

# Motion leadership and local interaction in two species of freshwater fish (*Danio rerio* and *Hyphessobrycon herbertaxelrodi*)

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## Abstract

The authors studied momentary motion leadership in small groups of black neon tetra (*Hyphessobrycon herbertaxelrodi*) and zebrafish (*Danio rerio*), its relationship with local interaction parameters, such as the acceleration and turning angle of the individuals, and the relative locations of the individuals within the group. The purpose was to know whether leadership tended to be monopolised by certain individuals or whether it was equitably shared between them and if there were differences in leadership sharing between these two species, which are known to have different degrees of cohesion and polarisation. The authors filmed groups of two, three, four and eight fishes of each species and tracked their individual motion by image analysis and trajectory extraction. In both species, motion leadership was not monopolized but egalitarian and very short lived, with leadership shifts distributed randomly over time. The duration of leadership episodes decreased as group size increased and was longer in black neon tetra than in zebrafish. Momentary leaders did not tend to be in the front positions, but closer to the centre of the group. Acceleration and turning angle were more extreme in zebrafish than in black neon tetra and in the momentary leaders than the followers in both species. In general, these differences between species and between leaders/followers were qualitatively similar with some differences in detail, indicating that the relationship between motion leadership and local interaction parameters is likely to conform to a general physical law.

## KEYWORDS

collective motion, *Danio rerio*, *Hyphessobrycon herbertaxelrodi*, local interaction, motion leadership

## 1 | INTRODUCTION

Coordinated collective motion (CCM) is a common phenomenon in many fish species. Through local interactions, individuals in a group (called shoal or school) synchronise their movements and achieve a

large-scale coordinated movement (e.g., Couzin *et al.*, 2006; Pitcher & Parrish, 1993; Radakov, 1973). Regarding the models proposed for CCM in fish, a common assumption is that individuals move based on the rules of attraction to and repulsion from their immediate neighbours, and that they align (or polarize) with respect to them by

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adjusting their headings and velocities (e.g., Aoki, 1982; Couzin *et al.*, 2002; Huth & Wissel, 1994; Lopez *et al.*, 2012; Reynolds, 1987; Strömbom *et al.*, 2022). Empirical studies have found that a set of local interaction rules on the relative position of the individuals and their acceleration and turning angles, among other measures, may explain the CCM observed (Herbert-Read *et al.*, 2011; Katz *et al.*, 2011; Perna *et al.*, 2014; Rosenthal *et al.*, 2015; Schaerf *et al.*, 2021). In addition, data-driven modelling shows detailed interaction rules in moving groups of fish (Escobedo *et al.*, 2020; Heras *et al.*, 2019; Zienkiewicz *et al.*, 2015; Zienkiewicz *et al.*, 2018). Moreover, two features (global cohesion and polarization) that characterize collective motion at the macro level can be explained by dyadic interaction rules based on changes in the direction and velocity of the individuals, with the kind of movement at the group level being inferred from the relationships between these variables at the micro level (Quera *et al.*, 2019).

Although the universality of the interaction rules from which CCM emerges remains to be explored, results indicate that the rules are similar in the species from three distinct families: (a) *Cyprinidae* (*Notemigonus crysoleucas* and *Danio rerio*), (b) *Poeciliidae* (*Gambusia holbrooki*) and (c) *Characidae* (*Hyphessobrycon herbertaxelrodi*, *Hemigrammus rhodostomus* and *Pristella maxillaris*). As the results published in the past 15 years show, a set of local interaction rules based on the relative position of the individuals and their accelerations, distances and turning angles, among other measures, underlie CCM (e.g., Calovi *et al.*, 2018; Herbert-Read *et al.*, 2011; Katz *et al.*, 2011; Quera *et al.*, 2019; Rosenthal *et al.*, 2015; Schaerf *et al.*, 2017), with differences between species likely to be quantitative rather than qualitative. Comparative studies have explored the differences in the CCM of different fish species (e.g., Leem *et al.*, 2012; Soria *et al.*, 2007). Gimeno *et al.* (2016) and Quera *et al.* (2019) compared zebrafish and black neon tetra and found that although the two species had different styles of CCM (a higher polarization in black neon tetra than in zebrafish), the relationships between acceleration, turning angle, relative angle and the distance from a fish to its neighbours followed similar rules in both species, with the differences between them characterized by different magnitudes of the parameters in the functions related to those variables.

Fish schools tend to show a weak dominance hierarchy and are considered egalitarian societies in which any individual can act as a leader at any given moment; leadership is assumed to be temporary and “equipotential” (Breder, 1954; Pavlov & Kasumyan, 2000). Breder used the term “equipotential” to indicate that each fish in a school shares the same capacity to influence the other individuals in the group. Nonetheless, some studies have found that the individuals at the front of a group have a strong influence on the direction of collective motion (Bumann & Krause, 1993). In some fish species, certain individuals consistently tend to initiate group motion and occupy the front positions (Burns *et al.*, 2012). Among conspecifics, fish with larger body sizes tend to swim faster, which could explain why they are likely to be at the front (Krause *et al.*, 1998). Moreover, empirical studies have found that leadership in fish schools can emerge from individual differences in body size (Krause *et al.*, 1998; Reeb, 2001),

hunger or food motivation (Krause, 1993; Krause *et al.*, 1992; Webster, 2016), exploratory tendencies or boldness (Harcourt *et al.*, 2009; Nakayama *et al.*, 2016) and knowledge or training experience (Ioannou *et al.*, 2015; Reeb, 2000). All these factors can also interact with one another (Reeb, 2001; Webster, 2016). In humbug damselfish (*Dascyllus aruanus*), Ward *et al.* (2013) failed to find a clear relationship between body size and leadership, but did find that leadership was consistent between trials. Recent studies have focused on the emergence of leadership in shoals of biomimetic robotic fish (Wang *et al.*, 2017); how leaders moving in front of a shoal benefit from being followed by others when predators attack (Ioannou *et al.*, 2019); the modelling of collective motion in guppies (*Poecilia reticulata*) based on simple interaction rules causing emergence of leadership (Landgraf *et al.*, 2020); the modelling of avalanches triggered by a small number of fish (“effective leaders”) in black neon tetra (*H. herbertaxelrodi*) (Múgica *et al.*, 2022) and the transitions from uncoordinated to coordinated shoals with defined leader–follower roles in stickleback fish (*Gasterosteus aculeatus*) (Georgopoulou *et al.*, 2022).

Some divergent results about leadership are likely to result from different definitions of that concept. Dominance is an ambiguous concept, as it depends on specific behaviour and context; that is, individuals that are dominant about food may not necessarily be dominant in controlling territory or access to sex partners. Regarding dominance in group motion, being at the front of a group may not necessarily be identical to being a leader. In a rather different field, Theveneau and Linker (2017) found that collective cell migration during development is not always governed by cells located at the front, with the authors stating that “it would be more accurate to dissociate the function of a cell (regarding group motion) from its position in the group” (p. 1), an idea that could be useful when studying motion leadership in fish. Likewise, certain types of dominance may change over short periods of time. Although it can be assumed that informed individuals may lead group motion for considerable time periods when a group of fish is migrating or foraging, that assumption may not necessarily hold when there is no specific goal in the group motion besides coordination as an anti-predatory tactic. In the latter case, very frequent changes in motion leadership could be expected, and leaders, if any, would be temporary.

Following Krause *et al.* (2000) and Collignon *et al.* (2019), the authors define a motion leader as an individual who initiates movement towards a certain direction and is followed by other group members. Such leadership can be assessed by analysing pair-wise time delays between changes in the fish headings over time, a method used in the studies of group motion in pigeons (Nagy *et al.*, 2010, 2013; Pettit *et al.*, 2015; Sankey *et al.*, 2022) and fish (Georgopoulou *et al.*, 2022; Katz *et al.*, 2011; Herbert-Read *et al.*, 2011; Schaerf *et al.*, 2017). Alternative methods, such as the analysis of transfer entropy between velocities in pairs of zebrafish, have been proposed (Butail *et al.*, 2016); Strandburg-Peshkin *et al.* (2018) reviewed the different methods of defining operationally and measuring leadership in moving animal groups. In this paper, the authors analysed the persistence and leadership sharing among fishes, and their possible differences

between species. As evidence exists that group size has an effect on CCM in fish (Calovi *et al.*, 2014; Shelton *et al.*, 2015; Soria *et al.*, 2007), the authors measured the movements of groups with different sizes ( $N = 2, 3, 4$  and 8). They also explored whether the relationships between acceleration, turning angle and relative angle between fishes were different for momentary leaders and followers, whether leaders tended to be located at the front of the group and whether there were differences between species in how these variables were related.

