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Making noise: emergent stochasticity in collective motion

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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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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. Introduction

Modelling the collective motion of animals remains a tantalising problem for scientists of a host of different disciplines. Both visually attractive and scientifically challenging, the concept remains useful because of its applicability to both animation (Reynolds, 1987) and control systems (Liu et al., 2003; 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 features seen in collective animal motion including group decision making (Couzin et al., 2005; Conradt and Roper, 2007), information flow (Sumpter et al., 2008) and response to predation (Wood and Ackland, 2007). This article focuses on the development of one-dimensional models that seek to describe some of the simplest observed features in collective motion. Such models are now known collectively as 1D self-propelled particle (SPP) models.

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

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

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

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

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

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

52 2. SPP Models

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

$$u_i(t+1) = G(\langle u(t) \rangle_i) + \xi_i, \quad (1)$$

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

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

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

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

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

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

112 **3. Modelling approach**

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

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

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

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

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

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

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

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

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

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

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

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

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

149 In our model individuals react deterministically to the positions and mo-
 150 tion of randomly selected neighbours. In previous work (Huth and Wissel
 151 , 1992), it has been suggested that interactions with single individuals are
 152 not able to mimic the properties of animal collective motion in the same
 153 way as averaging over a number of individuals. However, viewed over time-
 154 scales larger than Δt , our algorithm is qualitatively equivalent to reacting in

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

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

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

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

182 4. Model analysis

183 4.1. Coherence and direction switching

184 Here we show that our model preserves the interesting emergent be-
185 haviours previous models have found. We do not present a complete analysis
186 of the behaviour of our model. Rather, we focus on experiments which illus-
187 trate that our model produces coherent groups in which individuals do not
188 diffuse over long simulations and that our way of including noise results in
189 a phase transition from an ordered to a disordered state of simulated groups
190 for increasing noise and therefore that we are recovering previous results.

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

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

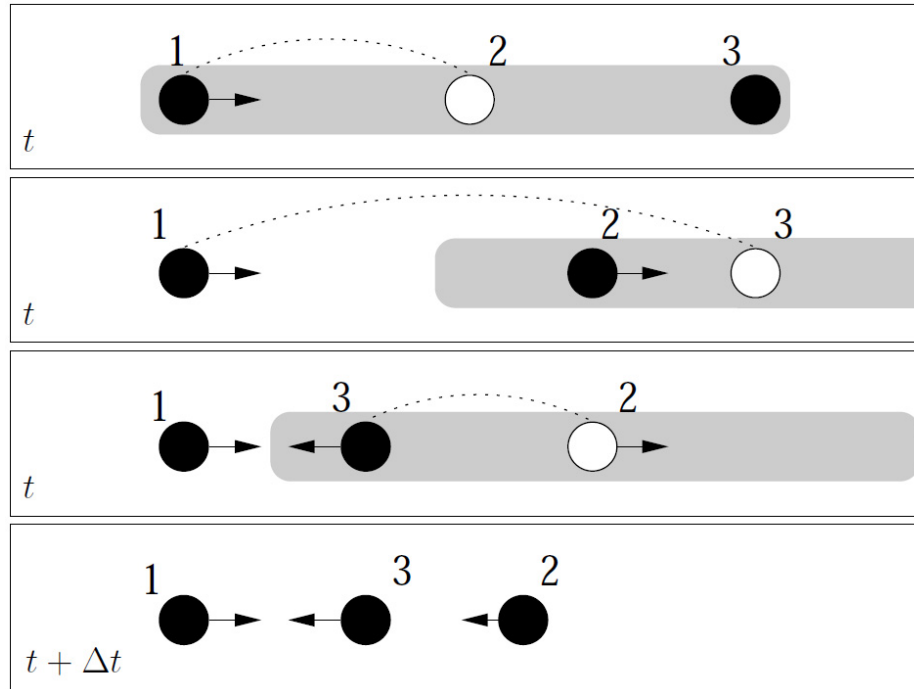


Figure 1: Schematic illustration of an example for one update step Δt of our model for $N = 3$ (top to bottom). The grey areas indicate the extent of r_O for updating individuals (in white) and the arrows show the direction of motion of the particles. Particles without arrows have zero instantaneous 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 Δt .

204 More commonly particles are assigned random initial velocities in simula-
 205 tion studies (Czirók et al., 1999; O’Loan and Evans, 1999; Raymond and
 206 Evans, 2006; Buhl et al., 2006). We chose our initial conditions to ensure
 207 that groups would not fragment within the first few time-steps of the sim-
 208 ulations. Long simulated time intervals before recording started (typically
 209 100,000 time-steps) ensured that no initial transitional data was used in our
 210 results.

