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Strategy selection under predation; evolutionary analysis of the emergence of cohesive aggregations

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Abstract

Why do animals form groups? This question has formed the basis of numerous scientific studies over the last hundred years and still remains a controversial topic. Predation is one of the foremost candidates, yet the precise mechanism remains quantitatively elusive. Here I investigate *in silico* the effect of ongoing predation on groups of heterogeneous individuals behaving according to a well documented individual based model. I examine the resultant evolutionary trajectories and describe the final selected states and their stability with reference to a qualitatively modified version of adaptive dynamics. The speed of individuals is found to dominate the selection of the final state over other parameters in the model. The relative stability of the groups and their internal configurations are discussed with reference to novel structural correlation functions that are defined and introduced. The results reveal the importance of tightly bound toroidal group structures as an intermediate state prior to the emergence of slow compact groups. The study also indicates the need to more accurately model the speed distributions in real aggregations.

1. Introduction

Conclusively linking an evolved behaviour to its underlying selective pressure remains a difficult problem in both complex models and the real world. Group aggregation, an example of collective behaviour exhibited ubiquitously across the natural world is no exception [Sumpter 2006, Parrish *et al.*2002, Parrish & Edelstein-Keshet 1999]. The preferential formation of groups has been linked to a host of causes: to feeding efficiency, to social hierarchy advantages, and prominently, to predation which has number of sub-divisions such as confusion, dilution, oddity and vigilance effects [Lima 1995]. Perhaps the best known example is the selfish herd hypothesis [Hamilton 1971] where individuals attempt to position themselves amongst their conspecifics so as to minimise their personal danger from predation and form a group as a consequence. Nonetheless there remain significant obstacles to understanding these problems, including the collection of appropriate experimental data, the clarification of conceptual issues and the need

to construct models that capture the necessary underlying behaviour without introducing simulation artifacts.

This latter topic, the modelling of collective animal aggregations, is a highly active area of current research, pursued by scientists from across the disciplines [Sumpter 2006, Parrish *et al.*2002, Parrish & Edelstein-Keshet 1999]. Despite this large effort there is little consensus on either the necessary level of complexity of the modelling or the details of the constituent parts. Even where a broad consensus of the modelling has been reached – models based on the nested variation of attraction originally introduced by Aoki [Aoki 1980] are now widely used at the biological interface – there are many variations in implementation that may, or may not, have profound effects on the qualitatively observed effects. For example, if a neutral zone (where no interaction occurs) is included [Tien *et al.*2004] or how strictly hierarchical the interaction zones need to be [Morrel & James 2008]; both these examples lead to different nearest neighbours distributions.

Recent work has sought to address the issue of model complexity and evolutionary pressure simultaneously with a view to clarifying issues in both [Wood and Ackland 2007]. This approach has made use of computational models to simulate predation and foraging challenges on groups of autonomous organisms, opening potentially new pathways to understanding both the emergence of successful evolutionary strategies and the veracity of the underlying models. In this article I look to build on this method and elucidate further details of the differing strategies that emerge. I will concentrate exclusively on the effects of predatory behaviour in this work and in particular on understanding the emergence and identification of the strategies that were previously reported. I will develop and contrast the difference between models that have constraints upon adaption and those which do not. Distinguishing between these two effects relates to the large difference in evolutionary timescales that must exist between them. My principle aim is to understand the reasons why strategy selection occurs and interpret it in terms of the differences between individuals, either at the level of their direct phenotype or in terms of their indirect positional preferences within the coherent structure.

2. Model Definition

I study a group of N boids (computational "birds", a general term to describe the computational representation of an individual [Reynolds 1987]), indexed by i, with position $\mathbf{r}_i(t)$ and velocity $\mathbf{v}_i(t)$. The model I use is based on that of Couzin *et al.*[Couzin *et al.*2002] and I implement a simple direction rule governing the repulsion, orientation and attraction with nested radii labelled R_R,R_O and R_A ($R_R < R_O < R_A$). If a boid or boids are detected in the repulsion region then the updating boid is directed away from it or them (note that because of turning constraints this is equivalent to the 90° turn adopted elsewhere [Huth & Wissel 1992]) and no further search is conducted. In the next two regions an averaged orientation with boids in the area between R_R and R_O and an averaged attraction with boids between in R_O and R_A is calculated. If boids are found in both then the contribution is averaged between them. These

calculations are modified by the presence of a blind angle and by detection of predators. The blind region to the rear is a feature present in real swarming creatures and is necessary for the maintenance of stability of some spatial flocking structures. Predator response is handled in a prosaic way: if a predator is detected then the boid moves in a new direction which is computed by taking the vectorial average of the direction it would have taken without the predator and a direction away from the predator, which is weighted with an evolvable parameter.

Finally once a new heading is calculated, some Gaussian stochastic noise is added with strength σ. If the turning angle required to move onto this new heading exceeds a maximum turn angle the boid will turn the maximum turn angle instead towards the new direction. Once new headings have been calculated for all the boids in the simulation then all are moved simultaneously to their new positions computed by multiplying their constant individual speed v_i by the constant time-step Δt in the direction of their heading (a displacement at time t $\Delta t \mathbf{v}_i(t)$.). Collisions are ignored, and in practice the precedence of the repulsing move makes them extremely unlikely. The headings are now recomputed in exactly the same way for the next time-step. The model so described can be implemented in two (e.g. Huth and Wissel [Huth & Wissel 1992]) or three dimensions (e.g. Couzin *et al.*[Couzin *et al.*2002]), and in this article I shall restrict attention to two dimensions, however the only difference in the implementation details is the use of solid angles for the turning and blind areas respectively. Preliminary simulations in three dimensions revealed that computational problems associated with warming up and simulating unbiased predator attacks are significantly greater with heterogeneous groups. One difference in my implementation is that I permit my groups to be composed of heterogeneous individuals, where each member of the group can adopt a different parameter set from its fellows. This model and its implementation have been described elsewhere ([Couzin *et al.*2002] and [Wood and Ackland 2007]) in greater detail to which I refer the reader for further details.

