

United by noise: Randomness helps swarms stay together

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Amongst the most striking aspects of the movement of many animal groups are their sudden coherent changes in direction. Recent observations of locusts and starlings have shown that this directional switching is an intrinsic property of their motion. Similar direction switches are seen in self-propelled particle (SPP) and other models of group motion. Comprehending the factors which determine such switches is key to understanding the movement of these groups. Here we adopt a coarse-grained approach to the study of directional switching in a SPP model assuming an underlying one-dimensional Fokker-Planck equation (FPE) for the mean velocity of the particles. We continue with this assumption in analysing experimental data on locusts and use a similar systematic FPE coefficient estimation approach to extract the relevant information for the assumed FPE underlying that data. We determine the mean time between direction switches as a function of group density for the SPP model. This systematic approach allows us to identify key differences between the SPP model and the data, revealing that individual locusts increase the randomness of their movements in response to a loss of alignment by the group. We give a quantitative description of how locusts use noise to maintain swarm alignment. We discuss further how properties of individual animal behaviour, inferred using the FPE coefficient estimation approach, can be implemented in the SPP model in order to replicate qualitatively the group level dynamics seen in the experimental data.

collective behaviour | locusts | swarming | density dependent switching | coarse-graining

While recent years have seen an explosion in the number of simulation models of moving animal groups, there is little detailed comparison between these models and data (1, 2). The models usually produce motion that ‘looks like’ that of a swarm of locusts, a school of fish or a flock of birds, but the similarities are difficult to quantify (3). Furthermore, the simulation models themselves are often difficult to understand from a mathematical viewpoint since, by their nature, they resist simple mean-field descriptions. These complications make it difficult to use models to predict, for example, the rate at which groups change direction of travel or how spatial patterns evolve through time. We are left with a multitude of models all of which seem to relate to the available data, but none of which provides clear predictive power.

One approach to the problem of linking data to model behaviour is the detailed study of the local interactions between animals. This approach has yielded better understanding of the rules which govern the interaction of fish (4, 5) and birds (6, 7). However, establishing these rules is technically difficult since it requires automated tracking of individuals over long periods of time and quantification of often complicated

interactions.

Coherent animal groups often make sudden changes in direction (1, 8, 9). In some cases a switch in direction is a response to an external influence, such as the presence of a predator, but in other cases animal groups appear to switch direction spontaneously. Recently, experiments on various densities of desert locusts (*Schistocerca gregaria*) in a homogeneous environment confirmed that directional switching can occur without changes in the external environment (8). In experiments with lower locust densities it was found that groups of locust nymphs were highly aligned and marched in one direction around a ring-shaped arena for up to two or three hours, before spontaneously switching direction in the space of only a few minutes and marching in the opposite direction, again for a number of hours. In experiments with higher densities marching groups formed travelling in the same direction for the 8-hour duration of the experiment. The group property of average velocity/alignment (as it will variously be denoted throughout the rest of this paper) of the locust experiments was previously modelled by a one-dimensional self-propelled particle (SPP) model similar to that in (10). In a manner analogous to the experiments in (8) this model also exhibits spontaneous direction switching where ‘particles’ rapidly change alignment.

In this paper we investigate directional switching in a SPP model and in our data of the motion of locusts. A coarse-grained model characterises the behaviour of a system in terms of a single ‘coarse’ variable (average locust velocity in our case) and does not take into account the ‘fine’ details of the behaviour of individual locusts. If such a model is explicitly available we can apply available mathematical techniques to study the properties of group switching as will be shown later for a simple toy model. In a more complicated scenario, where we are not able to write a coarse-grained model explicitly, we can often still assume that there exists a coarse-grained Fokker-Planck equation (FPE) describing the evolution of the average velocity of the particles in the SPP model. We use appropriately initialised computational experiments to estimate

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Abbreviations: FPE, Fokker-Planck equation; SI, Supporting Information; SPD, Stationary Probability Distribution; SPP, Self-Propelled Particle(s)

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the (explicitly unavailable) drift and diffusion coefficients of such a FPE. The drift coefficient represents the mean rate of change of the average velocity of the locusts, while the diffusion coefficient quantifies the randomness of the evolution of this coarse-grained variable (precise mathematical definitions are given later in Eqs. [13] and [14]). We also estimate the drift and diffusion coefficients of a coarse-grained FPE based on experimental data. Coarse-graining enables efficient description and analysis of these data and assists the refinement of the individual based model so as to simulate observed group properties more accurately.