## 2 | MATERIALS AND METHODS

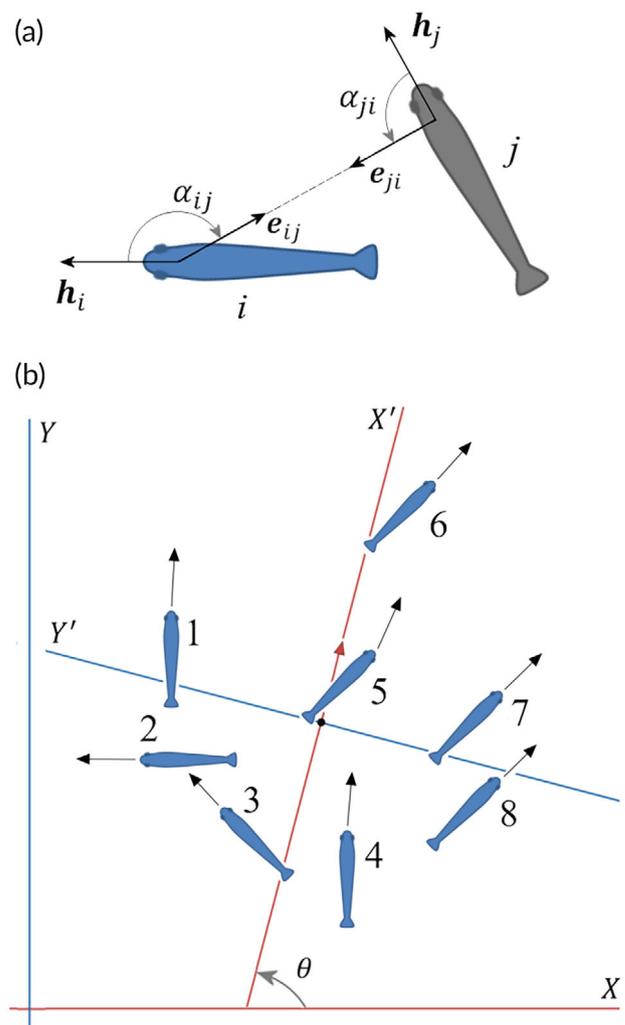
### 2.1 | Subjects

Thirty-four adult wild-type fishes were used in the experiment: 17 zebrafish (*D. rerio*; mean body length and S.D.:  $3.0 \pm 0.23$  cm) and 17 black neon tetra (*H. herbertaxelrodi*; mean body length and S.D.:  $2.5 \pm 0.20$  cm). For each species, 17 fishes were randomly selected from a big group in which females and males were mixed with a sex ratio close to 1:1, and assigned to four different groups (two, three, four and eight subjects). Each group was housed in a different aquarium ( $20 \times 14 \times 14$  cm for the groups of two, three and four individuals and  $34 \times 20 \times 22$  cm for the group of eight individuals) 1 week before the experiments started and during the experiments. The aquaria were maintained on a regular light/dark cycle and water temperature at  $25 \pm 2^\circ\text{C}$ , pH at 7.8–8, total hardness at 8–14° dH and carbonated hardness at 8–14° dH. Ammonium and nitrite concentrations were nil, whereas nitrate levels were below  $50 \text{ mg l}^{-1}$ . Water quality was kept optimal by performing weekly 15% water changes. Fish were fed to satiation on Ocean Nutrition Community Formula Flakes (Ocean Nutrition Europe, Essen, Belgium).

Institutional guidelines for the care and use of animals were followed. All the procedures performed were in accordance with the standards approved by the Ethics Committee of the University of Barcelona, where the studies were conducted (project no. 119/18, approval date 20 March 2018).

### 2.2 | Apparatus and procedure

An experimental tank measuring  $100 \times 93 \times 40$  cm and a water column with a height of 15 cm were used; that is, water volume in the experimental tank was  $0.1395 \text{ m}^3$ ; thus, fish densities in the experimental tank were 14.3, 21.5, 28.7 and  $57.3 \text{ m}^{-3}$  for groups of two, three, four and eight fishes, respectively. Water in the experimental tank was maintained at  $21\text{--}22^\circ\text{C}$ , with the same pH and dH levels as in the aquaria. Six lamps surrounding the tank provided homogeneous low-intensity light. Videos were recorded at 20 fps, 8-bit (grey scale) and a resolution of  $1176 \times 1016$  pixels, with a digital camera (uEye UI-1640-LE) mounted 2.2 m above the centre of the tank and linked to a computer. Given the experimental tank dimensions and the video resolution, the conversion factor was 0.084 cm per pixel. Durations



**FIGURE 1** Headings, relative angles and forefront index. (a) Headings ( $h_i, h_j$ ) and relative angles ( $\alpha_{ij}, \alpha_{ji}$ ) of two fishes *i* and *j* at frame *t*. Sign of the relative angle  $\alpha_{ij}$  is that of the vertical component of the vector product  $h_i(t) \times e_{ij}(t)$ , where  $e_{ij}(t)$  is the unit vector pointing from *i*'s to *j*'s position. (b) Translation and rotation of the (*X*, *Y*) axes to calculate forefront indexes for a group of eight fishes. The black dot close to fish 5 is the group centroid, and the red arrow under that fish is the group heading. The origin of the coordinates was moved to the group centroid and the axes were rotated to the (*X'*, *Y'*) axes, as indicated in the figure. Upon changes of the axes, fishes 6 and 4 had the highest positive and negative forefront indexes (*X'* coordinates), respectively

were originally measured in frames and subsequently converted into seconds by dividing them by 20.

Each experimental group (of two, three, four and eight individuals) was filmed daily for 5 min during spontaneous group swimming. The procedure was replicated first for 10 days with the zebrafish and then for 10 days with the black neon tetra. To ensure the fish became acclimatized to the temperature in the experimental tank ( $25^\circ\text{C}$ ), prior to the recording session, each group was transferred from its aquarium into a bucket containing a mixture of water from the experimental tank and the fishes' aquarium, and remained there for 5 min. The fish

were then transferred into the experimental tank. After another 5 min of habituation to the new environment, their activity was recorded for 5 min. Once the recording was made, the fish were captured with a net and transferred back to their aquarium, to which water from the experimental tank was added to facilitate re-acclimatization. At the end of the daily recording sessions, water was added to the experimental tank to compensate for the water transferred into the aquaria. As the four groups of each species were filmed in succession each day, the order in which they were recorded was randomly sorted daily to control for possible cumulative effects of the decrease in water temperature (because the heaters were removed from the experimental tank during recording) and any pheromones or chemical signals left in the water by the preceding group.

Eighty videos were recorded, with a total of 6 h and 40 min of footage. Video fragments were decomposed into frames, and a stack of 6000 frames per fragment was obtained. The authors randomly selected six packs of 500 consecutive frames for each fragment, resulting in six replicas of 25 s per group and day, *i.e.*, 60 replicas per group. In total, 1 h and 40 min of footage (120,000 frames) was analysed per species. The authors applied the method of Dolado *et al.* (2015) to resolve occlusions and acquired the individual fish coordinates in two dimensions from the stacks of occlusion-free frames by image analysis and trajectory extraction using Virtual Dub 1.9.11 (Lee, 2013), ImageJ version 1.48 (Rasband, 2014) and Image-Pro Premier 9.1 (Media Cybernetics Inc., 2015), in accordance with Quera *et al.*, (2019). The trajectory files were then processed using R scripts (R Development Core Team, 2020) to calculate the behavioural measures described in the next section.

## 2.3 | Measures

### 2.3.1 | Momentary motion leadership index and rank

The authors calculated motion leadership by analysing the pair-wise time delays between changes in the fish headings over time to determine which fish, if any, was directing group movement at each frame  $t$ . First, they calculated fish headings at each frame  $t$  (Figure 1a), which are the normalized velocities of the fish (unit vectors). For fish  $i$ ,  $\mathbf{h}_i(t) = \mathbf{v}_i(t)/|\mathbf{v}_i(t)|$ . Given the two-dimensional (2D) pixel coordinates of fish  $i$  at frames  $t-1$  and  $t$ ,  $[x_i(t-1), y_i(t-1)]$  and  $[x_i(t), y_i(t)]$ , respectively, its velocity was defined as the vector linking the two positions:  $\mathbf{v}_i(t) = (x_i(t) - x_i(t-1), y_i(t) - y_i(t-1))$ , with its module expressed in pixels per frame.