The principle focus of my attention in these models is the multiple expressed *phases* that Couzin *et al.*were the first to document. The phases are the different flocking behaviours that are represented in the model for different parameter choices and are best identified by the polarisation

$$p = \frac{1}{N} \left| \sum_i^N \hat{\mathbf{v}}_i(t) \right| \tag{1}$$

and the angular momentum about the group centre

$$m = \frac{1}{N} \left| \sum_i^N \hat{\mathbf{r}}_{ic} \times \hat{\mathbf{v}}_i(t) \right| \tag{2}$$

where $\mathbf{r}_{ic}$ is the displacement from the centre of the group, which is defined as the positional mean.

The model, in addition to non-aggregating regions of phase space, expresses four distinct modes of behaviour. Firstly a parallel phase with a very high

degree of alignment, $p \approx 1$, sometimes called a flying crystal. Secondly a dynamic parallel phase with a high degree of alignment which is identified by a clear polarisation plateau ($p \approx 0.9$) in the diagram. Thirdly a compact phase with group formation at low polarisation which forms three sub phases, which I call a swarm, a mill and a torus in order of increasing angular momentum. The swarm is simply a unordered cluster with no net angular momentum; the torus is a highly organised doughnut configuration with markedly high angular momentum ≈ 1 and the mill is a hybrid between the two which has non-zero angular momentum but is unable to sustain the order required for the toroidal configuration. Finally there is a "pack" phase with high polarisation but little lateral extent stabilised by high attraction and low orientation where the boids string out into a long "follow-my-leader" configuration which has non-zero angular momentum (caused by strung together turns). The first three of these were predicted in Couzin *et al.*, the latter was noted by Wood and Ackland as a result of their work on foraging configurations.

2.1. Evolutionary algorithm

Wood and Ackland [Wood and Ackland 2007] used the model presented above as a basis for running a series of evolutionary simulations that revealed different possible responses to predatory (and foraging) pressure. The principle for this is deceptively simple, that a predator is introduced and pursues prey until one is struck; this implies capture and a fitness penalty to that phenotype. Whilst intuitively clear this elementary methodology outlined above is a potential source of ambiguity in the study, both due to its own errors and, more interestingly, to limitations of the underlying model. For instance, the predators are chosen, at each time step, to pursue the closest individual. Yet this is one particular choice; it is also possible to head towards some average position of all visible individuals for instance. Different choices, or mixed ones, may correspond to differing predator types, e.g. ambush or chase [Neill & Cullen 1973]. There is limited empirical evidence for a computational choice for these parameters; predators have often been "left out" of predator prey studies in the wild [Lima 2002]. Whilst there is a significant body of work regarding predator strategies (e.g. [Quinn and Cresswell 2004]) the detailed individual *tactics* of predators remain elusive [Lima 2002] despite some ingenious experimental constructions [Krause and Godin 96, Ioannou *et al.* 2008]. There is more discussion of this topic in other modelling papers [Inada & Kawachi 2002, Zheng *et al.*2005].

The typical parameter values used in the simulation are listed in table 1. The size of the box was adjusted to the smallest parameter that had no further qualitative impact on the simulation results.

[Table 1 about here.]

In common with any simulation of a non-equilibrium process it is important that the system is run for significant periods of time so that the simulation can adopt a representative configuration: this is termed the warm-up step. This is

especially important when a heterogeneous population is present which may not necessarily be able to form a stable group. Even when stable group formation is permitted it is important that individuals have time to adopt an appropriate group position despite the correlation times and lengths for these processes being unquantified. For a full warm-up I run the simulation in a box of half the size (quarter the area) for 10^4 sime steps. This contraction of space is in order to more quickly ensure all the individuals come into contact. The space is then increased to the full size and run for the same quantity of time.

How many individuals to remove, or equivalently how many predators to introduce, must be monitored carefully. A larger number removed at any given evolutionary time-step significantly increases the speed of simulation as more evolutionary steps are made per warm-up, on average. The disadvantage of this is it can lead to significant and undesirable frequency dependent effects. It means that an unrepresentative configuration formed on one particular warm-up can either persist, or be the sole target of predation. Overall this permits a collection of unsuccessful individuals, surviving by chance, to adversely affect the group behaviour and by doing so unrealistically promote their fitness.

In this study, unlike [Wood and Ackland 2007] I will remove a single individual and then regenerate one in its place by replicating one of the survivors, with the chance of mutation. In principle this means that a single individual can persist for the length of the simulation, but in practice there is sufficient randomness for this to be unlikely. I exploit a simple trick in order to produce a qualitatively similar flock at each evolutionary time-step without forcing a particular configuration or phase or necessitating a full warm-up (described above) between each evolutionary time step. The spatial positions of individuals are permuted and then random vectors are added to their positions before running the simulation for shorter period of time than during a full warm-up. These steps are necessary in order to ensure that the group formed is representative of the individuals it contains whilst minimising computational time. To further contract the warming up time in between the evolutionary time steps I run the simulations for a short period of time (100 time steps) and then check that there is a large connected group component (90%). If so then the simulation proceeds. If not the short warm-up is repeated, with a check after each, until a group is formed or ten warmups are completed.

I can further manipulate the two timescales in the model, that is mutation and selection, by explicitly reducing the mutation rate; genetic mutations are rare, happening on average 0.003% of regenerations. As the inheritance of phenotypes was not modelled explicitly as genetic in origin it is not clear how to incorporate a biological realistic choice. I therefore chose a value such that, on average, one parameter is mutated at each evolutionary step i.e. the individual reinserted at that evolutionary step has, on average, one phenotypic mutation relative to the individual it replaced. Equally, in the absence of biological input, the simplest choice for mutation is a bounded uniform distribution around the original value. More realistic is a Laplacian, or double exponential, a form which encodes the mostly small but sometimes very large outcomes that are desirable. I contrast the two in this study, keeping the mean mutation fixed.

Genetic boundaries are dealt with using reflection, so as to minimise artefactual pinning effects. If a mutation would taken the value of a parameter outside of a prescribed range then the mutation is "bounced" back into the permitted parameter space.

