Physical Biology

Why swarming insects have perplexing spatial statistics

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Abstract

Unlike flocks of birds and schools of fish that show net motion and synchronized motion, insect mating swarms are stationary and lack velocity ordering. Their collective nature when unperturbed is instead evident in their spatial statistics. In stark contrast with bird flocks, wherein the number density can fluctuate enormously from flock to flock, the number density of individuals in laboratory swarms of the midge *Chironomus riparius* is approximately constant. Nonetheless, as swarms grow more populous, individuals cluster more and more. Here with the aid of stochastic trajectory models I show that these two seemingly contradictory behaviours can be attributed to the presence of multiplicative noise. The modelling also predicts that swarms are most stable when they are asymptotically large.

1. Introduction

Insect swarms are a form of collective animal behaviour that challenge basic notions of what constitutes such behaviour because unlike flocks of birds, schools of fish, and herds of ungulates they do not display ordered collective movements (Okubo 1986, Kelley and Ouellette 2013). Their collective nature when unperturbed is instead evident in their spatial statistics. But in this regard, they also differ from bird flocks (Ballerini *et al* 2008) and other groups of social animals because the number density of individuals of swarming insects can, as in the case of laboratory swarms of the midge *Chironomus riparius*, be approximately constant (Kelley and Ouellette 2013, Puckett and Ouellette 2014). Moreover, as the laboratory swarms of midges grow more populous, individuals cluster more and more (Kelley and Ouellette 2013, Puckett and Ouellette 2014). Here with the aid of stochastic trajectory models I show that these two seemingly contradictory behaviours can be attributed to the presence of multiplicative noise;—the noise experienced by an individual being dependent upon the number of local neighbours. The new results add to the growing realization that many of the emergent properties of insect swarms and other forms of collective motion can be attributed to the presence of multiplicative noise (Ahn and Ha 2010, Sun and Lin 2015, Reynolds 2019, 2021a, Jhawar and Guttal 2020, Haghsheno and Mehrafarin 2024).

2. Methods

The 3-dimensional trajectories of N swarming insects were simulated using the random walk model

$$
d\,\boldsymbol{x}_i = -k\,\boldsymbol{x}_i dt + \sqrt{2D + 2F \sum_{\substack{j=1 \\ j \neq i}}^{N} \exp\left(-\frac{(\boldsymbol{x}_i - \boldsymbol{x}_j)^2}{\sigma^2}\right)} \\ \times d\boldsymbol{W}_i(\boldsymbol{t}) \tag{1}
$$

where $\boldsymbol{x}_i$ is the position of the ith individual at time t, and $d\boldsymbol{W}_i(t)$ is an incremental Wiener process with correlation property $\overline{dW_i(t)\,dW_j(t+\tau)} = \delta(\tau)\,\delta_{ij}dt$. The first term on the right-hand side of equation (1) represents attraction to the swarm centre or 'swarm marker', a visually prominent feature over which swarm form. The constant part of the second term, the noise term, represents fluctuations in the individual movement that arise partly because of the limited number of individuals in the grouping and partly because of the nonuniformity in their spatial distribution. The position-dependent part of the noise term represents fluctuations which arise because of

the chance encounters with individuals that happen to be in the neighbourhood of the individual in question. The amplitude of this contribution to the noise is density dependent being relatively low when individuals are sparsely distributed throughout the swarm, and relatively high when, as will happen occasionally, some individuals crowd together; conditions that will result in q-Gaussian density profiles (Reynolds 2018), those occurrence in other settings has enriched the long-standing analogy between insect swarms and self-gravitating systems (Okubo 1986, Gorbonos *et al* 2016, Reynolds 2018, 2021b). The constants, k, D, F and σ determine the strength of the central attraction, and the magnitudes of the additive and multiplicative components of the driving noise. In the absence of multiplicative noise (i.e. when $F = 0$), equation (1) is the long-time limit of Okubo's (1986) classic stochastic model for the joint evolution of a swarming insect's position and velocity; extensions of which correctly predict the collective mechanical- and thermodynamic-like properties of insect swarms that emerge when they are subjected to external perturbations (Reynolds 2018, van der Vaart *et al* 2019, 2020, 2021 a).

