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RESEARCH ARTICLE

Polarized schooling emerges in tetra species with cohesive social networks

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ABSTRACT

Fish schooling depends on social interactions between animals. Studies on schooling overwhelmingly focus on a single species, which challenges our ability to resolve what features of this collective behavior are universal and how schooling has diversified over the course of evolution. Here, we studied interspecific variation in schooling behavior among five species of neotropical tetras to examine how social networks relate to schooling kinematics among species. We quantified differences in speed, polarization, spacing, mutual information and network properties within, and between, species. Our results demonstrate substantial interspecific variation in schooling behavior, with polarized species exhibiting higher speeds and more cohesive social networks. In contrast, shoaling species showed greater variability in their spatial arrangement and a less cohesive social structure. This comparison demonstrates how closely related species are capable of exhibiting distinct forms of schooling that reflect divergent traits in sensing, motivation and locomotor control.

KEY WORDS: Mutual information, Social networking, Collective behavior

INTRODUCTION

The way a school of fish moves together depends on the responses of its members to one another. A combination of attraction, repulsion and alignment provide rules for governing how individuals coordinate with neighbors to give rise to emergent group-level properties (Freeberg, 2019; Viscido et al., 2004; Couzin et al., 2002; Handegard et al., 2012; Katz et al., 2011; Herbert-Read et al., 2011). These properties are reflected in kinematic metrics of schooling, such as speed, nearest-neighbor distance, polarization and rotation (Fig. 1). An analysis of the temporal signature of kinematics can provide the basis for measurements of how a school functions as a social network (Szorkovszky et al., 2018; Sumpter et al., 2008; Butail et al., 2014; Lizier and Prokopenko, 2010). With these analytical tools, schooling offers a powerful system for exploring how social interactions relate to collective behavior (Viscido et al., 2004). The nature of these interactions may have emerged from selective pressures, as schooling has been linked to improved predator avoidance (Pitcher, 1993; Tosh et al., 2006; Wood and Ackland, 2007), foraging efficiency (Handegard et al., 2012) and other fitness-related outcomes. However, most studies of schooling have focused on single species, and consequently much less is known about how emergent group-level behaviors and social interactions vary across species.

Network-based analyses offer a powerful framework for examining the structure of social organization. In a school of fish, a network can be constructed from the similarity in kinematics between pairs of individuals, offering insight into how social structure emerges from the collective behavior of the group (Ward et al., 2018; Crosato et al., 2018; Peterson et al., 2024). A helpful metric in this framework is mutual information (MI) – a measure of the shared distribution between two variables or stochastic processes – which can be extracted from time-series data (Lizier and Prokopenko, 2010; Sumpter et al., 2008). MI has been used to capture temporal synchrony in swimming speed and heading between individuals (Peterson et al., 2024). Given that schooling fish attempt to maintain a similarity in kinematics with their neighbors, measurements of MI may be used to infer communication between fish, provided that the fish are not responding to a common source stimulus. By measuring MI between all pairs of fish in a school, one may construct a weighted, undirected network that reflects the overall distribution and strength of information shared by the motion of its members. Metrics of the emergent properties of a school's network – such as connectivity, modularity and path length – describe the organization of the group as a whole. When paired with conventional kinematic metrics of schooling (Patch et al., 2022; Johansen et al., 2010), a network analysis can be used to evaluate relationships between group social structure and collective motion.

Given the varied benefits and functions of schooling across fishes (Pitcher, 1993; Handegard et al., 2012; Zhang and Lauder, 2024), a reasonable expectation is that species will differ in their kinematics and network properties of schooling. Such an expectation follows from the ample support for adaptive divergence of morphological and biomechanical traits across species thought to emerge from selection (Wainwright and Reilly, 1994; Wainwright, 2007) and the evolutionary diversity of animal motion (Catavitello et al., 2018; Corn et al., 2021; Martinez et al., 2024). However, the extent to which species exhibit clear and observable differences in traits linked to collective behaviors is largely unknown. An important, but unanswered, question is whether behavioral specialization of schooling species results in greater interspecific variation in their kinematic and social network properties than the variation observed within species. Alternatively, the mutability of behavioral traits could allow species to exhibit a high degree of variability that overlaps in schooling behavior across species.

Neotropical tetras provide an ideal system to compare schooling across closely related species. Composed of over 1100 species, tetras represent a highly diverse clade of neotropical fishes that often aggregate in large groups in the wild (Fricke et al., 2025). These fishes are popular subjects of behavioral research and are

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List of symbols and abbreviations

C	connectivity
d	minimum-cost path between nodes
D	mean distance between fish
H	heterogeneity
I	intermittency
L	shortest path length
M	mutual information matrix
MI	mutual information
NND	nearest-neighbor distance
p_i	marginal probability
$p_{i,j}$	joint probability
Q	modularity
$\mathbf{r}$	radial position
S	speed
TE	transfer entropy
$\mathbf{v}$	velocity
θ	heading
μ_{str}	mean node strength
ρ	polarization parameter
σ_{str}	standard deviation of node strength
ϕ	rotation parameter
Ω	diagonal strength matrix

known schoolers (Priestley et al., 2006; Wilson et al., 2019; Gimeno et al., 2016; Ashraf et al., 2016). In addition, their small size permits examination of relatively large schools that may highlight subtleties in behavior not readily observed in small schools.

In the present study, we compared the kinematics and social networks of schools from five species of tetra that vary in the degree to which schooling is polarized. Polarization refers to the similarity in heading exhibited among the members of a school. Our study species were: the black neon (*Hyphessobrycon herbertaxelrodi* Géry 1961), pristella [*Pristella maxillaris* (Ulrey 1894)], rummy nose [*Petitella bleheri* (Géry & Mahnert 1986)], long-fin black skirt [*Gymnocorymbus ternetzi* (Boulenger 1895)] and Buenos Aires [*Psalidodon anisitsi* (C. H. Eigenmann 1907)] tetras. We will refer to the less polarized fishes as shoaling species, to reflect their propensity to move towards one another with relatively low similarity in direction (Pitcher, 1983).