Then, the authors calculated time directional dot products between the headings of each pair of fish ( $i, j$ ) within a moving time window of length  $2w$  centred at each frame  $t$ :

$$c_{ij}(t, \tau) = \mathbf{h}_i(t) \cdot \mathbf{h}_j(t + \tau)$$

with  $-w \leq \tau \leq +w$ . Nagy *et al.* (2010) measured global leadership over a period of time for every pair of pigeons in a flock by averaging the

directional dot products over that period and obtaining the lag that maximized the average. As the authors were interested in measuring momentary changes in leadership, they computed leadership indexes per frame, not globally. As  $c_{ij}(t, \tau)$  equals the cosine of the angle between the headings of fish  $i$  at  $t$  and fish  $j$  at  $t + \tau$ , it will be close to  $+1$  when the headings are very similar. In that case, if  $\tau > 0$ , then  $i$ 's heading will predict  $j$ 's at  $\tau$  frames after it. If  $\tau < 0$ , then  $i$ 's heading will be predicted by  $j$ 's at  $\tau$  frames before it. Conversely  $c_{ij}(t, \tau)$  will be close to  $-1$  when their headings at  $t$  and  $t + \tau$  are the opposite. Null correlations will indicate that the headings are independent of lag  $\tau$ . It should be noted that  $c_{ij}(t, \tau) = c_{ji}(t + \tau, -\tau)$ .

For each frame  $t$  and pair of fish, the authors obtained the maximum dot product,  $c_{ij}^*(t) = \max_{\tau} c_{ij}(t, \tau)$ , and the lag for that maximum,  $\tau_{ij}^*(t)$ .  $\tau_{ij}^*(t) > 0$  indicated that fish  $i$  tends to lead fish  $j$  with lag  $\tau_{ij}^*(t)$  (within the time window), whereas  $\tau_{ij}^*(t) < 0$  indicated that fish  $i$  tends to follow fish  $j$  with lag  $\tau_{ij}^*(t)$ . Thus, the momentary leadership index of fish  $i$  at frame  $t$  was defined as the average of its dyadic  $\tau_{ij}^*(t)$  indexes at that frame:

$$\tau_i(t) = \frac{1}{N-1} \sum_{\substack{j=1 \\ j \neq i}}^N \tau_{ij}^*(t)$$

with  $-w \leq \tau_i(t) \leq +w$ , and  $w = 30$  frames, *i.e.*, 1.5 s (see Herbert-Read *et al.*, 2011; Katz *et al.*, 2011). Fishes with values for  $\tau_i(t)$  that were close to  $+w$  tended to lead other fishes with lower values of that index, whereas fishes with values close to  $-w$  tended to be led by other fishes with a higher index than theirs.

### 2.3.2 | Duration of leadership episodes

A leadership episode was determined as a series of consecutive frames starting at  $t_A$  and ending at  $t_B$  in which one fish  $i$  had the momentary leadership rank  $r_i(t) = 1$ . The duration of the  $k$ -th episode of fish  $i$  was thus  $d_{ik} = t_B - t_A + 1$ . The mean duration of leadership episodes was a group measure:  $\bar{d} = T / \sum_i K_i$ , where  $T = \sum_{i=1}^N \sum_{k=1}^{K_i} d_{ik}$ , which equals the fragment length, and  $K_i$  the number of leadership episodes of fish  $i$ .

### 2.3.3 | Egalitarian leadership index

Collignon *et al.* (2019) measured the entropy of the distribution of motion leadership episodes in groups of zebrafish to determine whether leadership was equally shared among all the fishes or monopolized by certain individuals. If momentary leadership is shared by all the fishes equitably throughout a fragment, the proportion of frames  $p_i$  in which  $r_i(t) = 1$  will be identical for all  $i$ . Egalitarian leadership can be defined as the invariability of  $p_i$  and is expressed as the entropy,  $H = -\sum_{i=1}^N p_i \log_2 p_i$  (Shannon & Weaver, 1949), which is measured in bits. When  $p_1 = p_2 = \dots = p_N$ ,  $H$  will be the maximum and equal  $\log_2 N$ . Thus, a more convenient index of egalitarian leadership is  $E = H / \log_2 N$ . If

momentary leadership is shared equitably, then  $E = 1$ . If one fish monopolizes leadership throughout the fragment, then  $E = 0$ .

### 2.3.4 | Forefront index

This was defined as the distance from fish  $i$  to the axis passing through the centroid of the group, perpendicular to the axis defining group motion at frame  $t$  (Gimeno, 2018). First, the centroid coordinates of the group at  $t - 1$  and  $t$  were calculated as the averages of the individual fish coordinates at those frames,  $[x_c(t-1), y_c(t-1)]$  and  $[x_c(t), y_c(t)]$ , respectively. Group velocity  $\mathbf{v}_c(t)$  was the vector linking the former to the latter point, and the group heading was thus the unit vector  $\mathbf{h}_c(t) = \mathbf{v}_c(t)/|\mathbf{v}_c(t)|$ . Second, the origin of the coordinates was moved to  $[x_c(t), y_c(t)]$  and the  $(X, Y)$  axes were rotated to new  $(X', Y')$  axes, so that  $X'$  was aligned to the group heading and the transformed coordinates of fish  $i$  were given by the rotation matrix (Figure 1b):

$$\begin{pmatrix} x'_i(t) \\ y'_i(t) \end{pmatrix} = \begin{pmatrix} \cos\theta & \sin\theta \\ -\sin\theta & \cos\theta \end{pmatrix} \begin{pmatrix} x_i(t) - x_c(t) \\ y_i(t) - y_c(t) \end{pmatrix}$$

where

$$\cos\theta = (x_c(t) - x_c(t-1))/|\mathbf{v}_c(t)|$$

$$\sin\theta = (y_c(t) - y_c(t-1))/|\mathbf{v}_c(t)|$$

Thus, the forefront index of fish  $i$  was:

$$\phi_i(t) = x'_i(t) = (x_i(t) - x_c(t))\cos\theta + (y_i(t) - y_c(t))\sin\theta$$

Individuals with a positive  $\phi_i(t)$  would be at the front of the group, whereas individuals with a negative  $\phi_i(t)$  would be at the rear. The greater the absolute forefront index, the farther away the fish was from the  $Y'$ -axis.

### 2.3.5 | Acceleration

Following Herbert-Read *et al.* (2011) and Kartz *et al.* (2011), the authors defined acceleration as the rate of change of speed, which can take positive or negative values (*i.e.*, to calculate acceleration, they did not take the direction of motion into account). Given the velocities of fish  $i$  at frames  $t - 1$  and  $t$ , its acceleration at  $t$  was calculated as the difference between the module of its velocity at  $t$  minus that at  $t - 1$ , and is expressed in pixels per frame<sup>2</sup>:  $s_i(t) = |\mathbf{v}_i(t)| - |\mathbf{v}_i(t-1)|$ .

### 2.3.6 | Relative angle

The relative angle  $\alpha_{ij}(t)$  from fish  $i$  to fish  $j$  at frame  $t$  is the angle from  $\mathbf{h}_i(t)$  to the unit vector that points from  $i$ 's position to  $j$ 's position,  $\mathbf{e}_{ij}(t)$  (Figure 1a).  $\alpha_{ij}(t)$  will be positive when fish  $j$  is to the left of fish  $i$ , and

negative when it is to its right. When fish  $j$  is in front of fish  $i$ ,  $\alpha_{ij}(t) = 0^\circ$ , when it is behind,  $\alpha_{ij}(t) = \pm 180^\circ$ , and when it is alongside it,  $\alpha_{ij}(t) = \pm 90^\circ$ .

