Robustness of self-organised systems to changes in individual level behaviour: an example from real and simulated self-organised snail aggregations

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Abstract

Perfect behaviours that are optimal to the environment an agent operates within rarely exist in real animals or in robotic systems. The costs (be they biological or economic) of building sensors and processing the information they capture become excessive compared to the small advantages that occur from the modifications of behaviour. Many self-organised systems are thought to change their properties as a result of changes in individual behaviour. Here, using both natural systems and computer simulations, we demonstrate that intertidal snail aggregations slightly decrease in size when individuals forage for shorter periods due to hotter and more desiccating conditions – a non-optimal behaviour for the snails since aggregation reduces desiccation stress. However, this decrease only occurs in simple experimental systems (and simulations of these systems). When studied in their more complex natural environment, and when simulated in such an environment, using the same information-processing behaviours, no difference in aggregation behaviour was found between hot and cool days. These results give an indication of the robustness of self-organised systems to changes in individual-level behaviour. They demonstrate that information processing capabilities of self-organised groups may not need to be as great as for agents that perform solitary tasks, and also that oversimplified tests of swarm intelligence may not give a true indication of how tasks may be performed in a more complex environment.

Key words: Intertidal snails, Information processing, Developmental costs, Self-organisation, Aggregation
1.0 Introduction

While behaviours in real animals are normally adaptive, increasing survival and reproduction [1], they are not normally perfect. For example, many birds are unable to recognise the eggs of brood parasites, such as cuckoos [2], insects that manipulate the sex ratio of their offspring tend to pick suboptimal ratios at low foundress densities [3] and animals do not always select optimal habitats in which to breed, in terms of resource allocation [4].

To increase the optimality of behaviours requires bigger and more complex sensory and nervous systems. Larger brains and more neurons incur a higher metabolic cost than smaller brains [5] and have been shown to result in shorter life spans and lower fecundity in late life (e.g. in Drosophila [6]). Essentially, balancing the costs and the gains of a behaviour is an evolutionary trade off [3, 7-10].

In developing artificial systems, such as robots, conceptually identical principles should apply [11]. Increasing the ability of a robot to complete a task can be achieved by more technology, more sensors, more computational power etc., but these processes incur costs – be they economic, or physically restrictive in terms of weight, size or power consumption [11].

Swarm based robotics requires the interaction of large numbers of agents [12], so costs of each individual need to be minimised. While these agents collectively perform tasks, and therefore each individual can be simpler than a solitary task-performing robot, conventional theory on self-organising systems indicates that changes to individual-level behaviours will have effects on the behaviour of the collective system [13].
In this study we examine the role of individual behaviour on a self-organised system. If changes to individual behaviours occur, does the collective behaviour also vary? We study this in both a natural system and a simulation of this system (that of aggregation in intertidal littorinid snails). The system is well understood and previous simulations of the system, using just three well-documented behaviours, have demonstrated that both spatial and temporal predictions of aggregations using the simulation are statistically identical to patterns found on the real shore [14 - 16].

2.0 Methods

2.1 Study system
The study organisms are littorinid snails (*Echinolittorina malaccana* and *E. radiata*) on the intertidal rocky shores of Hong Kong. The snails form aggregations of 2 to >50 individuals during the retreating tide, as the rock surface dries out. During the incoming tide, the snails move up the shore to remain in the awash zone (wet by the waves, but not submerged). As the tide retreats the snails move back down the shore and form aggregations. Aggregations prevent desiccation [14, 17, 18] and this behaviour is important as the snails can emersed for >24h between tides high enough to wet them [14, 19]. Snails show three simple behaviours, that when simulated account for their distribution patterns. 1) If snails encounter another individual, through chance encounters then they can choose to aggregate (for details see below). 2) If snails encounter a crevice, they can choose to remain in the crevice. 3) Snails can follow previously laid mucus trails, which persist over tidal cycles. Using these rules, the simulated snails show the same distribution patterns as real snails [16]. Aggregations result from a process of self-organisation, essentially aggregations arise from chance encounters with other individuals, but these chance encounters are
facilitated by following of mucus trails. Where trails cross each other, or where trails cross crevices, are likely sites of large aggregations [16].