Our studies suggest that an individual's response to a loss of alignment in the group is increased randomness of its motion, until an aligned state is again achieved. This alignment-dependent stochasticity, using randomness to keep the group ordered, appears counterintuitive. While the constructive effects of noise at the level of an individual have been reported in other biological systems (11), here we present an example where noise has been found to be a constructive force at the collective level in an ecological system. Furthermore, the lack of sources of environmental noise in the experiment under consideration indicates the internal character of these fluctuations. Noise induced alignment seems, in this case, to be an intrinsic characteristic of collective coherent motion.

The paper is organised as follows: we start by providing an analytical result for mean switching times of the SPP model with global interactions and compare this to its equation-free approximation in the case of local interactions. After demonstrating that coarse-graining works well for our model simulations we adopt a similar FPE coefficient estimation approach to the locust data in order to find the drift and diffusion coefficients of the assumed underlying FPE. This analysis illuminates similarities and important differences between the model and the data and allows us to better understand directional switching in both cases. We conclude by proposing a new, modified model which reproduces the experimental observations more accurately than the previously used SPP models.

The self-propelled particle (SPP) model

We consider a group of N 'locusts'. Each locust adjusts its behaviour according to the behaviour of its neighbours which can be found less than a distance R (the interaction radius) from it. A locust's behaviour is described by its position, $x_i \equiv x_i(t)$, and velocity, $u_i \equiv u_i(t)$, $i = 1, \dots, N$, which evolve according to the model adapted from Czirók et al (10):

$$\Delta x_i = u_i \Delta t, \quad [1]$$

$$\Delta u_i = \left\{ G(\bar{u}_i^{loc}) - u_i(t) \right\} \Delta t + \Delta Q \eta(\bar{u}_i^{loc}), \quad [2]$$

where Δt is the time step between successive position and velocity updates. ΔQ is a random variable uniformly distributed in $[-\sqrt{\Delta t} \omega/2, \sqrt{\Delta t} \omega/2]$ with mean 0 and variance $\Delta t \omega^2/12$, where ω is the (constant) system noise amplitude.

$$\bar{u}_i^{loc} = \frac{1}{n_i(t)} \sum_{j \in \mathcal{J}_i^R} u_j(t) \quad [3]$$

is the mean of the velocities of the particles local to (inside the interaction radius of) particle i , where $\mathcal{J}_i^R \equiv \mathcal{J}_i^R(t)$ is the set of all $j \in \{1, 2, \dots, N\}$ such that $|x_i(t) - x_j(t)| < R$ (i.e. the set of particles (including particle i itself) located within the interaction radius, R , of particle i at time t) and

$n_i(t) = |\mathcal{J}_i^R(t)|$ (i.e. the number of particles located within the interaction radius of particle i at time t). The function $G: \mathbb{R} \rightarrow \mathbb{R}$ is chosen to be

$$G(z) = \frac{1}{1 + \beta} \{z + \beta \text{sign}(z)\}, \quad [4]$$

where β is a positive constant. Finally η is a function of the local mean velocity, \bar{u}_i^{loc} , which can be varied to change the behaviour of the model. We consider motion in a domain of constant length L with periodic boundary conditions, directly motivated by the experiments described in (8), where locusts march in a ring-shaped arena. Note that in this one-dimensional geometry we allow the particles to cross through each other.

In (8) and (10) the function η is chosen to be one. Similarly we will choose $\eta \equiv 1$ in our initial model and later revise this choice after analysis of the experimental data. Let us note that the model in (10) is a special case of model [1] – [2] where $\beta = \Delta t = 1$ and $\eta \equiv 1$ throughout.