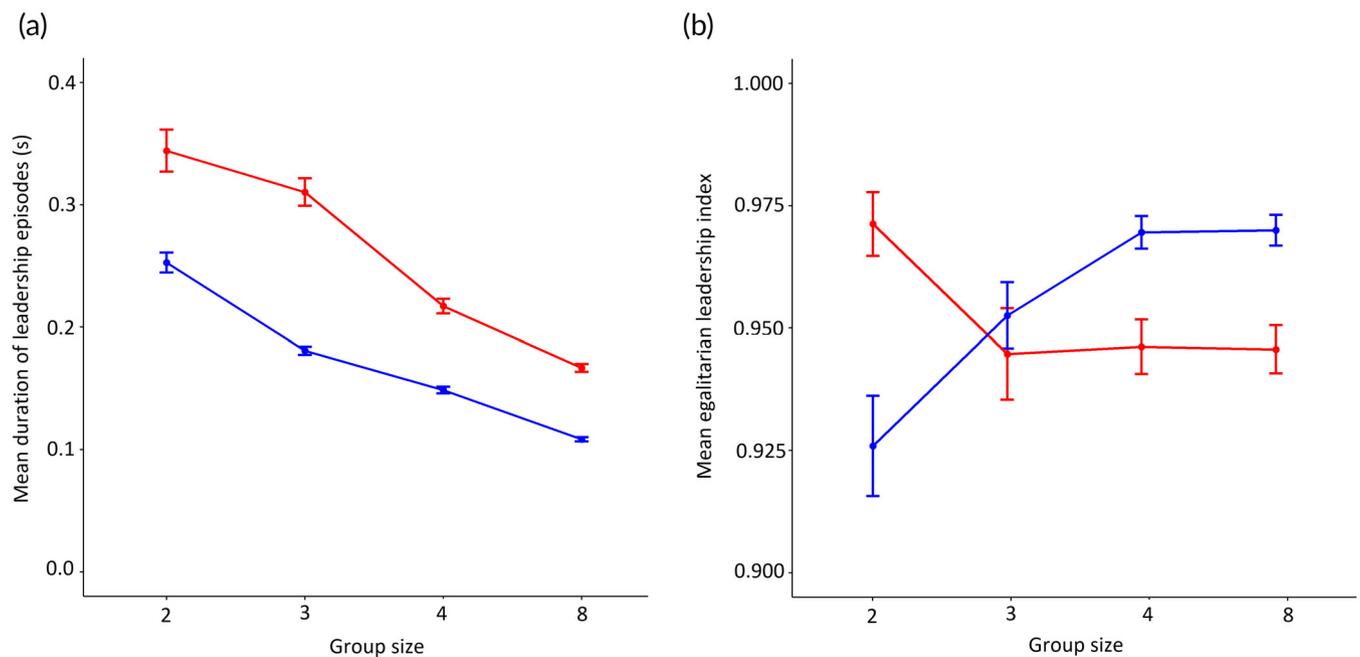
### 2.3.7 | Turning angle

The turning angle  $\beta_i(t)$  of fish  $i$  at  $t$  is the angle from its previous heading to its current one. When the fish turns left, its turning angle will be positive. When it turns right,  $\beta_i(t)$  will be negative. Turning angles are expressed in degrees per frame.

It is known that individuals in a group of zebrafish tend to distribute on several close strata on the water column, whereas individuals in a group of black neon tetra tend to swim in the same stratum (Gimeno *et al.*, 2016; Spence *et al.*, 2006). Nonetheless, it can be assumed that, even if two fishes were swimming on slightly different strata of the water column, their heading difference as recorded from a camera above would be the same as if they were swimming on the same stratum and, consequently, their momentary leadership indexes would not be distorted. Likewise for turning angles, because fish tended to turn horizontally. On the contrary, as fishes of those two species did not tend to swim vertically, the distance an individual travelled between two consecutive video frames (and, consequently, its speed and acceleration) could be reliably measured on the 2D image captured by the camera. Watts *et al.* (2017) showed that pair-wise leadership interactions identified through a 2D analysis matched those identified through a 3D analysis in which the position of fish on the water column was taken into account.

## 3 | RESULTS

Figure 2a shows the results for the mean durations of leadership episodes ( $\bar{d}$ ) as a function of group size and species. Data were averaged for each video fragment, resulting in 60  $\bar{d}$  values per group size and species. A mixed factorial ANOVA (with species and group size as between group factors and day as the within group one) indicated that  $\bar{d}$  was significantly different between the different group sizes [ $F(3, 40) = 154.94, P < 0.001, \eta^2 = 0.354$ ] and between species [ $F(1, 40) = 235.66, P < 0.001, \eta^2 = 0.179$ ]. The interaction between group size and species was significant as well, but its effect size was much smaller than the main effect sizes [ $F(3, 40) = 7.80, P < 0.001, \eta^2 = 0.018$ ]. Momentary leadership episodes were longer on average in black neon tetra than in zebrafish [0.260 s vs. 0.173 s,  $t(40) = 15.4, P < 0.001$ ], and decreased as group size increased from 0.344 s (black neon tetra) and 0.253 s (zebrafish) for the group size of 2 to 0.167 s (black neon tetra) and 0.108 s (zebrafish) for the group size of 8. Globally, days had a significant effect on  $\bar{d}$  [ $F(4.63, 185.12) = 3.45, P = 0.007, \eta^2 = 0.020$ ]. Mean duration of momentary leadership episodes was in average fairly stable in zebrafish (for all the group sizes) and in black neon tetra (for  $N = 4$  and  $N = 8$ ) throughout the days; in black neon tetra, for  $N = 2$  and  $N = 3$ , it decreased during the first half of the days and regained its initial value during the second half.



**FIGURE 2** Momentary motion leadership in *Hyphessobrycon herbertaxelrodi* and *Danio rerio*. (a) Mean duration of momentary leadership episodes and (b) mean egalitarian leadership index as a function of species and group size. Error bars are SEMs. Species:  $\blacktriangleright$ , Neon;  $\blacktriangleleft$ , Zebrafish

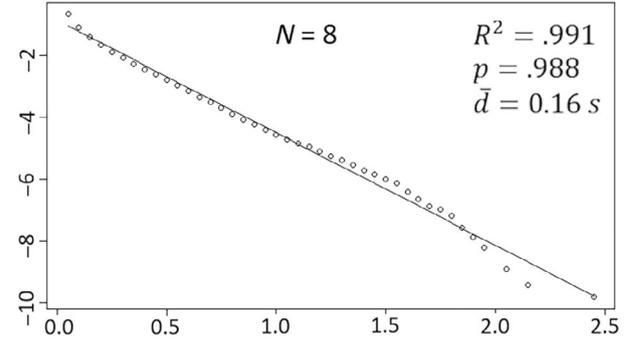
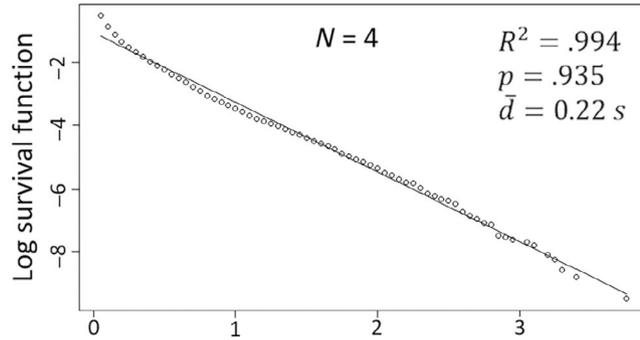
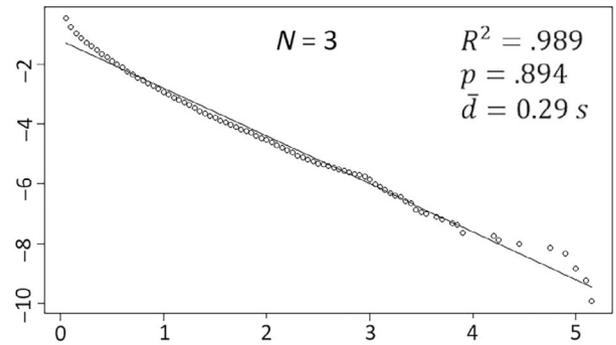
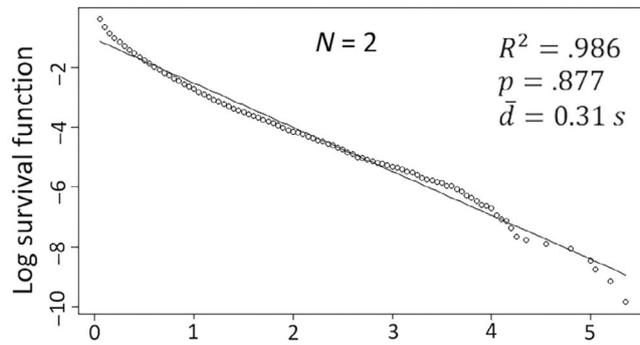
Results for the egalitarian leadership index ( $E$ ) are shown in Figure 2b as a function of group size and species, averaged for each video fragment, resulting in 60  $E$  values per group size and species. A mixed factorial ANOVA (with species and group size as between group factors and day as within group one) indicated that no significant differences existed in  $E$  between the different group sizes [ $F(3, 40) = 1.267, P = 0.299, \eta^2 = 0.006$ ] and between species [ $F(1, 40) = 0.290, P = 0.593, \eta^2 < 0.001$ ], whereas the interaction between the two variables was significant, with a small effect size [ $F(3, 40) = 12.039, P < 0.001, \eta^2 = 0.061$ ]. For the group size of 2,  $E$  was significantly greater in black neon tetra than in zebrafish [0.971 vs. 0.926,  $t(40) = 4.796, P = 0.007$ ], whereas no significant differences were found for the group sizes of 3 [0.945 vs. 0.953,  $t(40) = -0.832, P = 0.998$ ], 4 [0.946 vs. 0.970,  $t(40) = -2.468, P = 0.538$ ] and 8 [0.926 vs. 0.970,  $t(40) = -2.573, P = 0.483$ ]. Globally, days had no significant effect on  $E$  [ $F(6.98, 279.39) = 1.32, P = 0.242, \eta^2 = 0.017$ ].