Here I examine the effects of altering the simulations away from the choices made in previous work [Wood and Ackland 2007] focusing on suppressing any possible frequency dependent and group formation effects identified above, that may have been present in that study. A second aspect of this modelling is the choice of parameters to vary. Seven parameters are chosen: The velocity, the orientational radius, the attraction radius, the turning angle, the viewing angle, the preference to avoid the predator rather than align with flock mates and the magnitude of the perturbing noise. In [Wood and Ackland 2007], to suppress the immediate maximisation of the parameters the speed was coupled to the turning angle in effect creating a constant movement area, and the attraction radius coupled to the viewing angle in a similar fashion. This is denoted as a constrained simulation as the attraction radius/viewing angle (corresponding to eye position and capability) and the velocity/turning angle (corresponding to physical capability) are constrained, quickly fixed and associated with presumably slow evolving traits. Where the physical traits are uncoupled in the unconstrained simulation these parameters are free to evolve. The other traits: noise, preference and orientation radius are much less physiological in origin and offer the potential for dynamically changing over much shorter timescales, possibly even between simulation time-steps.

3. Simulation Results

3.1. Overview

The results of the simulations confirm those found previously with this model and parameter range and restrictions [Wood and Ackland 2007], demonstrating that the basic mechanism at work is robust to variation in methodological choices. What is striking is how correlated the transitions in the system are to the speed of the individuals, and less dependent on the other parameters in the system. Sample runs are shown in (Fig 1).

[Figure 1 about here.]

Overall the two phases in the system are characterised by a large orientation zone, low blind angle and high speed in the case of the fast, dynamic group whereas the slow groups have a negligible orientation region, a high blind angle and low speed. The blind angle, found to converge independent of strategy to a biologically plausible value of around 80° [Wood and Ackland 2007] is no longer so dependably found in the slower flocks; the result is still present for the case of fast, dynamics flocks but a blind angle of around 180° is selected when a low speed flock is created. By taking the parameters of final state evolved flocks averaged over runs (typically 5, as I have excluded end states where the final state was not representative due to switching) I find that the coefficient of

variation for the speed is approximately 0.3%, whereas for the attraction radius it is an order of magnitude larger (3%) and the radius of attraction is around 20 %. This gives a quantitative handle on the significance of the speed for phase selection.

One concern here is that the speed is bounded in the system. Yet this bounding is made with respect to the predator at the upper limit (modifying this would require co-evolution and energetic considerations, with the probable emergence of Red-Queen type dynamics [Van Valen 1973]) and the turning angle at the lower limit. It is clear from the simulations that although the speeds are pinned at the bounds there is clear selective pressure away from intermediate speeds.

I have also investigated the evolutionary trajectories of the model when the area constraints I impose are removed (Fig 1). This gives seven, rather than five, evolvable parameters. In this case the broad results are preserved: two different flocks types namely slow, compact and fast, dynamic groups are found. This aside there are some marked differences in the evolved flocks – a large attraction radius, as well as high value for both the viewing area and turning angle are now free to be chosen. More notable is that the selected strategy is now the opposite one with respect to mutation. In the unconstrained case low mutation selects slow moving compact groups and high mutation now selects for fast dynamical flocks.

This gives a broad observation of the effect of the evolutionary dynamics and makes it possible for us to focus exclusively on the speed as the phenotypic parameter of most significance. My goal now is to understand whether this is an indirect or direct effect and to relate this to the action of successive predatory events on the group.

3.2. Invasion dynamics

[Figure 2 about here.]

[Figure 3 about here.]

To investigate this dependence on the speed I have constructed an analogue to the pairwise invadability plot, well known in the field of adaptive dynamics. I am interested here in the relative fitness of a group of "invaders" to the resident population. This is simply implemented by creating boids with two different speeds and recording the probability of capture and whether this is greater or smaller than the unbiased removal probability. Care must be taken with this analogy as an assumption of a true PIP is that the invaders do not affect the fitness of the residents – I have no way of verifying this here. The PIP gives a strong indication of the stability's of different phases and likely evolutionary trajectories from a given starting configuration.

This study is restricted to only examine the speed, with plausible intermediate choices of the other parameters; with so many parameters in this model a wider scheme would be beyond the scope of this study. In the simulations described below I adopt the parameter choices shown in table 2.

[Table 2 about here.]

The coarse grained results can be seen in (Fig 2) from where the broadly parabolic shape of the fitness gives an indication of the reasons for the emergence of two differing strategies. It is clear from the large error bars in the plots is there is considerable underlying structure, and examination of the separate invasion speeds is required. The results of this are shown in (Fig 3)-5 What is immediately striking about the PIP's in (Fig 3) are that the unconstrained simulations (lower panel) produce a relatively smooth and simple landscape with gentle ridge giving local stability and a strong dip showing the resilience of faster flocks to the invasion of slower ones. The addition of the area constraint rules, forcing compromise, has a massive impact on the complexity of the structure (upper panel). The plots shown in (Fig 3) also reveal the existence of the salient features that result in the coarse differing outcomes shown in the simulations.

[Figure 4 about here.]

[Figure 5 about here.]

The two significant features present in the plot for the constrained model ((Fig 3), upper panel) are a well defined central ridge, indicating the stability of this configuration to small changes in speed (giving rise to the low variance within the speed distribution), and secondly a local fitness peak where the low speed invaders compete equally with the mid speed residents (the peak is prominently shaped but its height is only marginally greater than the unbiased removal, indistinguishable within the accuracy of this study). To explain these features it is instructive to examine PIPs corresponding to slight alterations in the properties of the evolutionary algorithm and computational setup. In (Fig 4) two plots are shown where the speed of the resident individuals have been made phenotypically heterogeneous – in order to mimic the effect of mutation smearing out the population – by the addition of Gaussian noise to the speeds. This results in the suppression of the local stability of the flock, but the susceptibility to invasion of mid speed flock by low speed ones is maintained. In (Fig 5) similar plots are shown but now showing the reduction in the number of invaders. Now the local stability effects are maintained but the mid-speed instability to low speeds is suppressed. The ability of low speed flocks to resist invasion by high speed is markedly strengthened.