A toy model with globally interacting particles

To illustrate our coarse-graining technique we will first study a modification of the model [1] – [2] where *all* particles interact with each other. The advantage of this model is that we can obtain the coarse-grained equations explicitly: we know that the assumptions, made later to justify coarse-graining, hold exactly and hence we can validate the approach. Moreover, we can obtain analytical results for this model, as shown below. We thus replace the local average [3] in formula [2] by the global average,

$$U(t) = \frac{1}{N} \sum_{j=1}^N u_j(t),$$

to obtain:

$$\Delta u_i = \{G(U(t)) - u_i(t)\} \Delta t + \Delta Q, \quad [5]$$

for $i = 1, 2, \dots, N$, where $\eta \equiv 1$ for simplicity and the marching group comprises all N individuals. Note that this toy model is the original model with the domain length, L , equal to $2R$. Equations [5] are now only one-way coupled with equations [1] (i.e. the positions of the locusts do not affect the velocities, but the velocities do affect the positions). Assuming that the number of locusts in the marching group is fixed and equal to N , this toy locust problem can be described by the system of N equations [5].

A quantity of interest is the mean switching time between different directions of motion of the group (left or right) for which, in this special case of global interaction, we can find an explicit formula. Adding equations [5] and dividing through by N and invoking the central limit theorem

$$\Delta U \approx \{G(U) - U\} \Delta t + \frac{\omega}{\sqrt{12N}} \Delta W, \quad [6]$$

where ΔW is the normal random variable with mean 0 and variance Δt (i.e. the standard Brownian process). Assuming the approximation in [6] to be exact, let $f_N(U, t)$ be the probability distribution function of the random variable U . Given initial condition $f_N(U, 0)$, the distribution $f_N(U, t)$ can be computed (as in (12)) as a solution of the FPE,

$$\frac{\partial f_N}{\partial t} = \frac{\partial}{\partial U} \left(\frac{\omega^2}{24N} \frac{\partial f_N}{\partial U} - \{G(U) - U\} f_N \right). \quad [7]$$

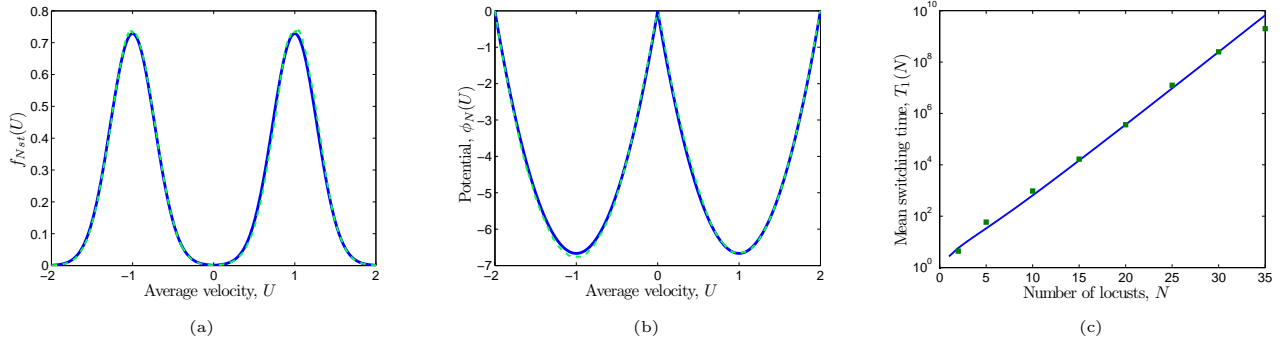


Fig. 1. The global interaction model [5]. For $\beta = 1$, $\omega = 3$ and $N = 10$ ((a) and (b) only). (a) The analytically derived SPD (solid line) of the approximate FPE for the average velocity, (see Eq. [6]) and the equation-free derived approximation to the SPD (dashed line). (b) The analytically derived potential (solid line) and the equation-free derived approximation to the potential (dashed line). (c) Mean switching time vs N : Analytically derived solution (solid line) and values simulated using the model [5] (squares). Note that there is a log-scale on the T_1 -axis. In this global interaction case it is clear that the mean switching time increases exponentially with the number of locusts.