Durations of leadership episodes showed exponential distributions in both species and for the four group sizes. Figure 3 shows the log-survival functions of the durations,  $\log_e S(d)$ . Log-rank tests showed statistically significant differences between the survival functions, both between group sizes [black neon tetra,  $X^2(3) = 3819, P < 0.001$ ; zebrafish,  $X^2(3) = 8540, P < 0.001$ ] and between species [ $N = 2, X^2(1) = 107, P < 0.001$ ;  $N = 3, X^2(1) = 714, P < 0.001$ ;  $N = 4, X^2(1) = 712, P < 0.001$ ;  $N = 8, X^2(1) = 1813, P < 0.001$ ]. Regression lines fitted to the log-survival functions had  $R^2$  ranging from 0.978 (zebrafish,  $N = 2$ ) to 0.994 (black neon tetra,  $N = 4$ ), indicating that the durations were exponentially distributed; that is, their rate parameter  $\lambda$  was largely

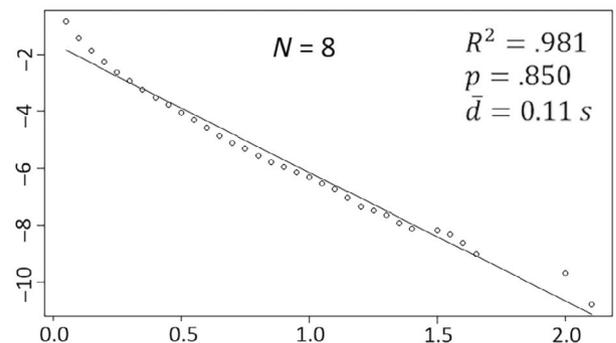
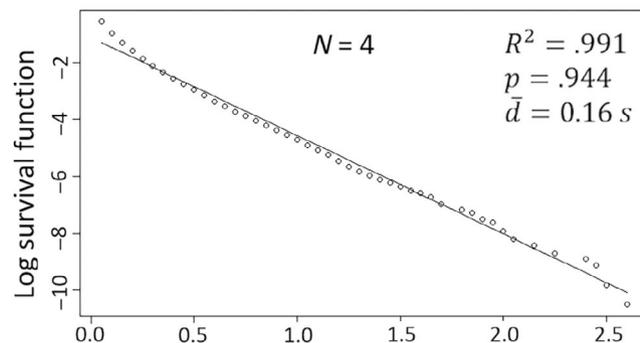
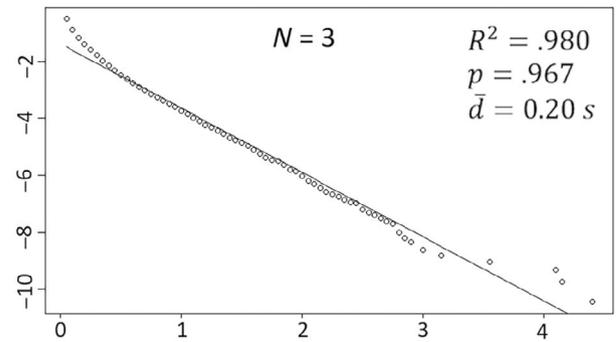
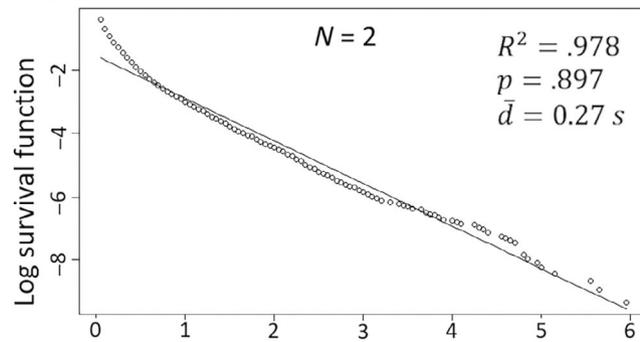
independent of the episode duration, with  $\log_e S(d) = -\hat{\lambda}d$ , where  $\hat{\lambda} = 1/\bar{d}$ . In other words, the probability of a leadership episode terminating did not depend on its duration and, therefore, leadership transitions were randomly distributed over time (e.g., Cox & Lewis, 1966; Haccou & Meelis, 1992; Lendrem, 1986), irrespective of the species and group size. Likelihood ratio tests of exponential against Weibull distributions (where the probability that an episode terminates would depend on its duration; Cox & Oakes, 1984) yielded  $P$ -values ranging from 0.850 (zebrafish,  $N = 8$ ) to 0.988 (black neon tetra,  $N = 8$ ), indicating that the null hypothesis of exponentiality could not be rejected.

The results for acceleration and turning angle as functions of the relative angle are shown in Figures 4–6. Accelerations and turning angles were aggregated based on 12 relative angle bins, from  $\alpha_{ij} = -180^\circ$  to  $\alpha_{ij} = +180^\circ$ , 30 degrees per bin (i.e., interval boundaries were  $-180^\circ, -150^\circ, -120^\circ, \dots, +180^\circ$ ). Data were averaged for day, video fragment, group size and momentary leadership rank 1 (leaders) vs. a rank greater than 1 (followers). As shown in Figure 4, both in black neon tetra and in zebrafish, an individual (fish  $i$ ) accelerated more when its neighbour (fish  $j$ ) was in front ( $\alpha_{ij} = 0^\circ$ ), decelerated when its neighbour was behind ( $\alpha_{ij} = \pm 180^\circ$ ) and tended to maintain its velocity when its neighbour was alongside it ( $\alpha_{ij} \cong \pm 90^\circ$ ). In both species, momentary leaders (Tau rank 1) accelerated more than the followers (Tau rank  $> 1$ ) regardless of their relative angle to their neighbours. Maximum acceleration occurred when  $\alpha_{ij} \cong 0^\circ$ , i.e., when fishes were one in front of the other: for a momentary leader (fish  $i$ ) when its neighbour (fish  $j$ , a follower) was in front, and for a follower (fish  $i$ ) when its neighbour (fish  $j$ , either a momentary leader or a follower) was in front. Maximum acceleration was greater in zebrafish

