**Stochasticity may generate coherent motion in bird flocks**

Andy M. Reynolds

*Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK*

**Abstract** Murmurations along with other forms of flocking have come to epitomize collective animal movements. Most studies into these stunning aerial displays have aimed to understand how coherent motion may emerge from simple behavioural rules and behavioural correlations. These studies may now need revision because recently it has been shown that flocking birds, like swarming insects, behave on the average as if they are trapped in elastic potential wells. Here I show, somewhat paradoxically, how coherent motion can be generated by variations in the intensity of multiplicative noise which causes the shape of a potential well to change, thereby shifting the positions and strengths of centres of attraction. Each bird, irrespective of its position in the flock will respond in a similar way to such changes, giving the impression that the flock behaves as one, and typically resulting in scale-free correlations. I thereby show how correlations can be an emergent property of noisy, confining potential wells. I also show how such wells can lead to high density borders, a characteristic of flocks, and I show how they can account for the complex patterns of collective escape patterns of starling flocks under predation. I suggest swarming and flocking do not constitute two distinctly different kinds of collective behaviour but rather that insects are residing in relatively stable potential wells whilst birds are residing in unstable potential wells. It is shown how, dependent upon individual perceptual capabilities, bird flocks can be poised at criticality.

Tel: +44 (0)1582 763133

Fax: +44 (0)1582 760981

Email: [andy.reynolds@rothamsted.ac.uk](mailto:andy.reynolds@rothamsted.ac.uk)

PACS 87.23.Ge - Dynamics of social systems

PACS 05.10.Gg – Stochastic analysis methods (Fokker-Planck, Langevin etc.)

**Keywords** flocking, collective animal movements, intrinsic noise

**1. Introduction**

Recently it has been found that flocking birds, like swarming insects, behave on the average as if they are trapped in elastic potential wells [Reynolds et al. 2022]. This can be attributed to the fact that flock cohesion may result from information exchange based on the projected view of each individual out through the flock [Pearce et al. 2014]; solid angles decrease as inverse-square power laws and averaging over such power laws results in a central attraction that increases with distance from the flock centre if the solid angles induce proportionate accelerations [Ramsey 1981]. The shapes of these potential wells fluctuate over time partly because of the limited number of individuals in the groupings and partly because of the nonuniformity in their spatial distributions. Here I show how such changes can account for four seemingly disparate observations: the emergence of coherent movement patterns which is the most beguiling feature of flocking and one that is frequently characterized by scale-free correlations [Ballerini et al. 2008a,b, Bialek et al. 2012, Cavagna et al. 2010, 2013, Ling et al. 2019a,b, O’Coin et al. 2022]; the nearly lossless propagation of global turning behaviors of starlings [Procaccini et al. 2011, Attanasi et al. 2014]; the presence of high density borders which may be of considerable biological importance but are otherwise poorly understood [Ballerini et al. 2008a, Cavagna et al. 2013]; and the complex patterns of collective escape of flocks under predation [Storms et al. 2019]. The analysis draws heavily on recent advances in the understanding and modelling of the central role played by multiplicative noise in determining the emergent mechanical and thermodynamic properties of insect swarms including, for example, their tensile strength and their equations of state [Reynolds 2019a, 2021a,b]. In contrast with bird flocks, insect swarms do not have high density borders, and under quiescent laboratory conditions are only weakly correlated [Ni and Ouellette 2015]. Nonetheless, *externa*l perturbations can induce correlations in laboratory swarms, just as they might do in wild insect swarms which must contend with environmental disturbances [van der Vaart et al 2020].