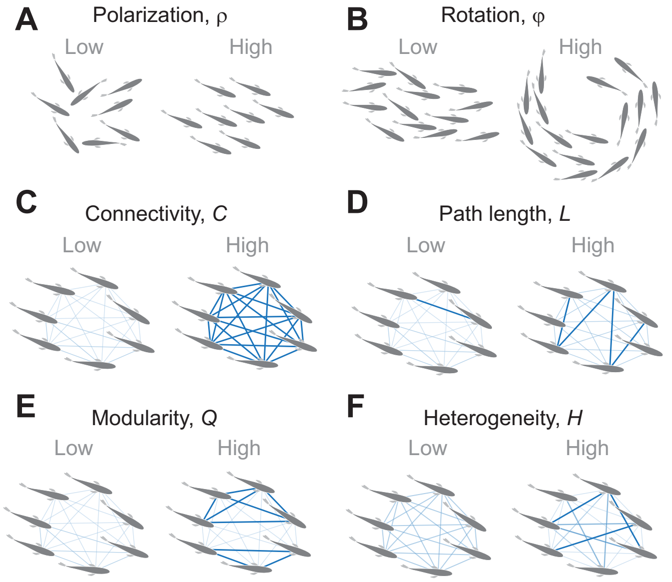

Fig. 1. Measurements of schooling kinematics and network properties. In addition to nearest-neighbor and average distance, we measured (A) polarization (Eqn 1) and (B) rotation (Eqn 2) parameters. Based on measurements of mutual information (MI, Eqn 3), we established (C–F) network properties of schools. These consisted of the connectivity (Eqn 4), path length (Eqn 5), modularity (Eqn 6) and heterogeneity (Eqn 7). For each, MI values provide a weighted edge (darker blue for higher MI) between the nodes (i.e. individual fish) in the network.

Drawing on principles of phenotypic evolution, we treated kinematic measurements as functional traits to evaluate divergence across species. Accordingly, our first aim was to test whether species differed in their patterns of group movement and social organization. We predicted that schools of different species would exhibit distinct kinematic traits and the emergent structure of their social networks. Our second aim was to examine whether variation in social structure was consistent with observed differences in kinematics – specifically, whether species-level differences in polarization, spacing and speed were associated with differences in MI and network properties in schooling fish. Together, these analyses link emergent social structure to schooling kinematics and evaluate how collective behavior varies across species.

MATERIALS AND METHODS

Animal husbandry

We obtained between 80 and 100 fish from the aquarium trade for each of the five focal tetra species described above. All selected species were similar in body length to minimize the influence of size on kinematic measurements. After an initial quarantine period of at least 1 week, fish were kept in a recirculating aquarium system in 9 l tanks at a density of ∼2 fish l^{-1}. Aquaria were kept at a temperature of ∼25°C, lighting was controlled on a 14 h:10 h light:dark cycle and fish were fed daily. All animal care and experimental protocols were in compliance with the Institutional Animal Care and Use Committee at the University of California, Irvine (IACUC protocol AUP-24-094).

Experimental setup

We constructed an experimental setup designed for the automated acquisition of schooling kinematics, based on a previous study (Peterson et al., 2024). A frame of extruded aluminium supported a custom-built tank that was filled with a depth of ∼3 cm of water. This shallow depth minimized occlusions of individual fish while allowing them to swim freely for viewing from above. A circular barrier of clear acetate (∼1.03 m at the water's surface) was placed in the tank to prevent fish from interacting with the tanks' corners. Water was continuously refreshed and circulated with a canister filter connected to a 75 l tank with a heater, ensuring a constant water temperature of ∼25°C. We placed an array of infrared light-emitting diodes (IR LEDs) under the tank to achieve even back-lighting. The experimental tank was additionally illuminated from above by white light from an LED panel directed upwards into a reflective photo umbrella. For even illumination, we wrapped the entire aluminium scaffold and tank in a reflective mylar sheet and the area above the tank was surrounded by diffuser cloth to prevent reflections on the water's surface.

We recorded swimming from above the tank for kinematic analysis. We positioned a mirrorless digital camera (Sony Alpha, A7III, Sony Electronics Inc., San Diego, CA, USA) ∼1.8 m above the center of the tank to record video with minimal parallax distortion. The camera's infrared filter was removed to maximize sensitivity to the IR LEDs, and video was recorded at 4k resolution (3840×2160 pixels), at a standard frame rate (29.97 frames s^{-1}).

Schooling experiments

We recorded the spontaneous swimming behavior of replicate schools of all five tetra species. Each school was created by randomly selecting 30 individuals from the larger pool of fish. The school was moved to the experimental tank and allowed to acclimate for 30 min prior to video recording. After acclimation, schools were recorded for three trials of 3 min duration, with a 12 min rest period between each recording. This was repeated for five schools of each species, yielding a total of 15 trials per species (5 schools×3 trials). The one exception was for the rummy nose tetras, for which we used 10 trials drawn from a previously collected dataset (Peterson et al., 2024). Thus, our kinematics were composed of 70 trials in total, among all species. Analyses that accounted for non-independence of observations treated the schools as a random effect (see 'Statistical analysis', below) and all reported tests accounted for the unbalanced number of trials across species.

Video recordings of schools were analyzed to acquire kinematic measurements. We used custom Python software (v.3.10) to (1) crop videos to the region of interest, (2) generate mean images for each trial to be subtracted from video frames and then (3) convert frames to binary images, with blob-size limitations to ensure that only fish were tracked. The selection of threshold values and a region-of-interest was performed manually to account for variation between trials. The pre-processed videos were then analyzed by TRex, open-source software for tracking individual fish (Walter and Couzin, 2021). TRex tracked the center of the area for each fish and calculated their speed and heading for all video frames. Heading was calculated independently for each frame, based on pattern recognition by moment invariants (Hu, 1962). The tracking failed primarily through occlusions, which could be detected through outliers (greater than 3 standard deviations) in the displacement between frames. This occurred on an average of 0.45% of our position measurements, though we removed those instances from our data analysis. The outliers were identified and removed using custom code in MATLAB (v.2023b, Mathworks, Natick, MA, USA) and missing data segments were interpolated using a spline-fit based on methods detailed previously (Peterson et al., 2024).

Analysis of kinematics

We performed a series of calculations from positional measurements of fish to characterize kinematic differences in schooling behaviors between tetra species. Average speed was calculated as the mean across all individuals in the school over the entire 3 min trial. Swimming intermittency was calculated as the proportion of time that fish swam below a threshold slow speed (5 cm s^{-1}). This speed was roughly two body-lengths per second for all species, which generally occurred when the fish were decelerating or moving little. The nearest neighbor distance (NND) was determined as the minimum euclidean distance between the centroid positions of each fish in the school. We also calculated the mean distance between each fish and all other individuals in the school, the grand mean of which was reported as the average distance. Though fish were of similar length across species, all variables involving linear measures (speed, NND and mean distance) were normalized by the average body length of individuals within a school to eliminate any effect of body size on the magnitude of the measurements.

