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# Making noise: emergent stochasticity in collective motion

Nikolai W.F. Bode<sup>a,b,\*</sup>, Daniel W. Franks<sup>a,b,c</sup>, A. Jamie Wood<sup>a,b,d,\*</sup>

<sup>a</sup> York Centre for Complex Systems Analysis, University of York, York, PO Box 373, YO10 5YW, United Kingdom

<sup>b</sup>Department of Biology, University of York, York, YO10 5YW, United Kingdom

<sup>c</sup>Department of Computer Science, University of York, York, YO10 5DD, United Kingdom

<sup>d</sup>Department of Mathematics, University of York, York, YO10 5DD, United Kingdom

#### Abstract

Individual-based models of self-propelled particles (SPPs) are a popular and promising approach to explain features of the collective motion of animal aggregations. Many models that capture some features of group motion have been suggested but a common framework has yet to emerge. Key to all of these models is the inclusion of "noise" or stochastic errors in the individual behaviour of the SPPs. Here, we present a fully stochastic SPP model in one dimension that demonstrates a new way of introducing noise into SPP models whilst preserving emergent behaviours of previous models such as coherent groups and spontaneous direction switching. This purely individual-to-individual, local model is related to previous models in the literature and can easily be extended to higher dimensions. Its coarse-grained behaviour qualitatively reproduces recently reported locust movement data.

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<sup>\*</sup>Corresponding author. Tel.: +44 1904 328650, Fax: +44 1904 328505.

*Email addresses:* nwfb500@york.ac.uk (Nikolai W.F. Bode), ajw511@york.ac.uk (A. Jamie Wood)

We suggest that our approach offers an alternative to current reasoning about model construction and has the potential to offer mechanistic explanations for emergent properties of animal groups in nature. *Keywords:* swarming, noise, coarse-graining, locusts, SPP model

#### 1 1. Introduction

Modelling the collective motion of animals remains a tantalising problem 2 for scientists of a host of different disciplines. Both visually attractive and 3 scientifically challenging, the concept remains useful because of its applicabil-Δ ity to both animation (Reynolds, 1987) and control systems (Liu et al., 2003; 5 Tanner et al., 2007) as well as the fundamental ecological understanding it brings (Sumpter, 2006). Many individual-based models have emerged in the last few decades that exploit advances in computational power to describe 8 features seen in collective animal motion including group decision making 9 (Couzin et al., 2005; Conradt and Roper, 2007), information flow (Sumpter 10 et al., 2008) and response to predation (Wood and Ackland, 2007). This 11 article focuses on the development of one-dimensional models that seek to 12 describe some of the simplest observed features in collective motion. Such 13 models are now known collectively as 1D self-propelled particle (SPP) mod-14 els. 15

In recent years the biological relevance of these models has been demonstrated as a result of the development of novel, approximately one-dimensional, experimental systems. By constraining marching bands of locust nymphs to a specially constructed annular arena Buhl et al. (2006), and more recently Yates et al. (2009), have shown that these insects do indeed behave in a

manner that is qualitatively comparable to one-dimensional SPP models. In particular this work demonstrated that SPP models capture the spontaneous turns of the locust bands, where the entire group reverses its direction of motion without external input. It is believed that the origin of these observations lies in internal, or intrinsic, stochastic effects or "noise" which may or may not correspond to inaccuracy of the individual movements (e.g Buhl et al. (2006); Couzin et al. (2005)).

Recently, the coarse-grained behaviour of 1D SPP models has been compared to locust movement in a more systematic way. From their study Yates et al. (2009) suggested that the insects respond to a decrease of group alignment by increasing the noise in their movement. The importance of this finding is that the addition of simple noise terms is not necessarily sufficient to describe and explain collective motion in animals. However, despite its great importance the origin of this stochasticity is far from clear.

