

Long-term environmental unpredictability increases social information use in zebrafish

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Lay summary:

In unpredictable environments, information becomes outdated faster, and animals must spend more time gathering and updating it, which is costly. Information can come either from personal experience or from observing others, which is cheaper and might therefore be preferred under instability. We show that zebrafish that live in unpredictable conditions pay more attention to social information than fish from stable environments. Flexible information-gathering strategies may help animals survive in a rapidly changing world.

Title: Long-term environmental unpredictability increases social information use in zebrafish

Running head: Social information use following unpredictability

Abstract

Human-induced environmental change increases unpredictability, disrupting habitats and social structures in ways that many animals are poorly adapted to. This may also reduce the reliability of information faster as contingencies shift. While independently acquired information is often more accurate, increased unpredictability may make recency the key to reliability, increasing the value of social information, which is cheaper and faster to update. Unpredictability might thus shift the balance between the values of these types of information, increasing reliance on more recent social information. Thus, independent of information quality, the predictability of background conditions may affect how animals make decisions. To test whether living in an unstable environment changes the inherent value of information, zebrafish (*Danio rerio*) were housed for three months under either highly unpredictable Dynamic (water temperature, feeding times, habitat complexity, group size and membership fluctuated) or Stable conditions. Across six behavioural assays, Dynamic condition fish showed more information-seeking, greater attention to social stimuli, more sensitivity to social cues, and were less coordinated but swam closer together in shoals. When personal and social information conflicted, they were also more likely to prioritize recent social information over previously learned personal information. Together, these results indicate that long-term housing in an unpredictable environment diminishes the value of information faster, raises the value of social information to allow for faster updating, shifts decision-making strategies independent of the quality of information itself, and disrupts coordinated schooling in zebrafish. This sensitivity may fundamentally alter how animal collectives navigate an increasingly unpredictable world.

Keywords: zebrafish, social information, schooling, environmental unpredictability

Introduction

Natural environments differ in predictability, with some exhibiting consistent changes that animals can anticipate (e.g., seasonal changes), while others experience abrupt stochastic perturbations, fluctuating unpredictably and making environmental cues less reliable predictors of future conditions (e.g., anthropogenic change; Bernhardt et al., 2020; Sih, 2024; Wingfield & Kitaysky, 2002). Environmental variation may be temporal (changes over time in temperature, habitat complexity, resource availability, or social group structure) or spatial (differences across locations in habitat structure, resource distribution, predation pressure, or population density; Rotenberry & Wiens, 1980; Wiens, 1985).

With the accelerating pace of human-induced environmental changes, including habitat disruption and climate instability, animals are increasingly confronted with unpredictable conditions (Acevedo-Whitehouse & Duffus, 2009; Domenici & Seebacher, 2020; Sih, 2024), which may require them to rapidly and flexibly adjust their behaviour. Ectotherms are especially vulnerable to extreme thermal variability, which can impair their metabolism, immune function, growth, and overall fitness (Angilletta et al., 2002), with unpredictable changes constraining anticipatory physiological regulation (Wingfield & Kitaysky, 2002). Rising water temperatures also disrupt ocean productivity, causing declines in fish populations (Lanz et al., 2009; Lluch-Belda et al., 1989; Lluch-Cota, 2000; Nevárez-Martínez et al., 2001). In response to warming sea surface temperatures and the resulting reduced prey availability, many species of seabirds rapidly adjust their reproductive strategies by changing their breeding time (Dobson et al., 2017) or increasing the spacing of egg-laying (increasing the survival chances of the first hatchling, which may outcompete or eliminate its sibling if needed; Bizberg-Barraza et al., 2024). Urgent questions remain about how animals make decisions and adjust their behaviour to adapt to unpredictable environments, defined by the lack of reliable anticipatory cues.

Environmental variability may reduce the reliability of all information as contingencies change more frequently (Riotte-Lambert & Matthiopoulos, 2020). The value of information depends on how closely it matches current conditions, and therefore declines faster in more variable environments, which require increased information updating behaviour (Boyd & Richerson, 1988). For example, tropical agamid lizards (*Psammophilus dorsalis*) from more spatially and temporally variable environments outperform those from stable environments on learning and cognitive flexibility tasks, demonstrating a higher capacity to track and use new information (Batabyal & Thaker, 2019). Similarly, in more variable environments, using the most recent information becomes more important, as older information is more likely to be outdated. For example, when payoffs change unpredictably, pigeons shift to using the most recent feedback for decision-making (Bell & Baum, 2002). As the value of new information increases in variable environments, individuals may benefit from engaging in more information-seeking behaviours, such as environmental vigilance (scanning) and sampling (Dall et al., 2005; Dridi & Lehmann, 2016).

There are two types of information that can be used to guide decision-making: personal and social. Personal information is gathered through direct interaction with the environment (Kendal et al., 2009). While often accurate and directly relevant to the individual, personal information can be costly to acquire, typically through trial-and-error, requiring significant time, energy, and entailing exposure to risks such as predation or competitive losses (Kendal et al., 2009; Coolen & Giraldeau, 2003). In contrast, social information is acquired by observing others, offering a cheaper (in time and energy) and safer alternative (Kendal et al., 2009; Laland, 2004). While the speed and low cost of acquisition makes social information easier to update, it can be misleading, outdated, or not relevant to the individual or current context (Kendal et al., 2009).

When possible, incorporating both types of information in decision-making has been shown to lead to more accurate decisions and is considered the optimal strategy (Templeton & Giraldeau, 1996; Valone, 1989; Valone & Templeton, 2002). However, the two sources may contradict each other, indicating different behavioural responses, in which case information of each kind should be weighted depending on its relative reliability (Pérez-Escudero & de Polavieja, 2011). For example, ninespine sticklebacks (*Pungitius pungitius*) tend to prefer their own personal information over conflicting social information (van Bergen et al., 2004), likely because personal information is typically more reliable and relevant to the individual (Kendal et al., 2009). However, sticklebacks do not show this preference if their personal information is unreliable or outdated, instead conforming to social information (van Bergen et al., 2004). A similar switch to relying on more recent social information has been observed across species when the quality of personal information decreases, and is sometimes referred to as a “copy when uncertain” strategy (Laland, 2004; Rafacz & Templeton, 2003; Smolla et al., 2016).

Animals’ environments may also be socially variable, such as in fission-fusion systems, where subgroup size and membership change on relatively short timescales (Croft et al., 2003). Primates from such variable-membership groups outperform those from less complex groups on multiple cognitive tasks involving learning, behavioural flexibility, and social cognition (Amici et al., 2008; Aureli et al., 2008; MacLean et al., 2012), possibly because frequent partner turnover increases the cognitive demands of constant updating of information about individuals and social dynamics (Amici et al., 2008). Due to the importance of social interaction to the survival of many species (Krause & Ruxton, 2002), social instability may have an outsized effect on the evolution of strategies to manage unpredictability.

Increased environmental unpredictability may shift the optimal balance between personal and social information (Valone & Templeton, 2002). Animals may shift to prioritizing social information in variable environments, as it is cheaper to obtain and faster to update (Kendal et al., 2009). However, social information is acquired second-hand and, as a result, might not have been updated by direct experience for some time (Boyd & Richerson, 1988). Making good decisions therefore relies on a complex interaction between the recency of information, its source, and the variability of the environment. Here, we explore one part of this relationship,

testing how living in highly predictable or unpredictable environments (both physically and socially) affects the relative weighting of personal and social information in zebrafish.

