**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.

**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, Haghsheno and Mehrafarin 2024, Jhawar and Guttal 2020, Reynolds 2019, 2021a, Sun and Lin, 2015].

**Methods**

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

$dx\_{i}=-kx\_{i}dt+\sqrt{2D+2F\sum\_{\begin{array}{c}j=1\\j\ne i\end{array}}^{N}exp\left(-\frac{\left(x\_{i}-x\_{j}\right)}{σ^{2}}^{2}\right)}dW\_{i}\left(t\right)$(1)

where $x\_{i}$ is the position of the *ith* individual at time *t*, and $dW\_{i}(t)$ is an incremental Wiener process with correlation property $\overline{dW\_{i}\left(t\right)dW\_{j}\left(t+τ\right)}=δ\left(τ\right)δ\_{ij}dt$. The first term on the right-hand side of Eqn. 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, Reynolds 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 $F=0$), Eqn. 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, 2021a, van der Vaart et al. 2019,2020].

**Results**

As observed by Kelley and Ouellette [2014], the model predicts that the number density is approximately constant (Fig. 1a). 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 (Fig. 1b). 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 $A+Bexp\left(-N/N\_{0}\right)$. 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 [Fig.1c,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 (Fig. 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] (Fig. 3a). 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 (Fig.3b). 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*.

**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, Fig. 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 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 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, Haghsheno and Mehrafarin 2024, Jhawar and Guttal 2020, Reynolds 2019, 2021a, Sun and Lin, 2015] 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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**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 $σ\_{x}∝N^{1/3}$ as would be expected if the number density were independent of the swarm size. As observed [Kelley and Ouellette 2013], there are deviations from $N^{1/3}$ 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 $A+Bexp\left(-N/N\_{0}\right)$is added to guide the eye.The quantity $N\_{0}≈25$ 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 $N\_{0}≈19.$ **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 Eqn. 1 with$k=1, D=\frac{1}{10} ,F=1$ and $σ=1$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.

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**Figure 2 Distributions of distances to nearest neighbours.** Predictions for swarms containing *N=5, 10 and 20* individuals were obtained using Eqn. 1 with$k=1, D=\frac{1}{10}, F=1$ and $σ=1$ a.u. $d\_{nn}$ is the distance to the nearest neighbour and $σ\_{x}$ is the root mean size of the swarms.



**Figure 3a) 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 (●).** The solid line is a fit to $q=A+Bexp\left(-N/N\_{0}\right)$is added to guide the eye.The quantity $N\_{0}≈17$ 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 Eqn. 1 with$k=1, D=\frac{1}{10}, F=1$ and $σ=1$ a.u.

**Supplementary Material**

**Algebraic Connectivity**

The numbers and sizes of the predicted clusters was determined by their algebraic connectivity. To do this, entries, $A\_{ij}$, in the adjacency matrix, ***A***, were set to unity if the multiplicative noise contribution $Fexp\left(-\frac{\left(r\_{i}-r\_{j}\right)^{2}}{σ^{2}}\right)$ in the stochastic model, Eqn. 1, associated with the pair of individuals ‘*i*’ and ‘*j*’ exceeded the additive noise *D*, i.e., if individuals ‘*i*’ and ‘*j*’ are ‘connected’. The eigenvalues of the associated Laplacian matrix $L=D-A$ were then calculated, where $D$is the degree matrix of the adjacency matrix**.**  The number of times 0 appears as an eigenvalue in the Laplacian is the number of clusters. Clusters are predicted to become less numerous but larger on average as the swarms grow more populous (Fig. S1). Conversely, clusters are predicted to become more numerous but smaller on average as the intensity of the multiplicative noise, *F*, increases (Fig. S2). The average Fielder value (the second smallest eigenvalue of the Laplacian matrix) increases as the intensity of the multiplicative noise, *F*, increases, indicating that the swarms are becoming better connected.