In this research we focus exclusively on a simple one-dimensional SPP 35 model, and show how a combination of an asynchronous updating scheme 36 and a novel implementation of particle interactions can produce a coarse-37 grained behaviour which reproduces findings by Yates et al. (2009) in locust 38 movement data. The novelty of our research lies in the fact that all noise in 39 the system emerges from the algorithmic implementation of our model rather 40 than being added to the movement of particles. We therefore work towards 41 explaining the origin of stochasticity in animal collective motion using our 42 modelling approach. 43

First we give an overview of selected 1D SPP models described in previous work and the results that they give. Second we introduce our modelling

<sup>46</sup> approach. We then show that our model can produce stable groups and <sup>47</sup> spontaneous direction switching and study the coarse-grained behaviour of <sup>48</sup> our model via an equation-free approach using numerical simulations. We <sup>49</sup> conclude by commenting on the potential of our modelling approach for inte-<sup>50</sup> grating individual-level characteristics and describing motion in dimensions <sup>51</sup> greater than one.

#### <sup>52</sup> 2. SPP Models

The first 1D SPP model simulated particles with a local aligning be-53 haviour on a continuous line with periodic boundary conditions (Czirók et al., 54 1999). In this model the individual and continuous velocities and positions 55 are updated sequentially and simultaneously for all individuals. Particles 56 tend to align with the average velocity of all particles within a fixed distance 57 from them. This alignment is subject to a stochastic error in the form of uni-58 formly distributed noise which is explicitly added to the particles' response 59 to the average local velocity. An anti-symmetric function G is applied to the 60 preferred velocity of individuals and introduces both propulsion and friction 61 to the system. The individual velocities  $u_i(t)$  are therefore updated as, 62

$$u_i(t+1) = G\left(\langle u(t) \rangle_i\right) + \xi_i,\tag{1}$$

where  $\langle u \rangle_i$  is the local average velocity for particle *i* and  $\xi_i$  is a random variable with uniform probability distribution over a finite interval  $[-\eta/2, \eta/2]$ (Czirók et al., 1999). The function G(z) is given by,

$$G(z) = \frac{1}{2}(z + \operatorname{sgn}(z)),$$
 (2)

which sets the average of the individual speeds in the absence of particle 66 interactions to magnitude 1 (Czirók et al., 1999). Analysis of the model 67 has indicated that the average velocity of all particles undergoes a phase 68 transition from an ordered state to a disordered state when the amplitude 69 of the noise  $(\eta)$  or the particle density is varied (Czirók et al., 1999). Such 70 phase transitions have also been observed for SPP models in two and three 71 dimensions which suggests that some features of higher dimensional systems 72 are preserved in 1D models (Vicsek et al., 1995; Chaté et al., 2008). For 73 certain parameter values the model exhibits a fascinating direction switching 74 behaviour - the average velocity of all particles in the system changes sign 75 spontaneously and on a short time scale compared to longer intervals of 76 sustained high absolute values of the average velocity. Several variants of 77 this scheme to introduce noise have been published (Chaté et al., 2008). 78

Another approach has been to implement SPP models on a one-dimensional 79 lattice with periodic boundary conditions over which particles move with ve-80 locities +1 or -1 (O'Loan and Evans, 1999; Raymond and Evans, 2006). In 81 the first model of this type particles align with the velocity of the majority 82 of particles around them with a given probability (O'Loan and Evans, 1999). 83 The magnitude of this probability is the first source of noise in the model. 84 The second source of noise and an important aspect of the model related to 85 this research is its asynchronous updating scheme. In each step only the posi-86 tion and velocity of one, randomly chosen particle are updated. Simulations 87 of the model showed a phase transition from high to low average particle 88 velocities for increasing sizes of the aligning probability. This is qualitatively 89 similar to the phase transition exhibited by the model of Czirók et al. (1999). 90

This asynchronous 1D SPP lattice model was subsequently extended sig-91 nificantly by the inclusion of repulsion and attraction into the individual 92 behaviour of the particles and the modification of the alignment behaviour 93 (Raymond and Evans, 2006). The authors justified their implementation of 94 the different behaviours by showing that they correspond qualitatively to 95 taking random samples of neighbours (Raymond and Evans, 2006). This 96 implementation results in two separate parameters which control the size of 97 the error or noise in the reaction of individuals to their surrounding neigh-98 bours. One parameter controls the error arising from stochastically sampling 99 the local group to determine the particle's preferred direction and the other 100 parameter introduces uncorrelated errors (Raymond and Evans, 2006). 101

