

# Collective Sensing: How animal groups scale noisy gradients

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## ABSTRACT

In the natural world, individuals constantly face the challenge of acquiring, interpreting and responding to complex sensory information. This is especially challenging when individuals must navigate heterogeneous environments. Recent empirical evidence suggests that animals may deal with this challenge by living in groups and processing information collectively. While these collective properties are manifested at a group level, they are an outcome of decisions made by individuals. In general, it is unclear how selection on behavioural rules adopted by individuals leads to evolution of group level properties such as collective information processing and distributed sensing. In this model, agents follow experimentally inspired decision rules used by schooling golden shiners (*Notemigonus crysoleucas*). Individual behavioural response to the environment along with social response provides groups the ability to filter high frequency spatial noise and collectively track a moving environmental cue. By varying interaction ranges of individuals, I also show an optimum in the inter-individual distance where groups detect large scale patterns and filter noise.

# **INTRODUCTION**

In the early 20th century, Edmund Selous, a naturalist, writer and observer of bird behaviour was enthralled at the sight of a flock of starlings. The birds clearly displayed structural order, even while the flock changed shape and direction. The whole flock appeared to move as a single coherent entity; a living sheet rippling through the sky. The remarkable synchrony displayed by individuals led Selous to conclude that such coordination must arise from thought transfer; that the minds of individuals in the flock must be connected, and that they must communicate using telepathy [7].

*“Each mass of them turned, wheeled, reversed and the order of their flight, changed in one shimmer from brown to grey, from dark to light, as though all the individuals composing them had been component parts of one individual organism. . . They must think collectively, all at the same time, or at least in streaks or patches — a square yard or so of an idea, a flash out of so many brains”.*

*- Edmund Selous (1931) [27]*

Researchers have since turned to more scientific explanations of the phenomenon, hoping to understand both the mechanistic and functional underpinnings of collective behaviour.

## **Functions of collective behaviour**

Collective behaviour is ubiquitous. We see it in the form of a flock of birds weaving through the evening sky; coordinated predator avoidance in fish schools; herds of ungulates migrating across the Serengeti; ants marching in long trails from nest to food and back; a locust swarm raiding crop fields; and even crowds of humans solving tasks collectively. In all these cases, individual identity dissolves, and the group takes on a life of its own.

Traditionally, anti-predation is thought to be among the major drivers of group living [16, 22]. Widely accepted mechanisms to explain such benefits are based on dilution effect [13], confusion effect [20], predator detection [12] and risk abatement [29]. It has also been shown that predators themselves prefer attacking solitary prey as opposed to schooling prey, thus allowing grouping to evolve, even without the prey being able to detect and respond to a predator [19]. However, anti-predation is not the only benefit of living in groups. More recently, it has been shown that group living allows for information pooling and consensus decision making [8, 6]. Behavioural coupling between neighbours allows for waves of information to travel across the group. Acquiring such indirect information allows individuals to respond to sensory stimuli that might otherwise be outside their reach, thus amplifying their effective sensory range. For example, foraging bats eavesdrop on

echolocating calls from group mates to locate prey [10], starling flocks respond to perturbations in any part of the flock [4] and fish schools detect favourable regions in environment by emergent gradient-tracking [2]. In this context, animal groups can be view as an array of sensors; information-processing entities with a collective awareness of their environment [7].

## **Mechanisms underpinning collective behaviour**

Coordinated movement in animal groups is now known to be facilitated by sensory modalities [28, 24, 3, 25]. Individuals acquire high-dimensional sensory information through vision, sound, odour, touch, pressure sensing and/or electroreception. The information is then processed and translated into low-dimensional motor output which manifests as behaviours. Individuals avoid near neighbours, whilst maintaining group cohesion via long range attraction. These aggregations were modelled by Aoki[1] & later by Reynolds [26]. The combination of these rules viz. close range repulsion and long range attraction in combination with intermediate alignment produced a number of life-like behaviours. Couzin et al. [9] extended this model to reproduce various collective states animal groups exhibit (swarming, torus forming and parallel states). The authors also demonstrated transition of groups from one state to another by varying the radii of individuals' zones of alignment and attraction. Similar models were further used to test decision making, information use and leadership in migrating animal groups [8, 15]. In contrast to the three zone model, experimental evidence suggests that individuals exhibit close range repulsion together with long range attraction, and that alignment is an emergent property of the system [21, 18]. In light of these findings, it is necessary to revisit this classical model.

The aim of this project is to use such experimentally inspired behavioural rules to examine how groups navigate a heterogeneous environment. Individuals' response rule to changes in the environment is based on Berdahl et al. [2]. The authors describe emergent gradient-tracking in schooling golden shiners (*Notemigonus crysoleucas*). Shiners exhibit a natural preference for darker regions in space. However, individuals do not possess the ability to track gradients. They slow down in darker regions and speed up in brighter regions. This means that a group moving perpendicular to the direction of gradient will have individuals moving at different speeds across it. In order to maintain group cohesion, faster individuals in the group (in the brighter region) eventually turn towards their slower schoolmates. This results in gradient descent and the group tracking the global optimum. Thus, the group shows phototaxis, an ability lacking in individuals forming it. What Berdahl et al. [2] also found was that larger schools perform better phototaxis in noisy environments.