3. Results

As observed by Kelley and Ouellette (2013), the model predicts that the number density is approximately constant (figure 1(a)). The model also predicts, as observed (Kelley and Ouellette 2013, Puckett and Ouellette 2014), that individuals cluster more and more, as swarms grow more populous (figure 1(b)). Here, as in Puckett and Ouellette (2014), this tendency to cluster is quantified in terms of the average distance between individuals and their nearest neighbours. As observed the asymptotic state is approach exponential slowly like $A + B\exp(-N/N_0)$. As observed by Puckett and Ouellette (2014), two closely related but distinct quantities, the volume per individual (which, as observed, is nearly constant for large swarms with $N > 10$), and the average distance between individuals and their nearest neighbours are also indicative of nearly constant number density and clustering (figures 1(c) and (d)). As noted by Puckett and Ouellette (2014), as opposed to the volume per individual, the nearest-neighbour distance may be more sensitive to any pairwise interactions in the swarm. Indeed, evidence for the predicted occurrence of clustering comes from the distribution of distances to nearest neighbours. The peaks of these distributions lie at ever shorter distances and the nearest neighbour distances fluctuate less strongly as the swarms become more populous (figure 2). Further analysis of the predicted clusters is presented in the Supplementary Material.

As expected, the simulated swarms have q-Gaussian profiles with $q < 1$ (Reynolds 2018) (figure 3(a)). Such density profiles have finite support, so that individuals are effectively more tightly bound to the swarm centre than they are in swarms with Gaussian density. The density profiles become more compact, and individuals become ever more rightly tightly bound to the swarm as q decreases. This is predicted to arise as swarms become more populous (figure 3(b)). This new result complements that of Reynolds (2021b) who showed that small (far from asymptotically larger) swarms have broader-than-Gaussian q-Gaussian profiles with $q > 1$.

4. Discussion

In contrast with bird flocks, fish schools and animal herds, laboratory swarms of the midge *Chironomus riparius* are a form of collective behaviour that lack collective order in their motions (Okubo 1986, Kelley and Ouellette 2013). Their collective nature is instead evident in the spatial statistics, and also in their responses to perturbations (Ni and Ouellette 2016, Sinhuber *et al* 2019, 2021, van der Vaart *et al* 2019, 2020). Herein with the aid of stochastic modelling it was shown how the near constant number density and clustering, two previously unexplained features of laboratory swarms of the midge *Chironomus riparius*, can be attributed to intrinsic multiplicative noise, as can the emergent mechanical-like and thermodynamic-like properties of these swarms (Reynolds 2019, 2021a). This mechanism for density regularization is distinctly