In summary, 1D SPP models show a wealth of emergent behaviours which 102 have increasingly been compared to real collective animal motion. The way 103 stochastic errors have been included into such models can roughly be di-104 vided into three categories. First, adding a random variable to the preferred 105 direction of individuals (Czirók et al., 1999). Second, asynchronous and 106 probabilistic updates (O'Loan and Evans, 1999; Raymond and Evans, 2006). 107 Third, varying the probability and accuracy with which individuals execute 108 their behavioural rules (O'Loan and Evans, 1999; Raymond and Evans, 2006). 109 In the next section we will introduce our model which takes inspiration from 110 the second and third approaches. 111

#### <sup>112</sup> 3. Modelling approach

In our model N individuals are represented by points on a continuous line and not by points on a lattice as in some of the models discussed above. The

individuals, indexed i, are characterised by their position  $x_i$  and instanta-115 neous velocity  $\theta_i$  and they react to their "neighbours" which are less than a 116 distance  $r_A$  away from them. We assume that each individual reacts with an 117 identical stochastic rate to its surroundings. This defines an implicit master 118 equation that in principle could be solved with a stochastic simulation algo-119 rithm (Gillespie, 1976). Instead, we exploit the identical rates and a simple 120 particle picking approach to simulate the system (O'Loan and Evans, 121 1999). The algorithmic implementation of our model is as follows: 122

- 123 1. Choose individual i at random, where i = 1, ..., N (equal probabilities, 124 with replacement).
- 2. If *i* has neighbours, choose a neighbour *k* of *i* at random (equal probabilities for all individuals within less than  $r_A$  of *i*).
- <sup>127</sup> 3. Update  $x_i$  and  $\theta_i$  (based on the interaction between k and i or on <sup>128</sup> previous  $\theta_i$  if i has no neighbours).

N realisations of steps (1) to (3) constitute one update step of length  $\Delta t$ 129 time-steps (see also figure 1). The duration of this update step corresponds 130 to the reciprocal value of the algorithmic rate at which individuals update. 131 Small values of  $\Delta t$  imply rapid updates, while large values of  $\Delta t$  imply slow 132 updates. The output of the model is obtained by recording the positions and 133 velocities of all individuals every  $T = \lambda \Delta t$  time-steps, where  $\lambda \geq 1$ . This 134 is analogous to how data of animal motion is obtained empirically where 135 individual positions and orientations are sampled according to the frame 136 rate of video recordings (Aoki, 1980; Buhl et al., 2006). In our simulations 137 we keep T fixed and only vary  $\Delta t$  and therefore also  $\lambda$ . 138

Suppose individual i and a neighbour k of i have been chosen in the algorithm described above. The interaction between i and k depends on the distance d between the two individuals. If  $d \leq r_O < r_A$ , i attempts to align with k and has desired velocity,

$$\theta_i^{desired} = G(\theta_k). \tag{3}$$

143 If  $r_O < d < r_A$  individual *i* gets attracted to *k* and has desired velocity,

$$\theta_i^{desired} = G\left(\operatorname{sgn}(x_k - x_i)\left(\frac{d - r_O}{r_A - r_O} + 1\right)\right),\tag{4}$$

where the fraction term in the argument is motivated by a distance rule such that at maximum distance maximal desired velocities are achieved. If *i* has no neighbours (there is no *k* such that  $d < r_A$ ),  $\theta_i^{desired}$  is given by,

$$\theta_i^{desired} = G(\theta_i). \tag{5}$$

The function G is given above in equation 2. Once  $\theta_i^{desired}$  is determined,  $\theta_i$ and  $x_i$  are updated according to,

$$\operatorname{new}(\theta_i) = \theta_i + (\theta_i^{desired} - \theta_i)\Delta t, \tag{6}$$

$$\operatorname{new}(x_i) = x_i + \operatorname{new}(\theta_i)\Delta t.$$
(7)

In our model individuals react deterministically to the positions and motion of randomly selected neighbours. In previous work (Huth and Wissel , 1992), it has been suggested that interactions with single individuals are not able to mimic the properties of animal collective motion in the same way as averaging over a number of individuals. However, viewed over timescales larger than  $\Delta t$ , our algorithm is qualitatively equivalent to reacting in

a noisy way to a random sample of neighbours and our results below show
that our simulations are comparable to empirical data. For a more detailed
discussion on the biological plausibility and interpretation of our model we
refer the reader to the discussion.