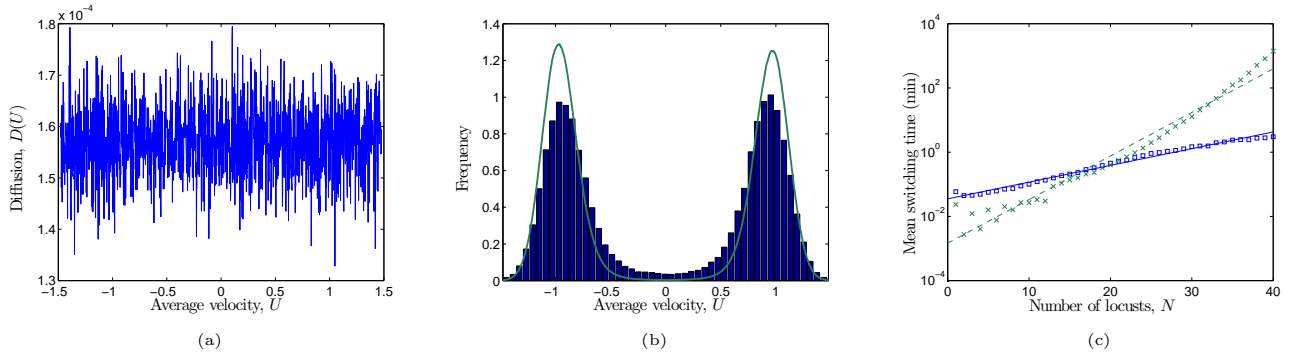


Fig. 2. Equation-free analysis of the local interaction model. $L = 90$, $R = 5$, $\beta = 1$, $\omega = 2.6$ and $N = 30$ ((a) and (b) only). (a) Estimation of the diffusion coefficient of the unavailable FPE for the coarse variable, U . (b) Two approximations of the SPD. The histogram represents a sample of the alignments (taken every 50 time steps) from one long simulation. The curve represents the equation-free estimation to the SPD. (c) Mean switching time as a function of the number of locusts, N , derived using the equation-free technique (crosses with dashed best fit line) and from simulation (squares with full best fit line).

Notice that, apart from the small approximation due to the application of the central limit theorem, this is an exact equation for the coarse-grained observable U . The steady solution of [7] is given by

$$f_{Nst}(U) = C \exp[-\phi_N(U)], \quad [8]$$

where C is a normalisation constant and the potential, $\phi_N(U)$, can be computed as

$$\phi_N(U) = \frac{12N\beta}{\omega^2(1+\beta)} [U^2 - 2|U|]. \quad [9]$$

The potential is symmetric with respect to $U = 0$. It has two global minima at $U_{\pm} = \pm 1$. Fig. 1 shows (a) the stationary probability distribution (SPD), $f_{Nst}(U)$, given by [8] and (b) the potential, $\phi_N(U)$, given by [9], both plotted as solid lines. The mean switching time can be computed (as in (12)) as a function of N ,

$$T_1 = \frac{24N}{\omega^2} \int_{-1}^0 \exp[\phi_N(U)] \int_{-\infty}^U \exp[-\phi_N(\xi)] d\xi dU. \quad [10]$$

The function $T_1(N)$ is plotted (full line) in Fig. 1(c), with approximations to the variation of the mean switching time with N (squares) given by stochastically simulating the model.

There is quantitative agreement between the simulations and the theoretical formula [10]. There is no doubt, in the case of global interaction, that the dependence of mean switching time on the number of particles in the system is exponential. It can be approximated (see SI) as

$$T_1 \approx \sqrt{\frac{\pi\omega^2(1+\beta)^3}{12N\beta^3}} \exp\left[\frac{12N\beta}{\omega^2(1+\beta)}\right]. \quad [11]$$