Zebrafish are highly gregarious, exhibiting a range of complex social behaviours (Miller & Gerlai, 2011). In the wild, they form large shoals ranging from 5 to 300 (Pritchard et al., 2001; Spence et al., 2008). In still water, zebrafish form relatively stable groups with an average of 3.5 fission-fusion events per minute, whereas in fast-flowing water this increases to around 8 per minute (Shelton et al., 2020). Their collective motion spans the range from loose aggregations (shoals) to highly coordinated schools, which are faster and less dense (Miller & Gerlai, 2012a). The physical habitats occupied by zebrafish often fluctuate in temperature, vegetation cover, food availability, and social composition (Engeszer et al., 2007; Lawrence, 2007; Shelton et al., 2020; Spence et al., 2008), and they are classified as one of the most eurythermal fish species (see Lawrence, 2007), tolerating temperatures from 6.7 to 41.7 °C (Cortemeglia & Beiting, 2005; Schaefer & Ryan, 2006).

Their remarkable tolerance to variable conditions and demonstrated complex social behaviours make zebrafish well-suited for studying responses to environmentally induced phenotypic plasticity. Both physical and social housing conditions have been shown to affect individual and group behaviour in zebrafish, even in adulthood (Shams et al., 2015; Dos Santos et al., 2020; Toni et al., 2025), consistent with their high levels of lifelong neuroplasticity and neurogenesis (Pushchina et al., 2024). For example, adult zebrafish housed at low temperatures (18 °C) show more anxiety-like behaviours, including more bottom-zone use and less exploration, whereas fish housed at high temperatures (34 °C) show increased shoal cohesion (Toni et al., 2025). Fluctuating thermal environments also have negative effects on development (Schaefer & Ryan, 2006) and adult reproductive performance (Massey et al., 2022). However, the existing literature on these effects has focused largely on predictable environmental cycles, rather than on how long-term exposure to unpredictable background environmental change shapes behaviour.

We housed zebrafish in either a Dynamic condition, where water temperatures and feeding times changed daily, and habitat complexity and group size and composition changed every third day, or in a Stable condition, where all variables were kept constant. It is important to note that our Stable condition is unusually consistent and not intended to represent a typical environment, as the natural habitats of zebrafish are quite variable. Rather, it provides a tightly controlled comparison to test how variation across physical and social factors influences behaviour. Because prolonged stability may itself have behavioural effects, differences in behaviour between the fish in our two conditions should be interpreted as consequences of differences in the relative predictability of environmental conditions.

Fish lived in these conditions for three months and throughout testing, during which we assessed differences in exploratory behaviour, social motivation, stress reactivity, group cohesion (closeness) and polarization (coordination), and decision-making strategies. We

hypothesized that living in a dynamic environment increases the value of recent information, leading to more information updating and seeking behaviour, and may also lead to increased reliance on social information. Based on this, Dynamic condition fish were expected to pay more attention to their surroundings, showing increased environmental sampling and social vigilance. Additionally, they should weight recent information more heavily when balancing conflicting information, ignoring older information independent of its quality.

Methods

Subjects and housing

Eighty 3-month-old experimentally naïve wild-type zebrafish served as subjects (excluding stimulus and demonstrator fish). Fish were bred in-house under standard laboratory conditions (12:12 h light:dark) and housed in one of eight 38 L glass tanks (50.8 × 25.4 × 30.5 cm; 4 Stable, 4 Dynamic) containing reverse osmosis (RO) water with added salt (Instant Ocean), with one filter, heater, and air-stone per tank. All housing tanks also contained plastic plants glued to small rocks. Water quality was monitored daily (salinity 450-750 ppm TDS; pH 6.8-7.8). Fish were fed twice daily (Skretting GEMMA Micro plus brine shrimp; ~ 0.10 g per 5 fish per feeding).

Environmental manipulation

Dynamic condition tanks completed five consecutive 18-day cycles of variation before Post-exposure testing, and continued under the same regime during the testing. Environmental variation consisted of daily changes in temperature and feeding times, and changes every three days in group size and composition and habitat complexity (see Table S1 for details). Mean environmental parameters matched those of the Stable group.

Stable condition tanks were kept at $23 \pm 1^\circ\text{C}$, fed at 10:00 and 14:00 h every day, retained a fixed four-plant layout, and always contained the same 10 fish. Handling matched the Dynamic condition, with brief bucket transfers on Switching days (fish from different tanks were placed into separate buckets). Every third Switching day (every ninth day), while fish were in buckets, all tanks received 25% water changes and tank/filter cleaning; on other Switching days, tanks were topped-up with RO water. Prior to housing assignment, fish were tested on three behavioural assays (Open-Field Test, Social Preference Test, and Novel Tank Diving Test; see below) to measure individual differences. Baseline scores were used to allocate fish to the two housing conditions such that mean values did not differ across conditions before exposure (see Results).

Behavioural assays

Fish were tested on six behavioural assays: an open-field test (OFT), a social preference test (SPT), a novel tank diving test (NTDT), a schooling test, a social information test (SIT), and

a conflicting information test (CIT). The OFT, SPT, and NTDT were conducted both before and after the 3-month housing exposure; the other assays were only conducted post-exposure. Each assay is briefly described below, and detailed methods for all assays are available in the Supplementary Information. All testing was conducted at least 2 h after lights-on, to avoid potential confounding effects from spawning behaviours (zebrafish typically spawn within the first hour of illumination under laboratory conditions; Darrow & Harris, 2004). Switching days were paused for assays that took over a day but continued otherwise. All tests were filmed to allow for subsequent coding of behaviors from the videos.

For the OFT (Figure S1), fish were placed alone in a novel tank with a shelter along one end; we measured the proportion of the session fish spent outside the shelter as a proxy for how exploratory they were (as in Guayasamin et al., 2017). For the SPT (Figure S1), fish were placed alone in a tank with two side chambers, one of which contained 5 novel stimulus fish; we quantified the proportion of the session that the test fish spent close (within 10 cm) to the chamber containing the other fish, indicating their social drive (Goncalves et al., 2022). For the NTDT (Figure S2), commonly used as an assay for stress, fish were placed alone into a small, novel, brightly-lit tank and filmed from the side; stressed zebrafish will often respond by staying close to the bottom of the tank in this situation; we measured proportion of the session spent in the bottom third of the tank, time spent frozen, and number of crossings between vertical thirds of the tank (Kysil et al., 2017).

For the schooling test (Figure S3), groups of 5 fish from the same home tank were placed into a circular tank and allowed to swim for 10 min while being tracked; we measured the mean distance between all the fish (called the inter-individual distance, IID), the mean nearest-neighbor distance (NND), the polarization of the group (the degree to which they were swimming in the same direction), thigmotaxis (the tendency to stay close to the wall, often linked to stress levels; Scharf & Farji-Brener, 2024), and the speed of the fish, all common measures of coordination and collective behaviour (Miller & Gerlai, 2012b). These measures were averaged over all fish in the group and over all frames in the video, and we also analyzed the 10 min session in 4 2.5 min segments.

For the SIT (Figure S4), fish were individually tested. Test fish were allowed to observe three demonstrator fish feeding on 10 floating food pellets at one of two feeders, and another three fish not feeding (at an empty feeder) on the other side of the tank. The demonstrators and any leftover pellets were then removed, the water between chambers was mixed, and the test fish was released into the empty arena to choose between the two sides; we quantified the number of pellets the demonstrators consumed (not always all of them), the test fish's first choice, and the proportion of the session the test fish spent on either side of the arena. This test is commonly used to explore the use of social information in the absence of any personal information (Coolen et al., 2003; van Bergen et al., 2004; Webster & Laland, 2011). Finally, for the CIT, test fish were trained to locate food at one of the two feeders in the same tank as the SIT for seven days (4 trials / day). Following this training, fish observed demonstrators feeding at the opposite

feeder to the one they had been trained on (i.e., the demonstrators provided social information that conflicted with the test fish's personal information), and the test fish were then released to select a feeder; we measured the test fish's initial choice, latency to choose a side, and time spent on either side of the arena (van Bergen et al., 2004). This test quantifies conformity (choosing based on social information in the presence of contradictory personal information).