2.1 Computer simulation.
The simulation was identical to that used in [16] except where indicated below. The simulated rocky shore was divided into a grid of 5 mm squares. Snails could move from one square to any of the eight neighbouring squares, giving an average distance between squares of ~6 mm, or the length of an average snail (this accounted for the diagonal distance being further than the orthogonal). One timestep in the simulation was defined as the time taken for each snail to move from one grid square to a neighbouring grid square. The simulation normally lasted 400 timesteps (but see below for modification). In most simulations, snails were prevented from moving off the top of the simulated shore by restricting upward movement directions, this typically only effected < 5% of snails in any given simulation [16]. Snails moving off the side of the simulated shore rejoined on the opposite side, moving in the same direction. Snails were able to leave the bottom of the simulated shore, and if they did so in the final tidal cycle of the simulation, were not included in further analysis. Snails leaving the bottom of the shore in simulations of more than one tidal cycle rejoined the simulation at the bottom of the grid at the start of the next tidal simulation, with their horizontal positions being randomly determined.

Simulated snails were initially randomly located in the lower 100 rows of the grid. Each individual moved up the shore with an initial bearing of 0°. At each timestep a new bearing was obtained by summing the previous bearing with a randomly generated angle from a normal distribution (mean = 0°, SD = 10°). A bearing of 0° was also applied at timesteps 10, 20, 40 and 80 to ensure simulated
patterns were similar to observed patterns in that the snails moved upshore [16]. Once in the top 40 rows of the grid (the position at high tide when snails would be washed by waves) the randomly generated angle was changed to give a more tortuous movement pattern (mean = 0°, SD = 100°) and when moving down the shore the snails were initially given a bearing of 180°, and then the bearing was again modified by a random angle (mean = 0°, SD = 10°). These bearings and angles mimicked real snail behaviour as they moved up and down the shore with the rise and fall of the tide. Patterns of simulated individual movement have previously been shown not to be significantly different from real snails’ movement patterns in terms of length of the trail and fractal dimensions of the trail [14, 15].

Decisions were made when snails encountered other snails, and when snails encountered the trail of another snail. To simulate a decision, a random number (from a uniform distribution between 0 and 1) was compared to the sigmoidal probability threshold, y, which increased with the time of the simulation:

\[ y = \frac{1}{1 + e^{-a(t-b)}} , \]

where \( t \) is the timestep, normally between 1 and 400 and values of parameters \( a \) and \( b \) indicate the probability of the decision occurring at a given timestep. These parameters are modified depending on the simulation and are shown in Figure 1. The likelihood of trail following or aggregating, therefore, increases with the increase in number of timesteps of the simulation. If the random number was lower than \( y \), snails aggregate and stop moving or follow mucus trails. Although aggregated snails are not moving, they could take part in further aggregation decisions if other snails encountered them – this may result in these aggregations increasing in size. The
crevice occupation rule, which was included in the original simulations [14, 16], is not included in the current study as all rock surfaces modelled were considered to be crevice-free (see below).

To create differences in individual-level variability, in some simulations the number of timesteps was reduced from 400 to 350 to simulate the snails behavioural response of stopping moving earlier in relation to increased desiccation stress. This reduction in time is indicative of the shorter foraging time experienced under hotter conditions, as measured in different treatments in the artificial environment experiment (see below). In some simulations, the behavioural rules of aggregation formation and trail following were also altered (see Figure 1), allowing decisions to occur with greater probability earlier in the simulation, since we predict that decisions (although modelled as time-based) are related to the dryness of the rock surface [15].

To provide simulation results to compare to the shore study (see below), 1 m$^2$ of shore was simulated with the same density of snails as recorded from the real shore (112 m$^2$). Persistence of mucus trails has previously been shown to be important in determining the spatial and temporal patterns of snails on the shore and degradation of mucus trails between tidal cycles was modelled as per [16]:

$$M_{t+1} = (M_t e^{0.78}) ,$$

where $M$ is the amount of mucus present in each 0.5 x 0.5 cm grid squares. To ensure the effects relating to persistence of mucus trails were incorporated into the simulation, each run of the simulation was repeated over three tidal cycles before results were collected, thus allowing simulation of mucus laid on the shore due to previous movements. A randomly selected area (500 x 500 mm quadrat – comparable
in area to the field study – see below) of the simulated shore was then investigated. Since we randomly selected quadrats on the shore, crevice distribution varied between replicate quadrats, and, as crevice distribution can affect the proportion of snails aggregating (although not significantly, [16]), we simulated all shores to have no crevices. Thus, our simulation results would not be expected to show exact matches to the observed data from real snails, but should be indicative of trends caused by changing physical factors.