This analysis now allows us to identify the principle mechanisms. When mutation is low the constrained system is dominated by the local ridges that are maintained by low variance in the population. In this case group effects are reduced and the individuals need to flee the predator results in a slow upwards drift in velocity. Conversely, when mutation rate is high, the phenotypic variance increases which reduces this local stabilising effect. The mid-speed group is now subject to destabilisation by low speed individuals which will give a transient evolutionary advantage to low speed individuals. The population may then cycle or excite in this configuration which gives rise to the higher error bars for the speed in this state. Once in the low state the population speed will drift upwards

once more and the behaviour described above will recur on the evolutionary timescales in the simulation. The process is constrained by the heterogeneity in the system precluding the need for invasion; leading to trapping in the low speed state. The effect of the Laplace operator is now also made clear. In the low mutation solution the speed variability is low but there is potential for discontinuous leaping from the local fitness ridge to the mid-speed peak; which would not be likely without the potential for large mutations. A rapid transition of this type can be seen by in the marked dip in the trajectory shown in the (Fig 1). In high mutation states the prevalence of low mutation rate events gives a less variable state than the simple box operator but the trough can now be leaped over rather than traversed, resulting in the sharp transition to the low speed state. The unconstrained simulations are much clearer, the only effect being that the variability in the speed alters the local slopes of the PIP and so high mutation states give rise to a fast group, a low to slow. Presumably this is due to greater manoeuvrability and vigilance potential.

4. Spatial sorting

[Figure 6 about here.]

[Figure 7 about here.]

Our goal is now to describe the origin of these features in terms of group dynamics. To do this I investigate statistics that are related to the structure of the group. This has received surprisingly little attention; even though previous work has analysed these effects in heterogeneous groups utilising rank Spearman techiques [Couzin *et al.*2002]. Here I complement this analysis by examining connected velocity correlation functions, with both the radial distance from centre and the angular position away from the group's forward direction. These two measurements contain significant information about both the position of individuals as a consequence of their properties as well as the groups behaviour and structural form. I define

$$\langle vr \rangle_c = \frac{1}{N} \sum_{i=1}^{N} v_i r_i^{\text{centre}} - \langle v \rangle \langle r^{\text{centre}} \rangle \tag{3}$$

$$\langle v\theta \rangle_c = \frac{1}{N} \sum_{i=1}^{N} v_i \theta_i^{\text{forward}} - \langle v \rangle \langle \theta^{\text{forward}} \rangle \tag{4}$$

as the velocity-radius $\langle vr \rangle_c$ and velocity-angle $\langle v\theta \rangle_c$ connected two-point functions. In the above definitions v_i is the ith individuals velocity, r_i^{centre} is the distance of the ith individual from the group centre and $\theta_i^{\text{forward}}$ is the angle the displacement vector from the centre of the group of the ith individual makes with average directional heading of the group. To summarise their behaviour – if there is no relation between the terms then both functions will be zero; if $\langle vr \rangle$ is positive then fast individuals are on the outside of the group and if it

is negative then the slow individuals are on the outside; if $\langle v\theta \rangle$ is positive then fast individuals are towards the rear of the group and if it is negative then they are towards the front of the group. A simple reading of the situation may give rise to the impression that fitness is related to the distance from the centre, but the reality is more complex: for instance being on the outside of the group can increase your individual vigilance.

I examined these velocity-distance ((Fig 6)) and velocity-angle ((Fig 7)) correlation functions both for the invasion situations described above and for the general case when noise is added to a static group. There is also a strong positive correlation for $\langle vr \rangle_c$ and a strong negative one for $\langle v\theta \rangle_c$ when high speed invaders are introduced to low speed residents – giving a clear indication that the high speed individuals are some distance at the front of a group of this type. This appears to have only a small impact on the fitness, a sign that the two parts of the group are almost independent.

The velocity-distance functions for mid speed residents show a strong positive correlation when low speed invaders are introduced(Fig 6). This implies that it is the residents, and not the invaders, that are on the outside of the group. Furthermore, there are only small correlations between angle and speed (Fig 7) in this regime. This indicates some radial symmetry of the group. It is also compact, either a mill or a torus, where invading individuals are migrating to the centre, giving them improved relative survival chances. An additional feature that emerges from the correlation graphs is the response to low speed invaders as the speed of the residents is reduced – there is a notable transition from the situation described above to one with zero or even negative $\langle vr \rangle$ and a strong negatively correlated $\langle v\theta \rangle_c$. This observation indicates a transition from the milling group to a slow moving dynamic group, with markedly different fitness implications. This result also provides evidence that homogeneity in speed is a necessary property in order to maintain a compact, radially symmetric group.

All of these transitions are smoothed out by both noise and lowering the number of invading individuals. The plot for $\langle v\theta \rangle_c$ is dominated by a peaking along the neutral line (at a value 0.0) implying that any deviation from this point will result in the faster moving individuals being at the front of the group. This is the source of the selection for fast individuals when mutation is small. The velocity-angle correlation function is also reveals additional features if the noise of the resident groups is altered – the central diagonal peak of uniform flocks is rotated onto a particular resident speed, around 3.75 for all values of invasion and is negative elsewhere. This reveals that this speed is the only value where the group is able to form stable compact shapes, where elsewhere is forms linear groups that spread out in time. This is almost certainly not a result of velocity, rather a function of the turning angle in these groups. For this value of the speed the turning angle will be $\approx \pi/3$ which indicates that this is a critical value where stable compact groups can form, i.e. it is not too small that lateral correlations cannot persist, or too large such that the groups are perpetually destabilised.