**Figure S1 Predicted numbers and sizes of clusters as a function of the swarm population size.** Predictions were obtained using Eqn. 1 with$k=1, D=\frac{1}{10}, F=1$ and $σ=1$ a.u. Here the ‘size’ of a cluster is taken to be the average number of connections that connected individuals have. The standard errors for the average numbers and sizes of the clusters are about 0.1 and 0.04 respectively.



**Figure S2 Predicted numbers and sizes of clusters as a function of the multiplicative noise intensity, *F*.** Predictions were obtained for a swarm containing *N=50* individuals using Eqn. 1 with$k=1, D=\frac{1}{10}$ and $σ=1$ a.u. Here the ‘size’ of a cluster is taken to be the average number of connections that connected individuals have. The standard errors for the average numbers and sizes of the clusters are about 0.1 and 0.04 respectively.

**Midge swarms are predicted to undergo a phase transition to states characterized by stellar polytropic sphere (q-Gaussian) distributions**

Here I show that stellar polytropic sphere distributions (q-Gaussians) which constitute the simplest, physically plausible models for self-gravitating stellar systems [Binney and Tremaine 1987], are predicted by minimally structured, stochastic models to characterize the trajectories of swarming midges once the swarms have become sufficiently large. The new result extends the long-standing similitude that insect swarms have with self-gravitating systems [Gorbonos et al. 2016, 2020, Gorbonos and Gov 2017, Okubo 1986, Reynolds 2018a, 2019, 2021, 2023a]. And somewhat paradoxically show how the presence of intrinsic noise can enhance the stability of swarms and sharpen their borders; thereby adding to the growing understanding as to how noise can facilitate order and structure in collective behaviour [Yates et al. 2009, Jhawar & Guttal 2020, Reynolds 2023b]. The new results arise from a simple modification to Okubo’s [1986] classic model for the trajectories of swarming midges.

Okubo’s [1] 1-dimensional stochastic model for one component of the midge’s position relative to the center of the swarm, *x*, and for one component of the insect’s velocity, *u*, is given by

$du=-kudt-ω^{2}xdt+\sqrt{2B}dξ\left(t\right)$ (S1)

$$dx=udt$$

The first term on the right-hand side of Eqn. (S1) tends to drive velocities back to their mean zero value. *k* is the ‘frictional coefficient’. Interactions between the individuals are not explicitly modeled; rather, their net effect is subsumed in a restoring force term (the second term on the right-hand side of Eqn.1). This is consistent with subsequent observations which have shown that to leading order insects appear to be tightly bound to the swarm itself but weakly coupled to each other inside it [Puckett et al. 2014]. In accordance with observations [Okubo 1986, Kelley and Ouellette 2013] the strength of the restorative force increases linearly with distance from the swarm centre. ω is the frequency of this average restorative force (a harmonic attractive force). The third term, the noise term, represents fluctuations in the resultant internal force. *B* is the magnitude of the stochastic noise and $dξ$ is an incremental Wiener process with correlation property $\left〈dξ\left(t\right)dξ\left(t+τ\right)\right〉=δ\left(τ\right)dt$ where the angular brackets denote an ensemble average. Simulated velocities are position-independent, and Gaussian distributed with mean zero and variance $σ\_{u}^{2}=\frac{B}{k}$. Simulated positions are Gaussian distributed with mean zero and variance $σ\_{x}^{2}=\frac{σ\_{u}^{2}}{ω^{2}}$. These predictions are broadly consistent with observations of laboratory swarms of the the non-biting midge *Chironomus riparius* [Kelley and Ouellette 2013].