different from how large bird flock self-organize to the maximum density at which a typical individual still can see out through the flock in many directions (Pearce *et al* 2014). Here it appears to be an accidental by-product of noisy dynamics. Nonetheless, the tendency of the midges to arrange themselves to maintain some empty space in their local neighbourhood could be advantageous because collisions are damaging and because the sharp manoeuvres required to avoid a collision when two individuals come close together are energetically costly. Indeed, midges rarely come closer together than about a wingspan distance (as predicted, figure 2) (Puckett *et al* 2014). The clustering precludes the emergence of scale-free behaviour which is a hallmark of starling flocks (Cavagna *et al* 2010); and one which is contingent on the flocks essentially having just relevant length scales, namely the inter-individual distance, which controls local interactions, and the overall size of the flock, which is an emergent property. The clusters in the midge swarms suggest a broader range of relevant length scales, with intermediate scales characterising the
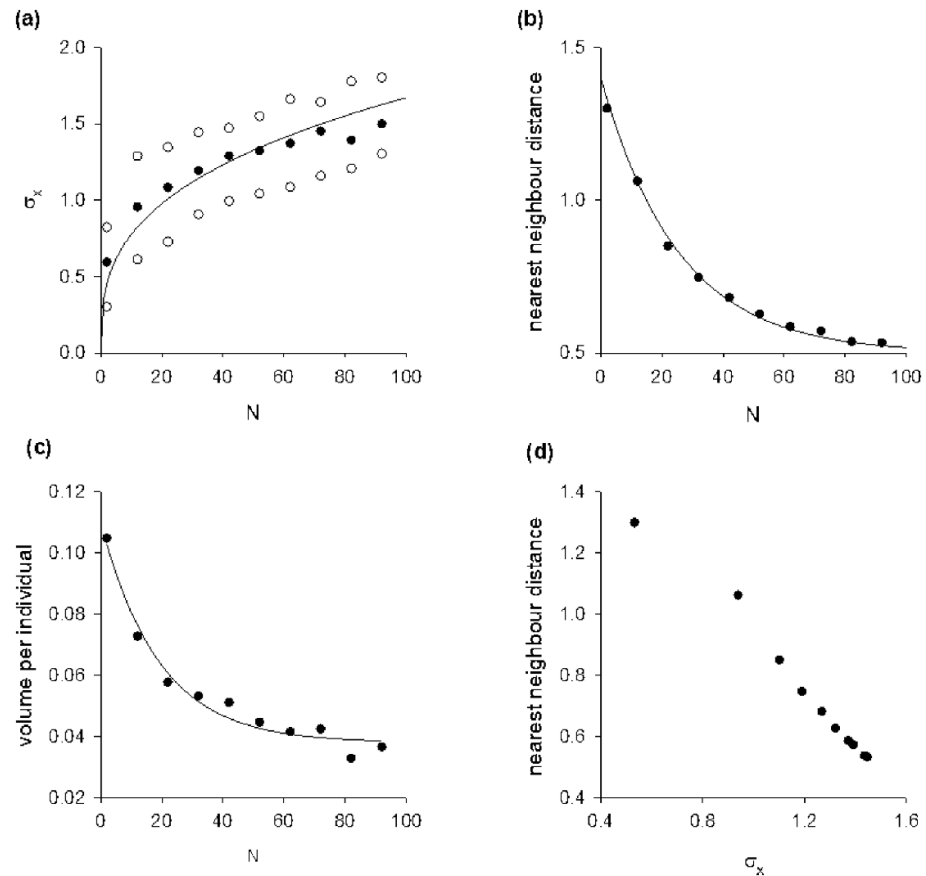
Figure 1. Predicted spatial statistics of insect swarms (●). (a) The root-mean-square size of a swarm as a function of the number individuals in the swarm. Also shown are the standard errors (o) which are comparable with the experimental uncertainties (Kelley and Ouellette 2013). The solid line is a fit $\sigma\_x \propto N^{\wedge}(1/3)$ as would be expected if the number density were independent of the swarm size. As observed (Kelley and Ouellette 2013), there are deviations from $N^{\wedge}(1/3)$ scaling. (b) The average distance between individuals and their nearest neighbours as a function of the number individuals in the swarm. The solid line is a fit to $A + B\exp(-N/N\_0)$ is added to guide the eye. The quantity $N\_0 \approx 25$ is a characteristic scale of approach to the asymptotic state. Standard errors decrease monotonically from 0.96 to 0.7 a.u. Similar trends are found for focal individuals within the core of the swarms, i.e. located within a distance σ_x from the centre of the swarm, and for focal individuals within the outskirts of the swarms. (c) Volume per individual. The solid line is an exponential fit with $N\_0 \approx 19$. (d) The average distance between individuals and their nearest neighbours as a function of the root-mean-square size of a swarm. Predictions (simulation data) were obtained using equation (1) with $k = 1$, $D = 1/10$, $F = 1$ and $\sigma = 1$a.u. Noisier swarms (e.g. with $F = 5$) are also found to have near constant number densities and clustering albeit with smaller number densities and faster approaches to saturation. The same behaviours are predicted to arise when instead of using the 'smoothed' density in the multiplicative noise, a discrete version, i.e. the actual local density within a given volume around each individual is used.