To compare the simulation with the semi-artificial environment experiment (see below), we simulated a shore of 300 x 300 mm – the same size as the marble slabs used in the semi-artificial environment study. We prevented simulated snails moving outside these dimensions by preventing movement off the edge until a new direction was established, as would occur with real snails that were restricted to moving solely within the artificial environment (see below). Since the snails were already in the awash zone when first immersed, and could not move fully down the shore with the retreating tide, the times of the simulations were restricted to 200 timesteps (from timestep 150 to timestep 350) for the low desiccation (shaded) treatments (see below) and 175 timesteps (150 to 325) in the open treatments.

2.3 Shore study.

The percentage of snails aggregating at mean high high water (MHHW = 2.17 m + C.D., the mean level of the highest of the two high tides during a day), was investigated at two shores on Hong Kong Island (Cape d’Aguilar [22.3037 °N, 114.2558 °E] and Wah Fu [22.2499 °N, 114.1304 °E]) in August and September 2001. Aggregations were defined as ≥ 3 individuals in direct physical contact with each other (after [14, 20]). Ten, randomly located, quadrat counts (0.25 m²) were taken
along a pre-determined 50 m stretch of shore. Three replicate sampling days were conducted for two different sets of environmental conditions: Hot Days (H) (air temperature 300 mm above the rock surface was > 35 ºC) and Cool Days (C) (temperature was < 28 ºC). Other factors, such as wave action, were kept as similar as possible between the different days, with low wave action (< 100 mm high waves) at Cape d’Aguilar but > 300 mm (though < 500 mm) at Wah Fu (predominantly due to wave action caused by passing boat traffic). The order in which the samples were taken at each shore was randomly determined with at least 48 h separating replicate sample days. Between sample days snails were seen actively foraging during high tide, confirming that individuals moved between sample days. To confirm the increased desiccation stress on Hot Days, cotton wool balls soaked in water (n = 5) were weighed before and after 1 h emersion on the rock surface at Cape d’Aguilar on each of the replicate days and the percentage water loss calculated.

2.4 Semi-artificial environment study.

Although we attempted to minimise possible confounding effects such as wave action on different replicate days in the Shore Study (see above), it is almost impossible to eliminate all possible confounds. To try and reduce these a manipulative experiment was carried out on artificial substrata (marble slabs) on the shore at Cape d’Aguilar. Slabs (300 x 300 mm) were placed flat on the shore at MHHW. Tree Tanglefoot gum (Tanglefoot Company, Michigan, USA) was placed around the perimeter of the slabs to prevent snails from escaping [21].

One of three treatments was assigned to 10 replicate slabs (∑n = 3 x 10 = 30). Ten slabs were shaded using a roof of aluminium foil wrapped around wire mesh (roof size 350 x 350 mm) supported 50 mm above the slab surface. The roof
prevented illumination of the experimental area by direct sunlight and therefore lowered temperature and desiccation. A second treatment was a procedural control consisting of a wire mesh roof (mesh size 7 mm) not covered in foil. The final treatment was an open treatment, with no roof and therefore subject to direct sunlight.

During low water, 7 *Echinolittorina malaccana* and 8 *E. radiata* (representative of the population density of each species on the shore, all ~ 7 mm in length) were placed on the slabs and allowed to attach by their foot or mucus holdfast. During high water, waves (< 100 mm in height) washed over the slabs for > 1 h and the snails were observed to move. The tide began to retreat just prior to midday, so ambient temperatures were high (> 35 °C) when the plates dried and the snails stopped moving. Once all animals had stopped moving the percentage of littorinids in aggregations on each slab was determined and slab surface temperature was measured with a K-type thermocouple (see [22] for details). Desiccation on each plate was estimated as above by measuring weight loss of cotton wall balls soaked in water (1 cotton wool ball per plate).

