Notes and commentary on *Self-Organization in Biological Systems*

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Contents

Chapter 1

What this book is about

This book is a compilation of my notes and comments on the book 'Self-Organization in Biological Systems' (Camazine et al., 2001).

Chapter 2

1. What is Self-Organization

- Self-organised ≈ de-centralised phenomena

- 'Self-organizationg is a process in which pattern (sic) at the global level of a system emerges solely from numerous interactions among the lower-level components of the systemn. Moreover, the rules specifying interactions among the system's components are executed using only local information, without reference to the global pattern.'

  - Not an original thought :p, but the word 'global' made me realise how much of anthropogenic climate change was originally caused by a tragedy of the commons type situations. In the tragedy of the commons, each individual player harms public goods with more benefit for himself, while damaging the sustainability of the common resource – without centralised control or command. In the absence of centralised regulation, this self-organised behaviour actually leads to unsustainable resource use!

- 'The terms *chaos* and *dissipative stuctures have precise scientific meanings that may differ from popularized definitions....*' : the authors discuss complexity, without discussing either chaos or dissipative structures. I had never heard of the term 'dissipative structure' and this is my attempt at explaining it (Notes from (Prigogine and Nicolis, 1971)):

  - in physical systems, objects at 'equilibrium' are assumed to generally lack structure (eg. two liquids in a contained will diffuse until there is a uniform mixture). Lowering the temperature in general promotes the appearance of order/structure (eg. ice formation).

However, lowering temperature need not be the only way to achieve order/structure.

– Order/structure can also result from systems that are far from equilibrium and are being *kept* away from it. The *Bénard flow* - where an oil layer heated from below forms hexagonal lattices. The lattices are formed through the action of convection, viscous and heat dissipation. These 'dissipative systems' thus form structures far from equilibrium because of the interaction of multiple processes.

- The 'ocular dominance stripes' shown in Figure 1.2e caught my sustained attention. While I may have come across this pattern in my undergrad, I never noticed how the black and white strips actually code for cortical regions that prefer one eye or the other! The patterns indicate stable regions of the visual cortex that preferrably fire to inputs from either eye. Reading up at (Calabrese, 2009) pointed out that the combination of a few phenomena may result in stripes:

    – cortical neurons that are connected to each other and are locally excitatory but inhibitory over longer ranges
    – Hebbian synapses (synapses that trigger more firings grow in strenght/connection)
    – similar/spatially patterned neural activity from the neurons coming into the cortex (from the eye)

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Chapter 3

2. How Self-Organization Works

- *"Most self-organizing systems use positive feedback"* - I wonder which systems are driven by negative feedback. As stated in the chapter, positive feedback tends to promote change, while negative feedback tends to suppress it. Can't think of any systems myself - I wonder which examples the authors had in mind..?
- *"Exhaustion or consumption of the building blocks is often an important mechanism for limiting positive feedback."* : as mentioned later in the chapter - termite/ant construction is a case where the 'building block' is an external exhaustible resource. In the case of social spiders (genus *Stegodyphus* & *Anelosimus*), web construction through silk investment is an energetically demanding resource, in the same vein, honeybee cells are also constructed by the use of the wax secretions (wonder how energy intensive wax production is).
- *"Signals are stimuli shaped by natural selection specifically to convey information, whereas cues are stimuli that convey information only incidentally."* : in the case of group echolocation an individual echolocator in a group is faced with lots of incoming sounds that may/not be relevant. I was wondering about two situations:
    1. The 'own' echoes are the *signal* while the echoes from other bats are potentially 'cues'. The others' echoes potentially inform the bat of the direction in which objects are, even though they don't necessarily provide distance/other information.
    2. The 'own' echoes the *signal*, while the calls of other bats are *cues*. The calls of other bats provide clear information about where neighbours are located, and this can be used to avoid colliding into them.
- *"In coordinating their movements in a school, fish use both positive and*

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negative feedback mechanisms": in the list of references I found (Huth and Wissel, 1992) who simulated schools of fish. Here are some notes from the paper:

- It looks like simulations of fish schools go back all the way to 1976!
- This paper assumes that there is no leader, and that fish in a group do not have access to any 'centre-of-mass' type quantity. Also that all members of a group follow the same 'rules'
- The authors propose a 'zonal model' and cite Aoki 1982, much like that in (Couzin et al., 2002) - somehow I didn't realise zonal models were a relatively established concept even in the 70's and 80's.
- Authors investigate two types of models - the 'D' model and 'A' model. In the D-model individuals react by prioritising the information from a few of the neighbours, in the A-model individuals averages information from all neighbours in its vicinity
- The A-model seems to mimic the behaviour of fish schools better than the D-model.

