

# Inherent noise can facilitate coherence in collective swarm motion

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**Among 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 and other models of group motion. Comprehending the factors that 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 self-propelled particle model assuming an underlying one-dimensional Fokker–Planck equation for the mean velocity of the particles. We continue with this assumption in analyzing experimental data on locusts and use a similar systematic Fokker–Planck equation coefficient estimation approach to extract the relevant information for the assumed Fokker–Planck equation underlying that experimental data. In the experiment itself the motion of groups of 5 to 100 locust nymphs was investigated in a homogeneous laboratory environment, helping us to establish the intrinsic dynamics of locust marching bands. We determine the mean time between direction switches as a function of group density for the experimental data and the self-propelled particle model. This systematic approach allows us to identify key differences between the experimental data and the model, revealing that individual locusts appear to 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 behavior, inferred by using the Fokker–Planck equation coefficient estimation approach, can be implemented in the self-propelled particle model to replicate qualitatively the group level dynamics seen in the experimental data.**

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

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 experimental 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 (4, 5). We are left with a multitude of models, all of which seem to relate to the available experimental data, but none of which provide clear predictive power.

One approach to the problem of linking experimental data to model behavior is the detailed study of the local interactions between animals. This approach has yielded better understanding

of the rules that govern the interaction of fish (6, 7) and birds (8, 9). However, establishing these rules is technically difficult because 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, 10–12). 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 (10). 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 2 or 3 h, 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 travelled in the same direction for the 8-h duration of the experiment. The group property of average velocity/alignment (as it will variously be denoted throughout the rest of this article) of the locust experiments was previously modeled by a 1-dimensional self-propelled particle (SPP) model similar to that in ref. 13. In a manner analogous to the experiments in ref. 10 this model also exhibits spontaneous direction switching where “particles” rapidly change alignment.

In this article we investigate directional switching in a SPP model and in our experimental data of the motion of locusts. A coarse-grained model characterizes the behavior 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 behavior of individual locusts. If such a model is explicitly available we can apply relevant 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 initialized computational experiments to estimate 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

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Eq. 9, both plotted as solid lines. The mean switching time can be computed (as in ref. 15) 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 *SI Appendix, Fig. S1C* 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 (Eq. 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 Appendix, section S1*) as

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

### Computer-Assisted Methodology

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 Eq. 7. However, we hypothesize 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 (16, 17) 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 (Eq. 12) for the mean velocity,  $U$ , of the locusts. Following refs. 16 and 18, we approximate

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

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

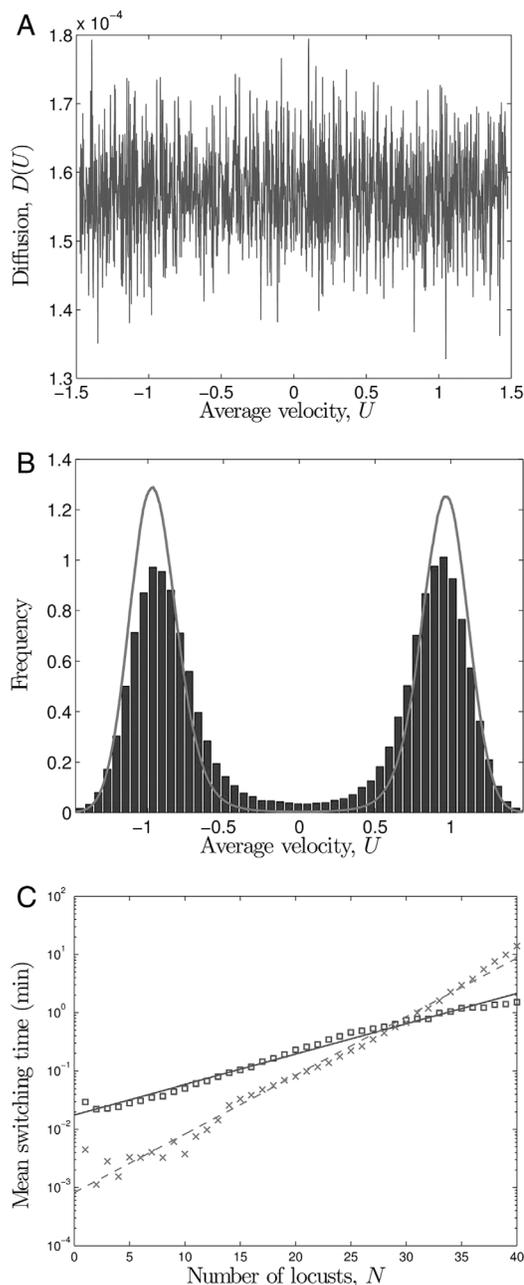
where  $\langle \cdot \rangle$  represents an ensemble average over several, consistently initialized, short replica simulations with the detailed model 1–2.  $\delta t$  is a small number of time steps of the process (typically between one and five) dictated by the timescale on which the coarse-grained Eq. 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 initializing the particles consistently [which is called “lifting” in the equation-free terminology (17)], so that their velocities give a specific value of alignment,  $U$ . We perform a large number of replica simulations (typically 1,000) allowing each one to evolve for a short time period  $\delta t$ . This provides representative averages for the drift and diffusion coefficients of FPE (Eq. 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 *SI Appendix, Fig. S1A* and *S1B*).