Equation-free approach

We now return to the original model [1] – [2] with finite interaction radius. Unlike in the case of the toy global interaction model, we are unable to derive an explicit, closed-form equation for the coarse-grained observable U , i.e. the analogue of equation [7]. However, we hypothesise that such a closed equation,

$$\frac{\partial f_N}{\partial t} = \frac{\partial^2 (D(U)f_N)}{\partial U^2} - \frac{\partial (F(U)f_N)}{\partial U}, \quad [12]$$

exists, where $D(U)$ and $F(U)$ are the diffusion and drift coefficients respectively. Using an equation-free approach (13,14) we are still able to approximate quantities such as the mean switching time by designing and performing short computational experiments to estimate, on demand, the drift and diffusion coefficients of the unavailable, coarse-grained FPE [12]

for the mean velocity, U , of the locusts. Following (13,15) we approximate

$$F(U) \approx \left\langle \frac{U(t + \delta t) - U(t)}{\delta t} \right\rangle, \quad [13]$$

$$D(U) \approx \frac{1}{2} \left\langle \frac{[U(t + \delta t) - U(t)]^2}{\delta t} \right\rangle, \quad [14]$$

where $\langle \cdot \rangle$ represents an ensemble average over several, consistently initialised, short replica simulations with the detailed model [1] – [2]. δt is a small number of time steps of the process (typically between one and five) dictated by the timescale on which the coarse-grained equation [12] becomes valid. We can then use the drift and diffusion coefficients to approximate, via quadrature, the potential:

$$\phi(U) = - \int_0^U \frac{F(s)}{D(s)} ds + \ln(D(U)) \quad [15]$$

and hence the SPD of the underlying FPE (using Eq. [8]).

The equation-free approach involves initialising the particles consistently (lifting), so that their velocities give a specific value of alignment, U . We perform a large number of replica simulations (typically 1000) allowing each one to evolve for a short time period δt . This provides representative averages for the drift and diffusion coefficients of FPE [12] using formulae [13] and [14] respectively. After we have found the values of these desired quantities at the first alignment we repeat the process on an evenly spaced grid of possible alignments. Applying this technique in the case of global interaction gives an excellent fit to the analytical solutions, as expected (see Fig. 1(b),(a)).

In the more biologically realistic ‘local’ model, [1] – [2], we found that slightly smoother results were obtained by initialising particles with both a prescribed alignment and a velocity

variance which, in long simulations, was observed to be consistent with the particular alignment value. The diffusion coefficient of a specific case ($N = 30$) of the local model is shown in Fig. 2(a) to be approximately constant, while the drift coefficient has a characteristic antisymmetric cubic shape, indicative of the symmetric double-welled potential (see SI). Such an effective potential is consistent with most particle velocities being aligned (in one direction or in the other) most of the time, with occasional switches between directions whose frequency depends on the height of the potential barrier between the wells relative to their depth. This is corroborated by the approximations to the SPDs given in Fig. 2(b). The histogram represents the proportion of time the mean velocity of the particles spends at each allowed value bin during a long-time simulation, while the curve is the equation-free approximation to the SPD.

For a range of N we used the short-burst equation-free derived potential to estimate the mean switching time using a modified version of Eq. [10]:

$$T_1 = \int_{U_-}^{U_+} \frac{1}{D(\xi)} \exp[\phi(U)] \int_{-\infty}^U \exp[-\phi(\xi)] d\xi dU, \quad [16]$$

where U_- and U_+ are the mean velocities at which the two minima of the potential occur. We also established the relationship between mean switching time and N by counting the switches during a long simulation for the same range of N . The two methods give similar, apparently exponential, relationships (see Fig. 2(c)).