Okubo [1986] attributed the fluctuations in the resultant internal force to the combined effects of the limited number of individuals in the swarm, the non-uniformity in their spatial distribution, and to chance close encounters of the modelled individual with other individuals. Okubo [1986] tactfully assumed that the stochastic noise term encapsulating these fluctuations was position independent. This seems appropriate because Okubo’s model [1986] and its subsequent extension to 3-dimensions are in close agreement with numerous observations of midge swarms studied under controlled laboratory conditions [Reynolds 2017, 2018b, van der Vaart et al. 2019, 2020]. These laboratory swarms contain less than 100 individuals but appear nonetheless to be asymptotically large, as their statistical properties saturate when the swarm contain of order 10 individuals [Puckett and Ouellette 2014]. Here, however, attention is focused on much larger swarms containing 1000’s or more individuals, as can occur in the wild [Attanasi et al. 2014]. In these cases, the chance close encounters can be expected to make the dominant contribution to the noise term, and such encounters can be expected to be more likely at the core of the swarm where the number of fast fliers is highest and more likely for slower fliers that are less able to head-off collisions with the fast fliers. The simplest form of the noise intensity that encapsulates these expectations, and the one adopted here, is $B=1-a\frac{x^{2}}{2}-b\frac{u^{2}}{2}$ where *a* and *b* are positive constants. Using the methodology of Reynolds [2017], it is readily shown that with this noise intensity, Eqn. 1 predicts that the positions and velocities of the modelled insects have stellar polytropic sphere distributions:

$P\left(u,x\right)=N\left(1-\left(1-q\right)ε\right)^{\frac{q}{1-q}}$ if $ ε<\frac{1}{1-q}$ (S2)

$ =0$ if $ ε\geq \frac{1}{1-q}$

where *N* is a normalization constant, $0<q<1$, and where $ε=\left(ω^{2}\frac{x^{2}}{2}+\frac{u^{2}}{2}\right)$ is the observable energy of an insect. Consistency contributions require that $a=\left(1-q\right)ω^{2}$, $b=1-q$ and that $k=1$. Notice that the noise intensity is seen, in retrospect, to be proportional to the joint distribution of *x* and *u* raised to the power of $\left(1-q\right)/q$.

Gaussian distributions of positions and velocities are recovered from Eqn. S2 as $q\rightarrow 1$. More generally, when $q<1$, the joint distributions of positions and velocities are more compact, having finite support. In the context of self-gravitating systems such cut-off corresponds, for each value of the radial coordinate *x*, to the corresponding gravitational escape velocity [Binney and Tremaine 1987].

The modelling therefore predicts that swarms undergo a phase transition to more stable, more compact forms when they become sufficiently large; the findings of Puckett and Ouellette [2014] regarding the asymptotic character of laboratory swarms notwithstanding. Moreover, because the entropic parameter *q* and the polytropic index *n* are related by $\frac{1}{1-q}=n-\frac{1}{2 }$ (Taruya, and Sakagami 2004), the modelling also predicts that these newly identified putative phases of swarm can, for example, have similitude with fully convective star cores(like those of [red giants](https://en.wikipedia.org/wiki/Red_giant)), [brown dwarfs](https://en.wikipedia.org/wiki/Brown_dwarf), [giant gaseous planets](https://en.wikipedia.org/wiki/Gas_giant) (like [Jupiter](https://en.wikipedia.org/wiki/Jupiter)), or even for [rocky planets](https://en.wikipedia.org/wiki/Terrestrial_planet); self-gravitating systems that are characterized by polytropes with index $n=3/2$ [Chandrasekhar 2016].This predictions mirrors the case of wild swarms of *Anopheles coluzzi* mosquitoes which can be driven into more robust states (characterized by $n=3/2$) by environmental perturbations [Reynolds 2018a].

It has been shown that as swarms grow, more cohesive states that are better able to withstand environmental disturbances become accessible even when individuals have the simplest possible (linear) flight dynamics. The swarms are predicted to become ever more stable, as they grow (as collisions become ever more likely) thereby making any potential gains from adopting non-linear dynamics redundant. Consequently, when swarms become sufficiently large, selection pressures for cohesiveness, could drive flight dynamics towards simplicity.

Enhanced stability is only required in the presence of perturbations. This may explain why natural swarms, which must contend with environmental disturbances, are typically much larger than laboratory swarms. The increasing simplicity that is predicted accompany the growth in swarm size may also account, in part, for why the largest, least agile males occur predominantly in larger swarms [Neems et al. 1992].