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



**Fig. 1.** 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 by using the equation-free technique (crosses with dashed best fit line) and from simulation (squares with full best fit line).

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. 1A to be approximately constant, while the drift coefficient has a characteristic antisymmetric cubic shape, indicative of the symmetric double-welled potential (see *SI Appendix, Fig. S2*). 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. 1*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 by using a modified version of Eq. 10:

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

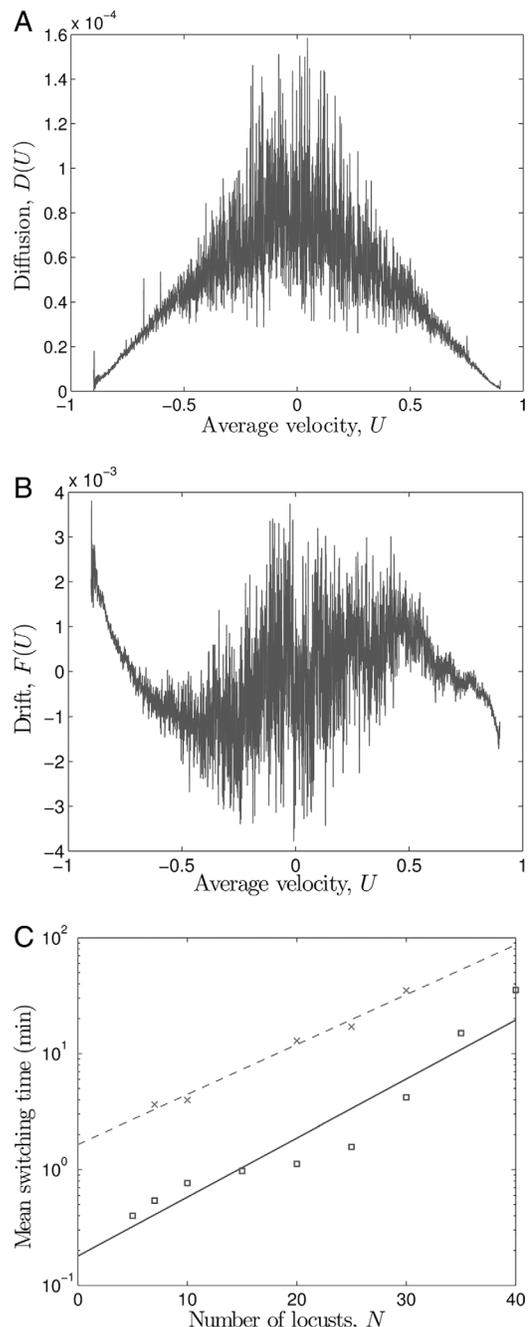
where  $U_-$  and  $U_+$  are the mean velocities at which the two minima of the potential occur. We also established the relationship between mean switching time and  $N$  by counting the switches during a long simulation for the same range of  $N$ . The two methods give similar, apparently exponential, relationships (see Fig. 1*C*).