Experimental data

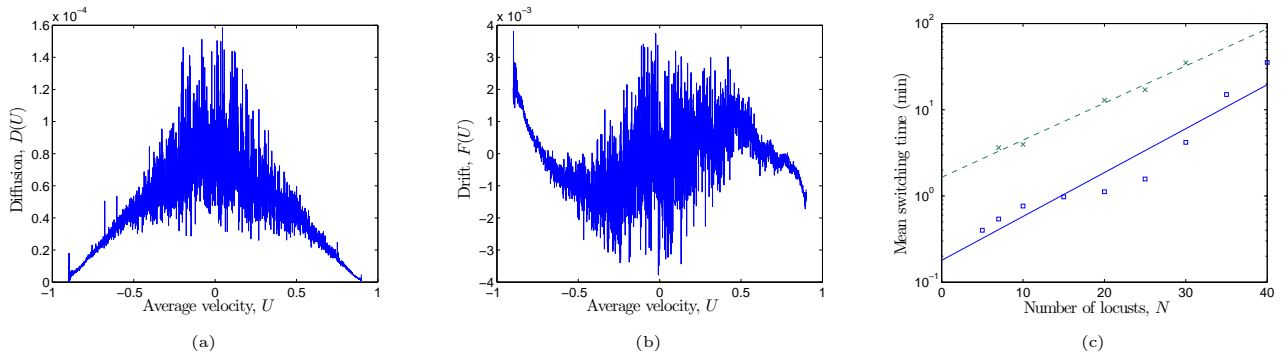


Fig. 3. Analysis of the experimental data. $N = 30$ ((a), and (b) only). The diffusion coefficient (a) and drift coefficient (b) estimated using [13] and [14] respectively. (c) Variation of the mean switching time with the number of locusts, calculated using the estimated potentials and Eq. [16] (crosses with dashed best fit line) and by counting the number of direction switches (squares with full best fit line). Note the log scale on the y -axis.

Locusts exhibit dynamic directional switching over a range of different densities. In previously reported experiments (8)

we recorded the directional alignment of groups of between 5 and 100 locusts for 8 hours. The ring-shaped arena in which the locusts were placed is analogous to the one-dimensional domain with periodic boundary conditions used in the SPP

model. We can thus use similar techniques to analyse the experimental data as we did with the long-term simulations. However, the equation-free approach (involving many consistent initialisations of the velocity - and even possibly of the variance of the velocity - of live locusts) is not practical in an experimental setting. Instead, we use a similar systematic FPE coefficient estimation approach from observations of the velocities of the locusts over a long period of time (an ‘equilibrium run’). During the first two hours of the experiments the activity of the locusts changed significantly, while in the latter six hours activity tended to be relatively consistent. We thus amalgamated, for each number of locusts up to 40, the observations of the locusts’ velocities over several experiments after the first two hours of each experiment. We collected instances of the same alignment, $U(t)$ and the alignment, $U(t + \delta t)$, a short time, δt , later and used these in equations [13] and [14] to estimate the drift and diffusion coefficients of the underlying FPE. Although experiments were carried out for numbers of locusts above 40 there were too few switches in the six hour interval to provide a meaningful estimate of drift and diffusion coefficients.

Fig. 3(a) and (b) show the estimated drift and diffusion coefficients of the alignment for the experiment with 30 locusts. The drift coefficient in Fig. 3(b), although noisy, still has a roughly cubic shape consistent with that estimated for the SPP model. Unlike the SPP model, however, the diffusion coefficient appears to have a quadratic shape, with its maximum at zero alignment. The potential (see SI), although not perfectly symmetric, is still double-welled, indicating the tendency of the particles to exhibit collective motion in one direction or the other.

We used Eq. [16] to calculate, for different N , the mean switching times from the potentials constructed by systematic estimation. We also found the mean switching time directly by taking the total time of the experiment and dividing it by the number of switches made. Both methods give an approximately exponential relationship between mean switching time and N (see Fig. 3(c)). This implies that the more locusts there are, the less often they switch and, as the

number of locusts becomes sufficiently large, there are effectively no switches over the duration of a day’s marching (~ 8 hours). There are quantitative differences between the results obtained by direct estimation of number of switches and the result of the coarse-grained approach. Two key sources may contribute to this: (i) The assumption that there exists a coarse-grained FPE for the average velocity, U , is valid only approximately. Such a discrepancy was already observed when we substituted the toy model [5] by model [1] – [2] (see Fig. 2(c)). In the case of the toy model [5] we know that there exists a closed FPE [7] and the results are exact, (see Fig. 1(c)). On the other hand, in the original model [1] – [2] the coarse-grained equation was not readily available and our computations revealed that it is valid only approximately. (ii) For the experiments there is also a second source of error since, unlike the computational model, we cannot obtain unlimited time series data. The length of the time series is limited by experimental restrictions. Binning the available time series as a histogram does not yield a symmetric SPD, which suggests that these time series are not long enough (see SI).