Along with this environmental rule, I implement a force based social interaction rule

[11]. This captures the fact that alignment is emergent rather than explicit in interaction among fish. The method represents the pairwise social interactions measured by Katz et al. [21].

Individuals are then faced with the task of navigating a noisy gradient to detect a moving gaussian resource peak. The aim of this project is to identify key features of the group (group size, density) and the environment (amplitude and frequency of both noise and the signal) that allows them to filter noise and scale gradients.

Another model examining gradient-tracking was developed by Hein et al. [17] where the authors show that groups match their size to the environmental scale. The authors describe groups to exist in one of three states - station-keeping, cohesive and dispersed states. Each state is separated from the neighbouring states by an abrupt change in potential energy. The authors found that the individuals evolve such that the group is poised at a transitional regime between station-keeping and dispersed phases (see Box 1 for details). The group undergoes a phase-like transition to switch between the two phases to balance exploring and exploiting gradient cues. However, in this model, agents track a moving gaussian peak in an otherwise homogeneous environment. Biological systems are rarely faced with environmental signals in isolation. Cues are inherently overlaid with noise, making detection of the global optimum harder. By overlaying the signal with noise, I create more realistic conditions where groups are required to filter noise to detect the underlying signal.

# **METHODS**

In this project, the movement of each individual is modelled using two behavioural rules: a social response rule and an environmental response rule. Both rules are based on experimental data on movement decisions made by freely swimming golden shiners (*Notemigonus crysoleucas*).

## Social response rule

To capture the features of observed social interactions among fish, the acceleration of individuals is modelled using a force-based method designed to represent the pairwise social interactions measured by Katz et al. [21]. As evidenced by Katz et al. [21] and Herbert-Read et al. [18], individuals in our model experience no explicit alignment. The property emerges in the system from close-range repulsion and long-range attraction in combination with self-propulsion.

The focal individual experiences a repulsive force from near-neighbours. This is interpreted as individuals expressing a need for personal space. As the distance between the focal individual and its neighbours increases, repulsion force experienced by the focal individual gradually decreases and it then displays attraction to neighbours. This helps maintain social cohesion within the group. Each individual has a perception range ( $l_{max}$ ) which represents sensory limitation of individuals. This determines the maximum distance till which they interact with near neighbours. A schematic of the social interaction forces is shown in Figure 1

The  $i^{th}$  individual responds to neighbours within  $l_{max}$  using the following rule (described by [11]):

$$m \frac{dv_{s,i}}{dt} = -\vec{\nabla} \left[ \sum_{j \in N_i} C_r \exp\left(-\frac{|x_i - x_j|}{l_r}\right) - C_a \exp\left(-\frac{|x_i - x_j|}{l_a}\right) \right] \quad (1)$$

## Environmental response rule

In order to model response of individuals to their environment, an environmental response rule is imposed based on experimental data from Berdahl et al. [2]. The authors found no signs of gradient detection by individual fish. Individuals respond to absolute light levels at their location; they accelerate in bright regions and decelerate in darker regions of the

environment. To capture this response, the environmental response of the  $i$ th individual was defined as a function of resource value at its location in space:

$$m \frac{dv_{e,i}}{dt} = (\psi(R(x_i)) - \eta |v_i|^2) \frac{v_i}{|v_i|} \quad (2)$$

Thus, each individual's movement is governed by two response rules: social and environmental. Combining the two allows for estimation of the force felt by each individual navigating through a noisy environment. Therefore, we have two equations that govern movement of each individual.

$$\frac{dx_i}{dt} = v_i \quad (3)$$

$$\frac{dv_i}{dt} = \frac{dv_{s,i}}{dt} + \frac{dv_{e,i}}{dt} \quad (4)$$

When travelling across a light gradient, the differences in individual speeds (attributed by response to the environment) in combination with desire to maintain social cohesion causes faster individuals to turn towards their slower school-mates. This allows groups to collectively descend light gradients.

## Environmental Gradient

The environmental signal itself is set up as a gradient depicted by a 2D gaussian peak. In order to mimic conditions experienced by biological entities, the peak is overlaid with a simplex noise (refer box 2) environment based on Stefan Gustavson's [14] implementation of the improved Perlin noise [23]. Creating a time varying noise function is computationally expensive. Hence, the gaussian resource peak is made to move in space with a temporally stationary spatial noise.

In order to make the noise function periodic, I use a function that samples the noise function four times from four different locations. It then mixes these samples, weighted by their proximity to edges. This effectively blends four regions of noise into one resulting in a noise function where the edges match up well and the function remains continuous. However, the blending process still produces certain artifacts. Due to the way the weighting is done, samples in the centre of the window in a more even mix of the four than samples near the edge. This creates low-frequency artifacts.