Analysis

Because we were unable to track individual identities across assays, results were analyzed at the group level, by housing condition (Stable or Dynamic). Additionally, because fish in the Dynamic condition were repeatedly mixed across tanks (part of the unpredictability of their environment), we could not consider different tanks as replicates, and we therefore did not include replicate as a random factor in the analyses.

After measures from all six assays were derived, they were each analyzed separately using JASP (JASP Team, 2024). Housing conditions were compared to each other using ANOVAs where there were more than two scores to compare (such as in the NTDT, which was run both before and after the housing manipulation), and t-tests and Anderson-Darling tests (when the data were not normally distributed) for pairwise comparisons; continuous measures were analyzed using linear regressions. In addition to test statistics and P-values, we also report means \pm SD for all measures (Table 1). For SIT and CIT, both categorical (first choice; χ^2) and continuous measures (time proportions; t-tests) are reported, as it has not yet been established which behavioural measures best capture different forms of information use in this species. All analyses are reported to ensure transparency and to provide a foundation for refining behavioural metrics in future studies of information use in zebrafish. Sexes were unknown (zebrafish are not highly sexually dimorphic), so sex differences were not examined, though sex-based differences in behaviour have been reported (Genario et al., 2020).

In the SIT, trials were excluded if fish failed to leave the start box ($n = 2$ Dynamic), procedural errors occurred ($n = 3$ Dynamic; $n = 2$ Stable), or less than 3 s were spent outside the neutral zone ($n = 1$ Stable); several fish died before completing this assay. A total of 61 fish (Stable, $n = 36$; Dynamic, $n = 25$) successfully completed the test. Time spent in all zones (including each chamber, the feeder zones in each chamber, and the neutral zone) was calculated, and preference scores were calculated as the proportion of time spent on the social information side, relative to the total time spent on both sides. In the CIT, trials were also excluded if fish failed to leave the start box ($n = 2$ Dynamic) or spent less than 3 s out of the neutral zone ($n = 4$ Stable, 4 Dynamic). Additionally, more fish had died before trials for this assay started. A total of 50 fish (Stable, $n = 31$; Dynamic, $n = 19$) successfully completed the test.

Results

Open-Field Test (OFT)

Exploratory behaviour scores in the open-field test (OFT) were measured as the proportion of time each fish spent outside the shelter. As intended, Pre-exposure scores did not differ significantly between fish that would eventually be assigned to different conditions (Figure 1A; Table 1; Anderson-Darling Test: $A = 0.41$, $P = 0.83$). After the three-month exposure period, exploratory behaviour increased significantly in both groups (Stable: $A = 11.99$, $P < 0.0001$; Dynamic: $A = 7.60$, $P = 0.0002$). There was no significant difference between conditions ($A = 0.75$, $P = 0.52$), indicating that the increase in exploration was due to general habituation and/or ontogenetic effects rather than differential effects of the treatment.

Table 1. Mean values \pm SD of key measures for all behavioural assays. OFT = Open-Field Test, values give the mean proportion of the session spent outside the shelter; SPT = Social Preference Test, values give the proportion of the session spent close to conspecifics; NTD T = Novel Tank Diving Test, values show the proportion of the session spent in the bottom third of the tank (Bottom) or frozen in place (Freezing), and the number of zone switches (Zones); Schooling = schooling test, values show the mean inter-individual distance (IID, in cm), nearest-neighbor distance (NND, in cm), group polarization (Pol), speed (Speed, in cm/s), and proportion of time close to the arena walls (Thig); SIT = Social Information Test, values show proportion of fish choosing the demonstrated feeder; CIT = Conflicting Information Test, values show proportion of all fish conforming to social information (Conform) or only “successful learners”, fish that passed Probe 1 (Conform SL).

Assay	Stable		Dynamic	
	Pre	Post	Pre	Post
OFT	0.41 \pm 0.21	0.66 \pm 0.18	0.42 \pm 0.22	0.61 \pm 0.22
SPT	0.84 \pm 0.18	0.72 \pm 0.21	0.82 \pm 0.16	0.80 \pm 0.23
NTDT (Bottom)	0.12 \pm 0.19	0.11 \pm 0.13	0.10 \pm 0.22	0.07 \pm 0.08
NTDT (Freezing)	0.13 \pm 0.15	0.03 \pm 0.13	0.16 \pm 0.18	0.02 \pm 0.07
NTDT (Zones)	118.38 \pm 96.71	101.23 \pm 65.70	120.10 \pm 74.53	136.23 \pm 68.15
Schooling (IID)		13.53 \pm 5.08		9.77 \pm 4.19
Schooling (NND)		6.45 \pm 2.39		4.52 \pm 1.48
Schooling (Pol)		0.57 \pm 0.09		0.53 \pm 0.10
Schooling (Speed)		1.09 \pm 0.22		0.93 \pm 0.39
Schooling (Thig)		0.806 \pm 0.016		0.806 \pm 0.017
SIT		0.59 \pm 0.34		0.49 \pm 0.4
CIT (Conform)		0.45 \pm 0.18		0.74 \pm 0.19
CIT (Conform SL)		0.43 \pm 0.16		0.87 \pm 0.23

Social Preference Test (SPT)

Social motivation in the social preference test (SPT) was assessed as the proportion of time each fish spent near the compartment containing a conspecific shoal. Pre-exposure scores did not differ significantly between housing conditions (Figure 1B; Table 1; $A = 0.36$, $P = 0.87$), confirming that groups were behaviourally matched at baseline. Following the three-month exposure period, shoaling preferences declined in the Stable condition (from 0.84 to 0.72 [proportion time spent close to the social stimulus]; $A = 5.16$, $P = 0.002$), but fish in the Dynamic condition showed no significant change (0.82 Pre- to 0.80 Post-exposure; $A = 0.80$, $P =$

0.48). Stable condition Post-exposure scores were significantly lower than the corresponding Dynamic scores ($A = 3.21$, $P = 0.022$).

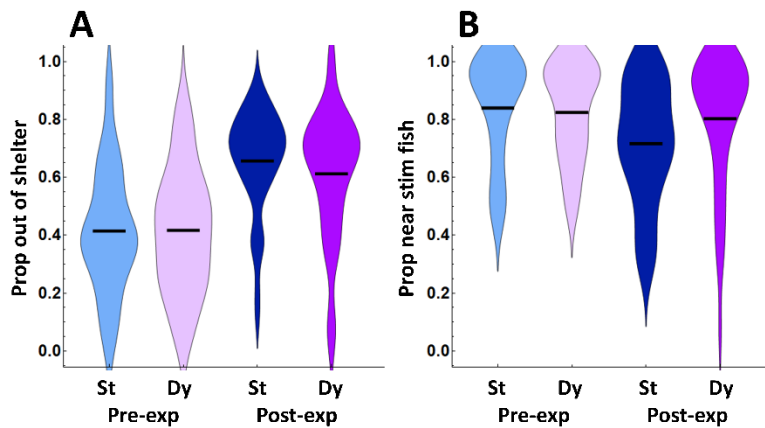


Figure 1: Effects of housing condition on exploratory behaviour and social motivation. Violin plots of, **A:** proportion of time spent outside the shelter in the Open-Field Test and, **B:** proportion of time spent near the social stimulus in the Social-Preference Test for both Stable (“St”, blue shades) and Dynamic (“Dy”, purple shades) condition fish, before (“Pre-exp”, light shades) and after (“Post-exp”, dark shades) a 3-month exposure to the housing conditions. Short horizontal black lines indicate group means

Novel-Tank Diving Test (NTDT)

Pre-exposure scores showed no significant differences between the Stable and Dynamic groups across any of the measures (Figure S5; Table 1; time spent in bottom third: $t(78) = -0.36$, $P = 0.721$; zone crossings: $t(78) = 0.089$, $P = 0.929$; freezing duration: $t(78) = 0.76$, $P = 0.450$). These results confirm that behavioural stress levels were equivalent across conditions prior to the experimental manipulation.

