

# 1 **Chapter 11: Conclusions**

2 The progress through coming together, information transfer, decision-making, moving  
3 together, synchronisation, structures, regulation to complicated individuals is one of  
4 increasingly complex aspects of collective animal behaviour. Each chapter has  
5 attempted to unify group behaviour of different species in these different situations and  
6 explain similarities in the underlying function and mechanisms. I will close this book with  
7 a brief discussion of how I believe that we should think of the science of collective  
8 animal behaviour and suggest some future directions for research.

## 9 **11.1 From toys to tools**

10 This book grew from a review article I wrote three years ago on 'principles of collective  
11 animal behaviour' (Sumpter 2006). There I outlined several guiding principles such as  
12 'positive feedback', 'individual variation' etc. which underlie many aspects of  
13 collective animal behaviour. These principles have again appeared at many points  
14 within this book.

15 Having a set of such principles is useful for grouping and categorising ideas and more  
16 quickly understanding new systems. Here, I have chosen a slightly different grouping of  
17 ideas under the different chapter headings, concentrating more on similarities between  
18 systems in spatial or temporal organisation. Again, these chapters provide a way of  
19 unifying our understanding of different systems.

20

21 Another way of unifying different systems is through mathematical modelling. One of  
22 the most remarkable features of the study of collective animal behaviour is the  
23 applicability of mathematical models. This is made all the more remarkable when we  
24 consider that animals are not as simple as physical particles. Individuals vary and  
25 experiments always involve intrinsic variation and noise. Despite, and sometimes  
26 because of this variation, it is possible to use one model to make predictions about very  
27 different types of groups.

28

29 Unifying principles are not however the be all and end all of science. In the 2006 article  
30 and now, I advocate a pragmatic view to unifying theories of collective behaviour. The  
31 study of collective animal behaviour should proceed on a case-by-case basis. For each  
32 particular system, we should classify how individuals interact with each other and build  
33 mathematical models based on observations. In many cases, models of one system  
34 may be applicable to other systems and this can help us understand the underlying  
35 mechanisms. This similarity between models should not in itself become the driving force  
36 in our research.

1

2 Instead, I see mathematical models and different theoretical approaches as a tool set  
3 for understanding a wide variety of systems. No single mathematical model provides a  
4 unique correct way of describing all aspects of a particular system. Neither can we  
5 expect to apply the same model to all systems. The art of understanding the world is not  
6 in mastery of particular models but in an ability to recognise and exploit connections  
7 where they exist.

8

9

10 It is for this reason that neither mechanistic nor functional approaches to group  
11 behaviour can claim precedence over the other. Both of these approaches have  
12 produced elegant models, which have been tested against experiments and suggest  
13 new ways in which systems can be viewed. In this book, I have emphasised the  
14 combination of functional and mechanistic approaches. Even if particular studies are  
15 likely to be more or less biased to either the functional or the mechanistic, it is important  
16 to bear in mind how the other approach can play a role in increasing understanding.

17

18 The idea that mathematical modelling has a role to play in understanding complex  
19 systems is not new. The last 30 years has seen the rapid growth of complexity science,  
20 the application of non-linear mathematics, statistical physics and the theory of networks  
21 to understanding biochemistry, biology and sociology. In many cases these models are  
22 'toy models' of systems. The Kuramoto model, self-propelled particles, the logistic  
23 equation, self-organised criticality, small world networks, voter models, preferential  
24 attachment, to name just a few, are ideas which are less inspired by details of particular  
25 systems and more an attempt to abstract from details and make general predictions  
26 about a wide range of systems.

27

28 In my opinion, the aim of complexity science today should be to move from these toy  
29 models towards a set of tools that can be applied to specific complex systems. Without  
30 a clear relationship to biological or sociological systems the role of toy models is limited.  
31 Or to put it more bluntly, as a biologist colleague once told me as I was trying to explain  
32 one such model to him, "leave your toys at home, we're trying to work here".

33

34 The models applied in this book are not just toys used to train our intuition before we get  
35 to work on the real thing. They are the tools of a serious approach to understanding

1 specific systems. From models of animal group size distributions; through cockroach,  
2 honey bee and ant emigration; to the collective motion of insects, birds and fish; to the  
3 structure of ant trails and termite nests, the interplay between experiment and model is  
4 clear. The models bring rigour to our assumptions about a system, make testable  
5 predictions and in many cases provide a quantitative as well as a qualitative match to  
6 the available data.

7

8 It is the combination of the relative sophistication of the individuals of which animal  
9 groups are composed and the empirical success in using mathematical models to  
10 predict and understand their behaviour, which makes the study of collective animal  
11 behaviour important. Despite the seeming complexity of the task of understanding  
12 social interactions, we do have tools that allow us to predict experimental outcomes.  
13 This should give hope to applications of similar methods in understanding ecosystems,  
14 brain function and other complex systems.