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

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

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

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

254 can only be understood as a an indicative approximation of the model's be-
255 haviour. In combination with our initial conditions the case $r_A = r_O$ leads
256 to a collective which moves in one direction, but diffuses as a result of the
257 asynchronous updating scheme. For larger r_A the groups quickly stabilise
258 and show a distinctive divide between an ordered and a disordered phase for
259 small and large values of Δt respectively.

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

270 *4.2. Coarse-grained behaviour*

271 The coarse-grained behaviour of a system can often be described in terms
272 of a small number or even single “coarse” variables. In some cases it is
273 possible to construct a “coarse-grained” model which accurately captures the
274 temporal development of these variables (Erban et al., 2006; Kolpas et al.,
275 2007; Yates et al., 2009).

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

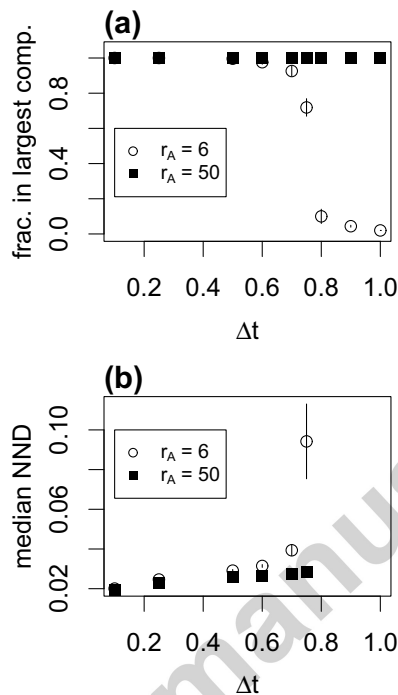


Figure 2: Coherence of simulated groups. Individuals within r_A of each other are considered to be connected. Components are defined as sets of individuals which are connected to each other either directly or via other individuals. If there is one component, all individuals are in the same group. (a) 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 Δt 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 Δt . The NNDs increased with increasing values of Δt . 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 $T = 1$.

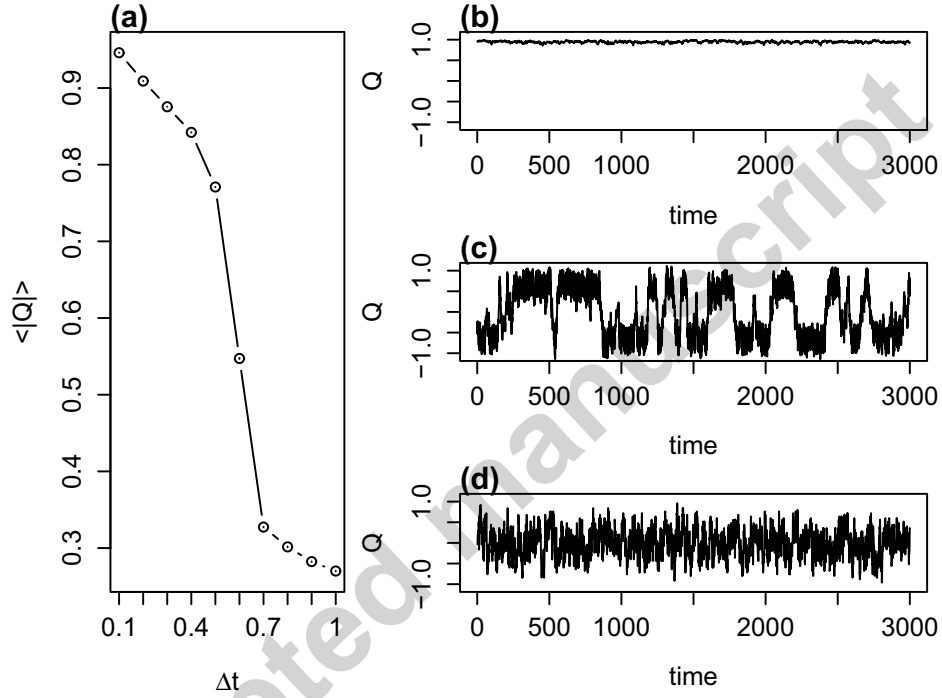


Figure 3: (a) $\langle |Q| \rangle$ as a function of Δt (mean over 5 replicas, error bars are smaller than the symbols). Parameters are as in figure 1 but $N = 50$ and $r_A = 50$. (b)-(d) illustrate direction switching in the simulations of our model, where $\Delta t = 0.1$ (b), $\Delta t = 0.6$ (c) 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.