Fish in both conditions exhibited slightly reduced bottom-dwelling Post-exposure, though this change was only significant in the Stable condition fish (Figure S5A; Stable: $A = 2.69$, $P = 0.04$; Dynamic: $A = 1.86$, $P = 0.11$; note that even though these tests compare the same fish before and after exposure, they are independent-sample tests, as individual identities could not be established). There was no difference between the conditions in Post-exposure time spent in the bottom third ($A = 2.05$, $P = 0.09$). As previous studies have assessed stress using shorter NTDT durations (Levin et al., 2007; Egan et al., 2009), we also analyzed time spent in the bottom third during only the first half of the trial (5 min). Results were consistent with the full-trial data (Figure S5B): fish in both conditions spent less time in the bottom zone following exposure than before, though this effect was not significant in either condition (Stable: $A = 1.16$, $P = 0.47$; Dynamic: $A = 0.81$, $P = 0.47$), and there were no significant differences between conditions ($A = 1.59$, $P = 0.16$).

Freezing behaviour also decreased significantly from Pre- to Post-exposure in both groups (Figure S5C; Stable: $A = 41.07$, $P < 0.0001$; Dynamic: $A = 37.32$, $P < 0.0001$), and also showed no difference between the groups ($A = 0.17$, $P = 0.99$). The reduction in both bottom-dwelling and freezing is consistent with habituation to the novel environment, as we also observed in the OFT, and may also reflect ontogenetic changes over the experimental period. Vertical zone switches Post-exposure revealed a significant effect of housing conditions (Figure

S5D). Dynamic condition fish switched zones more often than Stable condition fish (Table 1; $A = 2.68$, $P = 0.040$). Switching was not significantly different from Pre- to Post-exposure in either condition (Dynamic: $A = 1.25$, $P = 0.25$; Stable: $A = 0.49$, $P = 0.76$).

Schooling Test

Stable condition fish formed looser shoals, maintaining larger distances between the fish (Figure 2A; Table 1; IID: $A = 12.12$, $P < 0.0001$; NND: $A = 15.58$, $P < 0.0001$), were more polarized (Figure 2B; $A = 6.60$, $P = 0.0005$), and swam faster (Figure 2C; $A = 2.67$, $P = 0.04$) than Dynamic condition fish. The polarization of Dynamic condition shoals was significantly more variable (F-test of equality of variances: $F = 0.32$, $P < 0.0001$). Thigmotaxis, defined as the tendency to stay within the outer 10% of the tank radius, did not differ between conditions (Stable = 0.806 ± 0.016 ; Dynamic = 0.806 ± 0.017 ; $A = 0.66$, $P = 0.59$).

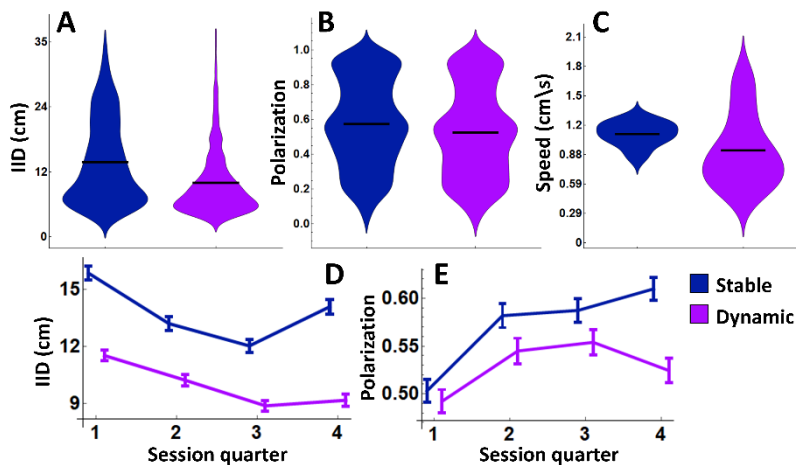


Figure 2: Effects of housing condition on schooling behaviour. **A:** violin plot of the mean inter-individual distance (IID, in cm); **B:** violin plot of the mean polarization of the group; **C:** violin plot of the mean speed of the shoal (in cm/s); **D:** plot of mean IID for each quarter of the session; **E:** plot of mean polarization across quarters of the session. Short horizontal black lines in A-C show group means; error bars in D-E show \pm SEM. Colours are as in Figure 1.

The characteristics of shoaling cohesion also varied across the 10 min sessions and differed across conditions. There was a significant interaction between condition and session segment for both IID (Figure 2D; two-way ANOVA: main effect of Condition, $F(1,3704) = 273.36$, $P < 0.0001$; main effect of Segment, $F(3,3704) = 33.27$, $P < 0.00001$; Condition * Segment interaction, $F(3,3704) = 4.056$, $P = 0.007$; post-hoc tests showed all segments differed except S2 and S4) and polarization (Figure 2E; Main effect of Condition, $F(1,3256) = 22.04$, $P < 0.0001$; main effect of Segment, $F(3,3256) = 15.41$, $P < 0.0001$; Condition * Segment interaction, $F(3,3256) = 3.13$, $P = 0.02$; post-hoc tests showed segment S1 differed from the other three).

Social Information (SIT)

To measure social information use, fish first observed demonstrators feeding at one of two feeders on opposite sides of the tank, and were then allowed to choose between the feeders, in the absence of the demonstrators. We measured demonstrator performance (number of pellets

consumed), the first chamber the test fish entered after release (first choice), and the time the test fish spent in both feeder zones. Mean feeder preference scores did not significantly differ between conditions (Table 1; $t(59) = 1.03$, $P = 0.308$). There was also no effect of condition on initial side choice ($\chi^2 = 0.12$, $P = 0.730$); 57.4% of fish chose the social information side first and first choice strongly predicted later chamber preference, with fish spending significantly more time on the side they initially entered (Spearman's $\rho = 0.91$, $P < 0.001$).

Demonstrator performance predicted preference for the social information feeder, with fish spending more time near it when demonstrators had consumed a greater proportion of the food pellets (Figure 3A; $\beta = -0.05 \pm 0.02$, $t(58) = -2.30$, $P = 0.025$), with a significant correlation in Dynamic condition fish ($\rho = -0.44$, $P = 0.041$) and a weaker, non-significant trend in Stable condition fish ($\rho = -0.30$, $P = 0.078$). When restricting the data to subjects whose demonstrators ate at least half of the pellets (5 or more), fish showed a significant preference for the social information side (Wilcoxon signed-rank test, $W = 479$, $P = 0.011$), but no difference between conditions ($t(36) = 1.06$, $P = 0.298$).

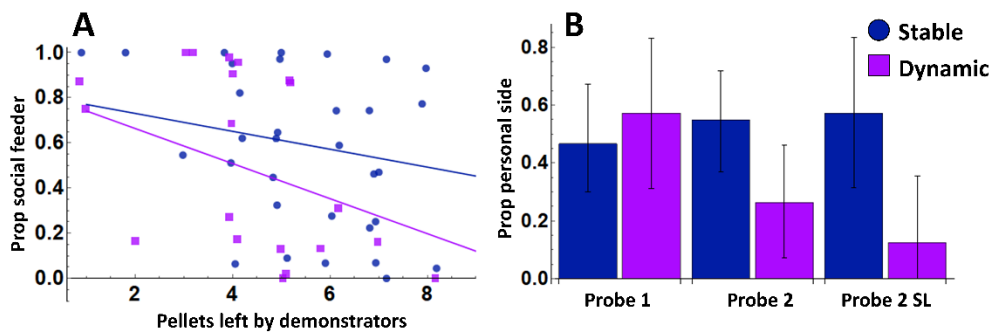


Figure 3: Effects of housing condition on the weighting of social information. **A:** scatter plot showing the relationship between demonstrator performance (number of uneaten food pellets) and test fish preference for the demonstrated feeder in the Social Information Test; lines show linear regressions on each group's data and data points have been jittered along the x-axis for clarity. **B:** Bar chart showing the proportion of fish in the Conflicting Information Test that chose the personal information side first in Probe 1 (retention test), Probe 2 (after exposure to conflicting social information), and in Probe 2 restricted to successful learners (SL, fish that chose personal information in Probe 1). Colours are as in Figure 1.

preference for the demonstrated feeder in the Social Information Test; lines show linear regressions on each group's data and data points have been jittered along the x-axis for clarity. **B:** Bar chart showing the proportion of fish in the Conflicting Information Test that chose the personal information side first in Probe 1 (retention test), Probe 2 (after exposure to conflicting social information), and in Probe 2 restricted to successful learners (SL, fish that chose personal information in Probe 1). Colours are as in Figure 1.