**2. A new model of flocking**

To good approximation the mean accelerations of flocking jackdaws are linear in the distance to the flock centre with a negative slope, indicating a harmonic potential field [Reynolds et al. 2022]. That is,

(1)

where the position *x* is along a principal axis of the flock and where is a frequency. One of the simplest models for the trajectory of a flocking bird consistent with this potential is given by

(2)

where *u* is the velocity of the bird at time *t*, *k* is an effective frictional coefficient (here after and without loss of generality set to unity) and where is a white noise such that and [Okubo et al. 1986]. The first term on the right-hand side of Eqn. (2) is a memory term that causes velocity fluctuations to relax back to their (zero) mean value. The third term, the noise term, represents fluctuations in the resultant internal force. 3-dimensional variants of this model are in close agreement with numerous observations of swarming insects made in the laboratory [Reynolds et al. 2017, Reynolds 2018, van der Vaart et al. 2019, 2020]. Nonetheless, because there are no interactions (correlations) between simulated individuals the model fails to capture the essential feature of flocking, namely coherent motion. This can be overcome by directly incorporating correlations into the stochastic trajectory simulation model, but such models are mathematical complex, and they do not explain how such correlations arise [Reynolds et al. 2022]. Here a different, simpler approach with explanatory capacity is adopted in which the noise contains both additive and multiplicative components so that

(3)

where is a free parameter and where Eqn. 2 now interpreted in the Ito sense. Changes in the overall intensity,, of the multiplicative noise can create new zones of attraction [Okubo 1986, Reynolds 2019a] and thereby induce coherent motion because each simulated bird will respond to these changes in a similar way. Below it is shown that the particular functional form of the multiplicative noise given in Eqn. 3 is consistent with various disparate observations of flocks of jackdaws [Ling et al. 2019a-c] and also starlings [Attanasi et al. 2015, Ballerini et al. 2008a,b, Bialek et al. 2012, Cavagna et al. 2010, 2013, Storms et al. 2019] under the assumption that starlings like jackdaws [Reynolds et al. 2021] are effectively trapped within elastic potential wells. The generality of this correspondence and independent justification for Eqn. 3 are discussed later. Nonetheless, because of the simplicity of the model and because the precise form of the noise is not known, comparisons between model predictions and observations are qualificative rather quantitative.

**3. Results**

It can be shown that the equilibrium density profile of the flock, associated with the noise intensity given in Eqn. 3 is determined by the stationary solution of the non-linear Fokker-Planck equation,

(4)

[Okubo 1986, Reynolds 2019a]. Eqn. 4 has stationary solution

(5)

In the absence of multiplicative noise (i.e., when *F=0*), is Gaussian (corresponding to confinement within an harmonic potential well) but is otherwise non-Gaussian and is broadly consistent with observations of bird flocks (Fig. 1) [Ballerini et al. 2008a,b, Bialek et al. 2012, Cavagna et al. 2010, 2013, Strong et al. 2019]. Relatively small amounts of multiplicative noise lead to high density borders, that are a characteristic feature of bird flocks [Ballerini et al. 2008a]. More generally, the potential for large changes in density is consistent with flocks existing with a wide variety of densities [Ballerini et al. 2008a]. And because the noise (and so the diffusivity) is relatively low at the borders, birds are, in accordance with observations [Cavagna et al. 2013], predicted to stay on the borders longer than internal birds keep their position inside the flock. Furthermore, increases in the overall intensity of the multiplicative noise can lead to ‘flash expansions’ (radial outward movements of the flock), ‘cordon’ formation (two relatively large parts of the flock that are interconnected by a thin string of individuals) and ‘splitting’ of the flock into multiple sub-flocks (Fig. 1). Flash expansions occasionally followed by cordon formation or even splitting characterise the collective escape of starling flocks under predation [Strong et al. 2019Sankey et al. 2021]. The increase in the multiplicative noise giving rise to these behaviours may be driven by cognitive limitations to simultaneously process visual information about the behaviour of the predator and that of other flock members; mirroring observations of guppies (fish) [Kimbell and Morrell 2015]. The model also accounts for the absence of ‘selfish’ herd dynamics in bird flocks under threat [Sankey et al. 2021], i.e., the strength of the central attraction (second term on the righthand side of Eqn. 2) does not depend on the noise level (threat level). The escape responses predicted by the above model were obtained by varying the strength of the multiplicative noise and not by explicitly modelling predators. An alternative model of collective escape is presented in Supplementary Material where the predator is considered explicitly, and noise is additive rather than multiplicative; a model which can accommodate internal sub-structure due to the presence of pair-bonded birds.