Measurements of heading provided the basis for metrics of polarization and rotation. The polarization parameter (ρ) describes the similarity of heading among individuals, and ranges from 0 (no alignment of heading) to 1 (all headings aligned; Fig. 1A). We calculated this parameter using the following equation (Couzin et al., 2002):

$$\rho = \frac{1}{n}\sqrt{\left(\sum_{i=1}^{n}\sin(\theta_i)\right)^2 + \left(\sum_{i=1}^{n}\cos(\theta_i)\right)^2}, \tag{1}$$

where θ_i is the heading angle of the ith fish and n is the number of fish. We additionally calculated a rotation parameter (ϕ), which approximates the circularity of the school's path, as a way of capturing the degree of 'milling' by the school (Fig. 1B). Values close to 1 indicate that the heading of all individuals is oriented tangent to the school's center. The rotation parameter was calculated using the following equation (Couzin et al., 2002):

$$\phi = \frac{1}{n}\left|\sum_{i=1}^{n}\mathbf{v}_i \times \mathbf{r}_i\right|, \tag{2}$$

where $\mathbf{v}$ is the velocity vector and $\mathbf{r}$ is the radial vector from the school's center to the focal fish.

Network analysis

The same positional measurements used for kinematic variables provided the basis for calculations of the social network properties of schools. MI is a measure of the joint statistical distribution between two sets of random variables. Here, we calculated MI using methodology adapted from previous work (Peterson et al., 2024), but the present calculations are based solely on measurements of speed. In particular, we binned speed measurements for each pairwise combination of fish over 2 s intervals, with a 1 s overlap between intervals. We then determined the marginal probability distribution of each fish, as well as the joint probability distribution of the pair. Marginal probability was measured as the proportion of the 2 s interval that an individual fish spent in a given bin, while the joint probability was the proportion of that interval that two fish occupied the same bin. We used these computed probability distributions to calculate the pairwise MI for each interval (Kraskov et al., 2004) using the following equation:

$$M = \sum_{i}\sum_{j} p_{i,j}\log_2\left(\frac{p_{i,j}}{p_i p_j}\right), \tag{3}$$

where M is the matrix of MI values for a given pair of fish, $p_{i,j}$ is their joint probability distribution, and p_i and p_j are the marginal probability distributions of each individual. We then averaged the resulting MI values across all pairs of fish in the school for the duration of the recording to get an overall, school-specific value for each trial.

We computed a series of network properties based on the MI measurements for each school using graph theory. The algebraic connectivity, which we refer to as simply 'connectivity', reflects the ease with which information spreads through a network. Higher values indicate greater robustness and network cohesion. Lower values suggest that the group is more loosely connected and potentially more vulnerable to breaking into disconnected components. We defined connectivity (C) as the second-smallest eigenvalue of the Laplacian matrix constructed from MI-based edge weights, calculated using the following equation (Chung, 1997):

$$C = \mathrm{eig}_2(\Omega - M), \tag{4}$$

where Ω is a diagonal matrix computed from the MI matrix (M, Eqn 3) as $\Omega_{i,i}=\Sigma_j M_{i,j}$.

The shortest path length (L) captures the 'minimum-cost' route between each pair of individuals in a network and is used here to quantify the efficiency of information transfer across the group. In fully connected networks, edge weights are derived from MI values between individuals, where higher MI values reflect stronger coordination. To ensure that higher coordination translates into shorter paths, we define the cost of an edge as the inverse of MI, such that more informative links are traversed more easily. We then used the Floyd–Warshall algorithm (Floyd, 1962), which evaluates all possible paths between node pairs, to identify the minimum-cost path. This algorithm allows for the possibility that indirect paths, through highly coordinated individuals, may be more efficient than direct connections. Lower values for shortest path length indicate more direct, or efficient, information transfer between individuals than higher values. We calculated the average of these pairwise shortest path lengths to provide a global measure of the efficiency of information transfer for each school, calculated using the following equation (Newman, 2010):

$$L = \frac{1}{n(n-1)} \sum_{i,j \in V, i \neq j} d_{i,j}, \qquad (5)$$

where $d_{i,j}$ represents the minimum-cost path between nodes i and j.

We calculated network modularity to describe the degree to which a network can be partitioned into subgroups. Higher modularity indicates more distinct subgroups within the school, while lower values reflect a more uniform or integrated structure. In addition, individuals form stronger connections to others within the same module than to those in different modules. We computed weighted modularity using the Louvain community detection algorithm, which identifies a partition of the network that maximizes the difference between observed and expected within-module edge weights (Blondel et al., 2008). Weighted modularity was calculated using the following the equation (Newman, 2010):

$$Q = \frac{1}{2W} \sum_{i,j} \left[M_{i,j} - \frac{s_i s_j}{2W} \right] \delta(c_i, c_j), \qquad (6)$$

where $M_{i,j}$ represents the edge weight (MI value) between nodes i and j; s_i and s_j represent the total node strength, defined as the sum of all edge weights connected to nodes i and j, respectively; and W is the sum of all edge weights in the network. Additionally, c_i and c_j are the community (module) assignments of nodes i and j, and $\delta(c_i,c_j)$ is an indicator function that equals 1 when i and j are assigned to the same module and 0 otherwise.

Finally, we quantified network heterogeneity (H), which describes the inequality of information strength across a network. We computed H as the coefficient of variation of node strength, defined as the sum of its MI values with all other nodes. Higher heterogeneity indicates that coordination is concentrated in a few individuals, whereas lower values imply a more uniform distribution of connectivity across the group. Heterogeneity was calculated using the following equation (Newman, 2010):

$$H = \frac{\sigma_{\mathrm{str}}}{\mu_{\mathrm{str}}}, \qquad (7)$$

where σ_{str} is the standard deviation in node strength, and μ_{str} is the mean node strength across all individuals in the school.

Statistical analysis

Our statistical analyses were designed to evaluate species-level differences in behavioral traits, identifying patterns of divergence in kinematic and network domains. All statistical testing was conducted in R v.4.4.1 (2024-06-14 ucrt; http://www.R-project.org/), and included all trial replicates for each school (black neon N=15, black skirt N=15, pristella N=15, Buenos Aires N=15, rummy nose N=10). For each kinematic and network variable, we implemented mixed effects models with school number as a random effect to compare school means using the emmeans package (https://CRAN.R-project.org/package=emmeans). This allowed us to account for potential non-independence due to repeated measures, while testing for species-level differences in trait values. Modeling was followed by *post hoc* Tukey's honestly significant difference (HSD) calculations to adjust for multiple pairwise comparisons between species using the glht function in the multcomp package (Hothorn et al., 2008). We also compared trait variances between species using Levene's test for homogeneity of variance from the car package (Fox and Weisberg, 2019), as it is robust to deviations from normality. We then performed *post hoc* comparisons of our variance model using Tukey's HSD (TukeyHSD function of the stats package) (http://www.R-project.org/).