## Box 2: Simplex Noise

Simplex noise is a procedural noise generating algorithm developed by Ken Perlin in 2001 [23]. This was created as an improvement on the classical perlin noise, which won Ken the academy award and has since been ubiquitous and the standard for creating procedural noise in computer graphics. Perlin noise has gradients arranged on a square grid (cube for 3D and a hypercube for higher dimensions). A gradient vector is obtained from each corner of the grid. The value at a given point is obtained by taking gradients from the surrounding grid points and computing the contribution of each. Perlin noise generates more grids with more corners than necessary. In case of simplex noise, the grid in  $N$  dimensions is composed of  $N+1$  points. In 2D, the shape is equilateral triangles. The major advantage of a simplex is that it has fewer corners than a hypercube in the same dimensional space. Therefore, the computational complexity in an  $N$  dimensional space is of the order  $O(N^2)$  as opposed to  $O(2N)$ . In this project, we use a C++ implementation of simplex noise described by Stefan Gustavson [14].

There are four major steps to implement the simplex noise:

1. Find surrounding corners
2. Get their respective gradients
3. Get contribution of each corner by applying a radial attenuation function
4. Sum up the contributions

Each step is described in further detail below. The description assumes a 2D simplex noise implementation.

1. In perlin noise, finding the surrounding corners is easy. Given a point, the four corner points are  $(int)i$ ,  $(int)j$ ,  $(int)i+1$  and  $(int)j+1$ . However, determining these corner points becomes harder in case of a simplex grid, where grid cells are equilateral triangles (Figure B1).

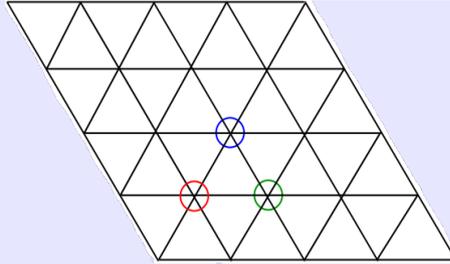


Figure B1: 2D simplex grid

The way to deal with this is to apply a skewing function to the grid. The skewing function extends the grid along its major axis such that each squashed hypercube of  $N!$  simplices transforms to a regular, axis-aligned  $N$ -dimensional hypercube. Figure B2 below shows a skewed 2D simplex grid.

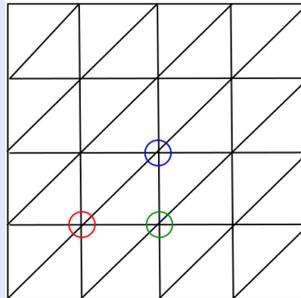


Figure B2: 2D simplex grid skewed to resemble a square grid

Skewing the grid gives it the semblance of a square grid. The first lower left (red) and upper right corners (blue) are easy to get from here. What is of concern is whether the point of interest lies in the upper or the lower triangle. By comparing the fractional part of  $X$  and  $Y$ , one can tell which triangle the point lies in. If the fractional part of  $X$  is greater than the fractional part of  $Y$ , the point is in the lower triangle. Otherwise, the point is in the upper triangle (shown in Figure B3).

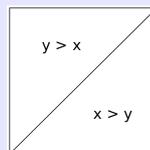


Figure B3: Location of our point of concern can be determined based on its  $x$  and  $y$  coordinates in a skewed simplex grid

2. Once coordinates of the surrounding corners is obtained, each corner is assigned a pseudorandom gradient vectors of length 1. A pseudorandom gradient is one that

has the appearance of randomness, but with the important consideration that it always returns the same gradient for the same grid point, every time it's calculated. It's also important that every direction has an equal chance of being picked. This is ensured by hashing simplex vertices to predefined gradient vectors.

3. A radial attenuation function is then used to determine contribution of each corner to the point of interest. In order to do this, we first calculate the attenuation radius ( $r$ ).

$$r = 0.5 - \Delta x^2 - \Delta y^2$$

where,  $\Delta x$  and  $\Delta y$  are distances along the x and y axes of the point of interest from the concerned vertex.

If the radius results in a negative value, the contribution of that corner is set to zero. If the value obtained is greater than zero, the contribution of that corner is evaluated as

$$n = r^4 * \text{dot product}(\langle \text{gradient}_x, \text{gradient}_y \rangle, \langle \Delta x, \Delta y \rangle)$$

where  $\text{dot}(x, y)$  represents the dot product of vector x with vector y and gradient is the gradient vector obtained for the corner in step 2.