A second phase transition is predicted to occur when $q<-1$. In these cases, the joint distributions of positions and velocities are no longer polytropes. Instead, individuals are most likely to located in the outskirts of the swarms, rather than in the cores of the swarms. This is reminiscent of starling (*Sturnus vulgaris*) flocks, as the birds are more tightly packed at the border than at the centre of the flock [Ballerini et al. 2008]. Moreover, because the swarming insects are predicted to have relatively low velocities in the borders, the insects like flocking starlings [Cavagna et al. 2016] are predicted to stay at the borders longer than the way internal individuals keep their position inside the collective. Although accidental this trait could be advantageous as males in the outskirts of swarms may be the first to detect the presence of incoming females. If this is the case, then there could be selection pressures of maintaining high density borders. But so far, such behaviour in insect swarms has not been reported on.

The two predicted phase transitions, from extensive to compacted density profiles, and from low density to high density borders, are not specific to noise intensities of the form $B=1-a\frac{x^{2}}{2}-b\frac{u^{2}}{2}$, and in this sense are robust model predictions. The predicted phase transitions do, for example, also arise when the noise intensities $B=exp \left(-a\frac{x^{2}}{2}-b\frac{u^{2}}{2}\right)$, in which case the joint distributions of positions and velocity are Gumbel-like (extreme value distribution-like), $P\left(u,x\right)∝exp \left(a\frac{x^{2}}{2}+b\frac{u^{2}}{2}-c\*exp\left(a\frac{x^{2}}{2}+b\frac{u^{2}}{2}\right)\right)$ where consistency conditions require that$a/b=ω^{2}$ and $bc=k$. More generally, Okubo’s [1987] model predicts the occurrence of the phase transitions whenever it is driven by multiplicative noise that is a monotonically decaying function of $a\frac{x^{2}}{2}+b\frac{u^{2}}{2}$. Forms of multiplicative noise that are not functions of $a\frac{x^{2}}{2}+b\frac{u^{2}}{2}$are incompatible with Okubo’s [1987] model. The phase transitions are also predicted by second-order variants of Okubo’s [1987] model in which the positions, velocities and accelerations of simulated swarming insects evolve jointly as Markovian processes [Reynolds 2024], when these models are driven by multiplicative noise that is a monotonically decaying function of $a\frac{x^{2}}{2}+b\frac{u^{2}}{2}+c\frac{\acute{A}^{2}}{2}$ where $\acute{A}$ are the fluctuations in the accelerations above and below that mean acceleration that effectively bind simulated individuals to the centres of the swarms (see above). This is biologically plausible because these fluctuations arise, in part, from collision avoidance manoeuvrers.

Finally, note that polytropic distributions albeit with *q>1* and with more complicated expressions for the observable energies can accurately characterise the properties of laboratory swarms of the midge *Chironomus riparius*, as reported on by Kelley and Ouellette [2013]. The added complexity is necessary because the effective forces that bind individuals to the centre of the swarm centre (and so the effective potential energies) are speed-dependent [Reynolds et al. 2017, see below].

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**Midges may maximize the cohesiveness of their swarms**

Here with the aid of stochastic modelling I show that the excess velocity flatness statistic of asymptotically large swarms of the non-biting midge *Chironomus riparius* may result in the maximum attainable cohesiveness of the swarm. One-dimensional stochastic models for the joint evolution of the positions, *x*, and velocities, *u*, are individual midges take the general form,

$du=a\left(u,x,t\right)dt+b\left(u,x,t\right)dξ\left(t\right)$ (1)

$$dx=udt$$

where $dξ(t)$ is an incremental Wiener process with correlation property $\overline{dξ\left(t\right)dξ\left(t+τ\right)}=δ\left(τ\right)dt$. The simplest such model, Okubo’s classic [1986] model, wherein $a\left(u,x,t\right)$ is linear in both *x* and *u*, and $b\left(u,x,t\right)$ is a constant, captures many of the properties of laboratory swarms of *Chironomus riparius* midges*.* The joint distribution of positions and velocities, $p\left(x,u\right)$, is a solution of the Fokker-Planck equation