A potential confound arises from demonstrators consuming significantly fewer pellets in Stable condition trials compared to Dynamic condition trials ($t(59) = 3.47$, $P < 0.001$). Dynamic condition fish also displayed a significant right-side bias, spending significantly more time in the right chamber regardless of where food had been delivered ($W = 248$, $P = 0.02$), though Stable condition fish did not ($W = 386$, $P = 0.414$). Demonstrator food consumption did not depend on the side either ($t(59) = 0.33$, $P = 0.744$).

Conflicting Information Test (CIT)

This assay tested how fish balanced personal and social information. Probe 1 measured first choice after one week of individual training on one feeder, to assess whether fish retained personal information. Immediately after Probe 1, fish observed a demonstration of conflicting

social information, where demonstrators fed at the opposite feeder. Test fish were then released into the empty arena for Probe 2, for which we measured first choice, choice latency, and time spent near each feeder, to assess whether fish conformed to social information that conflicted with their personal information. In Probe 1 (the retention test), seven fish (5 Dynamic, 2 Stable) were removed after not making a choice for 3 min. Of the remaining fish, 22/43 (51.2%) showed retention of personal information by swimming directly to the side on which they had been trained (we term these “successful learners”: Stable 14/29, Dynamic 8/14), with no difference between conditions ($\chi^2 = 0.30$, $P = 0.586$). Dynamic condition fish took significantly longer to choose a chamber once released from the start box ($t(48) = 2.36$, $P = 0.022$).

In Probe 2 (post-demonstration), Dynamic condition fish were more likely to conform to social information than Stable condition fish, making an initial choice that conflicted with their prior training (Figure 3B; Table 1; $\chi^2 = 3.89$, $P = 0.049$). Dynamic condition fish also chose the social information side significantly above chance ($\chi^2(1) = 4.26$, $P = 0.039$), whereas Stable condition fish did not ($\chi^2(1) = 0.29$, $P = 0.59$). Fish that conformed to social information tended to choose a side faster than those that relied on their personal information ($t(32.39) = -2.21$, $P = 0.034$), though choice speed did not differ between conditions ($t(48) = 0.17$, $P = 0.864$). This might be because decisions based on recently acquired information are made rapidly, whereas recalling older information and balancing conflicting sources requires more time. The number of leftover demonstration pellets was not related to preference ($\beta = -0.12$, $P = 0.558$), possibly because demonstrator foraging success was better overall than in the previous test.

Among the 22 fish that chose the trained side in Probe 1 (“successful learners”), indicating that they had learned the location of the rewarded feeder, Dynamic condition fish were significantly more likely than Stable condition fish to switch choices in Probe 2, conforming to the conflicting social information (Figure 3B; $\chi^2 = 4.13$, $P = 0.042$). Dynamic condition fish chose the social information side more than chance ($\chi^2(1) = 4.50$, $P = 0.034$), whereas Stable condition fish did not ($\chi^2(1) = 0.29$, $P = 0.593$).

Discussion

We examined how three months of living under extreme environmental unpredictability (Dynamic condition) or predictability (Stable condition) affected individual behaviour, collective movement, and information use in zebrafish. In all our assays, the information provided to fish did not differ across these conditions. In other words, the current experiment examines how relative differences in background environmental variability affect decision-making while controlling for any differences in the reliability of information.

Across most assays, Dynamic condition fish consistently showed greater attentiveness to and reliance on recent or current social information, higher social vigilance (paying more attention to conspecifics), and more information-seeking behaviour. This was evident in their increased environmental sampling (performing more zone switches in the NTDT) and closer

spacing in shoals (in the Schooling Test). However, the most direct evidence came from our explicit tests of social information use (SIT) and its relative weighting with conflicting personal information (CIT). Though fish from both conditions showed a preference for the socially demonstrated feeder when the demonstrators had consumed at least half the pellets (in the SIT), Dynamic condition fish displayed a stronger sensitivity to the quality of this social information, relying on it more when the demonstrators had consumed more of the pellets. The slope of this relationship was steeper (and only significant) in the Dynamic condition. Dynamic condition fish also showed stronger reliance on recent social information that conflicted with their personal information (in the CIT). Dynamic condition fish were the only group that significantly conformed in this test, and this effect was stronger when we only considered those fish that passed the personal information probe test. The SIT and CIT were conducted only after subjects had been exposed to their assigned environmental condition, so no comparison to pre-exposure measures was possible for these assays.

In the SIT, subjects were exposed to demonstrators either feeding or not, a form of social information, and then given a choice between the two feeders. Fish could learn by exploiting public information, in which they assess the success or failure of others to infer the quality of environmental resources (Valone, 1989). However, exploiting public information is cognitively demanding, and not all species can easily detect or use it (e.g., Coolen et al., 2003; Smith et al., 2001; Valone & Giraldeau, 1993); there are no published data on this issue in zebrafish. Although this test provided the opportunity for public information use, zebrafish may have relied on simpler forms of social information use to solve our task, such as local enhancement (attraction to the more active group) or stimulus enhancement (attraction to the rewarded feeding ring; Hoppitt & Laland, 2013).

In the CIT, fish were given a retention test (Probe 1) the day after the last day of training. Only about half of our fish showed reliable retention of the trained side, and the proportion of “successful learners” did not differ by condition. After observing a demonstration of conflicting social information (Probe 2), Dynamic condition fish were more likely to conform by choosing the social information side, whereas Stable condition fish did not show a clear preference. Successful learners (of personal information) conformed slightly more to the new social information, showing that this conformity was not simply due to forgetting their previously acquired personal information. Together, these two effects (Dynamic fish being more sensitive to the quality of social information in the SIT and conforming more in the CIT) suggest that simply living in an unpredictable environment for some time alters decision-making strategies, independent of the quality of the information itself. The CIT conformity test showed that Dynamic condition fish display a similar “copy when uncertain” strategy to other species when the reliability of their personal information is lowered (Laland, 2004; Rafacz & Templeton, 2003; Smolla et al., 2016). However, we additionally find that fish from dynamic environments shift to relying more heavily on social information (in the SIT), independent of the quality of the information itself, simply as a result of their long-term housing environment. Thus, their

behaviour may reflect a general “copy under uncertainty” strategy that is expressed across multiple contexts. Living in a physically and socially variable environment leads these fish to discount the reliability of (any) information faster and raise the value of the most recent information.

In the SPT, the social motivation of Stable condition fish decreased across exposure, while Dynamic condition fish maintained their social motivation. Living in socially dynamic environments has been shown to enhance the development of social skills and lead to higher reproductive success in male brown-headed cowbirds (*Molothrus ater*), possibly by allowing for a greater diversity of social experiences and learning opportunities (White et al., 2010). Such social competence may increase sociability through a positive feedback loop (Taborsky, 2021). Thus, it is possible that the lack of opportunities to interact with novel conspecifics in the Stable condition may have diminished their social competence and motivation. Stable condition fish may have also been less attracted or responsive to the novel stimulus fish after living in unchanging groups for three months, especially as their social environment was extremely consistent compared to that of wild zebrafish, who live in shoals that frequently change in size and membership (Lawrence, 2007). It is alternatively possible that the reduction in social motivation resulted from general habituation which was masked, in Dynamic condition fish, by an increase in social vigilance (see above).