Finally, we tested for differences in species' behavioral traits in a multivariate framework using a MANOVA, followed by a residual randomization permutation procedure (RRPP) to assess significance. We performed this test using the procD.lm function from the geomorph package in R (Baken et al., 2021; https://CRAN.R-project.org/package=geomorph; Collyer and Adams, 2018; https://CRAN.R-project.org/package=RRPP). This method is well suited for multivariate data and assesses significance using residual randomization, making it robust to departures from multivariate normality. To account for differences in the scale and units of component variables, trait values were standardized prior to analysis by scaling them to unit variance and centering their means at 0. Pairwise differences were assessed using the pairwise function with 999 permutations (Baken et al., 2021; https://CRAN.R-project.org/package=geomorph; Collyer and Adams, 2018; https://CRAN.R-project.org/package=RRPP). To confirm that observed differences were not the result of non-independence, we also performed all statistical testing on a dataset truncated to only schools that were fully independent of one another (N=2 per species) (see Table S1).

RESULTS

Schooling kinematics

Our measurements of schooling kinematics revealed distinct patterns of motion among the species. Representative recordings show differences in the spatial distribution of fish in our experimental aquarium (Fig. 2A). The different species exhibited contrasting temporal patterns of change in swimming speed and differing levels of variation in both speed and heading (Fig. 2B,C).

We analyzed the combination of all kinematic traits in a multivariate framework and visualized the functional space occupied by species. In a PCA of kinematic variables, the two primary axes together accounted for 86.03% of the kinematic variation. The species formed two main groups, separated primarily by differences in speed, intermittency and polarization (Fig. 3A). The more polarized species (black neon, pristella and rummy nose) were characterized by higher speed and lower intermittency than the less polarized ones (Fig. 3B,C). Variation within each of these groups, and within species, was accounted for by NND, mean distance and rotation (Fig. 3D,E,G). Pairwise multivariate analysis

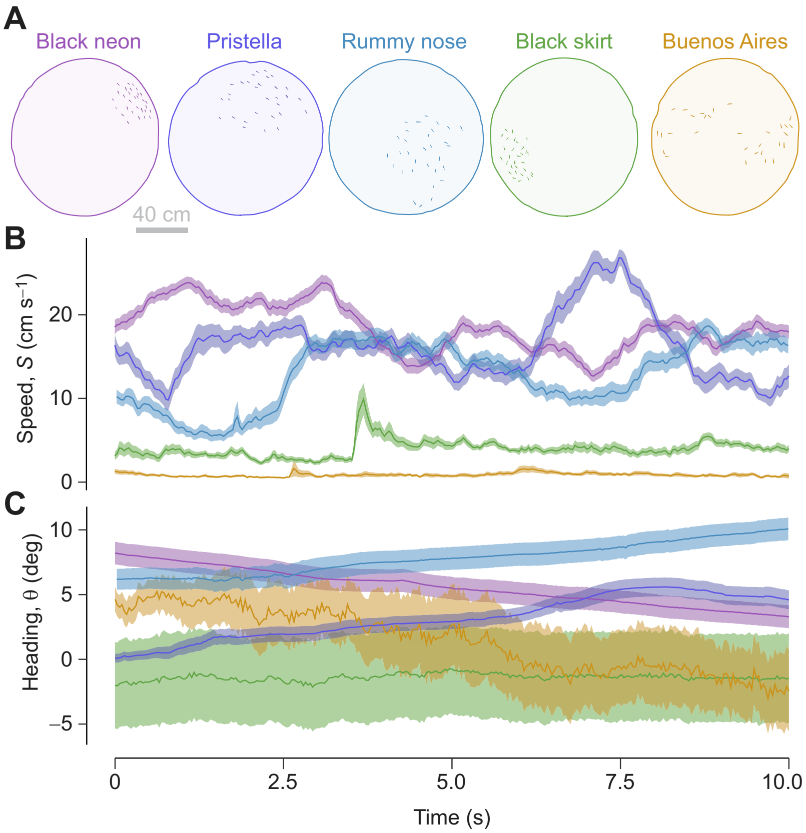

Fig. 2. Representative schooling kinematics for each species. Video frames (A) were extracted from behavioral recordings of each species (by color). The circular region encompasses the water's edge in the experimental aquarium and the fish appear as dark silhouettes. We calculated the (B) speed and (C) heading of each fish from centroid coordinates of their dorsal profile. Mean values and s.e.m. are shown by the solid lines and ribbons, respectively.

of variance (MANOVA) revealed significant differences ($P<0.02$) between almost all pairs of species. Buenos Aires and black skirt tetras were the only pair of species that did not differ in their overall kinematics ($P=0.062$).

We identified pairwise differences between species in all kinematic variables analyzed. This included measures of speed and intermittency, which exhibited three groups of species, each significantly different from one another. In particular, the two most polarized species (black neon and pristella) swam ∼50–70% faster and showed ∼10–15% less intermittency than the rummy nose tetra, which were of intermediate polarization (Fig. 3). The polarized species also swam ∼3–4 times faster and spent ∼60–70% less time motionless than the least polarized species (black skirts and Buenos Aires; Fig. 3B). We found that polarization differed significantly among all five species (Fig. 3F). Two intermediate species (rummy nose and pristella) exhibited at least ∼25% greater NND than both the most and least polarized species (black neon, black skirt and Buenos Aires tetras; Fig. 3D). The pattern was consistent for mean distance, except that Buenos Aires shifted into the group with greater distance (Fig. 3E). The rummy nose schooled with greater NND than Buenos Aires, while pristella tetras were not significantly different from either species. The tetra species were not substantially distinct in the rotation parameter, though pristella was significantly higher than rummy nose and black neon tetras (Fig. 3G).

Using variance tests, we found that species differed in their degree of behavioral modulation. With few exceptions, the least polarized species, the Buenos Aires tetra, exhibited the greatest variance in kinematic traits. The Buenos Aires tetras displayed significantly greater variance than all other species in both NND (Fig. 4C) and mean distance ($P<0.007$, in all cases), while their variance in intermittency was only greater than that of black neon tetras ($P=0.0001$). In addition, the Buenos Aires and black skirt tetras together had greater variance in polarization (Fig. 4A) than the more polarized black neon and rummy nose tetra (Buenos Aires versus black neon $P=0.0056$, versus rummy nose $P=0.020$; black skirt versus black neon $P=0.013$, versus rummy nose $P=0.039$). The relatively polarized pristella tetra also exhibited significantly greater variance in speed than black skirt tetra ($P=0.0051$). Black neon tetra had greater variance in rotation (Fig. 4B) than both black skirt and pristella tetra (black neon versus black skirt $P=0.006$, pristella $P=0.0076$).