5. Discussion

Models of collective behaviour are now frequent in scientific literature, across a spectrum of fields, but there is still little attempt to quantitatively match the models to what is observed in nature. The principle finding of this study is to draw attention to one particular feature of current models that has not received sufficient attention, namely the speed and speed distributions of the component individuals despite this being one of the rare features for which there exists sound experimental evidence [Aoki 1980]. In a paper which has had considerable significance in the literature, yet there has been little attempt to fit to, Aoki experimentally measured the velocity profile of individuals *within a group*. He found that the form was a gamma distribution, with probability density function

$$f(x) = \frac{\beta^{\nu}}{\Gamma(\nu)} e^{-\beta x} x^{\nu-1} \tag{5}$$

with numerical parameters $\nu = 1.08 - 3.87$ and $\beta = 0.22 - 0.6$. It should be stressed that these results were obtained from small groups of individuals in experimental conditions; whilst the basic functional shape of the data is clear it is easy to attach too much significance to the details of this curve fit. In particular it is impossible to judge whether this variation is the result of individual preference, ability or instantaneous choice; or a combination of all. Most models simply adopt a single, constant speed for all the individuals. It is furthermore clear that using constant identical velocity for each boid at each time-step promotes phases that whilst mathematically interesting are not physically plausible, notably the flying crystal phases seen in physics based models of aggregation [Viscek *et al.*1995]. If heterogeneity is introduced it is still at the level where each member has its own, constant speed. This creates a confusion between instantaneous speeds and phenotypic capabilities [Wood and Ackland 2007]. An alternative approach of many authors[Huth & Wissel 1992, Inada & Kawachi 2002] is to adopt an instantaneous velocity drawn from Aoki's observed distribution at each time step for each individual. This is dangerous as at each time-step, individual speed autocorrelations in time are destroyed with potentially serious consequences for individual manoeuvring.

This type of inconsistency within the model itself has severe implications for the evolutionary study attempted here. It is clear from both this study and earlier work[Wood and Ackland 2007] that the models of this type have preferences for two distinct collective behaviours when subjected to predatory pressure. Whilst qualitatively interesting, I have been unable to more precisely quantify the mechanism, due to underlying problems with the model rather than the evolutionary dynamics. With the fitness of individuals so tightly coupled to both individual and group speed it has become impossible to decouple what is the dominant response: speed determines both the chances of escape from a strike and the position within the flock. These subtleties lead to complex fitness landscapes, especially when characteristics are constrained, and are the origin of the differing, and surprising, response to mutation seen in this study. It is

regrettable that the precise mechanism as to this transition remains elusive, as it is masked by the models over dependence on speed; rapid transitions in alternate parameters may be more interesting but there is no statistical evidence for them within this study. Nonetheless we can draw one interesting observation from our results - we have clearly shown that the origin of the compact strategy is associated with the relatively high fitness of slower moving prey to faster moving prey when groups with some toroidal characteristics are formed. This is perhaps the origin of the "dutch auction" in speed that leads to the formation of stable highly compact groups in response to extreme predation pressure - bait balls being the most striking example [Parrish *et al.*2002]. I have also uncovered indicative evidence of the transient nature of these configurations.

Following this study, in addition to the speed distributions described at the beginning of this section, I can now highlight two further specific areas that I regard as important for further attention. There is now a significant body of work developing on understanding decision making in small animals [Conradt and Roper 2007]. This degree of analysis, applied to predatory species rather than prey, would provide considerable insight in the understanding of predator tactics and, by extension, strategy [Lima 1995]. Decoupling the target selection process from the chase would also help in understanding the evolutionary pressures, an area where there is already a growing body of work [Tosh et. al. 2006]. Ultimately such studies would enable us to better comprehend the details of predator-prey interactions and give considerable insight into understanding the co-evolution of these species on evolutionary timescales.

Finally, heterogeneity and spatial sorting need to be taken into account in the groups more rigorously and in particular understand how this impacts on individuals leading according to need [Couzin *et al.*2005]. In this article I have utilised correlation functions to expound these results and make the relationship between individual properties and positions clearer. There are implications in my study that suggest effective leadership requires certain components, faster speed, larger blind angle and so forth, that preferentially place the individual into key positions in the group when choices are made. A more extreme interpretation is that leadership is emergent and that a leader is simply an individual with those properties that place it in an influential group position when behavioural choices are made. Current studies typically represent leadership through addition of a goal function and propagation of information flow - the interaction and feedback between these components and other model parameters is not typically included and may be worthy of greater attention. Another area of interest is that some parameters may vary dynamically during the collective motion and those that are fixed for the duration. Significant behavioural differences could be created by, for instance, edge birds increasing their attraction radius, or lowering their orientational radius. Factors such as this need to be understood in terms of empirical findings [Ballerini et. al. 2008, Ballerini et. al. 2008] that find that it is the topological rather than metric structure of the group that is important and that the number of individual interacted with stays constant. This observation is motivated by a simple scaling argument, yet this argument may be deceptive; metric distance may still apply if the zones are strictly hi-

erarchical in nature and are flexible enough that for a wide range of densities the nearest neighbour distances are such that a constant number are found within an orientational radius. If metric models have any future, then they must replicate this result; yet it is far from clear how topological models can self-consistently incorporate attraction, it is either effectively infinite range or artificially truncated (or taken from a metric model).

In this study I have exposed a prominent model in the literature to a large-scale evolutionary study. Although I have uncovered many details about the potential evolutionary mechanisms the principle result is to highlight the shortcomings of the underlying models, and in particular their use of a constant speed, despite empirical evidence to the contrary. I hope that this study will inform the construction of future models that better fit both empirical data and lead to novel *in silico* experiments.