The instantaneous individual speed in our model tends to be increased 159 when particles get attracted to others (see equation 4). Such a dependence of 160 the instantaneous speed on the distance between individuals has previously 161 been used in models of collective motion for repulsion between individuals 162 (Reynolds, 1987; Hemelrijk and Hildenbrandt, 2008). Our assumption of 163 higher attraction speeds is based on the hypothesis that individuals need to 164 move faster if they are interacting with individuals further away (e.g. to catch 165 up with them), but is also necessary for the recovery of realistic distributions 166 of individual speeds (Bode et al., 2010). 167

To derive this model we use asynchronous updates similar to the ones sug-168 gested by O'Loan and Evans (1999) but we collect particle positions every T169 time-steps and thereby allow for different individual and average update rates 170 in real time with an approximately continuous velocity distribution. The im-171 plementation of alignment, friction and propulsion (see G(z)) are inspired 172 by Czirók et al. (1999) but our implementation of attraction is new. Our 173 random-neighbour-picking approach has parallels to the neighbour-sampling 174 argument Raymond and Evans (2006) invoked to justify the implementation 175 of their behavioural rules but we have made this sampling explicit and limited 176 interactions in our algorithm to pairwise interactions. The effect of varying 177 the length of update-steps in algorithms such as ours has been considered 178 previously, but not in a biological context (Tsitsiklis et al., 1986). The ratio-179

nale behind our model is to find a set of microscopic rules that are capable
of recovering empirical results.

#### <sup>182</sup> 4. Model analysis

#### <sup>183</sup> 4.1. Coherence and direction switching

Here we show that our model preserves the interesting emergent behaviours previous models have found. We do not present a complete analysis of the behaviour of our model. Rather, we focus on experiments which illustrate that our model produces coherent groups in which individuals do not diffuse over long simulations and that our way of including noise results in a phase transition from an ordered to a disordered state of simulated groups for increasing noise and therefore that we are recovering previour results.

Our simulations are performed in the absence of boundary conditions. 191 Typically, simulated collective motion is limited by periodic boundary condi-192 tions (Vicsek et al., 1995; Czirók et al., 1999; O'Loan and Evans, 1999; Ray-193 mond and Evans, 2006). This means that individuals crossing one boundary 194 are removed and appear at the opposite boundary which results in move-195 ment on a circle in one dimension. The advantage of this approach is that 196 simulated groups cannot disperse in space. Boundary conditions can form 197 a source of ambiguity in that it may not be clear in how far emergent be-198 haviours are a result of the model or the implementation of the boundary 199 conditions. 200

Initially, individuals were randomly distributed in an interval of length  $r_A$  to ensure that they were capable of perceiving at least one other particle. At the start of our simulations all individuals had velocity  $\theta_i = +1$ .



Figure 1: Schematic illustration of an example for one update step  $\Delta t$  of our model for N = 3 (top to bottom). The grey areas indicate the extent of  $r_O$  for updating individuals (in white) and the arrows show the direction of motion of the particles. Particles without arrows have zero instantaneous velocity. Dotted lines highlight interactions. In the first panel individual 2 is chosen and randomly picks individual 1 to interact with (alignment). In the second panel 3 is chosen and picks 1 to interact with. Since the distance between the two particles is larger than  $r_O$ , 3 gets attracted to 1. In the third panel 2 is chosen again and chooses to align to individual 3. The last panel shows the positions of 1,2, and 3 after one update step  $\Delta t$ .

More commonly particles are assigned random initial velocities in simulation studies (Czirók et al., 1999; O'Loan and Evans, 1999; Raymond and Evans, 2006; Buhl et al., 2006). We chose our initial conditions to ensure that groups would not fragment within the first few time-steps of the simulations. Long simulated time intervals before recording started (typically 100,000 time-steps) ensured that no initial transitional data was used in our results.