Communication and network properties

Our measurements of MI revealed differences in how the fish within schools interacted. More polarized species generally exhibited higher MI values, with the exception of the lower values for the polarized pristella tetra (Fig. 5). The most polarized black neon tetras had significantly greater (∼20%) MI than the intermediate rummy nose (Fig. 6). Schools of both pristella and black skirt tetra had ∼30% greater MI than the most non-polarized Buenos Aires, and ∼30% lower MI values than rummy nose. Therefore, more polarized species tended to exhibit greater synchrony in speed changes than the shoaling species.

The MI measurements provided the basis of our network analysis of schools. We found that the networks of the least polarized species (Buenos Aires) were significantly different from those of all other species (pairwise MANOVA: $P=0.0001$), as were those of the next most polarized species (black skirt) (Fig. 6A). Similarly, black neon tetra (the most polarized species) exhibited social networks that differed in multivariate space from all other species (pairwise MANOVA: $P<0.001$), except rummy nose (pairwise MANOVA: $P=0.13$). The intermediately polarized species (pristella, rummy nose and black skirt) did not significantly differ from each other in

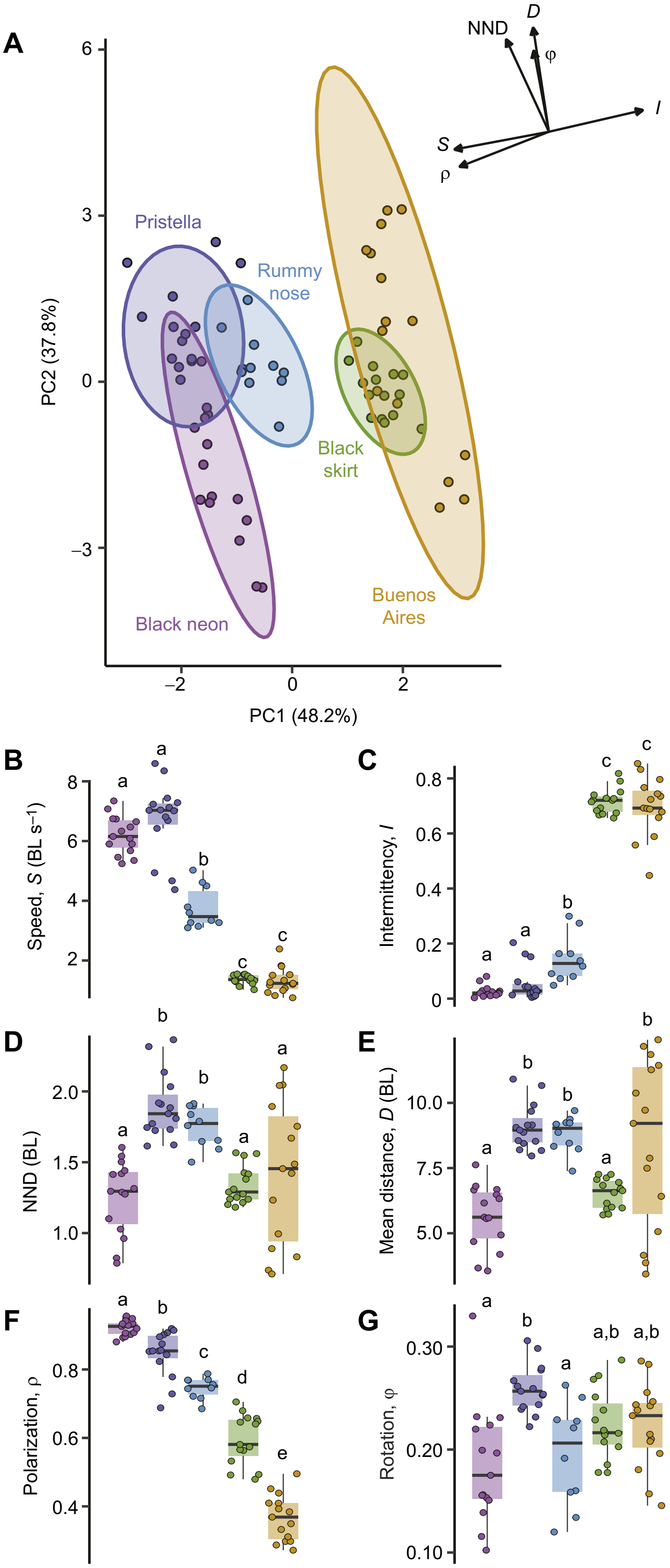

Fig. 3. Schooling kinematic traits across species. (A) Principal component analysis (PCA) of the kinematic trait space, including six kinematic parameters (speed, intermittency, NND, mean distance and the polarization and rotation parameters), with species identified by color. Points represent the position of an individual school in the trait space, with shaded regions denoting 95% data ellipses. The direction and length of the six axes (upper right) convey the relative contribution of the variables to the two principle component (PC) axes plotted. (B–G) Comparisons of individual kinematic traits across species. Points represent mean values for a school; boxes represent the 1st and 3rd quartiles, with the median (heavy black line) and range of the measurements across all trials for a species (error bars). The letters over each box indicate pairwise significant differences ($P<0.05$, $N=15$, for each species, except rummy nose tetra, *Petitella bleheri*: $N=10$), after correction for multiple comparisons using Tukey's honestly significant difference (HSD) method (groups with the same letters are not significantly different from one another). BL, body lengths.

