Collective gradient sensing in fish schools

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Throughout the animal kingdom, animals frequently benefit from living in groups. Models of collective behaviour show that simple local interactions are sufficient to generate group morphologies found in nature (swarms, flocks and mills). However, individuals also interact with the complex noisy environment in which they live. In this work, we experimentally investigate the group performance in navigating a noisy light gradient of two unrelated freshwater species: golden shiners (Notemigonus crysoleucas) and rummy nose tetra (Hemigrammus bleheri). We find that tetras outperform shiners due to their innate individual ability to sense the environmental gradient. Using numerical simulations, we examine how group performance depends on the relative weight of social and environmental information. Our results highlight the importance of balancing of social and environmental information to promote optimal group morphologies and performance.

I. INTRODUCTION

Collective animal behaviour arises from self-organising social interactions among individuals. While the functional form of these interactions is not trivial to determine from experiments, models have shown that simple local social interactions consisting of rules such as repulsion, alignment and attraction are sufficient to generate observed group morphologies, such as swarms, flocks and mills. However, in nature, individuals must balance social information with individually acquired environmental information.

Social interactions benefit group members in diverse ways. Living in groups has been shown to increase foraging ability and reduce predation risk through collective vigilance or escape waves. Individuals can also use social information to help navigate
noisy environmental gradients\textsuperscript{18-20}, where individuals may benefit from sharing information to overcome inaccurate estimates which is often called ‘wisdom of the crowd’\textsuperscript{21} or the ‘many wrongs’ principle\textsuperscript{22-24}. For each of these benefits, individuals combine social and environmental information which enhances information processing\textsuperscript{11}, possibly leading to emergent collective intelligence\textsuperscript{20,25,26}.

However, social benefits are weighed against possible downsides\textsuperscript{27,28}, such as de-valued individual information\textsuperscript{27} and decreased sensitivity to changing environments\textsuperscript{29}. Individuals must weigh information gathered from their senses along with social information\textsuperscript{30} or become isolated and face a greater risk of predation\textsuperscript{9,31,32}.

Despite the large number of studies on collective behaviour, there is little empirical or numerical work connecting group performance with the interplay of individual preference on social and environmental information. In a recent study, Berdahl et. al\textsuperscript{20} examined how a school of golden shiners (\textit{Notemigonus crysoleucas}) collectively navigated a noisy environment (a dynamic light field). While individual golden shiners could not detect the environmental gradient, the school was able to collectively swim toward darker waters. The emergent sensing arose from social interactions governed by a simple rule: golden shiners swim faster in bright regions and slower in dark regions. However, many animals, even those of microscopic scales such as bacteria\textsuperscript{33}, are able to sense environmental gradients.

In this work, we investigate the interplay of social and environmental information and how it impacts group performance. Building on recent work by Berdahl et al\textsuperscript{20}, our study combines empirical data with numerical simulations to examine the performance of schools of fish in navigating dynamic light fields. We experimentally examined group gradient sensing ability in two different species of freshwater fish: golden shiners (\textit{Notemigonus crysoleucas}) and rummy nose tetra (\textit{Hemigrammus bleheri}). While we find golden shiners are not able to sense the environmental gradient but are able to collectively find darker regions using an emergent sensing as Berdahl et al\textsuperscript{20}, the rummy nose tetras out-performed the shiners. This was due to the tetras individual ability to sense the light gradient. We propose a model based on the light intensity dependent speed-modulation proposed in the Couzin-Berdahl model\textsuperscript{20}. Our model includes an additional gradient sensing term that can be tuned to investigate the interplay of environmental and social information and its effect on group performance.

Our results show that while an individual’s ability to sense gradients generally improves the group’s performance, there are downsides. With greater weight given to environmental
Figure 1 | (Left) A schematic of the apparatus showing the infrared camera and projector placed overhead the experimental tank. The tank is lit from below with several infrared lights. (Right) The silhouettes of a group of 32 tetras are superimposed on the dynamic light field through which they navigate. The image is cropped, showing only a small region of the larger tank to illustrate the scale of dark spot to the body length of a fish.

information, the strength of social interactions decreases leading to larger nearest neighbour distance, eventually fragmenting the school. However, by balancing social and environmental information, the nearest neighbour distance can be minimised.