The fact that the diffusion coefficient increases when group alignment is low indicates that the locusts might respond to low group alignment by increasing the noisiness of their motion. To test this hypothesis we refined the SPP model [1] – [2]. Instead of taking the function $\eta(\bar{u}_i^{loc})$ (multiplying the uniform random variable, ΔQ , in the velocity update Eq. [2]) to be unity, we chose it to be a nontrivial function of the local mean velocity, \bar{u}_i^{loc} , specifically,

$$\eta(\bar{u}_i^{loc}) = \frac{3}{2} \left\{ 1 - \left(\frac{\bar{u}_i^{loc}}{|\bar{u}_i^{loc}|_{max}} \right)^2 \right\}, \quad [17]$$

where $|\bar{u}_i^{loc}|_{max}$ is the maximum of the absolute value of the mean local velocity; for this choice $\eta(\bar{u}_i^{loc})$ does not become negative. We specifically chose this functional form for η in order to obtain a quadratic shaped diffusion. The factor 3/2 is chosen to make the overall size of the noise in the original and revised models the same (see SI).

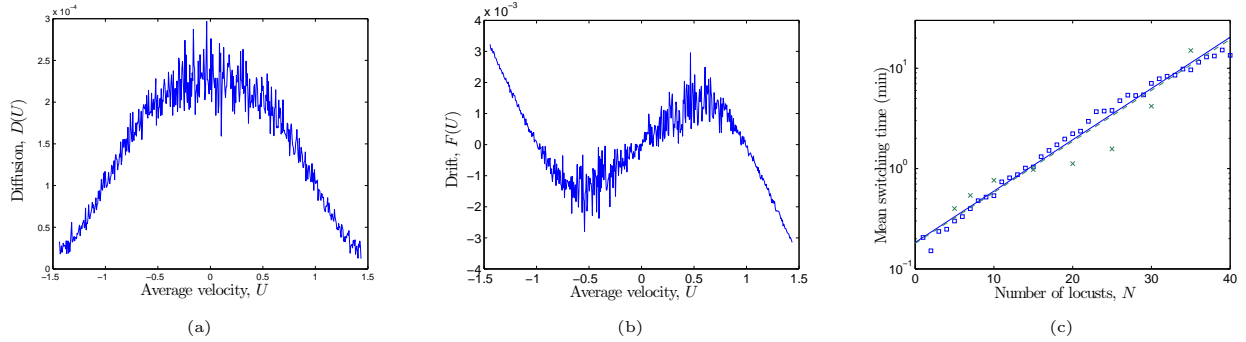


Fig. 4. Analysis of the revised model. $L = 90$, $R = 5$, $\beta = 1$, $\omega = 2.6$, $|\bar{u}_i^{loc}|_{max} = 1.5$ and $N = 30$ ((a) and (b) only). The interaction radius was chosen to be consistent with (8) and the noise was chosen so as to mimic the relationship between locust number and mean switching time given by the experimental data. (a) The diffusion coefficient of the revised model mimics the quadratic shape of the actual diffusion coefficient for the locusts, peaking at approximately zero alignment. (b) The potential has two deep wells giving further favourable comparison to the experimental data. (c) Comparison of the exponential relationship between the number of locusts and mean switching time, given by the revised model (squares with full best fit line) and the experimental data (crosses with dashed best fit line). Note the log scale on the y -axis.

In Fig. 4(a) the quadratic nature of the effective diffusion coefficient is recovered by the refined model. Qualitatively, the potential of the new model compares favourably with the potential of the actual locust data (see SI). A further useful validation of the revised model is that the mean switching time is significantly increased for all values of N in comparison to the original model (compare the simulation-derived mean switching times (squares with the full best fit lines) in Fig. 2(c) to Fig. 4(c)). A higher diffusion coefficient at lower alignments suggests that the locusts ‘prefer’ to be in a highly aligned state: when the locusts leave this state they increase the randomness of their movements and consequently a new aligned state is arrived at more quickly. The effect of this altered diffusion coefficient on the evolution of the coarse variable, U , is evidenced in Fig. 5. The transitions between ordered states in the original model are very sharp (see Fig. 5(a)), whereas the transitions for the experimental data are

relatively noisy (See Fig. 5(b)). The noisiness of the transitions appears to be replicated well by the revised model (see Fig. 5(c)). In general it can be seen that the marching band switches direction more frequently in the original model than the revised model.