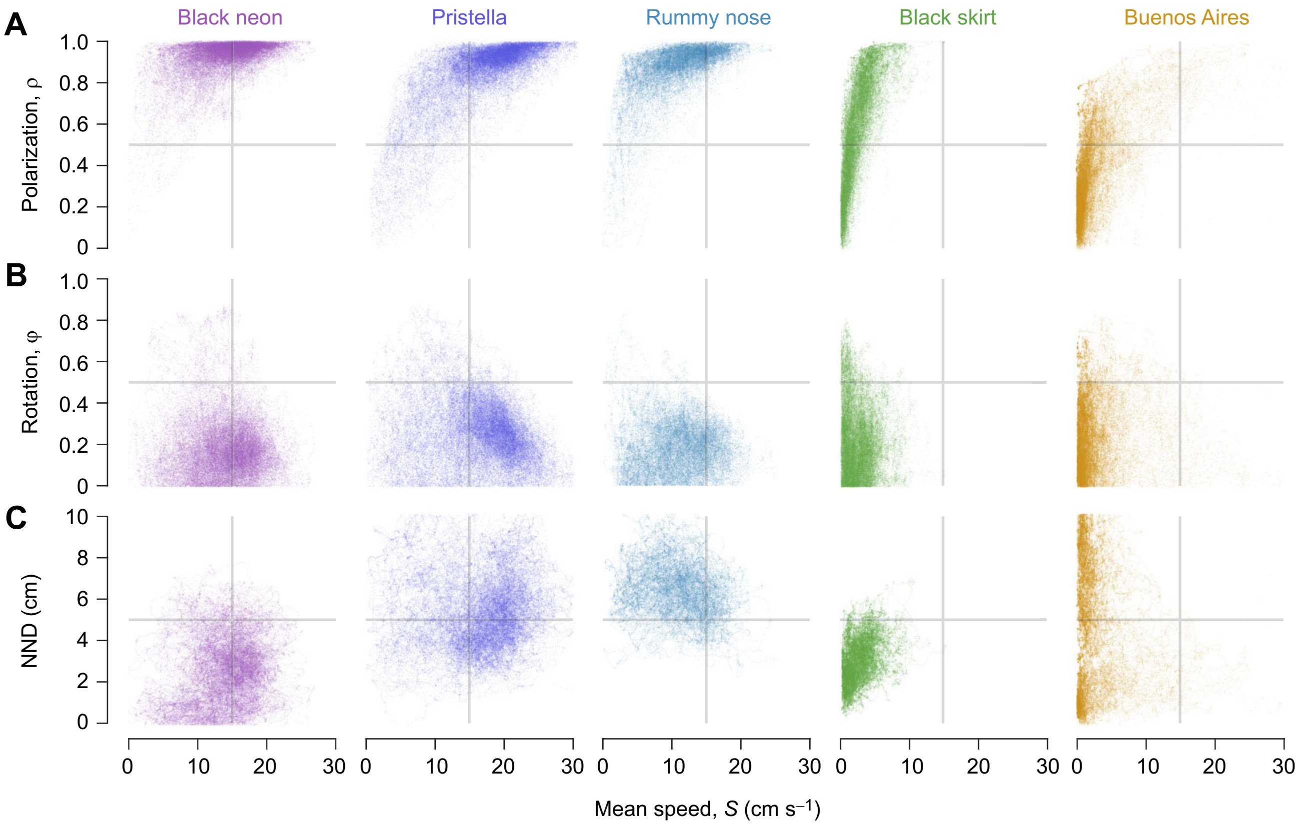

Fig. 4. Measurements of schooling kinematics. Each circle represents a single measurement and each panel includes all measurements, across all experiments, for each species (N=81,919 measurements, except for the rummy nose tetra, *P. bleheri* (N=53,946). (A) Measurements of the polarization parameter (Eqn 1), (B) rotation parameter (Eqn 2) and (C) mean nearest-neighbor distance (NND), with respect to the speed at the time of each measurement.

multivariate network properties (pairwise MANOVA: pristella versus rummy nose P=0.15; pristella versus black skirt P=0.23; rummy nose versus black skirt P=0.085). The primary axis of variation in this analysis is related to connectivity, heterogeneity and path length, while the secondary axis mostly reflects variation in modularity.

Our network analysis revealed pairwise differences between species in the structure of the social interactions within schools. The shortest path length, a measure of information transfer efficiency, was lower among the most polarized species (black neon; Fig. 6B), compared with the shoaling species (pristella, rummy nose and black skirt tetras), with Buenos Aires tetras exhibiting significantly greater values. Species values for connectivity, a measure of the average strength of relationships across a network, showed an inverse trend (Fig. 6C). However, the connectivity of pristella was intermediate to that of rummy nose and black skirt tetra, though it was not significantly different from either species. The most polarized black neon tetras maintained the highest connectivity of any species, followed by rummy nose, black skirt and Buenos Aires tetras. More polarized species showed lower heterogeneity, with black neons displaying the lowest values and Buenos Aires tetras being the most heterogeneous (Fig. 6D). Finally, differences in modularity were far more subtle than our other network parameters, but did follow similar trends such that the most polarized species tended to form subgroups (modules) less often than the least polarized species (Fig. 6E).

We found few differences in network variance between species. Using Levene's homogeneity of variance tests, there were no significant differences in variance for either shortest path length or heterogeneity between any pairs of species. Buenos Aires tetra displayed significantly greater variance in modularity than all other species (Buenos Aires versus black neon P=0.0003, versus black skirt P=0.001, versus rummy nose P=0.023) except for pristella tetra. Pristella tetra displayed significantly greater variance in modularity than black neon tetra (P=0.033). Pristella also showed greater variance in connectivity when compared with black skirt and Buenos Aires tetras (P=0.020 and P=0.043, respectively).

DISCUSSION

We examined species-level differences in schooling behavior across both kinematic and social network traits in neotropical tetras. Our results suggest that these closely related species do not share a common behavioral repertoire, but their kinematics exhibited distinct modes of group-level coordination and organization (Figs 2–4). These differences loosely correlated with the network characteristics of schools (Figs 5 and 6), indicating a link between social structure and schooling kinematics. In addition to trait means, we found significant differences in schooling variance between species. Taken together, these results are consistent with evolved divergence in collective behavior among tetras and reveal distinct forms of schooling among closely related species.

Our kinematic measurements allowed us to identify patterns of variation in collective traits between species. Consistent with previous observations (Gimeno et al., 2016; Wilson et al., 2019), polarized tetras (black neon and pristella) moved less intermittently,