It is clear from Eqn. 5 that any change in the overall intensity of the multiplicative noise is predicted to cause the birds to move coherently, as each individual will respond to the change in a similar way. This is supported by the results of numerical simulations using a 2-dimensional form of Eqn. 2 [Reynolds et al. 2021]. Two-point and four-point correlation functions characterizing movements following a change in the overall intensity of the multiplicative noise resemble observations [Bialek et al. 2012] (Fig. 2). Notice that the range of the spatial correlation, as determined by the position of the zero-crossing of the correlation function, is comparable with the flock size. More generally, in accordance with observations [Bialek et al. 2012, Cavagna et al. 2013, O’Coin et al. 2022], the range of the spatial correlation is not constant, but instead scales with the linear size of the flock. This indicates that the behaviour correlations are scale free, i.e., that the birds behave in the same way, irrespective of group size Similarly, because simulated birds will react at about same time, apparent initiators of collective turns will, in accordance with observations of flocks consisting of 4 to196 jackdaws [Ling et al. 2019b], appear to be located throughout the flock and can be far apart from each other. The presence of multiplicative noise can also give the impression of collective turns beginning in the borders of flocks because that is where the largest changes in the shape of the potential well can occur. This occurs, for example when , making the model consistent with very large starling flocks (more than 100 individuals) wherein the first birds that started to turn tended to be on the sides (in elongated tips) of the flocks rather than at the front [Attanasi et al. 2015].

More generally the salient features of quiescent flocks but not the collective responses of flocks to the presence of predators are reproduced by the model whenever the noise intensity decreases monotonically with increasing distance from the flock centre, e.g., when  or when . If, on the other hand, the noise intensity decreases rather than increases with distance from the flock centre then correlations are predicted to be scale-specific rather than scale-free. Note also that by utilizing multiplicative noises of the form, , for example, the above analysis can be readily extended to asymmetric flocks and to flocks with sharp boundaries (i.e., density distributions with finite support). These forms of the multiplicative noise are consistent with flock cohesion resulting from information exchange based on the projected view of each individual out through the flock as advocated by Pearce et al. [2014] (Fig. 3).

Further analysis reveals that the presence of multiplicative noise in the resultant cohesive force that binds together a flock may also benefit discrete pairs of individuals that are tied together by spring-like effective forces, as in the case of flocks of jackdaws, a species that form lifelong pair-bonds [Ling et al. 2019d]. The multiplicative noise is found to enhance the likelihood that the discrete pairs are close together, i.e., it enhances the strength of the spring-like effective forces that bind pairs together.

**4. Discussion**

Coherent motion is a self-evident and beguiling feature of flocking and much attention has been directed at quantifying and understanding the incumbent spatial correlations [Ballerini et al. 2008a,b, Bialek et al. 2012, Cavagna et al. 2010, 2013, Ling et al. 2019a,b]; a facet of flocking that has been directly incorporated into high-level models [Bialek et al. 2012, Reynolds et al. 2022]. Nonetheless, the origin of these correlations has remained elusive, although Charlesworth and Turner [2019] did show how coherent motion can emerge from the intrinsic tendency of individuals to make movements that maximize the number of different visual environments that they are expected to be able to access in the future. Here I showed how coherent motion of the kind that typifies flocking together with other facets of flocking (e.g., high density borders and collective escape from prey) can be attributed to a lower-level principle, namely to global changes in the effective elastic potential wells within which the birds reside [Reynolds et al. 2022]; changes that are induced by fluctuations in the overall intensity of the intrinsic multiplicative noise. In other words, the presence of intrinsic multiplicative noise may have been masking the simplicity that underlies flocking; namely the presence of non-interacting mobile individuals trapped within elastic potential wells. In this picture, distortions of the potential well due to the presence of multiplicative noise appear as a new, economical, unifying principle that underpins key, disparate characteristics of flocking. A picture in which correlations are the result of, rather than the cause of, coherent motion. Scale-free correlations and other salient properties of quiescent flocks [Attanasi et al. 2015, Ballerini et al. 2008a,b, Bialek et al. 2012, Cavagna et al. 2013, Ling et al. 2019a-c, O’Coin et al. 2022] were predicted to arise spontaneously in the presence of multiplicative noises that decrease monotonically in intensity with increasing distance from the centres of flocks. Accounting for collective responses of flocks (splitting and mobbing) due to the presence predators does, however, require either different kinds of multiplicative internal noise or distortions of the potential well by other means [Supplementary Material].