15

16 There is, of course, no clear cut distinction between toys and tools. Often a toy model  
17 based on very little experimental insight can serve as a basis for a more rigorous and  
18 detailed argument when fleshed out. Indeed, models of animal aggregations started  
19 as toy models of particle cohesion and self-propelled particle models of animal motion  
20 started as animations for computer games!

21

22 The important question is how to get the balance right between simplifying assumptions  
23 and biological detail. I believe the key to getting this balance right is as follows: one  
24 should concentrate on models that make predictions about a system which are both  
25 non-trivial and testable. Non-trivial means that the model is needed to make the  
26 prediction. We cannot simply arrive at the same conclusion by verbal argument alone.  
27 Here the rigour brought by mathematical modelling is important. Often the problem  
28 with verbal arguments is not that they cannot be used to make a particular prediction,  
29 but rather that verbal arguments can be made for all sorts of different predictions. It is  
30 determining which prediction follows from a set of well stated assumptions which is non-  
31 trivial and is the tool provided by mathematical modelling.

32

33 The work described in this book is testimony to the fact that ideas like self-organisation,  
34 emergence, complexity theory are not just fancy sounding names, but can be applied  
35 to make non-trivial and testable predictions about biological and sociological systems.

1 For this reason, scientists in all fields should be interested in collective animal behaviour  
2 and mathematical modelling of complex systems in general.

3

## 4 **11.2 Some open questions**

5 There are many open and interesting questions in collective animal behaviour. I have  
6 mentioned many of these during the course of the book, but it is worth listing some of  
7 them here for further consideration.

8

9 **Linking mechanisms and function in group size distribution (section 2.9).** While Niwa's  
10 model appears to provide a good empirical fit to data on fish schools and may be  
11 extendable to other animal groups, it does not include functional considerations. An  
12 interesting question is how individuals manipulate the average group size they  
13 experience, the key parameter in Niwa's model.

14

15 **How humans integrate many wrongs (sections 3.5 & 4.4)** The Milgram and Asch  
16 observations and experiments on humans reveal that humans use quorum-like rules to  
17 decide whether to copy the choices of others. It would be interesting to investigate  
18 these ideas in a context where there is a reward to be gained by making correct  
19 choices. Here, laboratory experiments, similar to those performed to investigate the  
20 prisoner's dilemma and other co-operative games in humans, could be used.

21

22 **Modelling realistic motion of bird flocks and fish schools (sections 5.2-5.4).** Many of the  
23 'mesoscopic' features of moving animal groups are not reproduced by current self-  
24 propelled particle models. The main restriction here is the availability of empirical data  
25 on the structure and dynamics of moving animal groups. It is currently difficult to  
26 quantify why the models are not quite right. Recent empirical work on starlings is  
27 beginning to provide this data, but it remains an important challenge in an area where  
28 so much theoretical modelling has already been done.

29

30 **Evolving self-propelled particles (section 5.7).** The Wood et al. model of how predation  
31 avoidance evolves is just one example of how natural selection might influence  
32 collective motion. One possibility is that natural selection acts to increase the  
33 complexity of group motion, so that the group is highly sensitive to changes in the  
34 environment (Sumpter et al. 2008a).

1

2 **Individual variation (sections 4.3 & 6.1).** Many of the models of collective behaviour  
3 assume that individuals are identical units, but the many wrongs idea and Kuramoto's  
4 model of synchronisation instead make predictions on the basis of differences between  
5 individuals. There are consistent differences between animals in their behaviour and a  
6 research challenge is to understand how these differences are integrated at the level  
7 of the group. Instead of seeing individual differences as simply 'noise' we should  
8 investigate their role in producing collective patterns.

9

10 **Modelling complex nest structures (section 7.3).** Although several models have  
11 explained formation of pillars and chambers via templates and stigmergy, how the  
12 complex structures such as harvester ant nests (figure 7.5) are constructed remains an  
13 open problem.

14

15 **Providing a useable formal framework for individual-based modelling (section 9.5).** One  
16 of the weaknesses of the individual-based approach to modelling is that because they  
17 are not expressed in a formal framework individual-based model results can be difficult  
18 to reliably replicate. The problem is agreeing on a tool for individual-based modelling  
19 and designing one that is flexible enough to encompass different types of models.

20

21 **Collective human behaviour (sections 3.5, 6.1 & 7.5 and chapter 8).** While there is a  
22 growing application of mathematical models to understand the social behaviour of  
23 humans, I would continue to classify many of the models as toys rather than tools. The  
24 studies discussed throughout this book are notable exceptions and other recent studies  
25 using network analysis to look at social interaction on, for example, the internet are also  
26 beginning to use data to inform models. The possibility for rigorous application to data  
27 on human social interactions is clear. It will be interesting to see how types of  
28 techniques used in studying collective animal behaviour can be applied in studying  
29 humans.

30

31

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