Chapter 4

3. Characteristics of Self-Organizing Systems

- The starting line of the first subsection 'The multiplicity of interactions...' is a really loaded sentence - could have been written in a simpler way.
- Bifurcation, or a sudden transition between states caused by small parameter changes is discussed as a characteristic of self-organising systems. The logistic growth equation is discussed. This here is my attempts at exploring the dynamics.
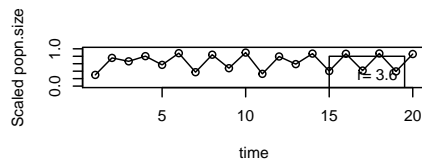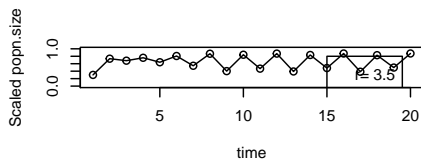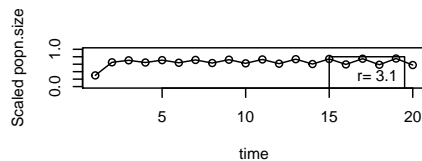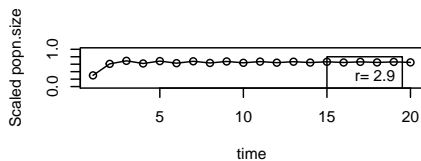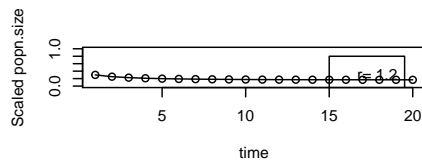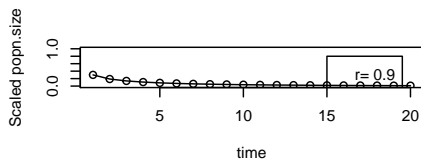
- On Figure 3.1: I didn't know stingless bees built such intricate nests. Makes me wonder whether the nests of the Indian stingless species have been investigated. The amount of detailed observations and photos in Chapter 3 of 'Stingless Bees' (Ed. Grüter,C. Springer) is preety fascinating.

- About the *Dendroctonus* beetle larvae example. The aggregation is weak when the density of larvae is low, but is very strong when the density is increased. The authors write *'The experiments demonstrated a simple emergent property–a cluster–in a group where the individuals initially were homogeneously distributed. At a certain density of larvae, the system spontaneously organizes itself'* : the formation of a single cluster is perhaps a 'new' form of organisation, but the formation of smaller clusters had already happened at lower densities. Where is the 'spontaneous organization' here - not sure. This example would make sense if in general there were small clusters formed until a particular threshold, where no matter the density only one big cluster forms. Perhaps this is what is actually known in reports?

- The idea of biological systems being 'tuned' by evolution to lie near bifurcation points is interesting. I'm kind of getting the hang of it now after playing around with the logistic equation model. Small changes in behavioural/morphological/physiological parameters could have much larger consequences at the collective/group level

- *'In many real-world systems, especially those in biology, it is difficult to control parameter values precisely enough to reveal such abrupt bifurcations..'* - true that! Moreover, the measurement error + field conditions etc. complicates parameter estimation - even if we know the exact dynamics underlying the phenomenon.

- About Figure 3.2: the interpretation of the bifurcation diagram would have been greatly aided with explicit X and Y labels! I'm wondering why the authors did not label the image directly but mention it in the *text*! I'm sure it wouldn't have taken anything away from the visual aesthetic of the image.

- The authors bring up the idea that self-organisation in biology is the consequence of both internal (biological) and external parameters (physical processes, ecological factors). '...strikingly different patterns may result from the same mechanism operating in a different parameter range.' - and highlight that cross-species differences in behaviour may actually be driven more by differences in environmental factors than generic differences perhaps.

- Box 3.2: highlights the fact that even weel defined mathematical models can show *deterministic chaos*, in that the model doesn't show any predictable switches in values/states. For instance in the logistic model, when

r>4, the system goes into deterministic chaos, where it is not possible to predict the populatin size from one timepoint to the other. However, in other parts of the parameter regime, the dynamics is qualitatively much more predictable.

- *'Here the term 'chaos' has a precise mathematical meaning that should not be confused with randomness or noise. Deterministic chaos is the unpredictable behavior of a nonlinear system within a certain parameter range.'*

- Authors suggest it is unlikely that the parameters of biological systems will lie in chaotic type regions, as the dynamics is then expected to be unpredictable and show great variation from one time point to the other. However, given the type of variation we see in biological/ecological data - it would seem a tough exercise to show that biological systems are actually not in a chaotic state?

Chapter 5

4. Alternatives to Self-Organization

- This chapter broadly looks at four somewhat intertwined alternatives that may describe biological phenomena :

    1. Leadership : the 'well-informed' leader that leads a pack. Perhaps there is evidence for this in elephant groups where the matriarchs lead the members to watering holes etc.?
    2. Blueprints: a fixed plan that will be executed where the process and end-product are fixed. eg. nest construction in some insects (as seen in Fig 4.3 - a potter wasp starts re-building its nest when the appearance is slightly altered)
    3. Recipes : a broad plan where the *what* is defined, but the 'how' is not so defined. Here I suppose bird nest building may be an appropriate.
    4. Templates: a fixed plan where each part of the work directly aligns/dictates the next part of the work.