Conversely, the incoherence of quiescent laboratory insect swarms [Okubo 1986, Ni and Ouellette 2015, Puckett et al. 2014] may be attributed to the relative stability of the confining potential well. In this regard, swarming and flocking do not constitute two distinctly different kinds of collective behaviour but rather are a single behaviour with differing noise intensities.

The results reported here complement those of Jhawar et al. [2020] who reported on a distinctly different way in which multiplicative noise can induce collective behaviour and consequently be of fundamental importance to the understanding of collective behaviours. They stand apart from previous works, such as the much-studied Vicsek model [1995], as correlations are a model prediction rather than an assumption. Future work could be directed at further understanding the sensory and cognitive mechanisms that could underpin the putative multiplicative noises, and at understanding how the overall magnitudes of these noises can vary over time. It is possible that some flocks are poised at the cusp of the phase transition, as suggested by Cavagna et al. [2010], since initial analysis suggests that depending on visual make-up of the flock (Fig. 3) and perhaps also the degree of localization [Reynolds 2019], the noise intensity can either increase or decrease with increasing distance from the centre flock, and as a consequence correlations can be either scale-free or scale-specific with the crossover occurring when the noise is purely additive. The analysis may therefore explain why flocks can appear to behave like critical systems (which also have scale-free correlations), poised to respond maximally to environmental perturbations; a phenomenon which until has defied explanation [Cavagna et al. 2010]. . Finally, the analysis reveals that individuals can in principle in bound together by pure noise (Eqn. 5 is localized even when the strength of the potential well vanishes) and thereby provides a new putative mechanism for maintaining cohesiveness that warrants further investigation.

**Acknowledgements**

Rothamsted Research receives grant aided support from RCUK.

**References**

Aarseth, S.J. Direct methods for n-body simulations, in Multiple Time Scales, edited by J. U. Brackbill and B. I. Cohen. Academic Press, Orlando (1985).

Attanasi, A. et al. Information transfer and behavioural inertia in starling flocks. *Nat. Phys.* **10**, 691-696 (2014).

Attanasi, A. et al. Emergence of collective changes in travel direction of starling flocks from individual birds’ fluctuations. *J. Roy. Soc. Int.* **12**, 2015039 (2015).

Ballerini, M. et al. Empirical investigation of starling flocks: a benchmark study in collective animal behaviour. *Anim. Behav*. **76**, 201-215 (2008a).

Ballerini, M. et al. Interaction ruling animal collective behaviour depends on topological rather than metric distance: Evidence from a field study. *Proc. Natl. Acad. Sci. USA* **105**, 1232-1237 (2008b).

Bialek, W. et al. Statistical mechanics for natural flocks of birds. *Proc. Natl. Acad. Sci. USA* **109**, 4786-4791 (2012).

Cavagna, A. et al. Diffusion of individual birds in starling flocks. *Proc.* *Roy. Soc. B.* **280**, 20122484 (2013).

Cavagna, A. et al. Scale-free correlations in starling flocks. *Proc. Natl. Acad. Sci.* **107**, 11865–11870 (2010).