The relative gradient sensing weight that minimises nearest neighbour distance avoids relying too much on one source of information and produces simulations that agree with our experimental data for rummy nose tetras.

II. MATERIALS AND METHODS

A. Husbandry

We studied the gradient sensing performance of schools of golden shiners (*Notemigonus crysoleucas*) and rummy nose tetras (*Hemigrammus bleheri*) in a laboratory. While both are freshwater fish that prefer to school in dark shallow water, shiners (a cyprinid found in cool waters of eastern North America) and tetras (a characin found in the tropical waters
of Amazon Basin of Brazil and Peru) require different water chemistry.

The golden shiners *N. crysoleucas* were acquired from Anderson Minnows. We kept approximately 500 juvenile shiners in three 30 gallon home tanks (∼ 150 in each tank) using de-chlorinated, aerated, and filtered tap-water kept at 21°C. Water changes of 30% were done twice weekly. Shiners were 5.3 ± 0.5cm in length.

The rummy nose tetras, *H. bleheri*, were acquired from Cichlid Exchange. We kept approximately 200 tetras in two 40 gallon home tanks (100 in each) at a constant temperature of 27.0 ± 0.5°C in a 1:3 de-chlorinated tap water to reverse osmosis water that was aerated and filtered. The RO water diluted the pH and gH of the tap water to 6.8 ± 0.2 and 100 ± 20ppm, respectively. Water changes of 20% were done once a week. Tetras were 3.4 ± 0.5 cm in length.

The home tanks for both species were illuminated with 12 h of light and 12 h of darkness per day. Both were fed a mix of crushed TetraMin flakes, Hikari brine shrimp, micro pellets, and freeze-dried blood worms four times a day. Before each experimental trial, fish were gently netted from their home tanks an hour after their first feeding and transferred to the experimental tank. We ensured that fish were not used in experiments on consecutive days by using a rotating schedule to select which home tank to gather fish. Fish were appropriately acclimatised to the water in the experimental tank before experiments took place. Further husbandry details are outlined in the Supplementary information.

**B. Experimental setup**

We conducted experiments with golden shiners and rummy nose tetra in a quasi two-dimensional acrylic tank (183 × 102 cm, 8 cm water depth).

Videos of schooling events were captured via a USB3 Point Grey camera mounted 180 cm above the tank which was back-lit by 850nm infrared LEDs positioned beneath the tank. The videos were captured in 2048 × 1280px at 30 frames per second by the camera which was hardware triggered to synchronise with the projected light field. The dynamic light field of 940 × 540px were generated by a projector positioned 226 cm above the experimental tank at 30 frames per second. As shown in Supplemental figure S2 and zoomed in Figure 1, the projected field consisted of a single dark spot which moved randomly around the tank at a constant speed and was overlaid on a noisy background which varied both spatially
and temporally, identical to\textsuperscript{30}. Measured light levels at the surface of the tank ranged from 10 lux (approximately twilight) to 500 lux (sunrise on a clear day), corresponding to the natural environment of the fish in the morning or evening.

For each species (tetra and shiner) and group size $N = 16, 32, 64$ and 128, we recorded five replicate experiments for 5 minutes. We used four different seeds to generate each projected video at a medium level of environmental noise ($\eta = 0.25$), and added a 50 pixel white border to the light field to discourage fish from interacting with the sides of the arena. Each experimental run was followed by a 10 minute rest period under neutral lighting (0.5 lux, deep twilight). See Supplementary information for further experimental details.