$\frac{∂p}{∂t}+u\frac{∂p}{∂x}=-\frac{∂}{∂x}\left(ap\right)+\frac{1}{2}\frac{∂^{2}}{∂x^{2}}\left(b^{2}p\right)$ (2)

Here for simplicity, I consider statistically stationary swarms with homogeneous velocity statistics and I consider models those deterministic terms are quadratic functions of *u* so that $a\left(u,x,t\right)=α\left(x\right)u^{2}+β\left(x\right)u+γ\left(x\right)$ and those intensity amplitude is constant, $b\left(u,x,t\right)=b\_{0}$. Following Franzese et al. [1999], a set of equations for the coefficients $α\left(x\right), β\left(x\right)$ and $γ\left(x\right)$ is obtained by multiplying the Fokker-Planck equation by $u^{n}$ and then averaging over all velocities:

$-\left〈u^{n+1}\right〉\frac{∂ρ}{∂x}=n\left[α\left〈u^{n+1}\right〉+β\left〈u^{n}\right〉+γ\left〈u^{n-1}\right〉\right]+\frac{b\_{0}^{2}}{2}n\left(n-1\right)\left〈u^{n-2}\right〉$ (3)

where $ρ\left(x\right)$ is the swarm’s density profile. Evaluating this equation for *n=1*, *2* and *3* provides expressions for $α\left(x\right), β\left(x\right)$ and $γ\left(x\right)$:

$α\left(x\right)=\frac{∂ρ}{∂x}\frac{\left[\frac{\left〈u^{4}\right〉}{3}-\left〈u^{2}\right〉^{2}\right]}{\left[\left〈u^{4}\right〉-\left〈u^{2}\right〉^{2}\right]}$ (4)

$$ β\left(x\right)=-\frac{b\_{0}^{2}}{2\left〈u^{2}\right〉}$$

$γ\left(x\right)=\frac{∂ρ}{∂x}\left〈u^{2}\right〉\frac{\frac{2}{3}\left〈u^{4}\right〉}{\left[\left〈u^{4}\right〉-\left〈u^{2}\right〉^{2}\right]}$

Such a prescription ensures that the position and velocity statistics of the simulated trajectories are approximately consistent with the model inputs, namely the moments of the velocity distribution and the swarm’s density profile. For swarms with Gaussian position and velocity statistics, the stochastic model reduces to Okubo’s [1986] model: $α\left(x\right)=0$, $ β\left(x\right)=-\frac{b\_{0}^{2}}{2\left〈u^{2}\right〉}$ , $γ\left(x\right)=-\frac{\left〈u^{2}\right〉}{\left〈x^{2}\right〉}x$ wherein individuals behave on the average as if they are trapped in elastic potential wells (since the effective forces are linear in position, *x*) that keeps them bound to the swarms. This is consistent with early observations [Okubo 1986, Kelly and Ouellette 2013]. More generally, the effective forces that bind individuals to the swarms are predicted to be speed dependent, as observed by Reynolds et al. [2017]. As the velocity flatness increases from unity, slower (faster) moving individuals become increasingly less (more) tightly bound to the swarm (Fig. 1). Nonetheless, the most slowly moving individuals are necessarily bound to the swarm by virtue of their not moving whilst the fastest moving individuals may be most susceptible to environmental disturbances, and so could benefit from enhanced binding to their swarms, i.e., could benefit from high excess velocity flatness values. In practice the excess velocity flatness values cannot be arbitrarily large because insects cannot fly arbitrarily fast. This analysis may therefore account for the positive excess velocity flatness, ~0.4, of asymptotic large midge swarms [Puckett and Ouellette 2014].



**Figure 1. The predicted strength of the central attraction for slow- and fast-moving individuals as functions of the velocity flatness.** Without loss of generality results are shown for $\frac{∂ρ}{∂x}=-1$. Results for velocity flatness values less than unity are shown for completeness even though the associated velocity distributions are pathological.