Collective movement, the characteristics of which are likely similarly determined by social motivation (Miller & Gerlai, 2007) also differed between conditions. Dynamic condition shoals were found to be more cohesive (swimming closer together), but less coordinated (lower polarization) and slower. Correlations between polarization, distance and group speed have been noted before, and may partly result from the physics of schooling (i.e., it is necessary to maintain greater distances when swimming faster, and fast-moving non-polarized groups will disintegrate; Hemelrijk & Hildenbrandt, 2008). In general, zebrafish exhibit two phases of collective movement, sometimes referred to as schooling (fast, polarized movement) and shoaling (slow, uncoordinated movement; Miller & Gerlai, 2012a). Our results suggest that Dynamic condition groups engaged in shoaling more, and in schooling less, than Stable condition groups. The lower polarization and higher cohesion we observed in Dynamic condition shoals is consistent with our predictions that unpredictable environments should increase social vigilance and information updating, though familiarity effects may have also played a role, as discussed below. Dynamic condition fish may have oriented themselves towards one another more often, at shorter distances, to more closely monitor their less-familiar shoal-mates. Monitoring the behaviour of other group members allows for faster and more accurate assessments of the environment (Valone & Templeton, 2002).

However, coordinated schooling is beneficial as it can reduce energetic costs through hydrodynamic gains (Heydari et al., 2024; Marras et al., 2015; Weihs, 1973; Zhang & Lauder, 2024) and coordinated schools may be targeted less often by predators than weakly polarized

groups (Ioannou et al., 2012). Differences in coordination between the conditions could have been a result of familiarity, as the Dynamic condition fish were less familiar with their current tankmates (though not entirely unfamiliar, as they interacted in buckets on Switching days and had likely been housed together at some point). Familiarization decreases signalling effort in fish (Riley et al., 2019) and may increase responsiveness to signals (Carter & Wilkinson, 2016; Micheletta et al., 2012; Thompson & Hare, 2010). However, the empirical evidence for better schooling in familiar groups is mixed. In tropical damselfish (*Chromis viridis*), there is no difference in cohesion or coordination between familiar and unfamiliar shoals (though familiarity improves escape performance; Nadler et al., 2021). In female guppies (*Poecilia reticulata*), familiarity increases polarization but has no effect on cohesion (Davis et al., 2017). Fathead minnows (*Pimephales promelas*) and Mediterranean killifish (*Aphanius fasciatus*) both show *greater* cohesion in familiar shoals, the opposite of our results (Lucon-Xiccato et al., 2022; Mathis & Smith, 1993).

Stable condition fish may also have swum further apart from each other as a result of competitive strategies. While grouping has benefits, such as protection from predators (Ward & Webster, 2016), it also entails costs, including competition among group members (Brockmann & Barnard, 1979; Ward & Webster, 2016). Such costs can outweigh the benefits, reducing sociality in species that evolved in resource-scarce environments (Sekulovski & Miller, 2025; Shier & Randall, 2004). For example, zebrafish have been shown to attempt to avoid kleptoparasitism when foraging in the presence of others (Sekulovski et al., 2025) and, when food delivery is predictable in time and space (as in our Stable condition), will attempt to monopolize the food source (Hamilton & Dill, 2002). Similar competitive strategies and aggression have been shown to arise in other species (e.g., Goldberg et al., 2001; Kleiber et al., 2022; Robb & Grant, 1998). It is possible that prolonged predictable food delivery in the Stable group, at a level of consistency unusual in the wild, shifted their behaviour towards competitive rather than cooperative strategies, further amplifying the difference in attitudes to social stimuli between the two conditions.

Exploratory behaviour (time spent outside of shelter in the OFT) increased and stress (time spent freezing in the NTDT) decreased after exposure in both conditions, suggesting that fish habituated to the testing tanks or, more generally, to frequent handling and being placed in novel arenas. Exploration is positively correlated with boldness in zebrafish (dos Santos et al., 2023), and fish tend to become bolder in captivity (Agnvall et al., 2015; Huntingford, 2004; Huntingford & Adams, 2005), likely due to the lower costs of risk-taking in such environments. For example, in laboratory settings, bolder and more aggressive fish have more reproductive and foraging success as there are no predation risks (Ariyomo & Watt, 2012; Ward et al., 2004). Fish in our study did not differ in the amount of time they spent near the bottom of the tank or freezing in the NTDT, nor in their tendency to stay near the walls while swimming in the Schooling Test, suggesting that the differences observed in the other assays are unlikely to be a result of heightened stress in one condition. However, the Dynamic condition had a higher

mortality rate throughout the experiment. While the cause of this mortality is unknown, and no overt signs of disease were observed, it may have involved stress-related immunocompromise, as reported in other fish species exposed to fluctuating water temperatures (Franke et al., 2024). Fish in the Dynamic condition were also exposed to social mixing, which is known to also increase the risk of disease transmission, a major cost of group living and possibly related to the reason many fish species prefer to school with familiar individuals (Croft et al., 2005).

Our findings provide empirical evidence that environmental unpredictability increases the value of recent information and promotes information-seeking behaviour, which may reflect a greater motivation to resolve uncertainty (Bennett et al., 2016; Dall et al., 2005; Dridi & Lehmann, 2016). They are also in line with existing studies that show that the quality of information shifts decision-making strategies: when personal information is less reliable, animals shift to using social information (Bell & Baum, 2002; Kendal et al., 2009; van Bergen et al., 2004). Our study adds that simply living in a highly variable environment is sufficient to change the perceived quality of information, degrading information faster and shifting to the “copy when uncertain” strategy, independent of the actual quality of available information (Bell & Baum, 2002; Kendal et al., 2009; van Bergen et al., 2004). This result supports theoretical models in which environmental change reduces the predictive value of older information and favours recent cues (Boyd & Richerson, 1988).

We also found that fish from unpredictable environments find social information more salient than fish in the Stable condition. The increased attention to and reliance on social information may be due to it being more easily and cheaply acquired and updated - keeping up with changing conditions - making it more reliable in variable environments than personal information (Kendal et al., 2009; Laland, 2004). Fish from both conditions tended to use more reliable (recent) information, but Dynamic condition fish were more likely to follow the most accurate social information and less likely to follow less reliable (older) or unclear information, possibly because information can become outdated more quickly and mistakes may entail more severe costs in unpredictable environments. Under stable conditions, information changes less. Animals may therefore develop a weaker sensitivity to uncertainty and devote less attention to environmental cues, such as social stimuli. Because less updating is required, information-seeking declines (Dall et al., 2005; Dridi & Lehmann, 2016). Additionally, living in a stable social group reduces the need to monitor and track group members and social dynamics (Amici et al., 2008; Aureli et al., 2008; MacLean et al., 2012), and the predictability of the group’s composition may lower the salience of social stimuli, because familiar individuals provide less novel information. This reduced salience of social stimuli may also translate into lower responsiveness to unfamiliar conspecifics, as we observed in the social preference test.

Importantly, our Stable condition did not constitute a neutral control, but rather an unusually predictable environment for a species that evolved in highly variable habitats and inhabits large, fission-fusion shoals (Bhat, 2003; Daniels, 2002; Engeszer et al., 2007, Lawrence,

2007; Shelton et al., 2020; Spence et al., 2008). From this perspective, the Dynamic condition may have provided a more naturalistic environment, with more realistic social learning opportunities. Accordingly, some of the behavioural differences we observed between conditions may be due to the unusually consistent information available to fish in the Stable condition, providing fewer opportunities for updating through learning.