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List of Figures

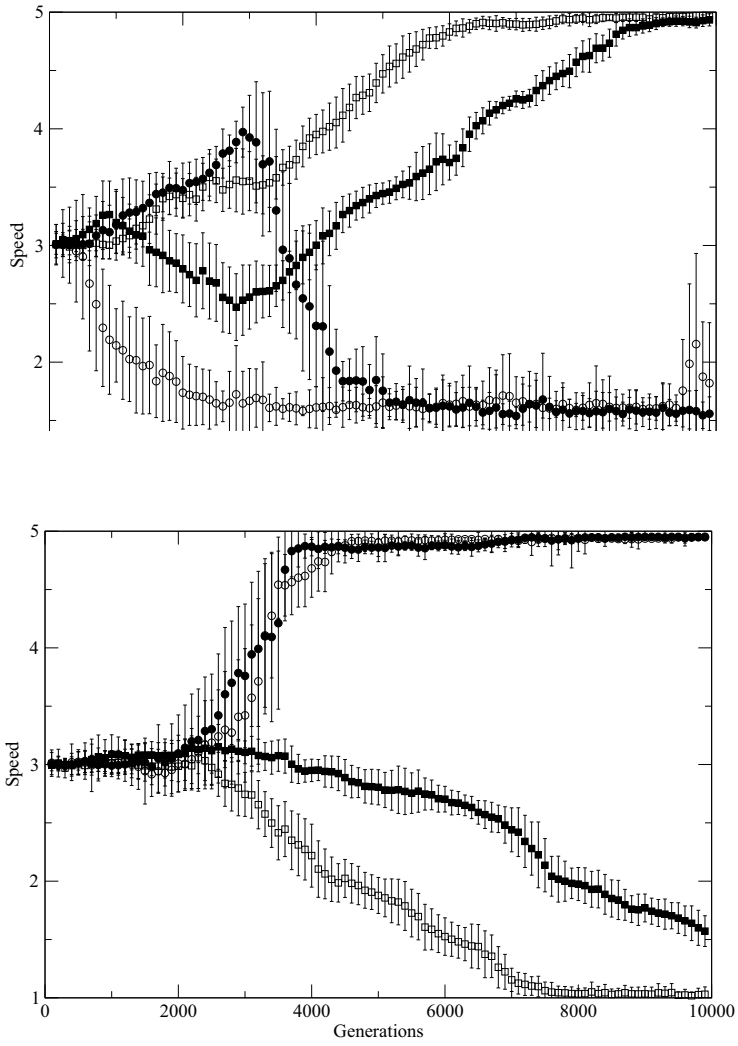

Figure 1: The evolutionary trajectories of groups starting with a common intermediate velocity. The data is binned, dropping 100 data points in between each shown for ease of viewing. The squares show simulations with a low mutation, the circles those with a high mutation. The solid symbols indicate the use of Laplacian mutation operator as apposed to a simple box mutation. The left panel shows simulations with constrained parameters values and the right hand where they are free (see text for more complete definition). The primary result is that the mutation differences cause a switching of the final state. The broad description is identical to that indicated in [Wood and Ackland 2007], with the emergence of either a slow group forming a compact flock shape or a fast group forming a dynamic shape (see text) depending on the mutation. Note that the lack of constraints reverses the impact of mutation. The use of the Laplacian operator complicates the simple selection by increasing the likelihood of switching between the configurations. Indeed other sample runs indicate switching out of the slow compact phase and into the fast phase, a transition that happens extremely quickly in evolutionary time.

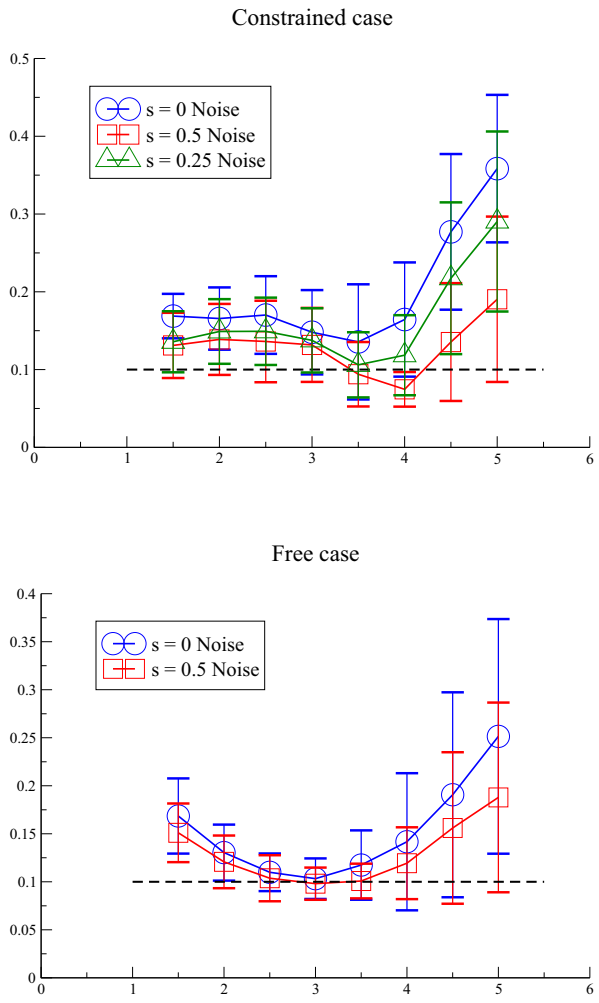

Figure 2: Plot showing a measure of the fitness of an invader relative to the fitness of the resident population given by $p_{\text{capture}}/p_{\text{random}}$ of the invader. The plots show that in both cases there is a parabolic relationship with intermediate speed values subject to invasion. This simple plot illustrates the existence of the two phase seen in the simulations. In both cases the addition of heterogeneity into the resident population increases the fitness of the invader. Each point is averaged both over 5 identical runs each of 16 different invading speeds (at intervals of 0.25 from 1.5 to 5 inclusive), i.e. 80 in total. The wide error-bars indicate the presence of considerable additional structure in the response to different speed invasion which I shall address in later figures.

