appear to need revision [15].
Furthermore, the results suggest that the state and structure of swarms are tuneable with
environmental noise as a control parameter. When mutual repulsion becomes sufficiently
140 strong, swarms are predicted to form near stationary crystalline states (Fig. 1c); states that
are consistent with occurrence of swarms of hovering insects [25].

Solid-like properties have been identified in dynamical tests with insect swarms [4,7], but this
is the first putative example of the most basic form of solid-like behaviour (crystalline
145 structure). The potential new state of swarming was predicted by a novel stochastic trajectory
simulation model for non-interacting individuals, Eqn. 2. Such models capture many of the
properties of laboratory swarms [1,7,15,19-23]. These models are founded on Gaussian
density profiles. The new model builds directly on this success, by replacing the Gaussian
density profiles with seemingly more realistic density profiles, Eqn. 1, that account of the fact
150 that two or more individuals cannot occupy the same location. In this sense crystalline states
and cooperate ring exchanges appear as inevitable predictions of highly successful models.
Analysis also indicates that when the strength of repulsion varies across a population then the
most reactive individuals aggregate preferentially in the outskirts of the swarms and if present
in sufficient large numbers can even form satellite ‘swarms’ – small swarms that are found
155 close to, but separate from, much larger swarms (Fig. 5), as observed in midges by Neems et
al. [26] and in mosquitoes by Sawadogo et al. [27]. An individual’s probability of mating is
greatest when located at the edge of a large swarm (i.e., where females enter the lek) or when
located in satellite swarm (i.e., adjacent to prominent landmark over which swarms form) as
they can intercept females on their way to the main swarm. Therefore, selection pressures for
160 mating should result in individuals with near maximal levels of repulsion, making satellite
swarms a rare occurrence, as observed [27]. The satellite swarms are predicted to be formed
exclusively from the highly reactive individuals. This is consistent with observations of the
smallest (most aerodynamic agile) individuals occurring predominantly in the smallest swarms
[26]. If present in sufficient numbers, then the strongly reactive individuals are predicted to
165 form a ring around the swarm.

The foregoing analyses is entirely consistent with that of Reynolds [16] who suggested that
the presence of a fluctuating environment drives the formation of transient, local order
(synchronized subgroups whose size and membership change rapidly over time), and that this

170 local order pushes the swarm as a whole into a new state that is robust to environmental
perturbations. It advances the analysis of Reynolds [16] by identifying a novel putative form of
collective behaviour that this transient, local order may take and by showing its formation may
be by-product of mutual repulsion – the most elementary kind of interaction between
individuals, and a necessary one. The new results add to the growing realization [15,16] that
175 different kinds of group morphologies and swarm dynamics are simply different phases of the
same phenomenon; and that correlations are not a universal feature of collective behaviour.
It would be interesting to test whether crystalline-like states and/or synchronized subgroups
resembling cooperative ring exchanges are evident in mosquito swarms [13] as the analysis
suggests, and in gnat swarms and in crane fly swarms, as casual (personal and other [28])
180 observations suggest.

Finally, a very different phase of swarming is predicted to occur at low Reynolds
(Supplementary Material). Reynolds number effects have, until now, not featured in the
literature on collective motion despite their occasional similitude with fluid motion [29]. This
185 analysis together with the foregoing and that of Reynolds et al. [18] suggests that the variety
of motions of swarming insects (freely roaming, hovering, looping, back and forth motions,
transient, local order) [25] are not distinctly different phenomena but are instead different
phases of a single phenomenon.

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Data Availability Statement

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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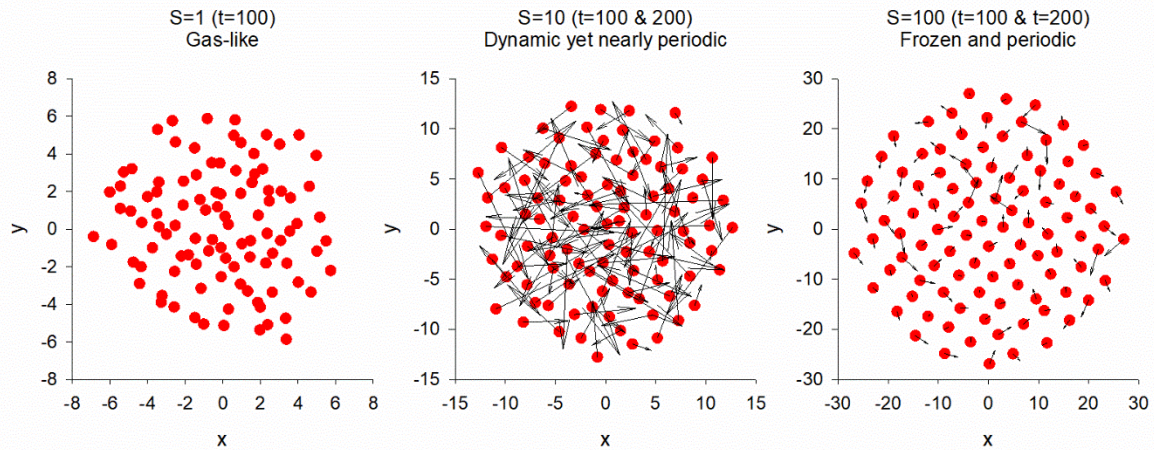