Dynamic environments simulated in the lab may capture some aspects of the variability animals experience in the wild, providing insight into how they might respond to intensifying global environmental change. Because we applied both social and physical manipulations, the behavioural differences we observed between conditions could have arisen from fluctuations in the social environment (such as group composition or size), physical environment (such as water temperature, feeding times, or habitat complexity), or from a combination of both. Future research could test these environmental variables separately to reveal which factors drove the observed effects. In addition, because fish were not individually identifiable, our analyses were limited to the group level, and pre- and post-exposure comparisons could not be made for individual fish. This limited our ability to determine the extent to which the observed condition differences were due to behavioural changes within individuals or group-level effects. Future research could include individual identification, such as tagging, to examine how individual differences shape behavioural responses to environmental unpredictability.

Although we did not directly measure aggression, social instability (as experienced by fish in our Dynamic condition) might increase conflict by repeatedly disrupting social hierarchies. Frequent group-membership changes elevate social uncertainty and may temporarily increase aggression until dominance hierarchies re-stabilize (Larson et al., 2006; Utne-Palm & Hart, 2000). For example, zebrafish often take up to five days to stabilize dominant-subordinate relationships, after which aggression decreases (Larson et al., 2006). In contrast, predictable food delivery may also increase aggression as dominant fish attempt to monopolize resources (e.g., Goldberg et al., 2001; Hamilton & Dill, 2002). Although no differences in aggression were observed between the conditions during the behavioural assays, future studies could include explicit measures of aggression. Future research could also test whether environmental predictability has developmental (organizational) effects by exposing subjects to stable versus dynamic conditions earlier in their lives. This was not possible in the current study, as we wished to equalize the initial mean personality trait values and stress levels across conditions, which required testing the adult fish before assignment to housing conditions.

Overall, our study shows that environmental instability shifts priority toward recent information, heightens information-seeking behaviour, and disrupts schooling by reducing group coordination. These findings may have important implications for how animals will alter their behaviour and decision-making strategies in an increasingly unpredictable world.

References

- Acevedo-Whitehouse, K., & Duffus, A. L. J. (2009). Effects of environmental change on wildlife health. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1534), 3429–3438. <https://doi.org/10.1098/rstb.2009.0128>
- Agnvall, B., Katajamaa, R., Altimiras, J., & Jensen, P. (2015). Is domestication driven by reduced fear of humans? Boldness, metabolism and serotonin levels in divergently selected red junglefowl (*Gallus gallus*). *Biology Letters*, *11*(9), 20150509. <https://doi.org/10.1098/rsbl.2015.0509>
- Amici, F., Aureli, F., & Call, J. (2008). Fission–fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology*, *18*(18), 1415–1419. <https://doi.org/10.1016/j.cub.2008.08.020>
- Angilletta, M. J., Jr., Niewiarowski, P. H., & Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, *27*(4), 249–268. [https://doi.org/10.1016/S0306-4565\(01\)00094-8](https://doi.org/10.1016/S0306-4565(01)00094-8)
- Ariyomo, T. O., & Watt, P. J. (2012). The effect of variation in boldness and aggressiveness on the reproductive success of zebrafish. *Animal Behaviour*, *83*(1), 41–46. <https://doi.org/10.1016/j.anbehav.2011.10.004>
- Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Di Fiore, A., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernández, G., Strier, K. B., & van Schaik, C. P. (2008). Fission–fusion dynamics: New research frameworks. *Current Anthropology*, *49*(4), 627–654. <https://doi.org/10.1086/586708>
- Bell, K. E., & Baum, W. M. (2002). Group foraging sensitivity to predictable and unpredictable changes in food distribution: Past experience or present circumstances? *Journal of the Experimental Analysis of Behavior*, *78*(2), 179–194. <https://doi.org/10.1901/jeab.2002.78-179>
- Bennett, D., Bode, S., Brydevall, M., Warren, H., & Murawski, C. (2016). Intrinsic valuation of information in decision making under uncertainty. *PLOS Computational Biology*, *12*(7), e1005020. <https://doi.org/10.1371/journal.pcbi.1005020>
- Bernhardt, J. R., O'Connor, M. I., Sunday, J. M., & Gonzalez, A. (2020). Life in fluctuating environments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1814), 20190454. <https://doi.org/10.1098/rstb.2019.0454>
- Bhat, A. (2003). Diversity and composition of freshwater fishes in streams of Central Western Ghats, India. *Environmental Biology of Fishes*, *68*(1), 25–38. <https://doi.org/10.1023/A:1026017119070>
- Bizberg-Barraza, I., Rodríguez, C., & Drummond, H. (2024). Do females plastically adjust hatching asynchrony as a reproductive tactic in response to climatic cues? *Animal Behaviour*, *215*, 251–261. <https://doi.org/10.1016/j.anbehav.2024.06.020>

- Boyd, R., & Richerson, P. J. (1988). An evolutionary model of social learning: The effects of spatial and temporal variation. In T. Zentall & B. G. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 29-48). Lawrence Erlbaum Associates.
- Carter, G. G., & Wilkinson, G. S. (2016). Common vampire bat contact calls attract past food-sharing partners. *Animal Behaviour*, *116*, 45–51.
<https://doi.org/10.1016/j.anbehav.2016.03.005>
- Coolen, I., & Giraldeau, L. A. (2003). Incompatibility between antipredatory vigilance and scrounger tactic in nutmeg mannikins (*Lonchura punctulata*). *Animal Behaviour*, *66*(4), 657–664. <https://doi.org/10.1006/anbe.2003.2236>
- Coolen, I., van Bergen, Y., Day, R. L., & Laland, K. N. (2003). Species differences in adaptive use of public information in sticklebacks. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1531), 2413–2419. <https://doi.org/10.1098/rspb.2003.2525>
- Cortemeglia, C., & Beitinger, T. L. (2005). Temperature tolerances of wild-type and red transgenic zebra danios. *Transactions of the American Fisheries Society*, *134*(6), 1431–1437. <https://doi.org/10.1577/T04-197.1>
- Croft, D. P., Arrowsmith, B. J., Bielby, J., Skinner, K., White, E., Couzin, I. D., Magurran, A. E., Ramnarine, I., & Krause, J. (2003). Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*. *Oikos*, *100*(3), 429–438.
<https://doi.org/10.1034/j.1600-0706.2003.12023.x>
- Croft, D. P., James, R., Ward, A. J. W., Botham, M. S., Mawdsley, D., & Krause, J. (2005). Assortative interactions and social networks in fish. *Oecologia*, *143*(2), 211–219.
<https://doi.org/10.1007/s00442-004-1796-8>
- Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, *20*(4), 187–193. <https://doi.org/10.1016/j.tree.2005.01.010>
- Daniels, R. J. R. (2002). *Freshwater fishes of Peninsular India*. Universities Press.
- Darrow, K. O., & Harris, W. A. (2004). Characterization and development of courtship in zebrafish, *Danio rerio*. *Zebrafish*, *1*(1), 40–45.
<https://doi.org/10.1089/154585404774101662>
- Davis, S., Lukeman, R., Schaerf, T. M., & Ward, A. J. W. (2017). Familiarity affects collective motion in shoals of guppies (*Poecilia reticulata*). *Royal Society Open Science*, *4*(9), 170312. <https://doi.org/10.1098/rsos.170312>
- Dobson, F. S., Becker, P. H., Arnaud, C. M., Bouwhuis, S., & Charmantier, A. (2017). Plasticity results in delayed breeding in a long-distant migrant seabird. *Ecology and Evolution*, *7*(9), 3100–3109. <https://doi.org/10.1002/ece3.2777>
- Domenici, P., & Seebacher, F. (2020). The impacts of climate change on the biomechanics of animals. *Conservation Physiology*, *8*(1), coz102. <https://doi.org/10.1093/conphys/coz102>
- Dos Santos, T. G., Mussulini, B. H. M., Frangipani, L. A., & de Oliveira, D. L. (2020). Differential impact of shorter and longer periods of environmental enrichment on adult