\textbf{C. Fish Tracking}

Our algorithm was implemented in Python using the OpenCV library, and followed a similar approach to SchoolTracker\textsuperscript{35}. Individual fish are located using detected line-segments in background subtracted frames of video. We then track fish from frame to frame by linking their two-dimensional positions over time using a Kalman filter. Due to the large number of fish, occlusions are frequent and the detection/tracking algorithm can fail to locate and track a fish over multiple frames. The tracks are spliced together by linking tracks in a four-dimensional position-velocity space\textsuperscript{41}. Our tracking algorithm recovers 90\% of trajectories for $N = 128$ and 92\% for $N = 16$. Since our focus in this paper does not rely on us maintaining identities for long periods of time, we have sufficient data to calculate velocities and accelerations.

Once the time-resolved trajectories are known, we compute velocities and accelerations by convolving the trajectories with a Gaussian smoothing and differentiating kernel\textsuperscript{36,42}. Derivatives computed using this convolution method are less noisy than what would be obtained from a simple finite difference scheme. For the data presented here, the convolution kernel was chosen to have a standard deviation of 1.5 frames, and the position information from 11 frames was used to calculate each derivative.
III. RESULTS

A. Experimental Results

We filmed schooling events of two freshwater species, golden shiners (Notemigonus crysoleucas) and rummy nose tetras (Hemigrammus bleheri), in a shallow tank (183 cm × 102 cm, 8 cm water depth). As shown in Figure 1a, a projector located 2.26 m over the experimental arena casts a dynamic light field at 30Hz onto the bottom of the tank. A cropped sample image of the light is shown in Figure 1b, with an overlay of the silhouettes of tetras for scale. Each noise image is the sum of a circular dark spot with gaussian decay (with length scale 38.1 cm) to white and a noisy greyscale light field that varies spatiotemporally. The dark spot moves with a constant speed of 5.7 cm/s in random directions. The noise level \( \eta = 0.25 \) was held constant throughout the experiments. See Berdahl et al. and our see Supplementary Information for further details on the light field.

We investigated the gradient tracking performance of schools of \( N = 16, 32, 64, \) and 128 individuals. For each species and group size, we conducted five replicate experiments with different random seeds used to generate the light fields. Each experiment consisted of fish navigating the dynamic light field for 5 minutes, which was captured by an overhead IR camera at 30fps as shown in Figure 1. Individual fish were tracked following a similar technique to Rosenthal et al. to obtain trajectories of individual’s positions. Velocities and accelerations were computed by convolving the position time-series with the first and second derivatives of a Gaussian, respectively. More details on our experimental methods and husbandry procedures are given in the Supplemental Information.

To quantify group gradient tracking performance, we calculate the mean gradient tracking performance as, \( \psi = \langle \langle 1 - L \rangle_{\text{fish}} \rangle_t \), which averages the local light level first over all fish in each frame and then over all time. This raw performance metric is then divided by the null performance, \( \psi_{\text{null}} \), which is defined similarly except by averaging over the level of darkness of fish trajectories if they instead experienced the temporal average of the light field. The un-biased gradient tracking performance is then,

\[
\Psi = \psi / \psi_{\text{null}}.
\]

The theoretical maximum performance for a single individual is obtained by minimising \( \Psi_{\text{null}} \) while remaining in the dark patch for the entire trial. Averaging over all five light fields
Figure 2 | (a) The average area of the school per individual for shiners (blue circles) and tetras (orange triangles) as a function of the group size $N$. (b) The group gradient tracking performance, $\Psi$, is shown as a function of group size $N$ for both shiners (blue circles) and tetras (orange triangles). The error bars represent the standard error of the group performance over replicates. The thick lines represent maximum group performance of a group of $N$ individuals with the average area per individual for shiners (solid line) and tetras (dashed line).

Generated with different random seeds, we calculate $\Psi_{max} = 2.32 \pm 0.72$. While $\Psi_{max}$ gives a hard upper limit on group performance, this inaccurately assumes that fish can minimize $\Psi_{null}$ (fish have no knowledge of the temporal average of the light fields) and occupy no volume. In fact, as shown in Figure 2a, the area per individual is independent of group size for both shiners and tetras and is approximately 0.24 and 0.49 $A_{fish}$, respectively, where $A_{fish} = \pi BL^2$.