- Of course, I had to think of the flexible web building of orb-web spiders (eg. (Peters, 1970) in *A. diadematus*). Individuals can complete the incomplete webs initiated by other spiders, and also actually complete webs that have been 'disassembled' (key parts of the web burnt off). This type of behaviour tells me spiders may be acting according to a mix of a blueprint, recipe and a template type mechanism. Perhaps less blueprint, but more recipe and template. The curvature/placement of the strings and the spider's own body determine the inter-string placement, while the broad overarching behavioural recipe might be - 'spin silk till you can walk from point A to B without feeling any gaps'

- Self-organization may play a stronger role in larger colonies of wasps, than in smaller colonies. In general this may perhaps be the case because the

importance of single inter-individual interactions gets 'averaged over', with increasing group size.

- The discussions of stigmergy reminded me of how the timing and number of social spiders on the web are so close tied together. The appearance of a few spiders triggers the appearance of more and so on. Studies by Deneuxbourg and colleagues have shown this with *Anelosimus* I think. Another example that came to mind may even be social waking/activity cycles in a bat colonies in caves or even in tree-hanging fruit-bats.

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Chapter 6

5. Why Self-Organization

This chapter delves into why self-organisation is so popular, in contrast to the some of the more 'centralised'/'deliberate' strategies outlined in Chapter 4 of the book.

- *'…. the reules in self-organizing systems can be quite economical in the physiological and behavioral machinery needed to implement them. …..'*

- "*arise through evolutionary processes and more likely to carry smaller costs than more complicated*" – what is a 'complicated' rules and does it *have* to be more costly. Does the energy/time/adaptation cost always trade-off 'linearly' with rule complexity? Perhaps different animal species already lie on the point where they have a lot of complex behaviours/rules built in for individual level behaviours, and for these animals the 'cost' is minimal? Moreover, many innate, individual animal behaviours the themselves are extremely 'complex' – what is the real difference between 'complexity' in innate animal behaviours and behaviours that involve pattern formation.

- '*It seems clear, however, that blueprints are not a widespread mechanism for guiding pattern formation in groups, with the obvious exception of human groups.. Why is this? Perhaps one important reason is that it would be extremely costly to encode genetically the vast quantity of information that would need to be expressed in a mental blueprint for a complex structure, such as a termite nest.*' – Yes, humans use 'blueprints' however, it's important to note that the blueprints are not genetically coded. Instead, perhaps our ability to communicate with each other is coded, which then facilitates the use/conception of blueprints.

- "*…that pattern-formation by cooperative groups usually arises through self-organization rather than external guidance because the latter mechanisms generally are exceedingly difficult to implement.*" - 'difficult to implement'

or rather that the tinkerer-nature of evolutionarymeans that in most cases self-organisation is the path of least effort, that still provides a results. For eg. there may be animalswith sufficiently sophisticated cognitive abilities, but they may still be following simple self-organisation type rules?

- in general, I have limited expertise in the field of evolutionary biology, but it seems like many of the arguments the authors make here about why self-organisation is the 'standard' parallels the arguments for why trait X is commonly seen instead of trait Y and Z. Here X = self-organisation and Y,Z = blueprints or templates. The arguments seems a bit wobbly. For instance the predominance of trait X, instead of Y or Z, could also be explained by the fact that it is an 'ancestral' state that never changed, or for which there was no selection pressure against?

Chapter 7

Investigations of Self-Organization

- the authors state two types of modelling approaches : 'bottom-up' - which is driven mainly by experimental findings and 'top-down'- which is driven mainly by intuition

  - I'm just wondering whether this is a false dichotomy, and wish there was a bit more detail.

- *'it may be temp(t)ing to vary the parameters of a model until the desired global pattern is produced'* - the authors caution against a forceful urge to find the parameters that best fit the data. After having set up a biologically reasonable parameter space to search, a failure to replicate certain patterns may indeed inform us of what is missing in the current model.

- '*A match that may be found between the global pattern and the output of the models is not particularly strong evidence of the model's validity.* ' - the match of just *one* pattern is definitely good proof of the model's validity. However, I would argue that in most phenomena, multiple 'patterns' at different scales of investigation can be extracted and compared. For instance, in shoaling behaviour, group polarity is a common property, but in addition the distributions of inter-neighbour distance, individual velocity, etc.must be taken into consideration. *REFERENCE MISSING HERE FOR MULTI-PATTERN MODEL CHECKING*

- the authors seem to reflect the then pre-dominant feeling that '...some biologists question the value of models.'. This may have been true a decade or two ago, but my feeling is that this feeling is declining fairly rapidly

- On how modelling exposes gaps in our knowledge: '*.. the investigator is forced to be explicit about each detail of the mechanics of a system. One*

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consequence of this is that in the process of model building, the investigator often realizes that no information is available about a particular part of the system.' : speaking from personal experience, I can definitely say modelling is a humbling experience. While qualtitative models already expose the lack of information, being forced to specify the relationship between variables and outcomes makes one think twice about how sure one can be at all!

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