3.0 Results

3.1 Computer simulation.

Simulations of real shores (equivalent to the Shore Study observations detailed above) were run 500 times for each treatment to ensure a good estimate of the true mean value (SE < 0.5 % of mean). The initial simulation predicts a mean of 41.8 % of snails in aggregations (Figure 2a). This percentage decreases to 25.1 % when the time of the simulation is reduced to 350 timesteps, but increases to levels similar to those initially recorded (42.1 %) when both the time and parameter values are altered as indicated above (Figure 2a).
The simulations of the slab experiments were run 2000 times for each
treatment to ensure a good estimate of the true mean value (SE < 0.5 % of mean). The
baseline conditions, in this case indicative of the coolest conditions (shaded
treatment), showed a mean of 48 % of snails in aggregations (Figure 2b). Decreasing
the time of movement resulted in a large reduction in the proportion of aggregating
snails (30 %). Altering the parameters of the behavioural rules (a and b), as well as
the reduction in time of movement, gave an intermediate mean value of 40 % (Figure
2b).

3.2 Shore study.
Desiccation differed significantly between the different temperature conditions (mean
± SE n = 15, desiccation = 71 ± 1.4 % h⁻¹ during Hot Days compared with 51 ± 0.7 %
h⁻¹ during Cool Days), although significant differences were also observed between
replicate days within the same conditions (Table 1). There were, however, no
significant differences in the percentage occurrence of aggregation behaviour between
Hot or Cool Days or replicate days within conditions at Cape d'Aguilar (Table 2;
Figure 3a) or at Wah Fu (Table 1; Figure 3b).

3.3 Semi-artificial environment study.
On artificial slabs, both temperature and desiccation were significantly lower (by ~20
°C and 30 %) in the shaded as compared to the open or procedural control treatments
(Table 3). No significant differences were, however, found between the percentages
of littorinids aggregating in different treatments (Table 2) although the mean
percentage of snails aggregating was higher, by almost 20 %, in the shaded treatment
(Figure 4). Snails stopped moving on the open treatments ~ 15 – 20 minutes before
the covered treatments, indicating changes in foraging time of ~ 50 model timesteps (see above).

4.0 Discussion

During hot, desiccating conditions, individual-level snail behaviour changes from that exhibited in cooler, less desiccating conditions. The time snails spend moving decreases, probably because the rock surface dries faster [15]. Essentially this should give snails less time to locate other individuals and form aggregations, therefore fewer or smaller aggregations should be formed, i.e. an individual-level change in behaviour has a direct effect on the self-organised behaviour [13]. This is clearly a sub-optimal behaviour, as aggregation reduces desiccation [14, 20], and the consequences of not aggregating on highly desiccating days should be higher. This hypothesis is supported by results from the semi-artificial environment studies and computer simulations of these studies. From these studies, it appears that there are cognitive constraints acting on the snails, influencing them to behave sub-optimally in some environmental conditions (i.e. perception of the dryness of the rock only is insufficient to optimise behaviour in a range of conditions).

However, when results from fully natural environments were analysed, there was no change in the collective behaviour. This was true of directly recorded results from the shore, as well as simulations of the snails in their natural environment (essentially the inclusion of mucus trails that were persistent between tidal cycles). This demonstrates that in natural environments, self-organised behaviours are robust to changes in individual level behaviour. These results have important ramifications for both evolutionary ecology and for the design of artificial self-organising systems such as swarms of robots.
In evolutionary ecology terms, self-organisation, at least in the case of littorinid snails, can overcome the need for complex sensory systems that deal with changing environments. By simply sensing the dryness of the rock surface, foraging time can be increased in cooler conditions and aggregation levels can remain high in both cool and hot conditions. Essentially, self-organisation allows the snails to overcome some of the evolutionary constraints of developing complex sensory systems to maximise their behaviours.