### Experimental Data

Locusts exhibit dynamic directional switching over a range of different densities. In previously reported experiments (10) we recorded the directional alignment of groups of between 5 and 100 locusts for 8 h. The ring-shaped arena [an annulus with outer radius 40 cm and inner radius 17.5 cm (see *SI Appendix*, section S4)] in which the locusts were placed is analogous to the 1-dimensional domain with periodic boundary conditions used in the SPP model. We can thus use similar techniques to analyze the experimental data as we did with the long-term simulations. However, the equation-free approach (involving many consistent initializations 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 2 h of the experiments the activity of the locusts changed significantly, but in the latter 6 h 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 2 h of each experiment. We collected instances of the same alignment,  $U(t)$  and the alignment,  $U(t + \delta t)$ , a short time,  $\delta t$ , later and used these in Eqs. 13 and 14 to estimate the drift and diffusion coefficients of the underlying FPE. Although experiments were carried out for numbers of locusts  $>40$  there were too few switches in the 6-h interval to provide a meaningful estimate of drift and diffusion coefficients.

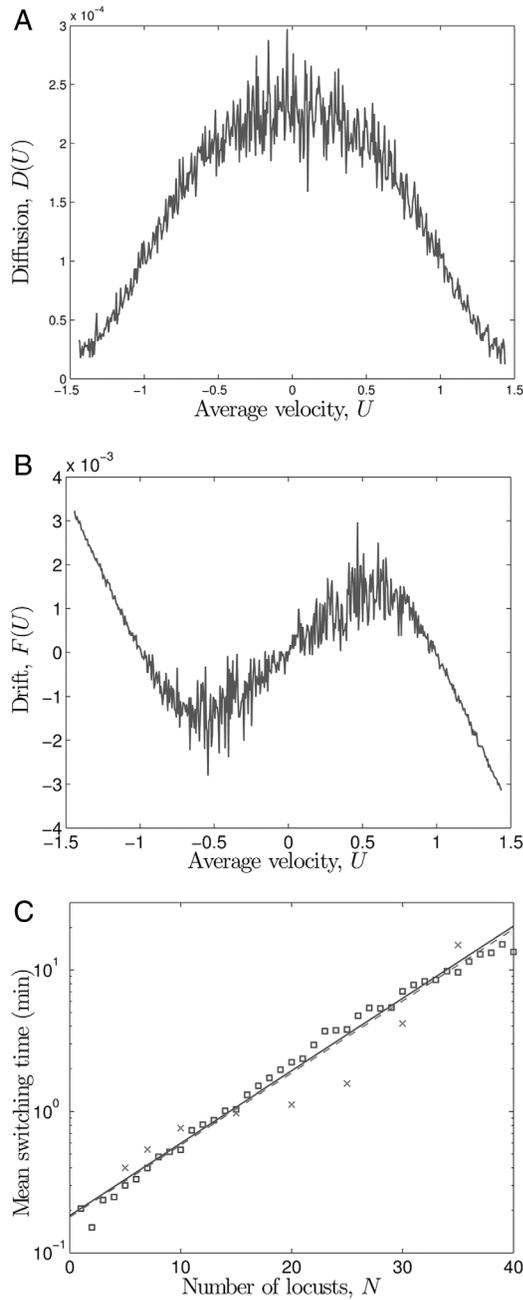
Fig. 2*A* and *B* show the estimated drift and diffusion coefficients of the alignment for the experiment with 30 locusts. The drift coefficient in Fig. 2*B*, although noisy, still has a roughly cubic shape consistent with that estimated for the SPP model. Unlike the SPP model, however, the diffusion coefficient appears to have a quadratic shape, with its maximum at zero alignment. The potential (see *SI Appendix*, Fig. S3), 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. 2*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 ( $\sim 8$  h). 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



**Fig. 2.** Analysis of the experimental data.  $N = 30$  (A and B, only). The diffusion coefficient (A) and drift coefficient (B) estimated by using Eq. 13 with  $\delta t = 4$  s, and Eq. 14 with  $\delta t = 0.2$  s, respectively. The rationale behind these choices of  $\delta t$  is explained in *SI Appendix*. (C) Variation of the mean switching time with the number of locusts, calculated by 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.

for the average velocity,  $U$ , is valid only approximately. Such a discrepancy was already observed when we substituted the toy model (Eq. 5) by model 1–2 (see Fig. 1*C*). In the case of the toy model (Eq. 5) we know that there exists a closed FPE (Eq. 7) and the results are exact, (see *SI Appendix*, Fig. S1*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



**Fig. 3.** Analysis of the revised model.  $L = 90$ ,  $R = 5$ ,  $\beta = 1$ ,  $\omega = 2.6$ ,  $|\bar{u}_i^{\text{loc}}|_{\text{max}} = 1.5$  and  $N = 30$  (A and B, only). The interaction radius was chosen to be consistent with ref. 10 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 favorable comparison with 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.