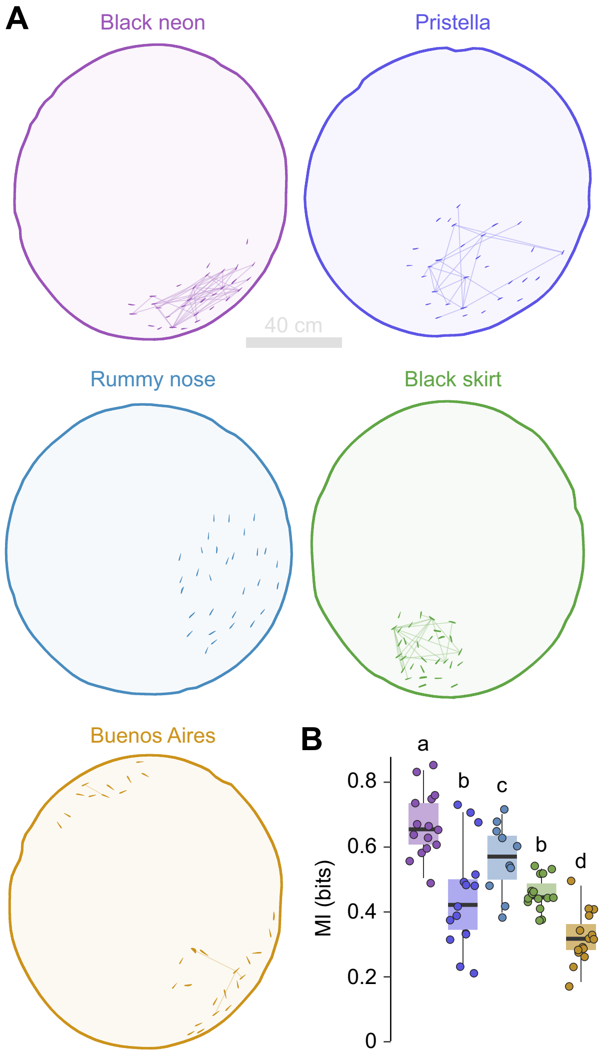

Fig. 5. Measures of MI between individual fish in a school. (A) As in Fig. 1, the position of fish is shown for representative video frames as silhouettes within the experimental aquarium. In addition, we have traced the edges between fish where MI levels are relatively strong (MI>1 bit) because of a similarity in temporal changes in speed (Eqn 3). (B) Mean values of MI for schools (points) of each species (color coded); boxes represent the 1st and 3rd quartiles, with the median (heavy black line) and range of the measurements across all trials for a species (error bars). The letters over each box indicate pairwise significant differences ($P<0.05$, $N=15$ for each species, except rummy nose tetra, *P. bleheri*: $N=10$), after correction for multiple comparisons using Tukey's HSD method (groups with the same letters are not significantly different from one another).

and hence faster, than shoaling species (Buenos Aires and black skirt; Figs 3B,C and 4A). Therefore, speed and the polarization parameter provided the primary means for differentiating species (Fig. 3A). In contrast, the spacing between fish (NND and mean distance) did not follow a consistent pattern with respect to polarization (Figs 3D,E and 4C). The spacing between fish, along with the tendency to rotate in unison (i.e. the rotation parameter), showed greater variation within species than between them (Figs 3A and 4B,C) and therefore did not distinguish forms of schooling.

The kinematics of schooling emerge from communication between fish and the rules that govern individual behavior. Previous analyses of the kinematic responses of individuals to a small number of conspecifics suggest that attraction and repulsion between individuals emerge largely from velocity control (Katz et al., 2011; Herbert-Read et al., 2011). Consistent with this view, our application of MI measurements quantifies statistical similarities in the temporal patterns of speed between pairs of fish. These similarities depend on signaling, behavioral motivation and the motor coordination of fish to keep up with each other. It is therefore reasonable to infer performance in communication and speed control from our measurements of MI. Based on this reasoning, polarized species may be predicted to exhibit higher values of MI and that expectation was largely supported by our measurements (Fig. 5).

Similar patterns of information transmission through a school have been observed in other species. The flow of information is commonly quantified by transfer entropy (TE), which has the advantage over MI of indicating the direction of information flow between individuals. Levels of both TE and MI between schooling fish tend to increase over time when the school increases speed and becomes more polarized (Kent et al., 2019; Peterson et al., 2024), with potentially greater levels at central positions (Ioannou et al., 2011). The essential role that vision plays in mediating information sharing may be shown by varying ambient illumination (Strandburg-Peshkin et al., 2013). Flow sensing via the lateral-line system has been shown to play a supplemental role in MI levels, but only in relatively large schools (Peterson et al., 2024). This information sharing through vision and flow sensing may be modulated by motivation or extrinsic factors. For example, schools that have not fed for a greater period of time share information at a relatively high level (Wilson et al., 2019). Similar effects are elicited through exposure to alarm pheromone or caffeine (Schaerf et al., 2017; Ladu et al., 2015). Thus, experimental studies that incorporate measures of MI and TE serve to develop an understanding of the major factors that govern the motion of schools.

In our analysis, MI measurements provided the basis for analyzing network properties. With MI values serving as the edges between the nodes of individual fish, it is perhaps unsurprising how each of these properties exhibited a rank order that was similar to mean values of MI measurements (Fig. 5B). The polarized species exhibited a shorter path length, greater connectivity and less heterogeneity than shoaling species (Fig. 6B–D). High connectivity indicates multiple alternative paths for information to travel, creating a resilient group that does not fragment easily (Chung, 1997). This redundancy in information flow is further reflected in low heterogeneity, which suggests balanced influence among individuals. A short path length additionally reflects rapid signal transmission across a group. Together, these properties suggest that polarized species school with cohesive, flexible and more decentralized collective behavior than shoaling species. We did not use networks based on TE measurements as the spontaneous behavior of some of the species considered does not lend itself to this approach. TE and time-delayed MI measurements require the identification of a time lag between signals, as may be achieved through cross-correlation (Schreiber, 2000). We found delays were not possible to identify during periods when fish were not well coordinated, which was more common in species such as the Buenos Aires tetra (Fig. 5). Although this lack of coordination offers a challenge to resolving the direction of information flow through a network, it reflects important behavioral differences across species. Therefore, MI calculations provided a basis for comparison between species that exhibit varying levels of coordination.

The cohesion of a school could present ecological trade-offs for a species. A cohesive school, such as black neon tetras, should facilitate rapid responses to a predatory threat, or other change in environmental conditions, among its members (Schaerf et al., 2017;