4. Contribution of each corner is then summed up to obtain noise value at the concerned point. Sample images of simplex noise is shown in multiple frequencies below (Figure B4)

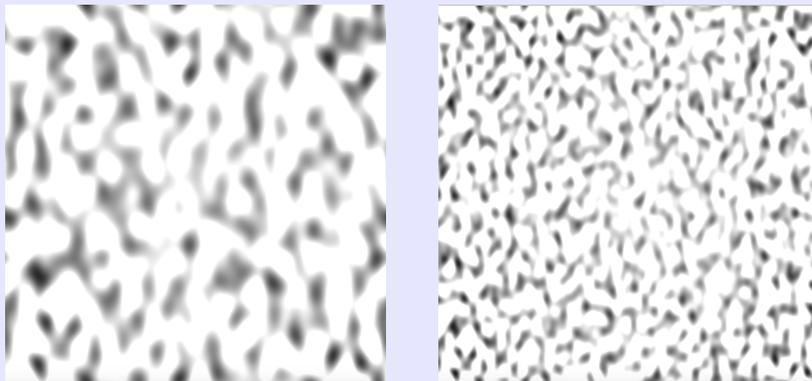


Figure B4: Sample images of simplex noise at two frequencies

## Agent based model

Individuals based simulations were used to analyse gradient-tracking by fish schools in noisy environments. The simulation was coded in C++ using Cinder for the graphical framework.

Each simulation is comprised of individuals (following the social and environmental rules) challenged with the task of filtering noise and tracking large scale environmental gradients. Efficient gradient tracking leads to groups spending more time in darker regions. Therefore, the amount of time individuals spent in darker regions was considered as a proxy for fitness. The signal to be detected was a moving gaussian peak placed in the middle of the window at the start of the simulation. The velocity of the peak was fixed across simulations. A list of static parameters used in the simulation is provided in Table 1.

Self-propulsion ( $\psi_0$ ) and individuals' response to changes in the environment ( $\psi_1$ ) were varied across simulations to plot a fitness landscape. Multiple fitness landscapes were generated for varying noise frequencies. Once the region in parameter space (self-propulsion and response to environment) for optimal gradient-tracking was identified, I varied length scale of the group keeping everything else constant. This was used to establish a relationship between the length scale of the group and its gradient-tracking ability. Table 2 contains a list of dynamic parameters and the values they take between simulations. An average of forty replicate runs was used to obtain fitness value for a given combination of parameters.

# **RESULTS**

Organisms were found to use one of two strategies to maximally exploit resource peaks in their environment. Relative acceleration due to self-propulsion with respect to social attraction determines which strategy individuals use.

- (i) Search strategy: Individuals using the search strategy increase their chances of finding an environmental cue by increasing their search rate. These individuals maximise their self-propulsion, thus exploring a larger region of space in a given time interval. When they lose a moving resource peak, individuals using this strategy leave quickly to try and find another peak in the environment. However, the need to explore their surroundings faster leads to these individuals being unable to effectively use social information, and hence, tracking a moving resource peak (Movie 1).
- (ii) Tracking strategy: A second choice would be to move slower and use social information from near neighbours. Individuals that use this strategy can track a moving resource peak using social information from neighbours already on it. Users of this strategy make the most of found resource patches rather than searching for new ones (Movie 2).

In a homogeneous environment, groups using the tracking strategy performed much better than groups using the search strategy. Figure 2 shows that an optimum exists in the fitness landscape. This is the region in parameter space where individuals maximise fitness by using social information to track a moving resource peak. A visualisation of individuals (in this region in parameter space) is shown in Movie 2.

With increasing self-propulsion, groups switch from the tracking to the search strategy. Movie 1 shows a region in parameter space where groups use the search strategy. Individuals here have increased self-propulsion, but their response to changes in the environment is increased proportionately i.e. the ratio of response to changes in environment to the self-propulsion ( $\psi_1/\psi_0$ ) is kept constant.

## **Gradient-tracking in noisy environments**

Once a fitness optimum was established, individuals were faced with the same gradient-tracking task in a noisy environment. Figure 3 depicts fitness landscapes for varying noise frequencies (increasing frequency from left to right). There is no optimum strategy in the parameter space following the introduction of noise. This suggests the loss of gradient-tracking in the presence of noise. In this case, adopting the search strategy gives individuals a slight benefit over the tracking strategy. Movie 3 shows loss of gradient tracking in noisy environments. However, reducing group density by manipulating the interaction range (repulsion and attraction) of individuals restored gradient tracking (Figure 4; Movie

4). Figure 5 depicts the relationship between school density and fitness at parameter conditions where groups exhibit gradient-climbing and noise-filtering. A quadratic model fit to the data indicates presence of an optimum density where individuals maximise their fitness.

# **DISCUSSION**

The aim of this project is to determine how groups filter noise and scale global peaks in environmental gradients. We found that noise-filtering in such animal collectives is density dependent. Groups have an optimal density (or inter-individual spacing) at which they filter noise to track large scale gradients in their environment.