Cavagna, A. et al. Marginal speed confinement resolves the conflict between correlation and control in natural flocks of birds (under review).

Charlesworth, H.J. & Turner, M. Intrinsically motivated collective motion. *Proc. Natl. Acad. Sci.* 116, 15362-15367 (2019).

Gorbonos, D. Long-range acoustic interactions in insect swarms: an adaptive gravity model.

# New J. Phys. **18** 073042 (2016).

Jhawar, J. et al. Noise-induced schooling of fish. *Nat. Phys.* **16**, 488-493 (2020).

Kimbell, H.S. & Morrell, L.J. ‘Selfish herds’ of guppies follow complex movement rules, but not when information is limited. *Proc. R. Soc. B.* **282**, 20151558 (2015).

Ling, H. et al. Behavioural plasticity and the transition to order in jackdaw flocks. *Nat. Comm*. **10**, 5174 (2019a).

Ling, H. et al. Collective turns in jackdaw flocks: kinematics and information transfer. *J. Roy. Soc. Inter.* **16**, 20190450 (2019b).

Ling, H. et al. Local interactions and their group-level consequences in flocking jackdaw. *Proc. Roy. Soc. B.* **286**, 20190865 (2019c).

Ling, H. et al. Costs and benefits of social relationships in the collective motion of bird flocks. *Nat. Ecol. and Evol.* **3**, 943–948 (2019d).

Ni, R. and Ouellette, N.T. Velocity correlations in laboratory insect swarms. *Eur. Phys. J. Special Topics* **224**, 3271-3277 (2015).

O’Coin, D., McIvor, G.E., Thornton, A., Ouellette, N.T., Ling, H. Velocity correlations in jackdaw flocks in different ecological contexts. *Phys. Biol.* (In Press).

Okubo, A. Dynamical aspects of animal grouping: swarms, schools, flocks and herds. *Adv. Biophys.* **22**, 1-94 (1986).

Pearce, D.J.G. et al. Role of projection in the control of bird flocks. *Proc. Natl. Acad. Sci. USA* **111**, 10422-10426 (2014).

Procaccini, A. *et al.*, Propagating waves in starling, *Sturnus vulgaris*, flocks under predation. *Anim. Behav.* **82**, 759-765 (2011).

Puckett, J.G. et al. Searching for effective forces in laboratory insect swarms. *Sci. Rep.* **4**, 4766 (2014).

Ramsey, A.S. Newtonian Attraction. Cambridge University Press, Cambridge UK (1981).

Reynolds, A.M.,SinhuberM. & Ouellette N.T. Are midge swarms bound together by an effective velocity-dependent gravity? *Euro. Phys. J. E* **40**,46 (2017).

Reynolds, A.M. Langevin dynamics encapsulate the microscopic and emergent macroscopic properties of midge swarms. *J. Roy. Soc. Inter.* **15**, 20170806 (2018)*.*

Reynolds, A.M. On the origin of the tensile strength of insect swarms. Phys. Biol. 16, 046002 (2019a).

Reynolds, A.M. On the emergence of gravitational-like forces in insect swarms. *J. Roy. Soc. Int.* **16,** 20190404 (2019b).

Reynolds, A.M. Intrinsic stochasticity and the emergence of collective behaviours in insect swarms. *Europhys. Lett.***44**, 22 (2021a).

Reynolds, A.M. Understanding the thermodynamic properties of insect swarms. *Sci. Rep.* **11**, 14979 (2021b)

Reynolds, A.M., McIvor, G.E., Thornton, A., Yang, P., Ouellette, N.T. Stochastic modelling of bird flocks – accounting for the cohesiveness of collective motion.*J. Roy. Soc. Int.* **19** 20210745 (2022).

Sankey, D.W. et al. Absence of “selfish herd” dynamics in bird flocks under threat. *Curr. Biol.* **31**, 3192-3198 (2021).