## Neon



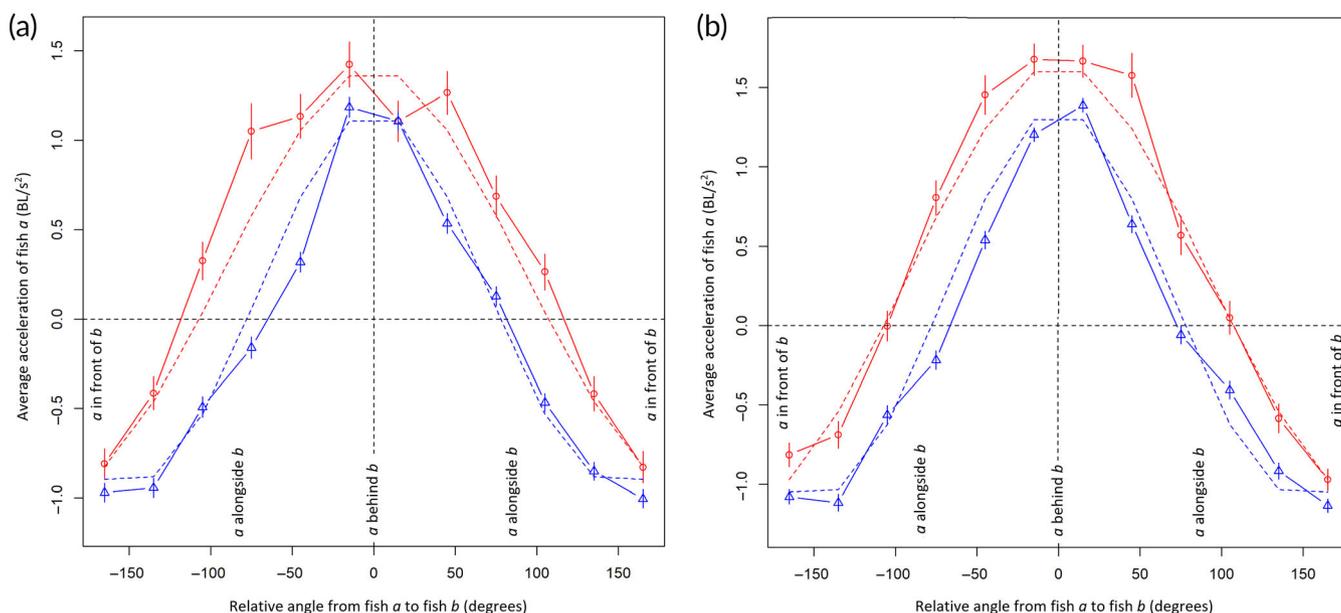
## Zebrafish



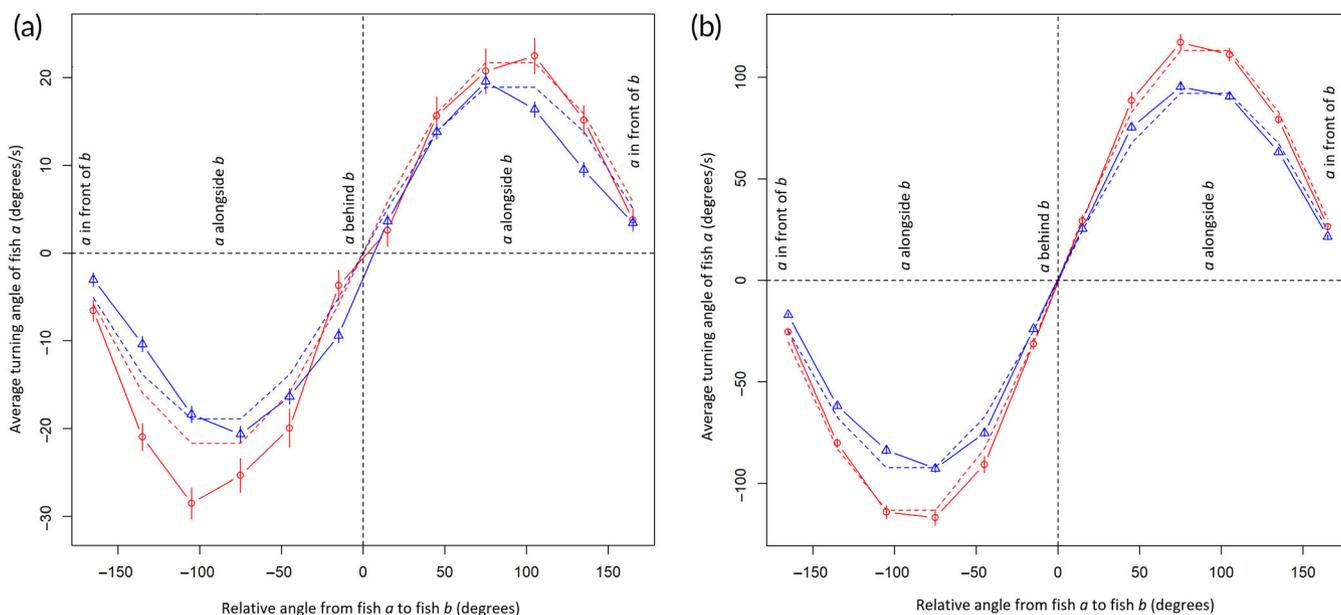
**FIGURE 3** Durations of momentary leadership episodes in *Hyphessobrycon herbertaxelrodi* and *Danio rerio*. Log-survival functions of durations of momentary leadership episodes as a function of species and group size, with regression lines and their  $R$ -squared values.  $P$ -values of likelihood ratio tests of exponential against Weibull distributions, as well as the average episode durations, are indicated

than in black neon tetra, and greater in the leaders than in the followers for both species. Maximum deceleration occurred when  $\alpha_{ij} \cong \pm 180^\circ$ , i.e., for a momentary leader (fish  $i$ ) when it was in front of

a follower (fish  $j$ ) and for a follower (fish  $i$ ) when it was in front of its neighbour (fish  $j$ , either a momentary leader or a follower). Table 1 shows the acceleration ranges based on species and leader/followers.



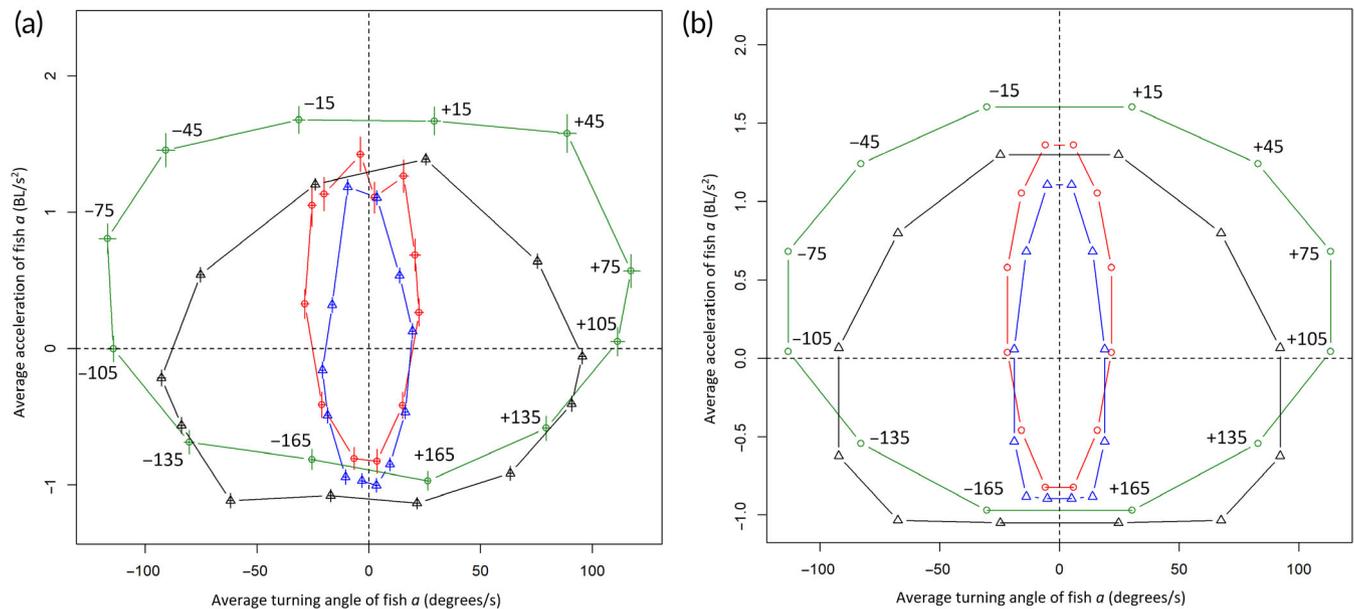
**FIGURE 4** Acceleration and relative angle in groups of *Hyphessobrycon herbertaxelrodi* and *Danio rerio*. Average acceleration of a fish (in BL s<sup>-2</sup>) as a function of the relative angle towards its neighbour, when the former is a momentary leader (*Tau rank* 1) and when it is a momentary follower (*Tau rank* > 1). Data are pooled from the groups of different sizes. (a) Black neon tetra and (b) zebrafish. Error bars are SEMs. Dashed lines indicate cosine models (see text). Specific relative angles are labelled. ◦, Leader, *Tau rank* 1; △, Follower, *Tau rank* > 1



**FIGURE 5** Turning angle in groups of *Hyphessobrycon herbertaxelrodi* and *Danio rerio*. Turning angle of a fish (in degrees s<sup>-1</sup>) as a function of the relative angle towards its neighbour, when the former is a momentary leader (*Tau rank* 1) and when it is a momentary follower (*Tau rank* > 1). Data are pooled from the groups of different sizes. (a) Black neon tetra and (b) zebrafish. Error bars are SEMs. Dashed lines indicate sine models (see text). Specific relative angles are labelled. ◦, Leader, *Tau rank* 1; △, Follower, *Tau rank* > 1