When exploring a homogeneous environment, individuals must converge to a single strategy that will help maximise their fitness (Figure 2). This optimum in the fitness landscape represents a trade-off between exploring the environment and exploiting found resources. On one hand, the rate of resource encounter increases with preferred speed of the individual (exploration rate increases with higher  $\psi_0$ ; search strategy). A high  $\psi_1$  ensures that individuals with a high exploration rate stop in areas rich in resources. On the other hand, once an individual is near a resource peak, social interactions allow it to track the peak as it moves. In this case, individuals with low  $\psi_0$  and  $\psi_1$  perform better at locating a lost peak (tracking strategy). The region below the diagonal in all fitness landscapes are parameter conditions where deceleration exhibited by individuals is insufficient for them to stop even at the global resource peak.

In nature, environmental cues are inherently overlaid with noise. In addition to tracking a moving resource peak, individuals have to filter such noise to avoid residing in sub-optimal resource peaks in the environment. Since individuals are unable to detect gradients in their environment, filtering noise also requires them to make use of social information, thus encouraging them to use the tracking strategy.

In order to effectively filter noise, groups are required to span across areas larger than the scale of the noise, yet smaller than the scale of the signal. The area spanned by the group can be modified in two ways: (i) by varying group size and (ii) by varying density of the group. Figure 3 and Figure 4 are fitness landscapes for dense and rare schools faced with the task of navigating noisy environments. The denser school was unable to filter noise and hence, performed poorly in the gradient-tracking task (Figure 3; Movie 3) while the rarer school spanning larger areas effectively filtered noise to track the underlying resource gradient (Figure 4; Movie 4). However, any further increase in the interaction range of individuals would result in groups filtering the signal as well as the noise. Figure 5 shows the relationship between pairwise inter-individual spacing (distance between pairs of interacting individuals experiencing zero force or minimal potential energy) and average fitness of the population. Dense schools are unable to filter noise in their environment resulting in inefficient gradient-tracking. Rare schools filter the environmental cue along with noise. Hence, there is an optimal school density that depends on the scale of the signal and the noise.

A systematic exploration of the three length scales (signal, noise and group) is required to confirm claims of group density affecting gradient-tracking. School density was varied

by varying repulsion ( $l_r$ ) and attraction ( $l_a$ ) length scales of individuals. I also varied the perception range ( $l_{max}$ ) of individuals to ensure the ratio of repulsive to attractive forces was maintained. However, the above procedure not only increases inter-individual spacing (decreases density), but also increases the distance at which individuals respond to each other. This might be true in the middle of the group where increasing density reduces perception range due to occlusion from conspecifics. But individuals at the edge of the school should have the same perception range outside the school.

It is also important to note that all simulations assume no depletion of the resource once individuals arrive at the peak. We speculate that using the search strategy might prove better in case of a fast depleting resource. However, using the search strategy isolates individuals from group mates. Such isolation might prove costly in species with high predation rates [13]. Further, high self-propulsion also involves higher energetic costs.

Such simple and robust rules may be used by animals to track large-scale gradients during migration events. However, groups are required to span such large distances to detect these gradients. Our work suggests that the ability of groups to respond to environmental information may drop as the population size decreases and groups start to fragment.

## **Future Directions**

The exploration-exploitation trade-off is at the heart of decision-making problems [5]. This model demonstrates that distributed sensing and collective computation may allow animals to effectively manage this trade-off. An evolutionary model may help gain further understanding into multiple strategies that individuals may use in a frequency-dependent manner. For example, too many individuals on the resource peak may result in a few individuals adopting the search strategy to exploit the noise peaks. The next step in this project would be to build an evolutionary framework for the model. Apart from this, an alternative way to implement periodic simplex noise needs to be explored in order to avoid low frequency artifacts. By varying the payoff for individuals exploiting the signal or the noise, we could recreate a scenarios where anthropogenic noise may hinder gradient detection. For example, industrial waste dumped in oceans may contain chemicals that exude resource odours (thus serving as noise) but may provide no fitness benefits to individuals that track it.