Figure 2 shows that our model is capable of producing groups which re-211 main coherent over long simulations in absence of boundary conditions. For 212 large values of  $\Delta t$  (here close to T) and small values of  $r_A$  the groups tend 213 to fragment. We show results for two particular values of  $r_A$  for unchanged 214  $r_O$  to illustrate that the relative size of the former parameter can be impor-215 tant for the coherence of the simulated groups. Non-zero distances between 216 individuals and their nearest neighbours in our simulations indicate that in-217 dividuals do not "collapse" onto one position in coherent groups - a potential 218 problem in deterministic simulations (figure 2). 210

In figure 3 we illustrate that simulated groups show spontaneous switches 220 in direction. To do so we measure  $Q = \sum_i \theta_i / N$ , the average velocity of indi-221 viduals. To get a feeling for how direction switches of groups can occur in our 222 model we refer the reader to figure 1. In this illustration the group initially 223 travels on average to the right hand side. After one update step is performed, 224 the group travels on average to the left hand side. The quantity  $\langle |Q| \rangle$  repre-225 sents the mean over a large number of the absolute value of measurements of 226 Q and is used to measure the order or alignment in the system. Large values 227 indicate high order and low values low order. Our model exhibits a phase 228

transition from an ordered state to a disordered state for increasing values 229 of  $\Delta t$  (see figure 3a). In figure 4 we show two examples for the characteristic 230 distributions of Q for our model. For low values of  $\Delta t$  the distribution of 231 Q peaks at two large values of |Q| which indicates that the group collec-232 tively moves in one direction with occasional and relatively quickly executed 233 switches in direction. Higher values of  $\Delta t$  result in a decreased distance be-234 tween the two peaks in the distribution of Q up to the point when the group 235 does not move collectively in one direction for prolonged periods of time any 236 more. This phase transition is captured by the sign of the skewness of the 237 distribution of |Q| which turns from negative to positive for increasing values 238 of  $\Delta t$  (figure 4c). The time which the groups spend travelling in one direction 239 between reversals in direction increases dramatically with decreasing  $\Delta t$  (see 240 figure 5). This trend is qualitatively similar to findings for other SPP models 241 in which reversal times increase for deceasing noise (O'Loan and Evans, 1999; 242 Yates et al., 2009). 243

We have seen that the parameters  $r_A$  and  $\Delta t$  control the stability and 244 state or phase of the simulated groups (ordered/disordered). To obtain a 245 more complete picture of our models' behaviour we performed a systematic 246 scan of the  $(r_A, \Delta t)$  parameter space for N = 50 (see figure 6). We used the 247 sign of the skewness of the distribution of |Q| as an indicator of the phase 248 as the change of sign in the skewness provided a clear and easily-defined 249 switching point (see figure 4c). Using the conditions for different phases 250 established above, we divided the parameter space into three regions of dis-251 tinctive model behaviours: unstable or fragmenting flocks, disordered flocks 252 and ordered flocks. As with all stochastic simulations this phase diagram 253

can only be understood as a an indicative approximation of the model's behaviour. In combination with our initial conditions the case  $r_A = r_O$  leads to a collective which moves in one direction, but diffuses as a result of the asynchronous updating scheme. For larger  $r_A$  the groups quickly stabilise and show a distinctive divide between an ordered and a disordered phase for small and large values of  $\Delta t$  respectively.

In summary, we have established that our model can produce a qualita-260 tively similar emergent behaviour to previous models. The level of noise in 261 the system is determined by the parameters  $r_A$  and  $\Delta t$ . Qualitatively similar 262 but quantitatively different phase diagrams for our model could be obtained 263 if particles were allowed to move at instantaneous speeds larger than two 264 (cf equation 4) or if they accelerated faster. The effect of N also leads to a 265 quantitative but not a qualitative change in the behaviour of our model. Our 266 model analysis is an illustration of principle and a more detailed investigation 267 of the effect of different initial conditions including different measures for the 268 stability of the group is beyond the scope of this work. 260

#### 270 4.2. Coarse-grained behaviour

The coarse-grained behaviour of a system can often be described in terms of a small number or even single "coarse" variables. In some cases it is possible to construct a "coarse-grained" model which accurately captures the temporal development of these variables (Erban et al., 2006; Kolpas et al., 2007; Yates et al., 2009).