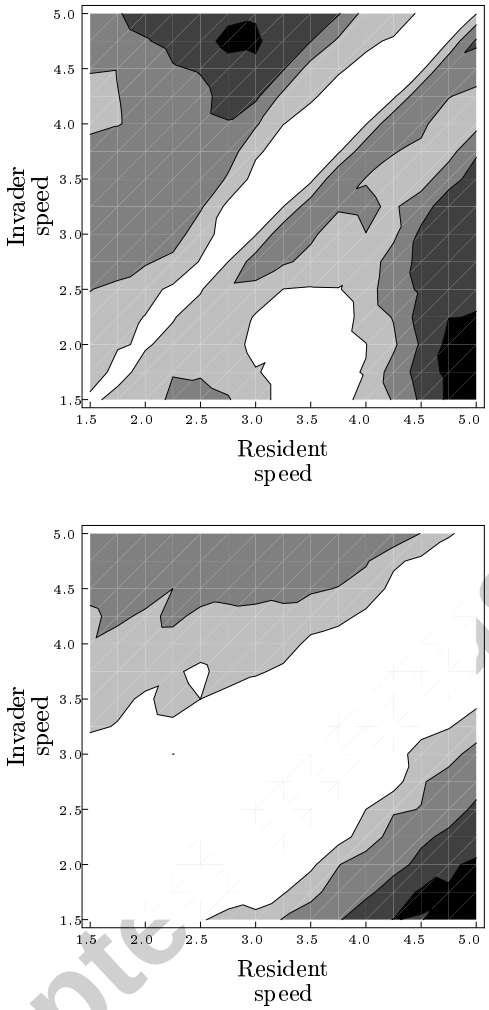

Figure 3: Plot showing a measure of the fitness of an invader relative to the fitness of the resident population again given by $p_{\text{capture}}/p_{\text{random}}$ but here broken down by individual responses at different speeds. The figure is analogous to pairwise invadability plots used in adaptive dynamics. The contour divisions here are qualitative rather than quantitative. White shaded areas indicate areas where the invaders are captured with same probability as a random individual – or better. Increased grey shading corresponds in greater likelihood of invader capture, approximated a unitary factor more for each change in shade (twice as likely, three times as likely etc.). This corresponds to an *increase* in fitness for the resident. In both plots the strong dark area at the lower right corner indicates the (predictable) high fitness of high speed residents to low speed invasion.

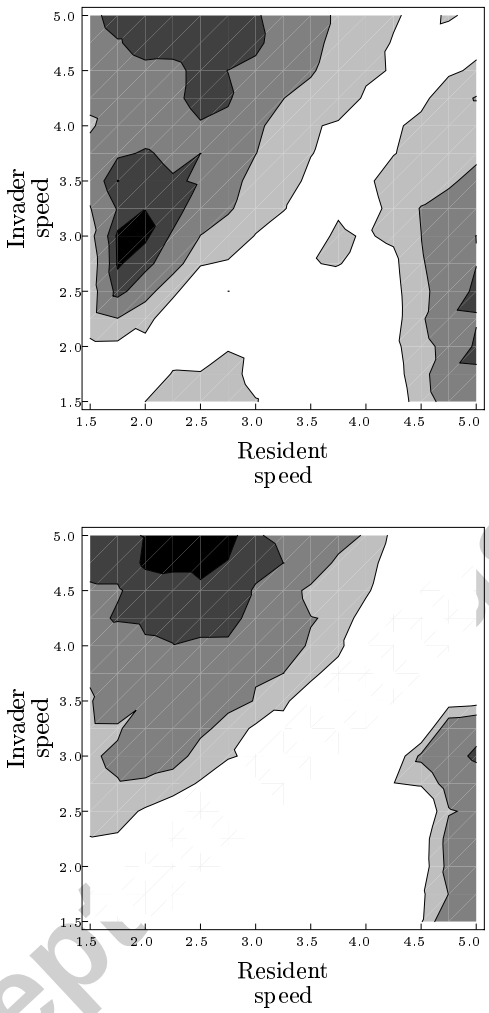

Figure 4: In both these plots the shading is identical to (Fig 3), with white indicating little fitness difference between invader and resident and darker areas increasing resident fitness. The upper plot shows the case where the resident speeds are perturbed by the addition of Gaussian noise of weight 0.25 (i.e. $v_{res} + 0.25N(0,1)$) and the lower with weight 0.5. The spreading of the white areas shows the loss of the local stability endowed by the central ridge. Note also how the fitness of the lower speed flocks is promoted relative to the high speed ones.

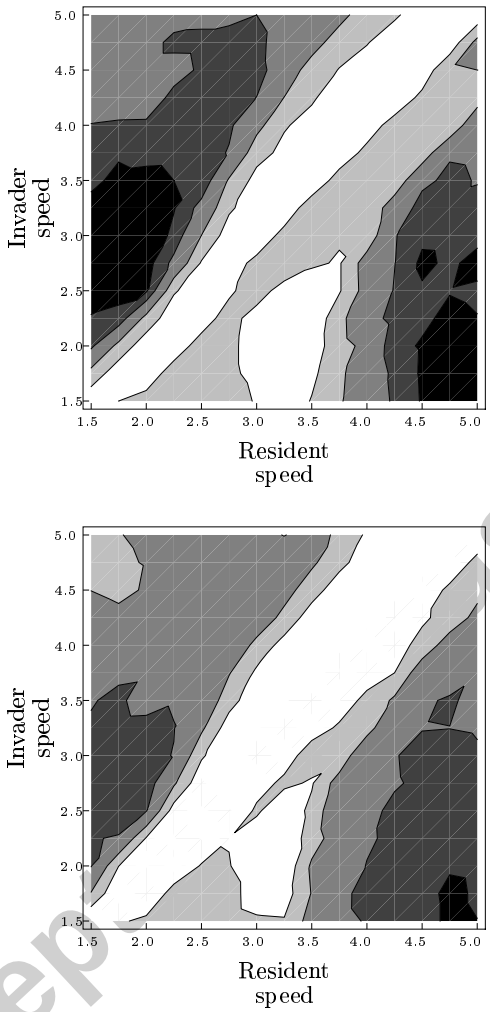

Figure 5: The shading is as described in (Fig 3). The upper plot here shows the fitness landscape for the introduction of 5 invaders (upper) and then 2 invaders (lower). Unlike (Fig 4) the features of the plot are largely unchanged, but the troughs separating them are filled in. The local stability ridge is widened – not surprisingly as less invaders have less impact and the fitness peak is reduced in prominence.