For both shiners and tetras, the level of performance, $\Psi$ is shown as a function of group size in Figure 2b. For shiners, our results generally agree with previous work by Berdahl et al. where $\Psi$ increases as a function of $N$. However, the group performance for rummy nose tetras exhibits the opposite trend, where $\Psi$ decreases with increasing number of individuals. The decreasing trend in group performance with increasing $N$ is due to the smaller and denser schools that tetras form compared to shiners. The average body length of golden shiners ($5.3\pm0.5$ cm) is about 50% longer than the tetras ($3.4\pm0.5$ cm) and therefore shiners occupy greater area for a given $N$. Another factor at play is the density of the school. In Figure 2b, we show that the average area per individual is fixed for each species, but tetras
school at about twice the density compared to shiners. The greater amount of area occupied by a school of shiners compared to tetras for a given $N$ decreases $\Psi_{max}$ since the size of the dark spot is kept fixed. The slightly larger size of our shiners compared to those used in Berdahl et. al (BL = 4.9 cm)\(^{20}\) is likely responsible for the small decrease in performance for large schools of shiners. For reference, we plot $\Psi_{max}$ for each $N$ given the average area of a school of each respective species, which shows that the finite size effect is responsible for the decrease in $\Psi$ for tetra. However, the increase in school area does not explain why tetras outperform shiners.

We investigate the mechanism for the increase in gradient tracking performance of tetras over shiners by examining the correlation in the social and environmental vectors with individuals’ acceleration. We estimate a social vector $\mathbf{S}$ which is calculated using neighbours within seven body lengths of the focal individual,

$$S_i = \sum_{j \in r_s, j \neq i} \frac{x_j - x_i}{|x_j - x_i|}.$$  \hspace{1cm} (2)

The direction of the social vector indicates the direction of social attraction and its length is a proxy for the strength of the attraction.

We take the environmental vector $\mathbf{G}_i$ to be the negative gradient of the light field $L$ evaluated at the position $x_i$ of each fish,

$$\mathbf{G}_i = -\nabla L|_{x_i}$$  \hspace{1cm} (3)

The environmental vector $\mathbf{G}_i$ points in the direction of steepest descent toward darkness and its length is the rate of change of the light field in that direction. To calculate the response of an individual fish to its social and environmental vectors, we calculate the correlation between the direction of the corresponding vector and the direction of the fish’s acceleration with the following,

$$C_{social} = \langle \hat{S}_i \cdot \hat{a}_i \rangle$$  \hspace{1cm} (4)

$$C_{environmental} = \langle \hat{G}_i \cdot \hat{a}_i \rangle.$$  \hspace{1cm} (5)
Figure 3 | Correlations between accelerations of shiners and the social and environmental cues (y-axis) are shown as functions of the magnitude of the social (a) and environmental (b) vectors (x-axis), respectively. Similarly, correlations between social and environmental vectors and the accelerations of tetras are shown as functions of the magnitude of the social (c) and environmental vectors (d), respectively. For all subfigures, the correlation between the accelerations and social vector are dark (blue) and between the accelerations and environmental vector are light (orange).

Using $C_{social}$ and $C_{environmental}$, we determine whether the motion of individuals is more strongly correlated with social or environmental information. In Figure 3a, we show $C_{social}$ and $C_{environmental}$ for shiners as functions of the magnitude of the social vector $S$. As expected, $C_{environmental}$ is independent of the magnitude of the social vector. In Figure 3b, we show that $C_{environmental}$ is independent of the magnitude of the environmental vector, suggesting that individual shiners do not sense the environmental gradient, in agreement with recently reported results.20 In contrast to the data we reported for the golden shiners, we find that the accelerations of tetras are not strongly correlated with the social vector as shown in Figure 3c, as $C_{social} < C_{environmental}$. However, as shown in Figure 3d, tetras respond strongly to the
Figure 4 | (a) Group performance shown as a function of weight $w$ for group size $N = 8$, 16, 32, 64, 128, and 256. (b) The performance gain $\Delta \Psi = \Psi_{max}(w) - \Psi(w = 0)$ shown as a function of group size for different noise scales $\eta = 0.10, 0.25$ and 0.40. (c) Gradient tracking performance $\Psi$ shown as a function of weight $w$ for different $\eta$ and $N = 32$. The dashed vertical line shows $w_0$ the weight at which $\Psi$ reaches half maximum, where $\Psi = \Psi(w = 0) + 0.5\Delta \Psi$. (d) The $w_0$ shown as a function of $N$ for different noise scales $\eta$.