We adopt the approach pioneered by Yates et al. (2009) in which they study the coarse-grained behaviour of 1D SPP models in terms of the average particle velocity Q. Yates and co-workers hypothesised that the temporal



Figure 2: Coherence of simulated groups. Individuals within  $r_A$  of each other are considered to be connected. Components are defined as sets of individuals which are connected to each other either directly or via other individuals. If there is one component, all individuals are in the same group. (a) the fraction of the total number of individuals within the largest component. (b) the median of individual's distance to their nearest neighbour (NNDs). We show the average over 1000 equally spaced sampling points during the last 200,000 time-steps of a simulation over 300,000 time-steps (5 replicas). Error bars show one standard deviation from the mean. For larger values of  $\Delta t$  the groups did not maintain coherence which led to a low average proportion of individuals within the largest component. For larger  $r_A$  the groups maintained coherence over the simulation, even for large values of  $\Delta t$ . The NNDs increased with increasing values of  $\Delta t$ . For  $\Delta t > 0.6$  and  $r_A = 6$  the groups did not maintain cohesion over the length of the simulation which led to very large NNDs. Parameters: N = 100,  $r_O = 5$  and T = 1.



Figure 3: (a)  $\langle |Q| \rangle$  as a function of  $\Delta t$  (mean over 5 replicas, error bars are smaller than the symbols). Parameters are as in figure 1 but N = 50 and  $r_A = 50$ . (b)-(d) illustrate direction switching in the simulations of our model, where  $\Delta t = 0.1$  (b),  $\Delta t = 0.6$  (c) and  $\Delta t = 1.0$  (d). The groups remained coherent for the duration of the simulations (compare to figure 1). Simulations lasted for 1,600,000 time-steps and output started after 100,000 time-steps.



Figure 4: Distribution of Q for different values of  $\Delta t$  over 400,000 time-steps (T) at the end of 10 million time-steps. (a)  $\Delta t = 0.6$ , the particles switch direction occasionally and the group is mostly well aligned (high values of Q). (b)  $\Delta t = 0.9$ ), the group is not well aligned and Q fluctuates about zero. N = 50,  $r_A = 50$ ,  $r_O = 5$ , T = 1. (c) Skewness of the distribution of |Q| against  $\Delta t$  extracted from simulations of 400,000 time-steps at the end of a 10 million time-step simulation. The sign of the skewness switches from negative to positive for increasing values of  $\Delta t$ . N = 50,  $r_A = 9$ ,  $r_O = 5$ , T = 1.

evolution of Q can be approximately described by the Fokker-Planck equation
(FPE),

$$\frac{\partial f_N(Q,t)}{\partial t} = \frac{\partial^2 (D(Q)f_N)}{\partial Q^2} - \frac{\partial (F(Q)f_N)}{\partial Q},\tag{8}$$

where the function  $f_N(Q, t)$  is the time-dependant probability distribution 281 for the random variable Q. D(Q) and F(Q) denote the diffusion and drift 282 coefficients, respectively. These two coefficients can be interpreted as follows: 283 the drift captures the mean rate of change of Q while the diffusion denotes 284 the magnitude of the randomness in the evolution of Q. Since the explicit 285 form of the FPE is not available, the drift and diffusion coefficients need to 286 be estimated using computer simulations (for details, see Yates et al. (2009)). 287 While it is possible to approximate interesting quantities such as the mean 288 switching time from the estimated form of the FPE (Erban et al., 2006; Yates 289



Figure 5: Average reversal times for simulated flocks for varying  $\Delta t$ . The quantity  $\langle \tau \rangle$  is the average time for which sgn(Q) remains unchanged. We collected 1000 values of  $\tau$  for 10 replicas of each parameter combination. Error bars show one standard deviation from the mean. For smaller values of  $\Delta t$  the sign of Q remained unchanged over a simulation of 100 million time-steps. Note the log-scale on the y-axis.  $r_A = 50$ ,  $r_O = 5$ , T = 1.



Figure 6: Phase diagram for simulations over 10 million time-steps. Groups were considered to be unstable if at some stage during the simulation at least one particles had no neighbours (i.e. no particles within  $r_A$ ). The ordered state was defined by a negatively skewed distribution of |Q|. The behaviour of the model was robust over five replicates. Dashed lines are for guidance of the eye only. N = 50,  $r_O = 5$ , T = 1.

et al., 2009), we will limit our study to the functional form of the drift and diffusion coefficients as this provides a sufficiently detailed insight into the behaviour of Q.