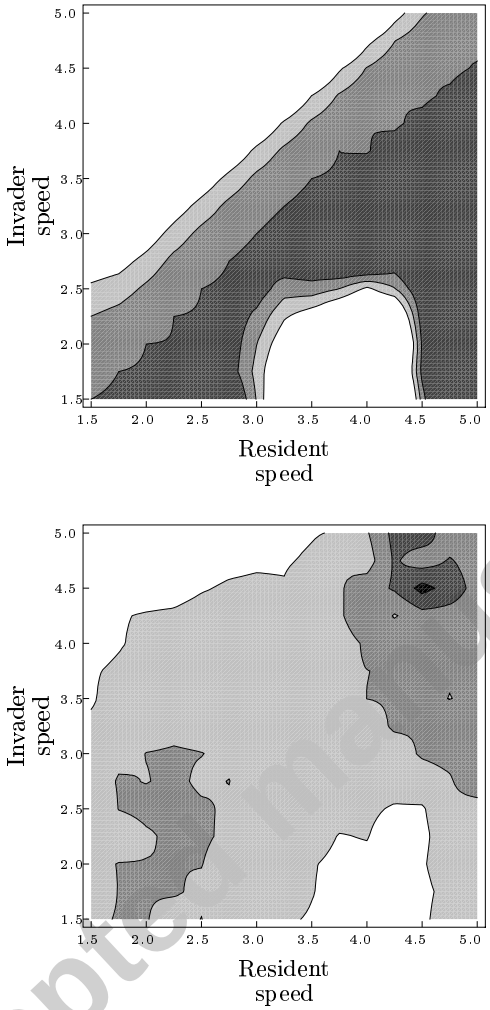

Figure 6: The plot shows the velocity-radius correlation function for the unperturbed system with ten invaders (upper) and the Gaussian perturbed system (with 0.5 weight added to the resident speeds). White indicates positive correlations, dark increasingly lower correlations, but the plot should be regarded as qualitative rather than quantitative. The upper left corner indicates that here the higher speed invaders are clearly at the front of slow moving resident flocks. The prominent feature in the lower part of the plot shows the parameter area were radially symmetric groups may form and how strongly sorted these are with respect to velocity. The lower plot indicates how all these effects are markedly damped, and the overall correlations raised, when phenotypic variation in the speed is added.

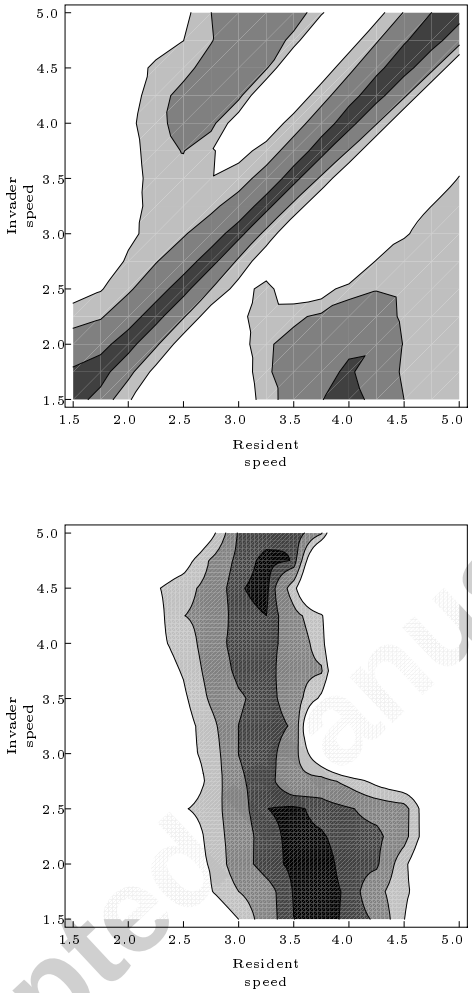

Figure 7: The plot shows the velocity-theta correlation function for the unperturbed system with ten invaders (upper) and the Gaussian perturbed system (with 0.5 weight added to the resident speeds). Once more this is an indicative plot, with white now indicating larger negative values and dark higher values, approaching zero (I have inverted the colour scale for ease of viewing). The upper clearly shows that lack of sorting in the purely homogeneous case along the central diagonal and also in the radially symmetric situation in the lower part of the plot and also potentially in the upper part. The lower plot shows the remarkable rotation of this plot to the radially symmetric group formation being confined to a particular value of the speed.

List of Tables

Table 1: The basic simulation parameters used unless otherwise stated in the text.

Parameter	Symbol	Value or constraint	Notes
System Size	L	240	periodic b.c.
No. of Boids	N	100	
Repulsion Radius	R_r	1	Fixed
Orientation Radius	R_o	$R_r < R_o < R_a$	Evolvable
Attraction Radius	R_a	$R_a > \sqrt{\frac{A_s}{2\pi}}$ or free	Evolvable
Speed	v	$1 < v_i < 5$	Evolvable
Viewing Angle	θ	$\theta < 360°$	$A_s/(R_a^i)^2$ or Evolvable
Turning Angle	ϕ	$\phi < 180°$	$A_m/2(v^i)^2$ or Evolvable
Food Pref.	Ω^f	free	Evolvable
Anti-Predator Pref.	Ω^p	free	Evolvable
Noise	σ	free	Evolvable

Table 2: The simulation parameters used in the section on invasion dynamics. These values are chosen based the on the mean values resulting from the evolutionary simulations. For comparison and due to the extreme dependence on the speed of the states, I have chosen the values uncoupled to the speed and taken this parameter alone to be my indicative parameter of the final state. Each point on each of the diagrams presented in this section is the result of 10^4 simulated predator attacks.

Parameter	Symbol	Value or constraint	Notes
Attraction Radius	R_a	25	
Orientation Radius	R_o	$(R_A + R_R)/2 = 13$	
Speed	v	$1 < v_i < 5$	
Viewing Angle	θ	$3\pi/2$	
Turning Angle	ϕ	$0.1\pi \lessapprox \phi < \pi$	$9\pi/4(v_i)^2$
Anti-Predator Pref.	Ω^p	4	
Noise	σ	0.1	