light gradient as $C_{\text{environmental}}$ increases with the magnitude of the environmental vector.

While our results for shiners show that individuals are more strongly influenced by social information, tetras appear to exhibit the opposite trend and are more strongly influenced by the environmental gradient. This result clarifies the findings in Figure 2b, where tetras outperformed shiners in navigating the dynamic light field toward darker regions. This stark contrast in performance between tetras and shiners in solving the same problem is due to the different gradient sensing mechanisms. Shiners rely strongly on social cues which leads to an emergent group level gradient sensing\textsuperscript{20}, but tetras can individually sense the environmental gradient.
B. Simulation model

As we have seen, different species of fish vary in the degree to which they base their movement on social and environmental information. To investigate this relationship, we explore how group performance depends on the relative weighing of environmental and social information via a tunable weight parameter, $w$.

We propose a new model, built on the recently proposed agent based Berdahl-Couzin model\textsuperscript{16,20,37}, to which we augment with an environmental gradient sensing for each individual. Individuals interact socially via the canonical Couzin model where motion is determined via repulsive, aligning, and attractive interactions that depend on distance to neighbours. The direction given by social cues is $\hat{d}_{\text{social}}$. Explicit details of the calculation of $\hat{d}_{\text{social}}$ are outlined in the Supplemental Information. We calculate the gradient of the noisy light field $d_{\text{environmental}} = -\nabla L|_{x_i}$.

The updated direction of each individual is given by

$$d = \hat{d}_{\text{social}} + w \hat{d}_{\text{environmental}}, \quad (6)$$

where $w$ is the relative weight and $\hat{d}_{\text{social}}$ and $\hat{d}_{\text{environmental}}$ are unit vectors corresponding to the social and environmental vectors, respectively. To determine the velocity of each individual, we then normalise $d$ and multiple by the speed $s$,

$$v = s \hat{d} \quad (7)$$

To determine the speed of individuals, we follow the light intensity dependent speed-modulation proposed by Berdahl et al\textsuperscript{20}, where individuals slow down in dark regions and speed up in bright regions. The speed grows linearly with the brightness, given by $s = s_{\text{min}} + L (s_{\text{max}} - s_{\text{min}})$. Note, the speed modulation is the basis for the shiner’s emergent sensing. Further details and a flowchart for our model algorithm are given in the Supplementary Information.

In the limit that $w \to 0$, social interactions entirely determine individual behaviour and our model reverts to the Couzin-Berdahl model\textsuperscript{20}. In the opposing limit where $w \to \infty$, individuals lose all social information and respond only to their local environmental gradient and no longer respond to social information. We investigate the group performance as a function of group size $N = \{8, \ 16, \ 32, \ 64, \ 128, \ 256\}$, the weight given to gradient
information $w$ is 32 log-spaced values between $10^{-2}$ and $10^3$, and the noise level of the environment $\eta = [0.10, 0.25, 0.40]$. We performed 20 replicate simulations for each weight and noise level. Each simulation was run for $10^4$ time steps and data was recorded every 100th time step. In our simulations, the parameters used for the Couzin model were fixed throughout the simulations and were: zone of repulsion 0.5; zone of orientation 3.0; zone of attraction 5.5; field of perception 270 degrees; turning rate 100 degrees; social error 0.01 radians; time step increment 0.125. These values correspond to the parameters fit for golden shiners as previously reported by Berdahl et al. Note that the simulations are not parametrised to fit our specific schools of fish.