When a similar technique was applied to long time-series of the alignment 293 (Q in this case) of locust bands marching in an annular arena, the functional 294 form of F(Q) and D(Q) revealed fascinating properties of the evolution of 295 Q (Yates et al., 2009). Previous research had shown that the locusts were 296 highly aligned and marched in one direction for prolonged periods of time 297 before spontaneously switching the direction of their motion within a few 298 minutes and marching in the opposite direction (Buhl et al., 2006). The drift 299 coefficient estimated from this empirical data had a roughly cubic and anti-300 symmetric shape which is consistent with particle motion in aligned states 301 with occasional switches in direction (Yates et al., 2009). For large positive 302 values of Q, F(Q) took large negative values, and vice-versa. This indicated 303 that for very high average group speeds the group speed was likely to decline 304 over time. There were three points for which F(Q) = 0. These corresponded 305 to one unstable and two stable stationary points of Q(t). The two stable 306 stationary points indicate that groups of locusts had a preferred group speed 307 which was approximately the same in either direction. Interestingly, the dif-308 fusion coefficient had a quadratic shape with its maximum at zero alignment 309 (Yates et al., 2009). An equation-free analysis of a simple 1D SPP model (a 310 variant of Czirók's model (Czirók et al., 1999)) indicated that the approxi-311 mated diffusion coefficient for the evolution of the average particle velocity 312 in this model was roughly constant for different values of Q, while F(Q) had 313 the same antisymmetric cubic shape as found in the locust data. Yates et al. 314

(2009) hypothesised that the quadratic shape of D(Q) for the empirical data 315 could be a result of locusts responding to "low group alignment by increas-316 ing the noisiness of their motion". The authors tested their hypothesis by 317 refining their original model. In the new model the stochastic error added to 318 the preferred direction of individuals was increased if individuals perceived a 319 low local group alignment around them. This model produced a better fit to 320 the empirical data and its equation-free analysis confirmed that the estimate 321 for D(Q) now had a quadratic form. 322

We performed an equation-free analysis on our model following the ap-323 proach by Yates et al. (2009). To facilitate a comparison to previous empir-324 ical data and models, we restricted the particles to a line of length L with 325 periodic boundary conditions and used the same parameters as Yates and co-326 workers wherever possible. We found that the estimated drift coefficient for 327 our model had a cubic shape and the diffusion coefficient a roughly quadratic 328 shape with maximum at Q = 0 (see figure 7). The diffusion shows a notice-329 able increase for large values of |Q|. This phenomenon was not found in the 330 empirical data (Yates et al., 2009) and is a sign that the drift coefficient af-331 fects the diffusion coefficient. In other words, the cubic drift is so pronounced 332 or sharp that it impacts on the diffusion. For our model this effect could be 333 explained by the fact that the groups cannot maintain high velocities as a 334 result of the friction implemented in the function G. This cannot happen in 335 the measurements Yates et al. (2009) made from the locust data since the 336 absolute value of their coarse variable was bounded above by 1. 337

These findings indicate that our model produces a coarse-grained behaviour qualitatively similar to the coarse-grained behaviour of bands of

marching locusts. The higher noise in the evolution of Q in our simulations emerges from our model which does not assume larger stochastic errors for low values of |Q|. Yates and colleagues noted that the randomness in their models is not necessarily indicative of random decision making in locusts. They suggest that there may be small-scale detailed interactions between individuals which result in noise in the coarser experimental observations (Yates et al., 2009). This is precisely what our model achieves.