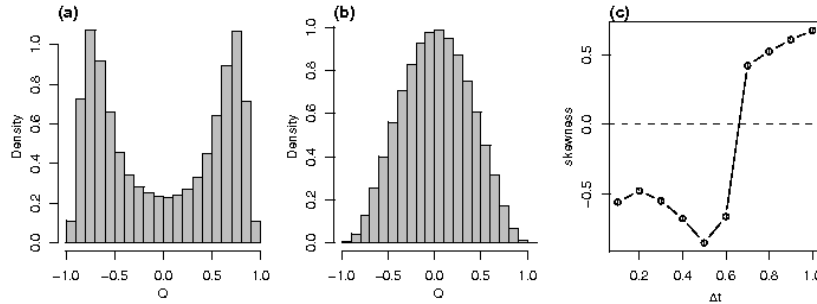


Figure 4: Distribution of Q for different values of Δt over 400,000 time-steps (T) at the end of 10 million time-steps. (a) $\Delta t = 0.6$, the particles switch direction occasionally and the group is mostly well aligned (high values of Q). (b) $\Delta t = 0.9$, the group is not well aligned and Q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

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

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

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

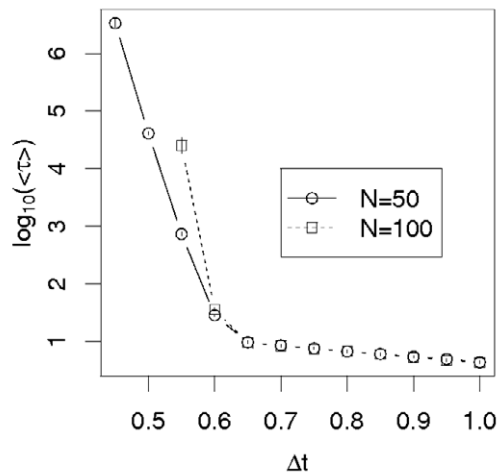


Figure 5: Average reversal times for simulated flocks for varying Δt . The quantity $\langle \tau \rangle$ is the average time for which $\text{sgn}(Q)$ remains unchanged. We collected 1000 values of τ for 10 replicas of each parameter combination. Error bars show one standard deviation from the mean.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

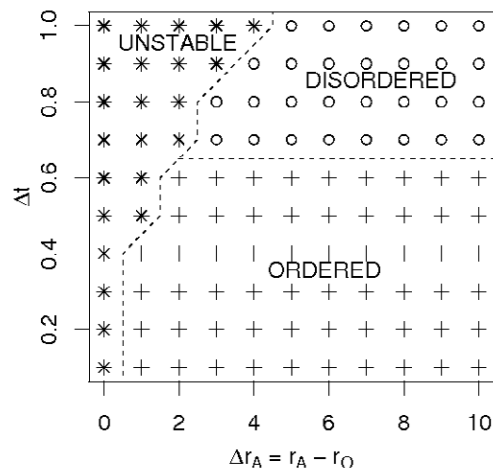


Figure 6: Phase diagram for simulations over 10 million time-steps. Groups were considered to be unstable if at some stage during the simulation at least one particles had no neighbours (i.e. no particles within r_A). The ordered state was defined by a negatively skewed distribution of $|Q|$. The behaviour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

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

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

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

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

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

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

347 5. Discussion

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

358 For our model it is important to maintain a clear separation between algo-
359 rithmic implementation and biological interpretation. We do not claim that
360 updates in our model translate directly into interactions between individuals.
361 The length of update-steps, encoded in the size of Δt , does not explicitly re-
362 late to biological or neurological reaction times of animals. Furthermore, the
363 instantaneous positions and movement of individuals on time-scales close to

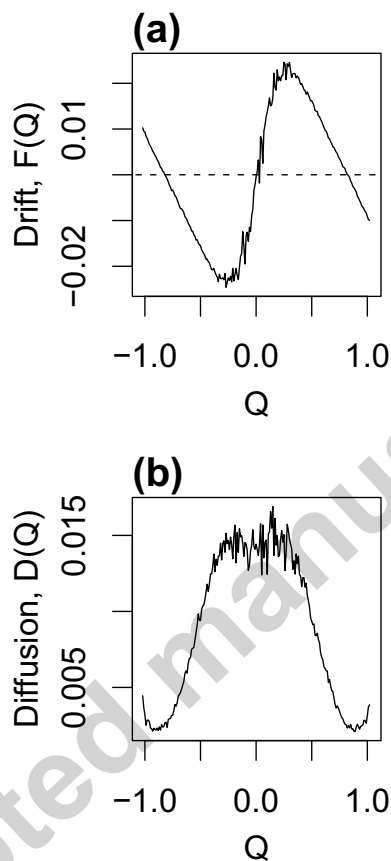


Figure 7: Equation-free analysis of our model. $L = 90$, $N = 30$, $r_A = 6$, $r_O = 5$, $T = 1$ and $\Delta t = 0.5$. All parameter values were chosen as close as possible to the ones by Yates and coworkers and otherwise to produce a similar coarse-grained behaviour to the locust data (Yates et al., 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.

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

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

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

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

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

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