clusters, as in the case of the mosquito *Anopheles gambie* (Shishika *et al* 2014). Insect swarms may therefore be dynamically more complex than flocks.

The modelling showed how multiplicative noise determines the spatial statistics of swarms and governs how these statistics saturate as the swarms enter an asymptotic regime. Swarms containing order 10 individuals were predicted to be asymptotically large, as the addition of more individuals does not change the spatial statistics. This surprisingly small threshold is consistent with the observations of Puckett and Ouellette (2014) which provided a strong constraint on how rapidly swarm models must produce collective states.

The new modelling together with previous analysis (Reynolds 2021b) predicts that swarms transition from having expansive q-Gaussian density profiles (with $q > 1$) to having compact, more tightly bound, q-Gaussian density profiles (with $q < 1$) as swarms grow more populous. The first prediction has experimental support (Reynolds 2021b). The second prediction awaits experimental verification, as the largest laboratory swarms which contain on average 92 individuals have Gaussian (i.e. have $q = 1$ q-Gaussian) density profiles (Reynolds 2021b). It would therefore be interesting to analyse the spatial statistics of larger swarms, such as those measured in the wild which can contain orders of magnitude more
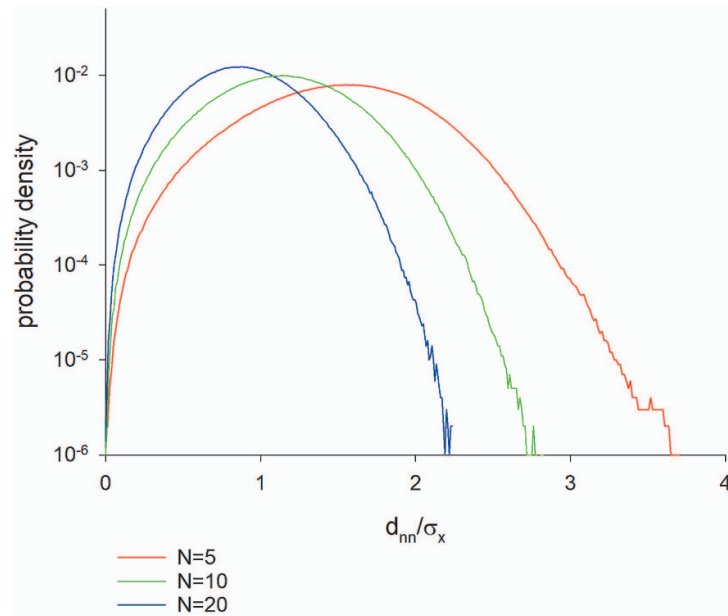
Figure 2. Distributions of distances to nearest neighbours. Predictions for swarms containing $N = 5$, 10 and 20 individuals were obtained using equation (1) with $k = 1$, $D = \frac{1}{10}$, $F = 1$ and $\sigma = 1$ a.u. d_{nn} is the distance to the nearest neighbour and σ_x is the root mean size of the swarms.
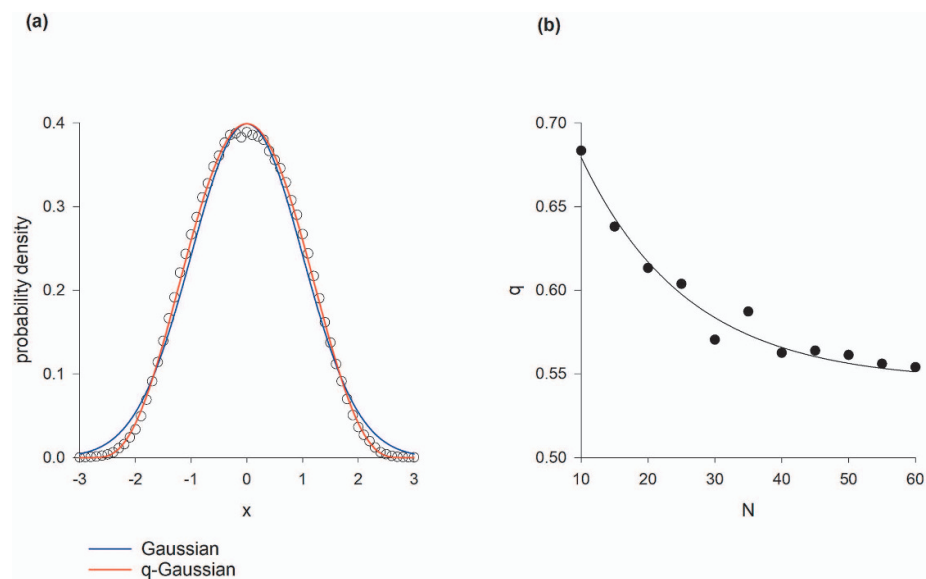

Figure 3. (a) Swarms are predicted to have q-Gaussian density profiles. Simulation data (o) for a swarm containing $N = 10$ individuals are shown together with the best fit Gaussian and best fit q-Gaussian which has $q = 0.67$. (b) Swarms are predicted to be most stable when they are asymptotically large ($\bullet$). The solid line is a fit to $q = A + B\exp\left(-N/N_0\right)$ is added to guide the eye. The quantity $N_0 \approx 17$ is a characteristic scale of approach to the asymptotic state. Standard errors for the estimates for q are about 0.01. Predictions were obtained using equation (1) with $k = 1$, $D = \frac{1}{10}$, $F = 1$ and $\sigma = 1$ a.u.

individuals (Armitage *et al* 1995). The new prediction complements that of Reynolds (2018) who showed that environmental perturbations can drive insect swarms into more robust states characterized by q-Gaussian density profiles with $q < 1$, as in the case of wild swarms of the mosquito *Anopheles gambie* (see also Supplementary Material).

To summarize: With the aid of stochastic trajectory models, I showed how two seemingly contradictory properties of insect swarms, namely approximate constancy of the number density of individuals and the tendency for individuals to cluster more and more as swarms grow more populous, can be attributed to the presence of intrinsic

multiplicative noise. This new result adds to the growing realization (Ahn and Ha 2010, Sun and Lin 2015, Reynolds 2019, 2021a, Jhawar and Guttal 2020, Haghsheno and Mehrafarin 2024) that rather than being a disruptive influence, the presence of intrinsic noise is, in fact, fundamental in bringing about many of the emergent collective behaviours of swarms and flocks.

Data availability statement

No new data were created or analysed in this study.

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