# **FIGURES**

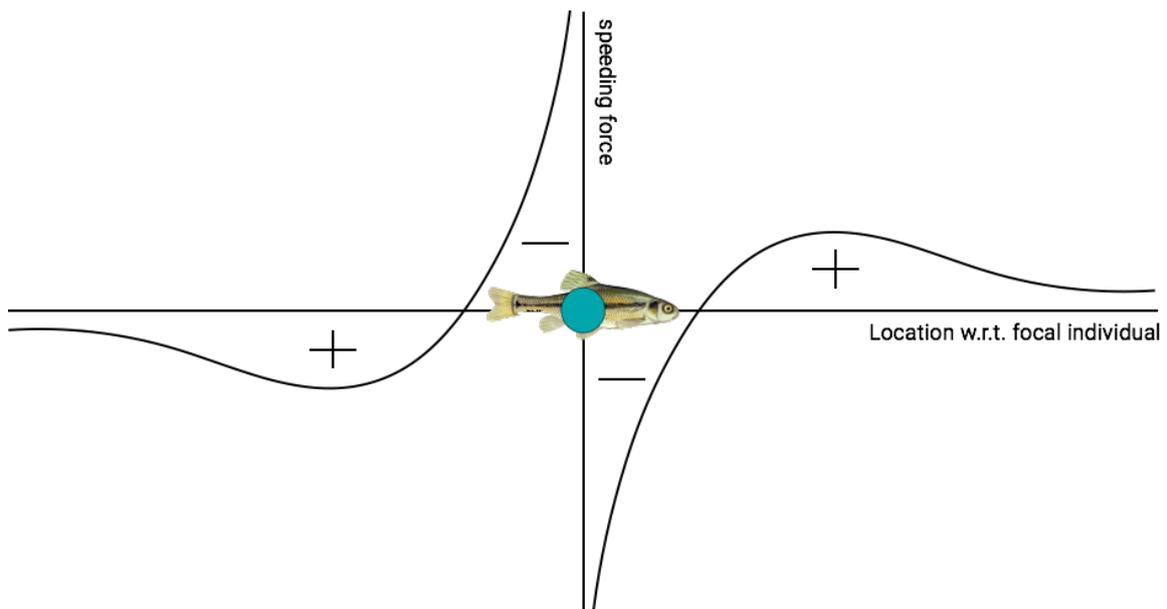


Figure 1: Speeding force as a function of location of a single neighbour. The focal fish is located at the origin facing right. A minus sign indicates repulsion whereas a plus sign indicates attraction. Therefore, the focal fish depicts close range repulsion and long range attraction [21, 18]. A positive speeding force indicates acceleration of the focal fish while negative speeding force indicates deceleration. This is an outcome of social forces described above

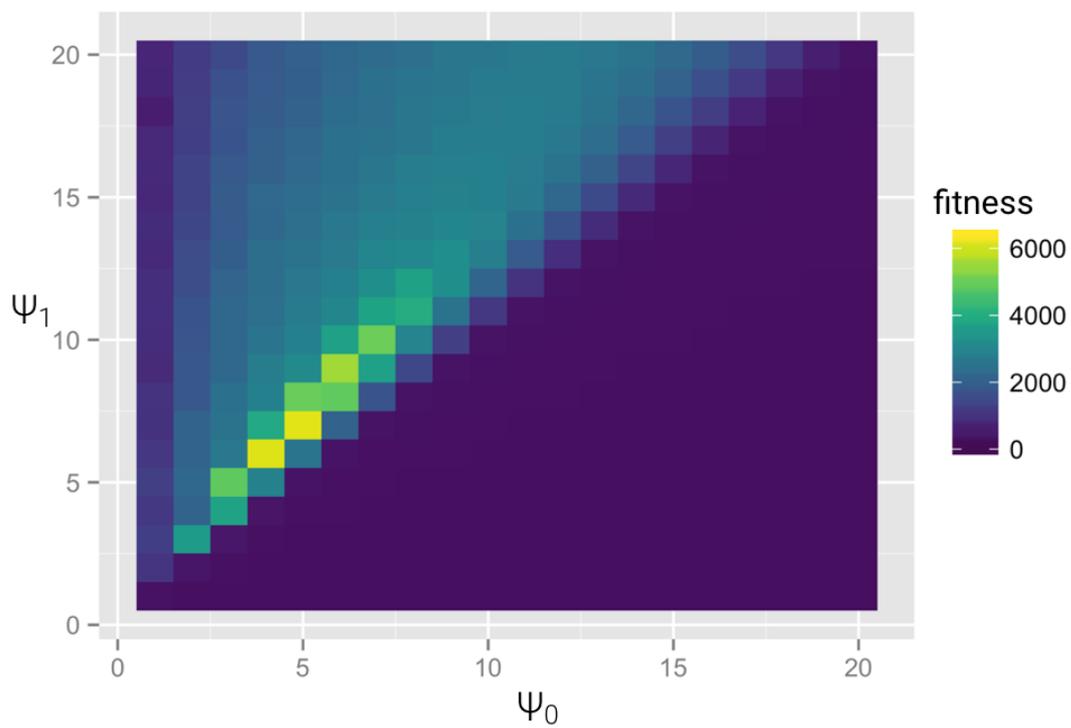


Figure 2: Fitness landscape for individuals trying to detect a moving gaussian peak in a noiseless environment. Observed peak in the landscape is the region of optimal gradient-tracking. This is the region in parameter space described by Hein et al. (in press) as being in a critical regime between station-keeping and dispersed phases