Figure 1 Predicted transition from a gas-like state to a crystalline state exhibiting cooperative ring exchange. Predictions are shown for a 2D swarm containing 100 individuals. Movements in the x- and y- directions were obtained using independent pairs of the stochastic model given in Eqn. 2. The vectors indicate the displacements made between times $t=100$ and $t=200$ a.u. Cooperative ring exchange is also evident in simulated 3D swarms but is harder to discern.

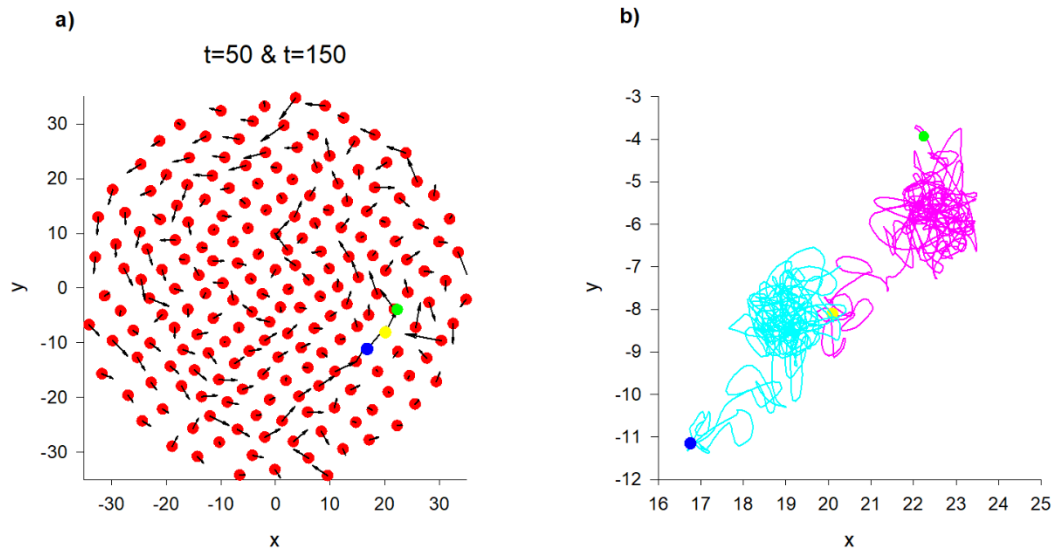
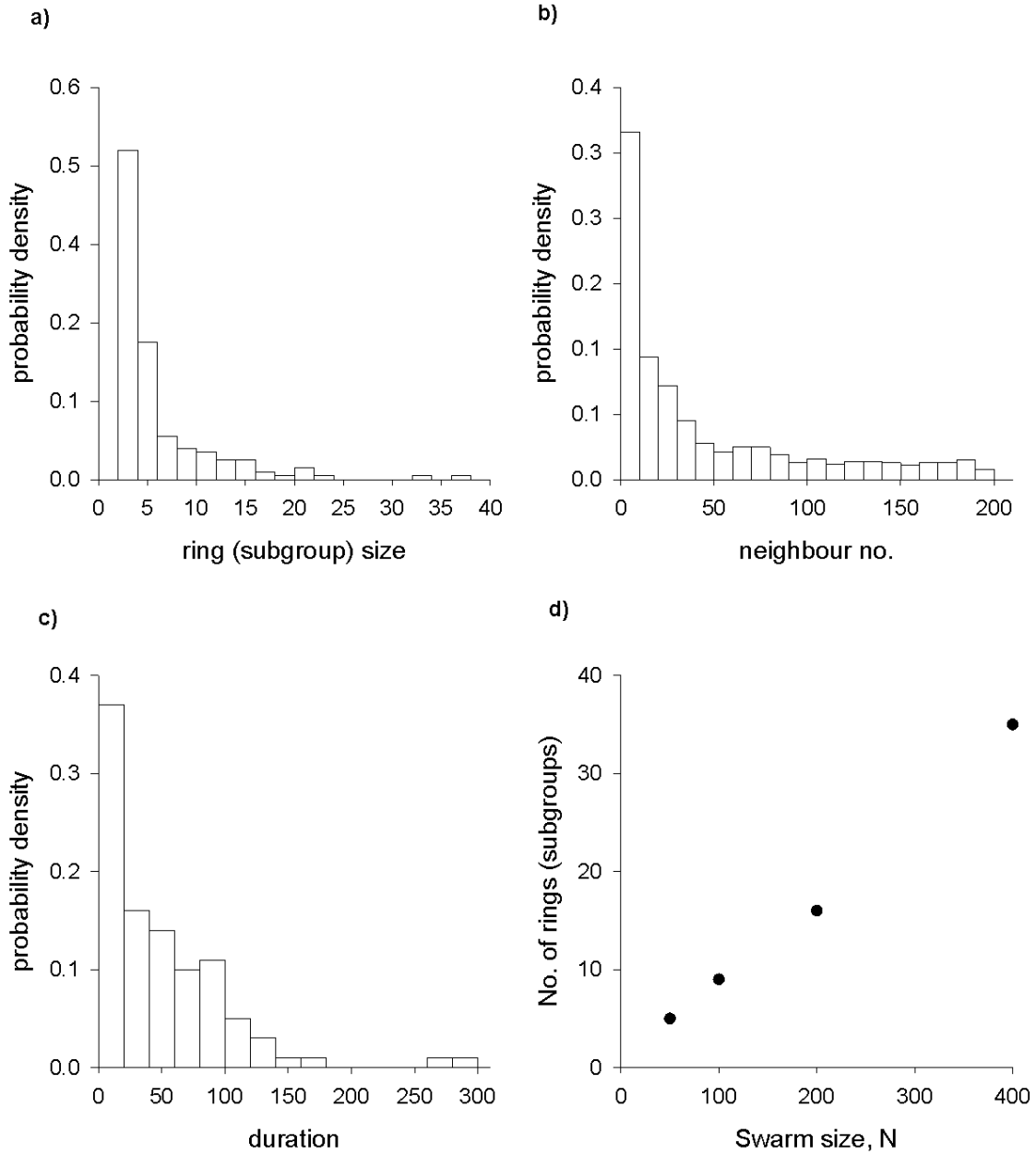