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.

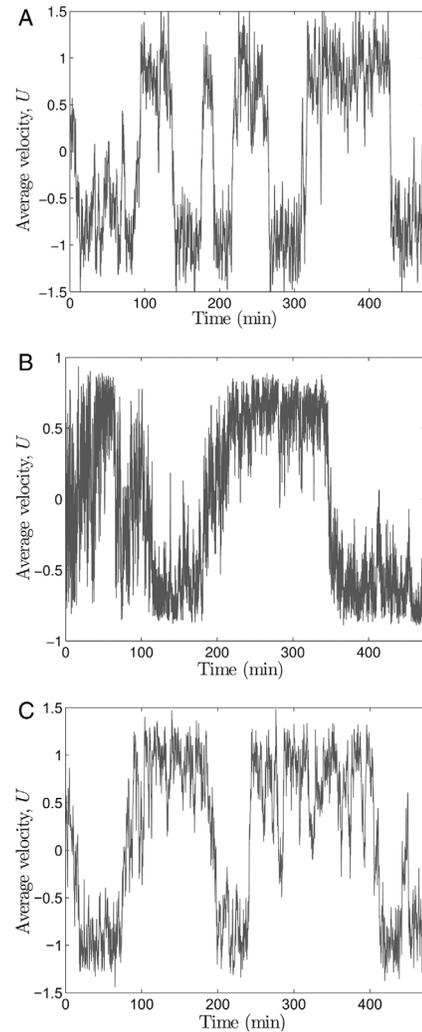
The fact that the diffusion coefficient increases when group alignment is low indicates that the locusts might respond to low

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  $\eta(\bar{u}_i^{\text{loc}})$  (multiplying the uniform random variable,  $\Delta Q$ , in the velocity update Eq. 2) to be unity, we chose it to be a nontrivial function of the local mean velocity,  $\bar{u}_i^{\text{loc}}$ , specifically,

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

where  $|\bar{u}_i^{\text{loc}}|_{\text{max}}$  is the maximum of the absolute value of the mean local velocity; for this choice  $\eta(\bar{u}_i^{\text{loc}})$  does not become negative. We specifically chose this functional form for  $\eta$  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 Appendix*, section S5).

In Fig. 3A the quadratic nature of the effective diffusion coefficient is recovered by the refined model. Qualitatively, the potential of the new model compares favorably with the potential of the actual experimental locust data (see *SI Appendix*, Figs. S3 and S4).



**Fig. 4.** Typical evolution of the average velocity,  $U$ , for the original model (A), the actual locust data (B), and the revised model (C).  $N = 30$ ,  $L = 90$ ,  $R = 5$ ,  $\beta = 1$ ,  $\omega = 3.9$  (A and C, only) and  $|\bar{u}_i^{\text{loc}}|_{\text{max}} = 1.5$  (C, only). In A and C, we have used an altered value of  $\omega$  and a rescaled time axis to better illustrate the similarities and differences between the models and the experimental data.

A further useful validation of the revised model is that the mean switching time is significantly increased for all values of  $N$  in comparison with the original model [compare the simulation-derived mean switching times (squares with the full best fit lines) in Fig. 1C with Fig. 3C]. 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. 4. The transitions between ordered states in the original model are very sharp (see Fig. 4A), whereas the transitions for the experimental data are relatively noisy (see Fig. 4B). The noisiness of the transitions appears to be replicated well by the revised model (see Fig. 4C). 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 unique features. First, 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. Second, we used the systematic Fokker–Planck equation coefficient estimation approach on experimental data. Our results indicated that the individuals move more randomly in locust 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 on the behavior of individual locusts from group-level information: we alter individual behavioral 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 modeling, changing the noise term for the individual locusts so that it becomes larger when the alignment is smaller. It should be noted that the randomness in the model does not necessarily mean

that the locusts are making random choices. It could be that there exist underlying small-scale individual interactions that manifest themselves as noise in the individual motion of the locusts at the level of our experimental observation. 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 (19) can provide a rationalization 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 (19), there may be selection pressure on an individual to minimize the time spent in the disordered phase. A longer interswitch 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 (7, 20–22). Noise in response to lost alignment may be an example of a general property of organization of collective motion. Another example is found in traffic-jam models where one way of avoiding “phantom traffic jams” is to introduce additional noise to traffic motion (23–25).

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

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