In terms of artificial self-organising systems, the results suggest that tests of effectiveness of collective behaviour could be limited, if they are conducted in simplified environments (for example, the use of real robots may provide more realistic results and potentially better performance than the use of simulation packages). If agents need to interact with their environment, then it is important to ensure the environment that they operate in is fully realistic; this is akin to problems that have previously been identified in other non-swarm-based bio-inspired technology applications [23, 24]. Furthermore, the importance of optimising the individual-level ‘behaviours’ of each agent are perhaps less important than previously realised. From these results, it is not clear what the implications of variations between different agents would be, but it is suggestive that self-organised systems should be relatively robust to small amounts of between agent variability.

Acknowledgements

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References


Table 1. Summary of comparisons using nested ANOVA to determine variation in desiccation of cotton wool balls and aggregation behavior of littorinids during different environmental conditions (Factor = Temperature, fixed with 2 levels, Hot or Cool Days) on three replicate occasions (Factor = Day, random with 3 levels). Values in bold indicate significant differences between treatments (P < 0.05). (For all comparisons: Levene’s test for homogeneity of variance p > 0.05, not significant).

<table>
<thead>
<tr>
<th>Comparison</th>
<th>Shore</th>
<th>Factor</th>
<th>F</th>
<th>d.f.</th>
<th>p</th>
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<td>Desiccation of cotton wool balls at different temperatures</td>
<td>Cape d'Aguilar</td>
<td>Day(Temperature)</td>
<td>2.50</td>
<td>8, 20</td>
<td>0.043</td>
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<td></td>
<td></td>
<td>Temperature</td>
<td>96.00</td>
<td>1, 20</td>
<td>&lt;0.001</td>
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<tr>
<td>Aggregation behavior at different temperatures and low wave action</td>
<td>Cape d'Aguilar</td>
<td>Day(Temperature)</td>
<td>0.40</td>
<td>4, 54</td>
<td>0.806</td>
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<tr>
<td></td>
<td></td>
<td>Temperature</td>
<td>3.99</td>
<td>1, 54</td>
<td>0.166</td>
</tr>
<tr>
<td>Aggregation behavior at different temperatures and high wave action</td>
<td>Wah Fu</td>
<td>Day(Temperature)</td>
<td>0.39</td>
<td>4, 54</td>
<td>0.390</td>
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<td></td>
<td></td>
<td>Temperature</td>
<td>5.22</td>
<td>1, 54</td>
<td>0.084</td>
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Table 2. Summary of comparisons using ANOVA to determine differences between surface temperature, desiccation and sheltering behavior of littorinds on marble slabs with different treatments (open to full sunlight, shaded with a roof and a procedural control). Values in bold indicate significant differences between treatments (P < 0.05). (For all comparisons: Levene’s test for homogeneity of variance p > 0.05, not significant).

<table>
<thead>
<tr>
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<th>d.f.</th>
<th>p</th>
<th>SNK tests</th>
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<td>2, 27</td>
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<td>Desiccation</td>
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<td>Aggregation</td>
<td>0.98</td>
<td>2, 27</td>
<td>0.388</td>
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Aggregation behavior
Figure 1. The probability of trail following or aggregation given a local encounter between two snails or an individual snail and a previously laid mucus trail. Right of the arrows indicates ‘standard’ parameters for equation 1 as in Stafford et al. (2007); trail following $a = 0.9$, $b = 290$, aggregation $a = 0.7$, $b = 360$. Left of the arrows indicates modified parameters used to indicate higher levels of desiccation stress; trail following $a = 0.9$, $b = 240$, aggregation $a = 0.7$, $b = 310$. The vertical dashed line indicates when snails stop moving in hotter, more desiccating conditions.

Figure 2. Mean ($\pm$ SD $n = 500$ or 2000) percentage of snails aggregating in (a) simulated shore experiments and (b) simulated semi-artificial environment experiments

Figure 3. Mean ($\pm$ SD $n = 30$) percentage of snails aggregating on Hot Days (> 35 $^\circ$ C) and Cool Days (< 28 $^\circ$ C) at (a) Cape d’Aguilar and (b) Wah Fu.

Figure 4. Mean ($\pm$ SD $n = 10$) percentage of snails aggregating in semi-artificial environments (marble slabs) under three different treatments.
Figure 1. Stafford et al.
Figure 2. Stafford et al.
Figure 3. Stafford et al.
Figure 4. Stafford et al.