C. Simulated results

In Figure 4a, we show the group performance $\Psi$ of our simulation as a function of the weight $w$ with a noise level $\eta = 0.25$. The shape of $\Psi(w)$ is sigmoidal. We find that increasing $w$ (the gradient sensing weight) greatly increases $\Psi$ of the group. In this limit, individuals follow the gradient eventually finding the moving dark region. However, inside the dark region $d_{\text{environmental}} = 0$, since the gradient is zero, and the motion of individuals is determined by social interactions. Increasing group size $N$ decreases the maximum $\Psi$, which is due to the increasing size of the school. Therefore, larger group sizes do not benefit from large gradient sensing weight as much as smaller groups. To quantify this effect, we calculate the max gain in group performance $\Delta \Psi = \max(\Psi) - \Psi(w = 0)$. In Figure 4b, we show $\Delta \Psi$ as a function of group size, $N$ for three different noise levels $\eta = 0.10, 0.25,$ and 0.40. We find that $\Delta \Psi$ decreases monotonically with increasing $N$ and decreases with increasing $\eta$, showing that larger groups benefit less from an individual’s ability to sense the gradient regardless of the noise level of the environment.

The group performance decreases with increasing noise level $\eta$ at large $w$, as shown in Figure 4c. In more noisy environments, individuals who strongly rely on gradient sensing benefit less, as they respond to local variations in light level instead of large scale features.

Another trend of increasing $\eta$ is the shifting of the sigmoidal $\Psi(w)$ toward smaller $w$. The sigmoid reaches half the max, $\Psi_{1/2} = \Psi(w = 0) + \frac{1}{2} \Delta \Psi$, at $w_0$ as shown in Figure 4d. In Figure 4d, we show the shifting of the group performance $\Psi$ toward smaller $w$ by showing $w_0$ as a function of $N$ and $\eta$. The weight at half-max, $w_0$, decreases with increasing environmental...
noise level $\eta$. We also find a maximum of $w_0$ for groups of $N = 32$, demonstrating that small (and large) group benefit more from smaller weights $w$ than intermediate group sizes.

Up to this point, our study did not account for the ubiquitous presence of error in individual environmental gradient sensing. To introduce this effect, we include a gaussian random error with standard deviation $\sigma_w$ which is added at each timestep to the local gradient direction. For small $w$, the amount of error added to the gradient direction is nullified as individuals base their direction on social interactions. For large weights, $w > 100$, increasing the amount of error $\sigma_w$ destroys the individual ability to sense the gradient and turns the simulation into non-interacting random walkers.

While increasing $w$ increases the group performance $\Psi$, large $w$ destroys social information. To quantify this effect, we calculate the nearest neighbour distance $d_{nn}$. For all group sizes $N$, nearest neighbour distance decreases with increasing $w$ to a minimum $\min(d_{nn}^N)$. We find that $d_{nn}$ decreases for increasing group size $N$, corresponding to the increasing density of the group near the dark spot. Note that $d_{nn} < 0.5BL$ for $N \geq 128$ which is due to overcrowding in the dark spot and low time resolution. With shorter $\Delta t$ for the simulation, the repulsive social interaction would prohibit such overcrowding and should yield a minimum $d_{nn} \geq 0.5BL$. For large $w$, we find that $d_{nn}$ increases, as long range attractive social

![Figure 5](image_url)  