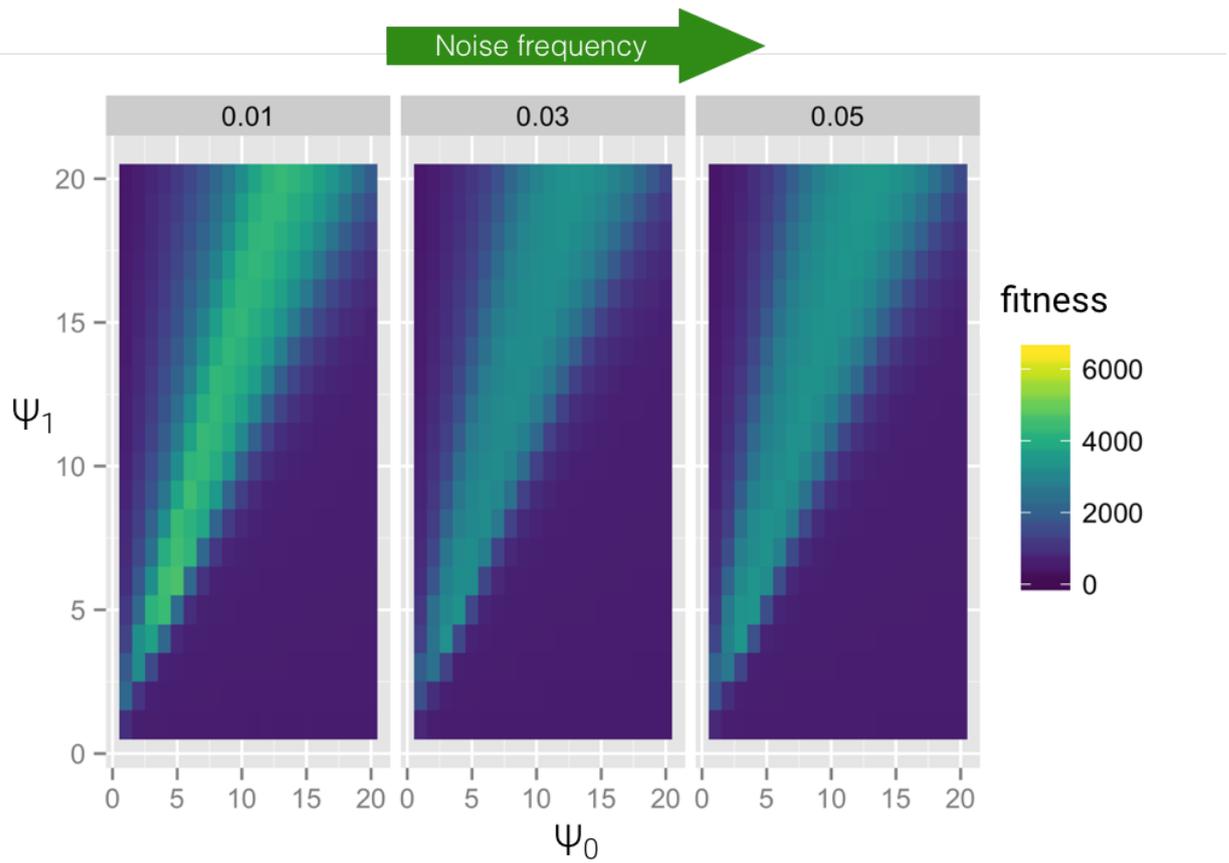


Figure 3: Fitness landscape for individuals trying to detect a moving gaussian peak in a noisy environment. We observe that there is no peak in the fitness landscape once noise is introduced. This suggests that groups are unable to track a moving gaussian peak in a noisy environment