Figure 2 a) An example of the emergence of sporadic cooperative ring exchange. The locations of the individuals at time $t=50$ a.u. are shown (solid circles) together with their net displacements during the time interval $t=50$ to $t=150$ a.u. (black arrows). Note that other snapshots show both clockwise and anticlockwise rotations. **b) The trajectories of the individuals located at the positions shown in dark blue and yellow at $t=50$ a.u.** The individual starting at the location marked in dark blue is seen to move to the location previously occupied by the individual that started from the location marked in yellow. And the individual starting at the location marked in yellow is seen to move to the location previously occupied by the individual that started from the location marked in green. Movements in the x - and y -directions were obtained using independent pairs of the stochastic model given in Eqn. 2. Predictions are shown for a 2D swarm containing 200 individuals with $S=100$.



285 **Figure 3 Characteristic features of the cooperative rings.** **a)** Probability of the size of a
 ring in which an individual may be included at any moment – omitting rings of size 1. **b)**
 Probability of interacting with the kth nearest neighbour. **c)** Durations of ring exchanges, i.e.,
 time elapsed between first arriving at a previously occupied location and moving to another
 previously occupied location. **d)** Number of rings as a function of swarm size. Predictions are
 290 shown in panels a) and b) for a 2D swarm containing 200 individuals with $S=100$. Analyses

include both closed (complete) and open (incomplete) rings. Open rings end with individuals that have moved to a location that was previously vacant rather than occupied by other individuals. Open rings lead to the appearance of apparent 'leaders' and 'followers'.