**Figure 5** | The gradient tracking performance $\Psi$ is shown for $N = 128$ as a function of weight $w$ for different gradient sensing error $\sigma_w$. 
We propose that nature selects the weight $w$ which balances individually acquired gradient information with social information such that nearest neighbour distance $d_{nn}$ is minimised for all group sizes. Smaller nearest neighbour distance reduces predation risk. We find the weight which minimises the sum of the squared difference of $d_{nn}$ for group sizes $N = 16, 32, 64$ and $128$ to be $\tilde{w}_{\text{min}} = 31.6$, and is shown in Figure 6a. Therefore, by weighing their individually acquired gradient information around thirty times stronger than social interaction, individuals can optimise both $\Psi$ and $d_{nn}$. However, we emphasise the granularity of $w$ due to computational cost. Using $w = \tilde{w}_{\text{min}}$, we show the group performance $\Psi$ as a function of $N$ in Figure 6b. We find good agreement between our model and experimental data for the rummy nose tetras. In Figure 6b, the shaded region represents the $\Psi$ for the range of $w$ that minimise $d_{nn}$ in simulations for each group size $N$, $w = 14.7$ to $68.1$. For groups $N = 128$, the group performance for $\Psi$ for the tetras falls below the range predicted by our simulation. We attribute this disagreement largely to distraction of individual fish with the edge of the tank.

**Figure 6** | (a) Nearest neighbour distance of simulated schools is shown as a function of the weight $w$ for group sizes $N$. The dashed vertical line is the weight $\tilde{w}_{\text{min}}$ which minimises $d_{nn}$ for all $N$. (b) Gradient tracking performance of the numerical results for $w = \tilde{w}_{\text{min}} \approx 32$ (dark green squares), where the shaded region shows the range of $\Psi$ corresponding to simulated weights from $w \approx 14$ to $64$. These weights are those which minimise $d_{nn}$ for $N = 256$ and $16$ respectively. The experimental results are overlaid for the rummy nose tetras (orange triangles) and shiners (blue circles).
Note that the simulations are not parametrised to fit the schools of tetra. In all the numerical results, we fixed the repulsion, orientation and attraction zonal distances to match those reported for golden shiners previously reported. We use the simulations to display a generic quality of self-propelled particle models that aligns with our experimental observations of tetrars which have some innate environmental gradient sensing ability. One could further improve the model’s ability to match the tetra data by tuning parameters of the Couzin model \( r_o \) and \( r_a \) or determining \( \tilde{w}_{\text{min}} \) more precisely.

IV. DISCUSSION

This work presents experimental and numerical studies on group performance of fish schools navigating a spatiotemporally varying light field. First, we experimentally investigate the collective gradient tracking performance of two freshwater species: golden shiners (\( N. crysoleucas \)) and rummy nose tetrars (\( H. bleheri \)). We find that tetrars outperform shiners at this task for all group sizes. Our results agree with previous findings that the motion of shiners is based strongly on social interactions and is not correlated with the light gradient. On the other hand, tetrars can individually sense the gradient of the light field, which accounts for their high group performance compared to shiners.

Second, we have used these observations to propose an agent based model based on the Couzin-Berdahl model, where we include a gradient sensing ability for each agent. In our simulations, we find that group performance increases with increasing dependence (weight) on gradient sensing information. This result is robust to group size and noise scale. However, when individuals rely too much on their individual information, nearest neighbour distance increases and the school fragments.

We propose that nature balances the weight attributed to an individual’s gradient sensing ability and social information to minimise nearest neighbour distance. This adaptation is important because decreasing nearest neighbour distance reduces risk of predation. Using the gradient sensing weight which minimises the nearest neighbour distance, we find good agreement with our experimental data for rummy nose tetrars. Additionally, we find that increased error associated with local gradient sensing can lead to poor performance especially for large weights.

Our model shows the disadvantages of relying too strongly on either social information
(poor group performance) or individually acquired environmental gradient information (fragmented groups). Further work is needed to determine experimentally how individuals of various species weigh social and environmental information. Another course for future research is to investigate the role of individual differences and aptitude on group performance.

**Ethics.** All experiments were conducted in accordance with federal and state regulations and were approved by the Gettysburg College Institutional Animal Care and Use Committee.

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**Author contributions.** J.P. devised the study. A.P. and J.P. wrote the simulation code and performed the simulations. All authors conducted the experiments. All authors analysed the data, interpreted the results and wrote the manuscript.

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