#### 347 5. Discussion

In this work we have introduced a new approach to include noise into 1D 348 SPP models. Our approach yields a good qualitative fit to empirical data 349 and can easily be extended to higher dimensions. It therefore suggests a 350 mechanism whereby small-scale stochastic interactions can produce an emer-351 gent behaviour which is comparable to the coarse-grained behaviour of bands 352 of marching locust nymphs. Our model suggests that stochasticity in ani-353 mal movement could be a result of incomplete information intake (neighbour 354 sampling) and small variations in instantaneous rates of information intake 355 (asynchronous updates). This mechanism is parsimonious as it only relies on 356 asynchronous updating and stochastic neighbour-sampling of individuals. 357

For our model it is important to maintain a clear separation between algorithmic implementation and biological interpretation. We do not claim that updates in our model translate directly into interactions between individuals. The length of update-steps, encoded in the size of  $\Delta t$ , does not explicitly relate to biological or neurological reaction times of animals. Furthermore, the instantaneous positions and movement of individuals on time-scales close to



Figure 7: Equation-free analysis of our model. L = 90, N = 30,  $r_A = 6$ ,  $r_O = 5$ , T = 1 and  $\Delta t = 0.5$ . All parameter values were chosen as close as possible to the ones by Yates and coworkers and otherwise to produce a similar coarse-grained behaviour to the locust data (Yates et al., 2009). (a) The drift coefficient shows a characteristic antisymmetric cubic shape. (b) The diffusion coefficient has a roughly quadratic shape with maximum approximately at Q = 0. Notice the "ears" in D(Q) for large values of |Q|. The estimates for drift and diffusion were obtained from long time series of model simulations in agreement with the analysis of empirical data.

 $\Delta t$  have no direct physical meaning. We merely record the response of indi-364 viduals to their surroundings averaged over multiple updates (model output 365 every T time-steps). Therefore, it is the average behaviour of individuals in 366 our model at time-scales larger than  $\Delta t$  that should be considered in a bio-367 logical interpretation of our model. The importance and impact of variable 368 update rates in our model opens up questions regarding the length of and dif-369 ference between reaction and decision times in animals and their individual 370 information processing capabilities. 371

We aim to hint at under-explored possibilities in formulating SPP mod-372 els. Most SPP models implement interactions in a deterministic way and 373 then add stochastic errors (e.g. Vicsek et al. (1995); Czirók et al. (1999)). 374 Absence of noise terms in such models would result in accurate interactions 375 of individuals in perfect knowledge of each other. In contrast, in our ap-376 proach the algorithmic implementation of interactions itself leads to noisy 377 interactions. We feel this is an important difference with the potential of 378 improving our understanding of collective animal motion by suggesting pos-370 sible mechanisms for seemingly imperfect or erratic animal interactions. We 380 have previously demonstrated, for example, that an asynchronous updating 381 scheme coupled with varied updating rates provides a mechanism that could 382 explain both continuous speed distributions of collectively moving individu-383 als and the way in which these distributions change in response to external 384 stimuli (Bode et al., 2010). This work has also suggested that the length of 385 update steps in algorithms such as the one presented here could be related 386 to the level of threat animals perceive. The length of the update steps is one 387 of the parameters that controls the level of noise in our model. Therefore, 388

<sup>389</sup> our model suggests a meaningful explanation and mechanism for different <sup>390</sup> levels of noise in a biological system and makes testable predictions as to <sup>391</sup> when and why phase transitions might occur in this system. Furthermore, <sup>392</sup> a mechanism based on stochastic sampling of individal's sensory zones as <sup>393</sup> in our model also offers a potential explanation for the anisotropy observed <sup>394</sup> in the internal structure of large starling flocks (Ballerini et al., 2008; Bode <sup>395</sup> et al., in press).

SPP models commonly assume that all individuals are identical. How-396 ever, this does not necessarily hold in nature. Research has begun to inves-397 tigate the effect of individual features of gregarious animals onto collective 398 behaviour (Couzin et al., 2005; Leblond and Reebs, 2006). Our framework 399 facilitates the inclusion of individual characteristics. One could, for exam-400 ple, consider different updating rates for individuals, possibly related to their 401 individual state of agitation (Bode et al., 2010). These individual updating 402 rates could vary over time in response to environmental stimuli or simply 403 the number and updating rates of neighbouring individuals. The advantage 404 of our modelling approach, with a detailed microscopic description, is that 405 additional features such as decision making and information transfer can be 406 incorporated into the framework that we propose in the future. 407

In conclusion, we suggest that noise in models for collective motion of animals should not be considered as a necessary error to account for imperfect interactions but as an opportunity to find out more about how animals function within collective aggregations.

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