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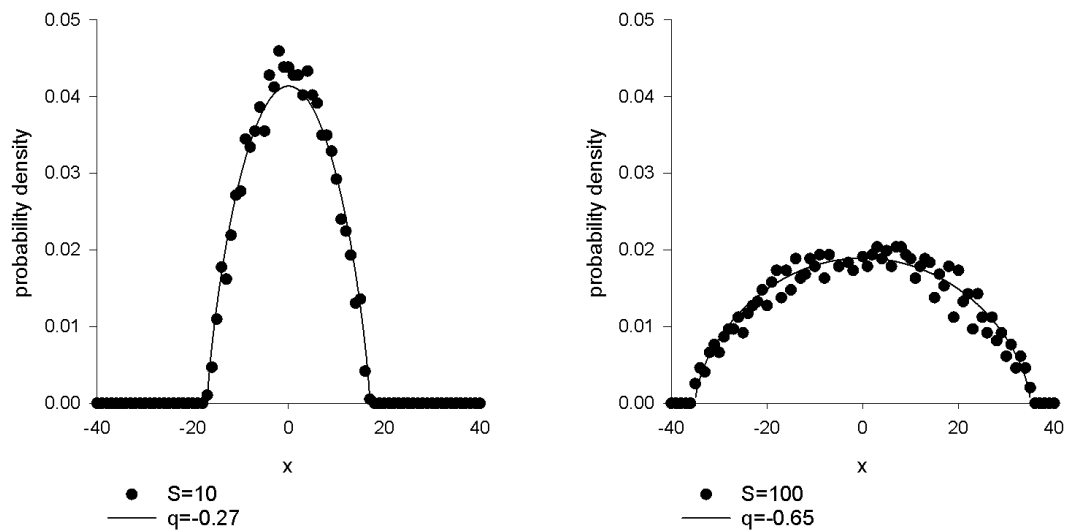


Figure 4 Density profiles are predicted to transition from being Gaussian to q-Gaussian as the strength of the mutual repulsion increases Movements in the x- and y- directions were obtained using independent pairs of the stochastic model given in Eqn. 2. Simulation data are shown (•) together with the best fit q-Gaussians.

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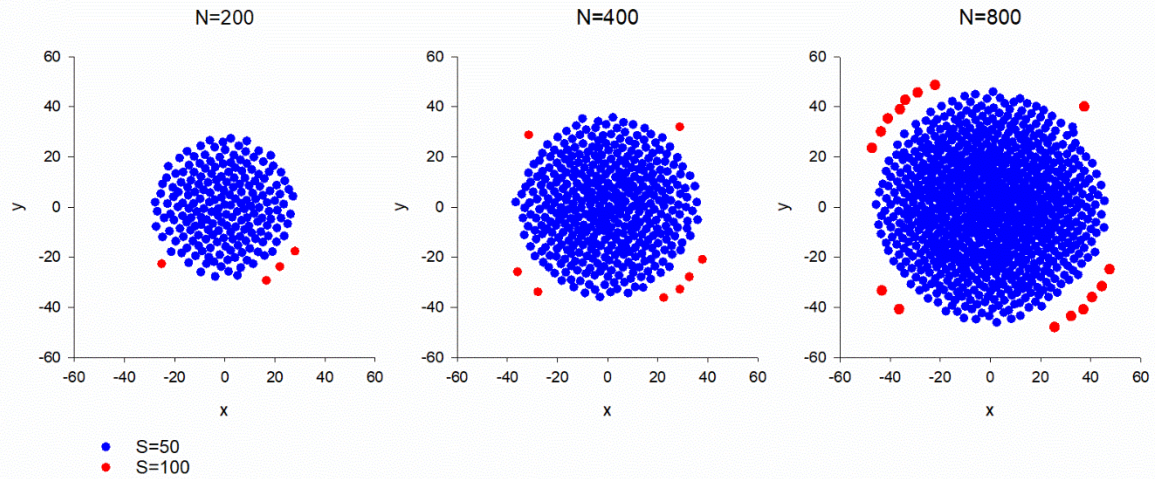


Figure 5 Predicted emergence of satellite swarms - small swarms that are found close to, but separate from, much larger swarms. Satellite swarms become more discernible, larger and more distant as the population of the patent swarm increases. The positions and compositions of the satellites are stable. Movements in the x- and y- directions were obtained using independent pairs of the stochastic model given in Eqn. 2. Predictions are shown for a 2D swarms wherein 98% of individuals have $S=50$ and 2% have $S=100$. The satellite swarms are formed exclusively from the highly reactive individuals with $S=100$. Comparable predictions were obtained with $S=5$ and $S=10$.