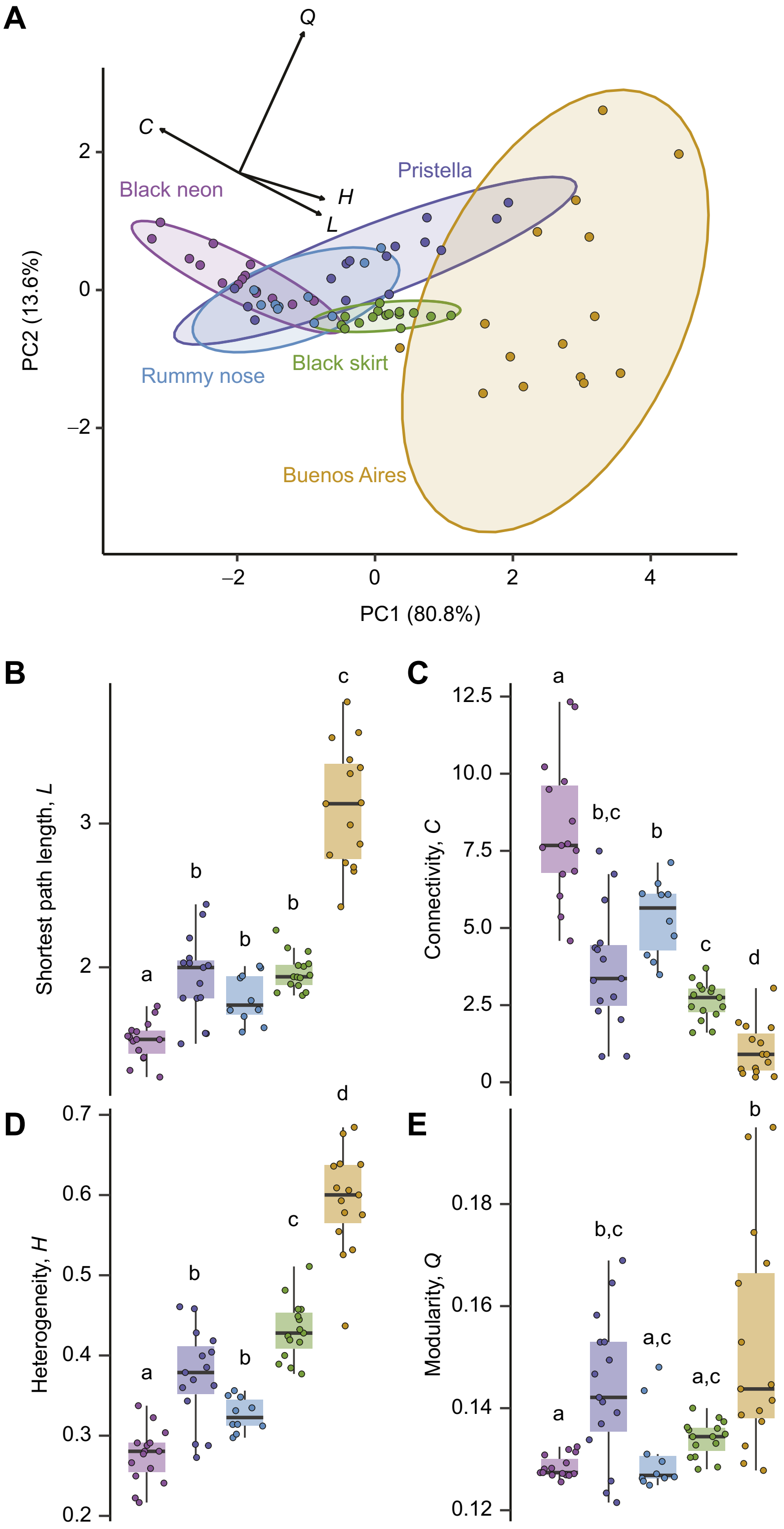

Fig. 6. Comparison of network properties across species. (A) PCA of the network trait space, including four network parameters (shortest path length, connectivity, heterogeneity and modularity parameters), with species identified by color. Points represent the position of an individual school in the trait space, with shaded regions denoting 95% data ellipses. The direction and length of the four axes (upper left) convey the relative contribution of the variables to the two principle components plotted. (B–E) Mean values of MI for schools (points) of each species (color coded); boxes represent the 1st and 3rd quartiles, with the median (heavy black line) and range of the measurements across all trials for a species (error bars) for the (B) shortest path length, (C) connectivity, (D) heterogeneity and (E) modularity. The letters over each box indicate pairwise significant differences ($P<0.05$, $N=15$ for each species, except rummy nose tetra, *P. bleheri*: $N=10$), after correction for multiple comparisons using Tukey's HSD method (groups with the same letters are not significantly different from one another).

Sosna et al., 2019). The ability to rapidly respond to the motion of neighboring fish could also assist in coordinated swimming to lower the metabolic costs of locomotion (Zhang and Lauder, 2024; Li et al., 2020; Seo and Mittal, 2022). However, cohesive schools may be less exploratory and therefore could be less likely to discover and exploit a refuge, food source or other resources. Species such as the Buenos Aires tetra exhibit a high degree of variance in the spacing between fish and their low polarization reflects large variance in heading among members of a school (Fig. 3D–F). Such sparse arrangements of fish could present a number of advantages. While there are potential hydrodynamic benefits to schooling, there are also regions in a flow field that adversely affect locomotor energetics compared with swimming in isolation (Li et al., 2019; Heydari et al., 2024; Seo and Mittal, 2022). A predator might more easily capture multiple prey if they are close together. Strongly cohesive schools might therefore not present a superior performance in all ecological contexts, but may instead exploit resources differently from shoaling species.

While our comparative framework reveals clear species-level differences in the behavior of schools, a few methodological constraints should be considered when interpreting our findings. Our analysis was largely restricted to two-dimensional kinematics, whereas schools have the potential to move in a three-dimensional volume, if permitted (Ko et al., 2025). This difference in dimensions can affect measurements such as NND, should alter the geometry of sensory occlusion (Strandburg-Peshkin et al., 2013) and may thereby change the relative strength of network connections. We emphasized 2D kinematics because it enabled reliable tracking of all individuals in a school in a manner challenging for 30 individuals in a 3D volume. The 2D limitation is also an ecologically relevant condition for tetras schooling in shallow or near-surface waters common in freshwater habitats. We additionally did not consider a possible role of sex ratios, as most tetras lack external dimorphism and invasive sexing of all individuals was not compatible with our repeated-measures design. While sex-specific effects cannot be ruled out, there is currently little evidence that they strongly modulate schooling in these species. Our focus was on emergent group-level patterns, rather than inferring individual interaction rules. Individual-level properties could be considered through agent-based modeling or trajectory-level causal inference, which are outside the present scope. Future studies integrating 3D kinematics, causal interaction metrics and incorporation of phylogenetic inference could offer additional insight.

Conclusion

Our findings demonstrate significant interspecific variation in schooling behavior among closely related neotropical tetras. These results underscore the diversity of collective behaviors within this group. Differences in kinematic and network properties, particularly polarization, speed and MI, indicate distinct collective behavioral patterns and information exchange across species. In particular, we found that polarized species are distinguished by rapid swimming and a more cohesive social network than shoaling species. The relationship between kinematic traits and network metrics emphasizes the interconnectedness of motion and social structure within schools. Such comparisons among closely related schooling species offer the promise of understanding how evolution is capable of diversifying collective behavior.

Competing interests

M.J.M. is an Academic Editor of Journal of Experimental Biology. M.J.M. was not involved in the editorial assessment of this submission. The authors declare no other competing interests.

Author contributions

Conceptualization: N.E.S., C.M.M., M.J.M.; Data curation: M.J.M.; Formal analysis: N.E.S., C.M.M., M.J.M.; Funding acquisition: C.M.M., M.J.M.; Investigation: N.E.S., A.N.P.; Methodology: N.E.S., A.N.P., C.M.M., M.J.M.; Project administration: C.M.M., M.J.M.; Resources: C.M.M., M.J.M.; Software: N.E.S., A.N.P., M.J.M.; Supervision: C.M.M., M.J.M.; Validation: N.E.S.; Visualization: N.E.S., M.J.M.; Writing – original draft: N.E.S.; Writing – review & editing: A.N.P., C.M.M., M.J.M.

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Data and resource availability

Supplementary data and code are available from Dryad (Swanson et al., 2026): https://doi.org/10.5061/dryad.x0k6djj0f. All other relevant data and details of resources can be found within the article and its supplementary information.

ECR Spotlight

This article has an associated ECR Spotlight interview with Nathan Swanson.

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