Storms et al. Complex patterns of collective escape in starling flocks under predation. *Behav. Ecol. & Sociobio.* **73**, 10 (2019).

van der Vaart et al. Mechanical spectroscopy of insect swarms. *Sci. Adv.* **5**, eaaw9305 (2019).

van der Vaart et al. Environmental perturbations induce correlations in midge swarms. *J. Roy. Soc. Inter.* 20200018 (2020).

Vicsek, T.S. et al. Novel Type of Phase Transition in a System of Self-Driven Particles. *Phys. Rev. Lett*. **75** 1226–1229 (1995).

**Diagram, histogram

Description automatically generated**

**Figure 1 a, b)** **Predicted density profiles and c) their variance as functions of the overall intensity of the multiplicative, F.** In the absence of multiplicative noise, the density profile is Gaussian. As the intensity of the multiplicative noise increases, the density profile gradually develops high density borders before expanding rapidly, forming a cordon and then splitting. Predictions were obtained from Eqn. 5 with (for illustrative purposes) and with all other parameters set to unity. Predictions shown in a) unlike those shown in b) are generic and arise when the multiplicative noise decreases monotonically with increasing distance from the centre of the flock. Justification for being comparable with the flock size can be found in Fig. 3.

Chart

Description automatically generated

**Figure 2 Predicted velocity correlations as the flock expands in response to an increase in the intensity of the multiplicative noise (expansion of the potential well).** Predictions were obtained using a 2-dimensional (polar) form of Eqn. 2 for a flock containing 100 birds with a Gaussian density profile with unit variance and with Gaussian velocities with mean zero and unit variance (i.e. with all model parameters set to unity) [Reynolds et al. 2022]. The flock initially had a Gaussian density profile with variance 1/4**.** Predictions are shown for the longitudinal (parallel to the mean velocity) and perpendicular components of velocities, and where the average is formed over all pairs of birds *ij* with separation *r*. Also shown are smoothed predictions for the four-point correlation where the average is founded over all quadruplets of birds ijkl; with separation . Similar predictions (not shown) are obtained when the flock initially had a Gaussian density profile with variance 2, i.e., as the flock contract in response to a decrease in the intensity of the multiplicative noise. Although these correlations are small they are nontrivial and extend across the entire the flock. Note that if the equilibrium density profile is always maintained because it changes sufficiently slowly (rather abruptly as above) then it is readily shown that a change in variance, , of a flock with a Gaussian density profile induces a mean flow [Reynolds 2017]. More generally, there is a net flow into (out of) regions where the probability density is increasing (decreasing); resulting in correlations.

**Chart, histogram

Description automatically generated**

**Figure 3 a) Predicted elastic well potentials and b) multiplicative noises resulting from information exchange based on the projected view of each individual out through the flock, as advocated by Pearce et al. [2014].** It is assumed that birds accelerate towards neighbouring birds. The magnitude of these accelerations is taken to be proportional to solid angles which decrease as a softened inverse-square power law, with softening parameter a.u. Th softening parameter is used prevent the development of analogously large accelerations in simulations of gravitational-like systems [Aarseth et al. 1985]. Ensemble average resultant accelerations and root mean square accelerations are shown as a distance from the centre of the flock. The ensemble consists of 100 flocks each containing 100 birds randomly and uniformly distributed within a circle of radius 10 a.u. Predictions are shown for birds with equal sized silhouettes (solid lines) and for birds in one hemisphere appearing to be twice as large as those in the other hemisphere perhaps mimicking localized coherent motions, i.e., mimicking hemisphere specific flight orientations or banking angles (dashed lines). The former is consistent with the behaviour of unperturbed swarms of the non-biting midge *Chironomus riparius* [Reynolds 2019] and is predicted to result in scale-specific correlations (see main text). The later resemble the modelled multiplicative noise term, Eqn. 2 which has a local maximum at the centre of the flock and two minima in the outskirts. Results do not change significantly after accounting for adaptation following the approach of Gorbonos et al. [2016].