Discussion

Our analysis of self-propelled particle models and of animal movement data has revealed a number of novel features. Firstly we established that the mean switching time increases exponentially with the number of particles/locusts. As locust density increases the turning rate of the group rapidly decreases. This observation has implications regarding attempts to control the locusts’ motion: at high densities it becomes increasingly difficult to influence a group’s direction. Secondly we used the systematic Fokker-Planck equation coefficient estimation approach on experimental data. Our results indicated that the individuals move more randomly in locust

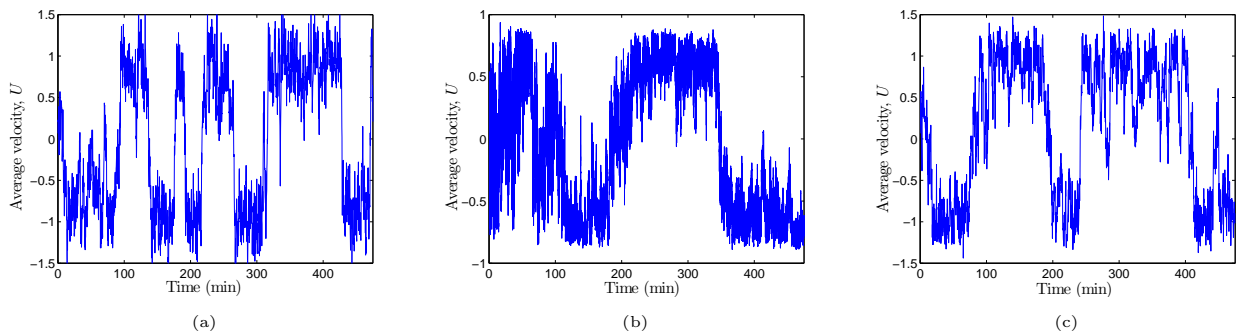


Fig. 5. Typical evolution of the average velocity, U , for (a) the original model, (b) the actual locust data and (c) the revised model. $N = 30$, $L = 90$, $R = 5$, $\beta = 1$, $\omega = 3.9$ ((a) and (c) only) and $|\bar{u}_i^{loc}|_{max} = 1.5$ ((c) only). In (a) and (c) we have used an altered value of ω and a rescaled time axis in order to better illustrate the similarities and differences between the models and the data.

groups with low alignment. This appears to enable the group to find (and remain in) a highly aligned state more easily.

One of the most useful aspects of our agent-based approach is that it enhances our ability to speculate about the behaviour of individual locusts from group level information: we alter individual behavioural rules and use self-propelled particle models to test the effect that these alterations have on the coarse variable, U . This enables us to verify the validity of these individual-scale alterations. We thus used our experimental observations to guide our modelling, changing the noise term for the individual locusts so that it becomes larger when the alignment is smaller. We found the relationship between group number and mean switching time to again be exponential, but with longer mean switching times than in our previous model.

It would be interesting to consider whether recent findings about cannibalistic interactions between marching locusts (16) can provide rationalisation for the observation of apparently increased individual randomness in response to a loss of alignment at the group level: given the risk of exposing the rear of the abdomen to oncoming insects (16), there may be

selection pressure on an individual to minimise the time spent in the disordered phase. A longer inter-switch time might also be selected for in an evolutionary scenario since it allows the locusts to remain in a coherent group for longer periods, potentially increasing harvesting efficiency and reducing predation (5, 17–19).

We have provided evidence that our revised model is more biologically justifiable than our original model; new functional forms such as [17] may be useful in the formulation of other self-propelled particle models characterising collective animal behaviour. Our findings provide strong evidence for the seemingly unexpected phenomenon of randomness contributing to the creation of coherent behaviour at the collective level.

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