In both species, the average turning angle of a fish depended on its relative angle to its neighbour (Figure 5). Positive (left) turns were maximum when the neighbour was on the left (relative angle  $\alpha_{ij} \cong +90^\circ$ ), whereas negative (right) turns were maximum when the neighbour was on the right ( $\alpha_{ij} \cong -90^\circ$ ). The average turning angle

was zero when the neighbour was either in front or behind (relative angles equal to  $0^\circ$  or to  $\pm 180^\circ$ , respectively). As shown in the figure, the relationship between the average turning angle and relative angle had a peak at  $\alpha_{ij} = +90^\circ$  and a trough at  $\alpha_{ij} = -90^\circ$  in both species, and when fishes were both momentary leaders (*Tau rank* 1) and



**FIGURE 6** Acceleration and turning angle in groups of *Hyphessobrycon herbertaxelrodi* and *Danio rerio*. Relationship between the average acceleration (in  $\text{BL s}^{-2}$ ) and turning angle (in  $\text{degrees s}^{-1}$ ) per species and momentary leader/follower rank as parametric functions of the relative angle (in degrees) of a fish to their neighbours. (a) Data are pooled from the groups of different sizes. Error bars are SEMs. (b) Model. Relative angles are indicated for the zebrafish momentary leaders (Zebrafish. Leader),  $\circ$ , Neon Leader;  $\Delta$ , Neon Follower;  $\diamond$ , Zebrafish Leader;  $\triangle$ , Zebrafish Follower

**TABLE 1** Minimum and maximum accelerations and turning angles for the momentary leaders (Tau rank 1) and followers (Tau rank > 1), in groups of *Hyphessobrycon herbertaxelrodi* and *Danio rerio*

Fish species		Acceleration ( $\text{cm s}^{-2}$ )		Acceleration ( $\text{BL s}^{-2}$ )		Turning angle ( $^{\circ} \text{s}^{-1}$ )	
		Min.	Max.	Min.	Max.	Min.	Max.
<i>Hyphessobrycon herbertaxelrodi</i>	Leader	-2.07	3.56	-0.83	1.42	-28.54	22.48
	Followers	-2.51	2.96	-1.00	1.18	-20.65	19.57
<i>Danio rerio</i>	Leader	-2.91	5.03	-0.97	1.68	-116.85	117.29
	Followers	-3.40	4.16	-1.13	1.39	-92.68	95.5

followers (Tau rank > 1). Nonetheless, for a given relative angle to their neighbours, momentary leaders tended to turn more than the followers. Peak-to-peak amplitude was greater in zebrafish than in black neon tetra. In both species, the amplitude was greater in the leaders than in the followers. The minimum and maximum average turning angles are shown in Table 1.

Acceleration and the turning angle of a fish are approximate sinusoidal functions of the relative angle from that fish to its neighbours. When the data were analysed separately for momentary leaders vs. momentary followers, the acceleration of fish  $i$  was modelled as a cosine function of the relative angle (in degrees) from fish  $i$  to fish  $j$  with different parameter values depending on whether fish  $i$  was a leader ( $k = +0.5$ ) or a follower ( $k = -0.5$ ):

$$s_i = p \times \left(1 - \frac{|\alpha_{ij}|}{4 \times 180}\right) \times \cos\left[\left(1 - \frac{k}{180}\right)\alpha_{ij}\right]$$

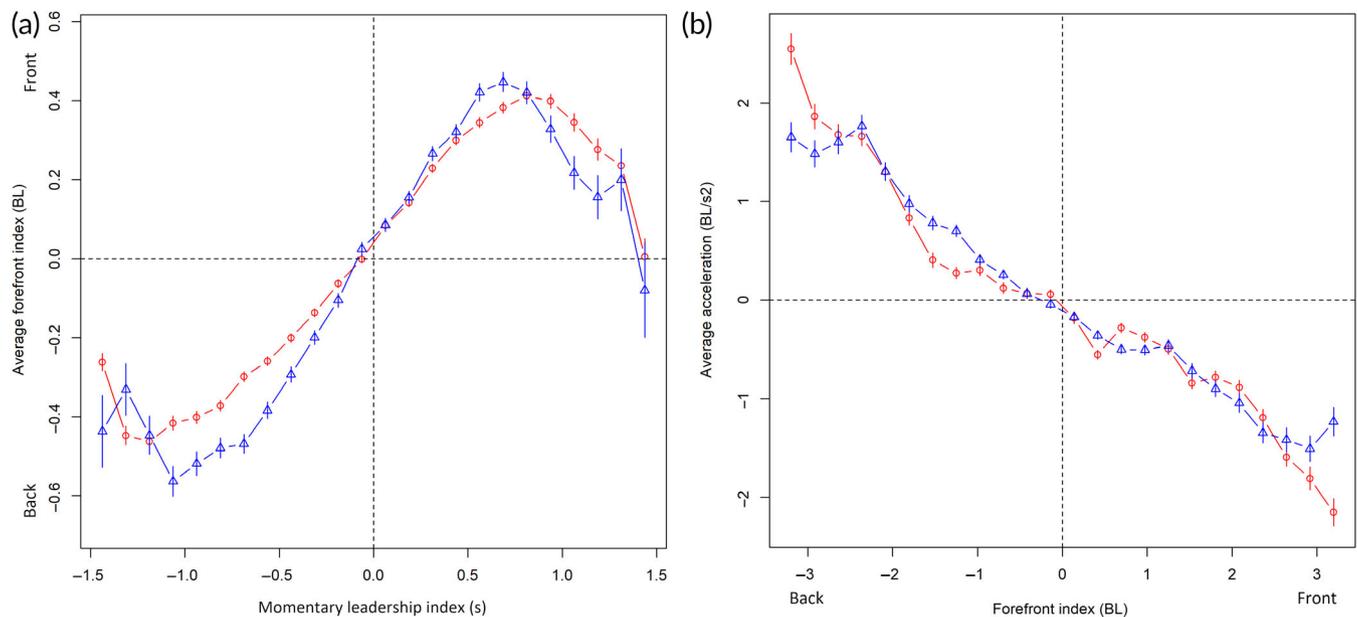
where  $p$  is the maximum acceleration, a function of the species and leader/follower rank (Table 1). Similarly, the turning angle of fish

$i$  could be modelled as a sine function of the relative angle from fish  $i$  to fish  $j$ :

$$\beta_i = q \times \sin \alpha_{ij}$$

where  $q$  is the maximum positive turning angle, a function of the species and leader/follower rank (Table 1). The cosine and sine models are shown in Figures 4 and 5. When the data for leaders and followers were pooled (Quera *et al.*, 2019),  $k = 0$  and the values for the parameters that were intermediate or close to the maxima in Table 1 provided a reasonable model for the data (black neon tetra,  $p = 1.34 \text{ BL s}^{-2}$ ,  $q = 20.04^{\circ} \text{ s}^{-1}$ ; zebrafish,  $p = 1.61 \text{ BL s}^{-2}$ ,  $q = 94.35^{\circ} \text{ s}^{-1}$ ). Figure 6a shows the relationship between acceleration and the turning angle for a set of relative angles as a function of species and the leader/follower rank. The corresponding modelled parametric functions are shown in Figure 6b.

Momentary leadership and the forefront indices were related (Figure 7a) for the group sizes of 3, 4 and 8 pooled together. On average, the forefront index was positive when the fish had a positive



**FIGURE 7** Forefront index and acceleration in groups of *Hyphessobrycon herbertaxelrodi* and *Danio rerio*. (a) Average forefront index (in BL) of a fish as a function of its momentary leadership index (in s). (b) Average acceleration (in BL s<sup>-2</sup>) of a fish as a function of its forefront index (in BL). Data are pooled from the groups with sizes larger than two fishes. ◻, Neon; ◻, Zebrafish

leadership index (i.e., when it tended to lead other fishes) and negative when the fish had a negative leadership index (i.e., when it tended to follow other fishes). In other words, momentary leaders tended to be at the front of the group, whereas followers tended to be at the rear. Nonetheless, as indicated by the peaks and troughs in Figure 7a in both species, whereas fishes with moderately positive indexes tended to be at the front and fishes with moderately negative indexes tended to be at the back, those with the highest positive indexes, as well as those with the lowest negative indexes, tended to be close to the centroid of the group. The forefront index showed a greater range in zebrafish than in black neon tetra, which is consistent with zebrafish maintaining a greater mean interindividual distance, even when adjusted for body length (Quera *et al.*, 2019).

Figure 7b shows that the mean acceleration and forefront index were negatively related. In both species, fishes in the front positions tended to decelerate, those in the rear positions tended to accelerate and those in the central positions tended to maintain their velocities. Decelerating while in a front position favours cohesion with fishes that are in the rear positions, whereas accelerating in a rear position favours cohesion with those at the front. As fishes with moderately positive leadership indices tended to be at the front, it is them that decelerated the most. Likewise, as fishes with moderately negative leadership indices tended to be at the back, it is them that accelerated the most.