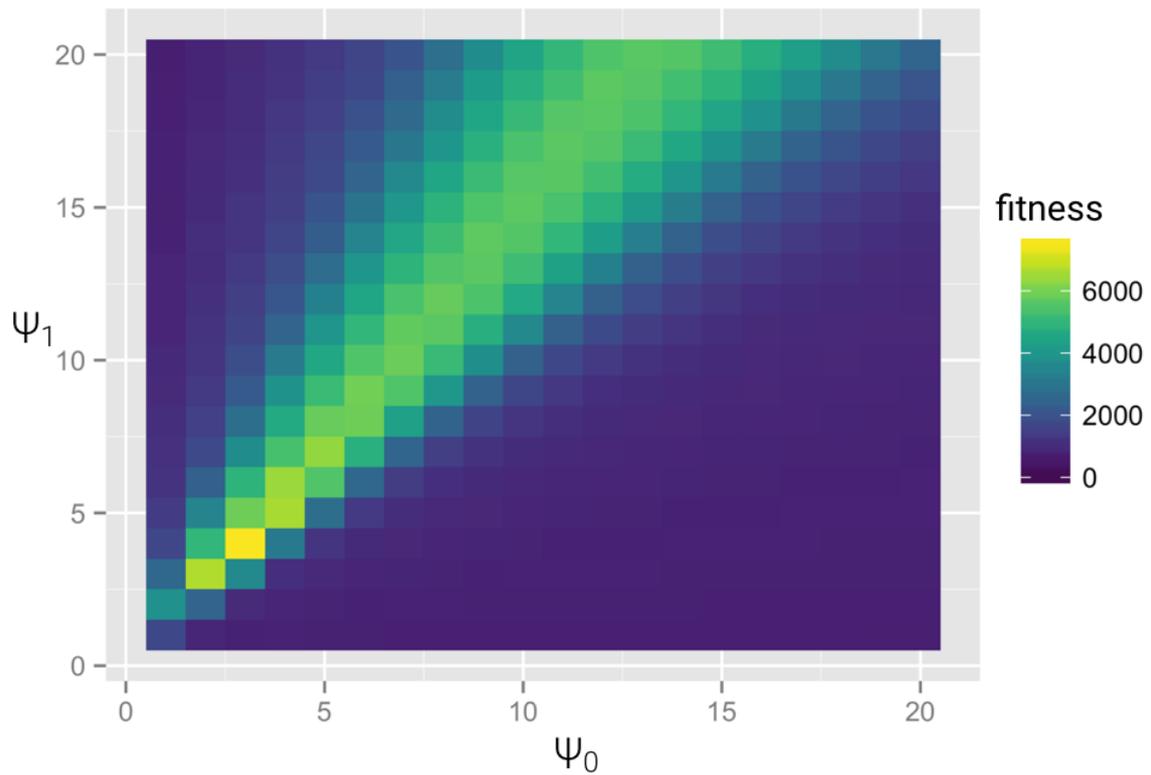


Figure 4: Fitness landscape for individuals trying to detect a moving gaussian peak in a noisy environment. This graph is identical to the first noise condition in 3 except density of the school. Reduced group density allowed groups to filter noise and track large scale gradients in their environment.

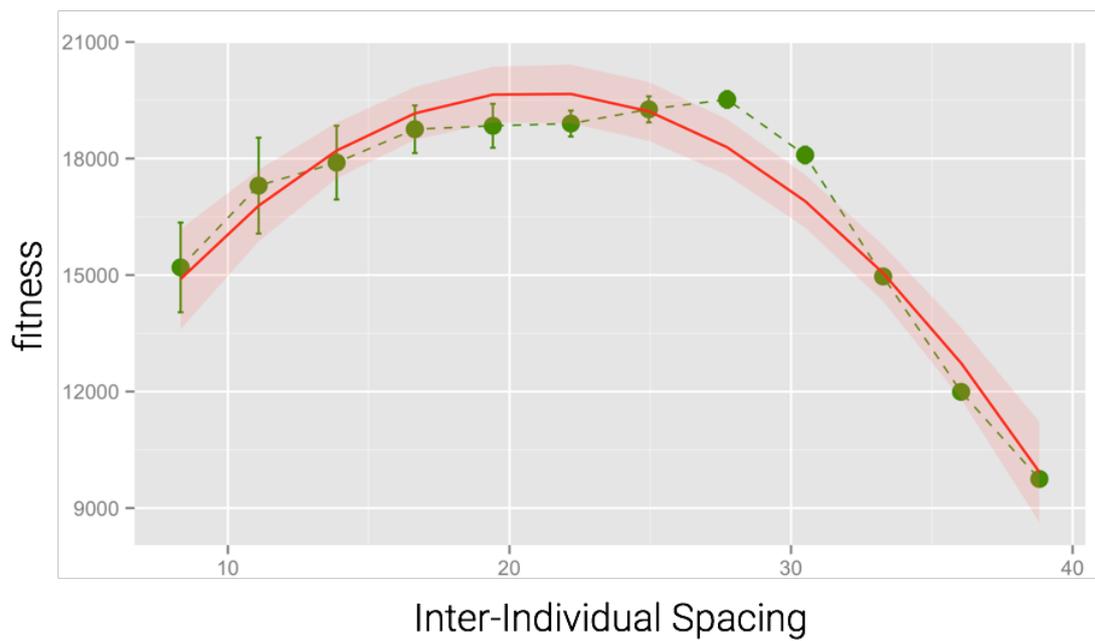


Figure 5: Fitness and a function of inter-individual spacing (distance between pairs of interacting individuals experiencing zero force or minimal potential energy). The data points show mean fitness over simulations and the error bars show twice the standard error. The solid red line is a quadratic model fit to the data, and the shaded region is its 95% confidence interval.

# **TABLES**

Table 1: Summary of static model parameters with the value each took through simulations

Static Parameters List		
Symbol	Meaning	Value
$A_n$	Noise amplitude	1
$A_s$	Signal amplitude	1
$\mu_{se}$	Mean sensory noise	0
$\sigma_{se}$	Standard deviation of sensory noise	0.05
$\eta$	Damping coefficient based on individual's speed	1
$C_r$	Amplitude of repulsive potential	150
$C_a$	Amplitude of attractive potential	75
$\tau$	Timestep	0.05

Table 2: Summary of manipulated model parameters with the range of values each took through simulations

Dynamic Parameters List		
Symbol	Meaning	Value
$\Psi_0$	Self-propulsion of individuals	1 - 20
$\Psi_1$	Individual's response to changes in environmental cues	1 - 20
$\nu_n$	Noise frequency	0 - 0.05
$\sigma_s^*$	Standard deviation of the gaussian signal	40, 80*
$l_r^*$	Range of repulsive potential	50, 10*
$l_a^*$	Range of attractive potential	10, 20*
$l_{max}^*$	Perception range of individuals	25, 50*

\*These parameters were varied for density control of schools (values used are also marked with an asterisk)

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