## 4 | DISCUSSION

In general, as group size increased in both black neon tetra and zebrafish, the mean durations of leadership episodes decreased and the

probability of the episodes terminating was independent of their durations. In other words, leadership transitions among individuals were distributed randomly over time (in a different field, a similar result has been reported for sheep flocks; Gómez-Nava *et al.*, 2022). In both species, the duration of momentary leadership episodes decreased when group size increased, but that duration was greater in black neon tetra than in zebrafish regardless of group size. Nonetheless, the duration of the leadership episodes was very short in both species, indicating that the shift of momentary leadership occurred at a high rate. These results were related to those on the egalitarian leadership index. During a video fragment, the shorter the leadership episodes, the more frequent the shift among momentary leaders and the higher the egalitarian leadership index was on average. The egalitarian leadership index was high in both species, being slightly higher in zebrafish. It has been suggested that a great frequency of leadership changes in groups of mosquitofish (*Gambusia hoolbrooki*; Burns *et al.*, 2012; Ward, 2012) might be a consequence of the uncertainty when moving in unfamiliar environments (Ward & Webster, 2016).

In zebrafish, Collignon *et al.* (2019) found that the egalitarian leadership index decreased as the group size increased, whereas the authors of this study observed that trend only in black neon tetra, with zebrafish showing the highest egalitarian leadership when the group size was 8. Nonetheless, Collignon *et al.* defined leaders as the individuals that initiated movement in successive trials from one room to another through a corridor, not as individuals whose momentary changes in heading predicted changes in others. This makes it difficult to compare the results of this study about that index with theirs. Therefore, further studies on the pattern of the egalitarian leadership index in zebrafish and other species are required. As the authors observed only one group of fish per each group size, the results

regarding group size effects cannot be seen as generalizable but rather exploratory. The study should be replicated with independent groups of fish for each group size to obtain more generalizable results for the two species.

In both species, acceleration and the turning angle depended on their momentary leadership rank and the relative angle between the fishes. In general, momentary leaders tended to accelerate more and had larger turning angles than the followers. When a momentary leader and a follower swam alongside each other, both tended to turn to each other, with the former accelerating and the latter tending to maintain its velocity. Furthermore, the magnitude of the turning angle was greater in the former than in the latter. Likewise, when a follower swam alongside another fish (either a leader or another follower), it tended to maintain its velocity. When a momentary leader swam in front of a follower, the former kept its heading and did not turn, and decelerated. Conversely, when a momentary leader swam behind a follower, the former accelerated, while keeping its heading. That same pattern of acceleration and turning was observed in the followers when they swam in front or behind their neighbours (either leaders or other followers), except that they accelerated less (when they were behind their neighbours) and decelerated more (when they were in front of them) than the leaders did. Schaerf *et al.* (2021; Figure 4a) obtained similar results in pairs of eastern mosquitofish (*Gambusia holbrooki*) about the relationship between acceleration (or change in speed) and relative position between a leader and a follower, although they defined a leader as the individual that was in front and represented acceleration (change in speed) as a function of relative ( $x$ ,  $y$ ) positions between the fish, not as a function of their relative angle.

As leadership rapidly alternated among the group members, the changes in acceleration and turning angles tended to maintain instantaneous coordination in the group. Therefore, the leadership shifts can be viewed as dynamic adjustments that keep the group polarized and cohesive. Momentary leaders lead by accelerating and turning more, thus changing the group heading and velocity instantaneously. The magnitude of turning angles, both for the momentary leaders and followers, was greater in zebrafish than in black neon tetra. In the former, such abrupt changes in heading can explain their lower polarization and cohesion (Quera *et al.*, 2019). On the contrary, the magnitude of acceleration was fairly similar in both species when scaled to their average body lengths; that is, momentary leaders accelerated and decelerated at similar rates in both species depending on the relative angle towards their followers, as shown by the empirical and modelled data in Figures 4 and 5. Although the results shown in Figure 6 indicate that zebrafish were less polarized than black neon tetra (as zebrafish show frequent heading changes, *i.e.*, greater turning angles, the ellipsoids have larger horizontal axes than those observed for black neon tetra), they also show that the differences in the acceleration-turning angle pattern between the two species were a matter of scale. Likewise, within a species, the differences in that pattern between momentary leaders and followers were probably a matter of both translation (along the acceleration axis) and rescaling (along the turning angle axis).

Although the authors found that momentary leadership was short lived and mostly egalitarian, experiments with moving groups of mosquitofish (*Gambusia holbrooki*; Burns *et al.*, 2012) and humbug damselfish (*Dascyllus aruanus*; Ward *et al.*, 2013) found that certain individuals consistently lead the group on successive trails. Nonetheless, similar to Collignon *et al.* (2019), neither of those studies measured momentary leadership by calculating pair-wise time delays in a moving shoal, as the authors of this study did, but by recording which individuals in a stationary shoal initiated movement through a corridor towards the arms of a Y-maze (Burns *et al.*, 2012) and movement towards a boulder that offered refugia (Ward *et al.*, 2013) and were followed by the rest of the group. Thus, the different ways in which leadership was measured made it difficult to compare the results of this study with theirs; according to Krause *et al.* (1998), “the initiation of new swimming directions in stationary shoals does not follow the same principles as positioning behaviour in shoals that are already on the move” (p. 1031).

Momentary leaders tended to be at the front of the group, whereas followers tended to be at the back both in black neon tetra and in zebrafish. Katz *et al.* (2011) studied motion leadership in golden shiners (*Notemigonus crysoleucas*) based on analysing pair-wise time delays between changes in the fish headings, and determined that frontal group members tended to lead the group, but “that speed information flows bidirectionally, with fish responding to the speed changes of those swimming both ahead and behind” (p. 18724). In general, leaders do not have to be necessarily always in frontal positions, as results obtained by Theveneau and Linker (2017) on leadership in cell migration during development indicate. In this study, individuals with the highest (“strong” leaders) and lowest (“strong” followers) momentary leadership indexes tended to be close to central positions, whereas individuals with moderately positive (“weak” leaders) or negative (“weak” followers) indexes tended to be in more extreme front and rear positions, respectively. If a strong leader was in front of the group, strong followers should be close to it, *i.e.*, near the front of the group, as well to be able to rapidly detect changes in the former’s heading. When the group size was larger than 2, the fact that both strong leaders and followers tended to be closer to central positions whereas the remaining individuals were in peripheral ones could be explained as a trade-off solution that maintains dynamic equilibrium in the group, preventing group crowding. As motion leadership was highly egalitarian and momentary strong leaders did not tend to be in peripheral positions, individuals keep rotating their positions; if we assume that individuals in a shoal tend to avoid peripheral positions to minimize predation risk (Hamilton, 1971), then strong leaders tend to minimize that risk. The fact that momentary leaders tended to decelerate and followers tended to accelerate could be explained as a mechanism favouring group cohesion by preventing the average individual distance from increasing. Thus, in groups of more than two fishes in both black neon tetra and zebrafish, the relative positions of momentary leaders and followers, as well as their deceleration and acceleration, respectively, tended to avoid crowding, while also maintaining group cohesion.

In conclusion, both in black neon tetra and in zebrafish, motion leadership during spontaneous group swimming is very short lived and unstable. Changes in leadership tend to be distributed randomly across time, and leadership is largely egalitarian and not monopolized. Although leadership vanishes rapidly, its episodes are longer on average in black neon tetra than in zebrafish, with their duration tending to decrease as group size increases. In both species and for groups of more than two fishes, momentary leaders do not tend to be in the front of the group, but closer to its centre. Although acceleration and turn are dependent on their relative angle towards their neighbours, momentary leaders tend to accelerate and turn more than momentary followers. Zebrafish leaders (and followers) tend to accelerate and turn more than black neon tetra leaders (and followers), with differences between the species and between the leaders/followers being quantitative rather than qualitative.

### AUTHOR CONTRIBUTIONS

V.Q.: design of experiments, data collection, software development, data analysis, manuscript preparation. F.S.B.: design of experiments, data collection, data analysis, manuscript preparation. E.G.: data collection, software development, data analysis. R.D.: design of experiments, data collection, data analysis, manuscript preparation.

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### DATA AVAILABILITY STATEMENT

Data recorded in this study are available at this site: <https://drive.google.com/drive/folders/1mTI3W5Wh9zHukKRx4JPrpwALeFWkw3G?usp=sharing>

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