- zebrafish exploratory activity (*Danio rerio*) in the novel tank paradigm. *Behavioural Processes*, 181, 104278. <https://doi.org/10.1016/j.beproc.2020.104278>
- dos Santos, C. P., de Oliveira, M. N., Silva, P. F., & Luchiari, C. A. (2023). Relationship between boldness and exploratory behavior in adult zebrafish. *Behavioural Processes*, 209, 104885. <https://doi.org/10.1016/j.beproc.2023.104885>
- Dridi, S., & Lehmann, L. (2016). Environmental complexity favors the evolution of learning. *Behavioral Ecology*, 27(3), 842–850. <https://doi.org/10.1093/beheco/arv184>
- Egan, R. J., Bergner, C. L., Hart, P. C., Cachat, J. M., Canavello, P. R., Elegante, M. F., Elkhayat, S. I., Bartels, B. K., Tien, A. K., Tien, D. H., Mohnot, S., Beeson, E., Glasgow, E., Amri, H., Zukowska, Z., & Kalueff, A. V. (2009). Understanding behavioral and physiological phenotypes of stress and anxiety in zebrafish. *Behavioural Brain Research*, 205(1), 38–44. <https://doi.org/10.1016/j.bbr.2009.06.022>
- Engeszer, R. E., Patterson, L. B., Rao, A. A., & Parichy, D. M. (2007). Zebrafish in the wild: A review of natural history and new notes from the field. *Zebrafish*, 4(1), 21–40. <https://doi.org/10.1089/zeb.2006.9997>
- Franke, A., Beemelmans, A., & Miest, J. J. (2024). Are fish immunocompetent enough to face climate change? *Biology Letters*, 20(2), 20230346. <https://doi.org/10.1098/rsbl.2023.0346>
- Genario, R., de Abreu, M. S., Giacomini, A. C. V. V., Demin, K. A., & Kalueff, A. V. (2020). Sex differences in behavior and neuropharmacology of zebrafish. *European Journal of Neuroscience*, 52(1), 2586–2603. <https://doi.org/10.1111/ejn.14438>
- Goldberg, J. L., Ward, P., & Cresswell, W. (2001). Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove (*Zenaida aurita*). *Behavioral Ecology*, 12(4), 490–495. <https://doi.org/10.1093/beheco/12.4.490>
- Gonçalves, C., Kareklas, K., Teles, M. C., Varela, S. A. M., Costa, J., Leite, R. B., Paixão, T., & Oliveira, R. F. (2022). Phenotypic architecture of sociality and its associated genetic polymorphisms in zebrafish. *Genes, Brain and Behavior*, 21(5), e12809. <https://doi.org/10.1111/gbb.12809>
- Guayasamin, O. L., Couzin, I. D., & Miller, N. Y. (2017). Behavioural plasticity across social contexts is regulated by the directionality of inter-individual differences. *Behavioural Processes*, 141, 196–204. <https://doi.org/10.1016/j.beproc.2016.10.004>
- Hamilton, I. M., & Dill, L. M. (2002). Monopolization of food by zebrafish (*Danio rerio*) increases in risky habitats. *Canadian Journal of Zoology*, 80(12), 2164–2169. <https://doi.org/10.1139/Z02-199>
- Hemelrijk, C. K., & Hildenbrandt, H. (2008). Self-organized shape and frontal density of fish schools. *Ethology*, 114(3), 245–254. <https://doi.org/10.1111/j.1439-0310.2007.01459.x>
- Heydari, S., Hang, H., & Kanso, E. (2024). Mapping spatial patterns to energetic benefits in groups of flow-coupled swimmers. *eLife*, 13, RP96129. <https://doi.org/10.7554/eLife.96129>

- Hoppitt, W., & Laland, K. N. (2013). *Social learning: An introduction to mechanisms, methods, and models*. Princeton University Press.
<https://doi.org/10.23943/princeton/9780691150703.001.0001>
- Huntingford, F. A. (2004). Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *Journal of Fish Biology*, *65*(1), 122–142.
<https://doi.org/10.1111/j.0022-1112.2004.00562.x>
- Huntingford, F., & Adams, C. (2005). Behavioural syndromes in farmed fish: Implications for production and welfare. *Behaviour*, *142*(9–10), 1207–1221.
<https://doi.org/10.1163/156853905774539382>
- JASP Team. (2025). *JASP* (Version 0.95.0) [Computer software]. <https://jasp-stats.org/>
- Kendal, R. L., Coolen, I., & Laland, K. N. (2009). Adaptive trade-offs in the use of social and personal information. In R. Dukas & J. M. Ratcliffe (Eds.), *Cognitive ecology II* (pp. 249–271). University of Chicago Press.
<https://doi.org/10.7208/chicago/9780226169378.003.0013>
- Kleiber, A., Le Calvez, J.-M., Kerneis, T., Batard, A., Goardon, L., Labbé, L., Brunet, V., Ferreira, V. H. B., Guesdon, V., Calandreau, L., & Colson, V. (2022). Positive effects of bubbles as a feeding predictor on behaviour of farmed rainbow trout. *Scientific Reports*, *12*, 11368. <https://doi.org/10.1038/s41598-022-15302-7>
- Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press.
<https://doi.org/10.1093/oso/9780198508175.001.0001>
- Kysil, E. V., Meshalkina, D. A., Frick, E. E., Echevarria, D. J., Rosemberg, D. B., Maximino, C., Lima, M. G., Abreu, M. S., Giacomini, A. C., Barcellos, L. J. G., Song, C., & Kalueff, A. V. (2017). *Comparative analyses of zebrafish anxiety-like behavior using conflict-based novelty tests*. *Zebrafish*, *14*(3), 197–208. <https://doi.org/10.1089/zeb.2016.1415>
- Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, *32*(1), 4–14.
<https://doi.org/10.3758/BF03196002>
- Lanz, E., López-Martínez, J., Nevárez-Martínez, M. O., & Dworak, J. A. (2009). Small pelagic fish catches in the Gulf of California associated with sea surface temperature and chlorophyll. *CalCOFI Reports*, *50*, 134–146.
- Larson, E. T., O'Malley, D. M., & Melloni, R. H., Jr. (2006). Aggression and vasotocin are associated with dominant–subordinate relationships in zebrafish. *Behavioural Brain Research*, *167*(1), 94–102. <https://doi.org/10.1016/j.bbr.2005.08.020>
- Lawrence, C. (2007). The husbandry of zebrafish (*Danio rerio*): A review. *Aquaculture*, *269*(1–4), 1–20. <https://doi.org/10.1016/j.aquaculture.2007.04.077>
- Levin, E. D., Bencan, Z., & Cerutti, D. T. (2007). Anxiolytic effects of nicotine in zebrafish. *Physiology & Behavior*, *90*(1), 54–58. <https://doi.org/10.1016/j.physbeh.2006.08.026>
- Lluch-Belda, D., Crawford, R. J. M., Kawasaki, T., MacCall, A. D., Parrish, R. H., Schwartzlose, R. A., & Smith, P. E. (1989). Worldwide fluctuations of sardine and anchovy stocks: The regime problem. *South African Journal of Marine Science*, *8*(1), 195–205.
<https://doi.org/10.2989/02577618909504561>

- Lluch-Cota, S. E. (2000). Coastal upwelling in the eastern Gulf of California. *Oceanologica Acta*, 23(6), 731–740. [https://doi.org/10.1016/S0399-1784\(00\)00121-3](https://doi.org/10.1016/S0399-1784(00)00121-3)
- Lucon-Xiccato, T., Cattelan, S., & Griggio, M. (2022). Familiarity effects on fish behaviour are disrupted in shoals that contain also unfamiliar individuals. *Behavioral Ecology and Sociobiology*, 76, Article 100. <https://doi.org/10.1007/s00265-022-03210-9>
- MacLean, E. L., Matthews, L. J., Hare, B. A., Nunn, C. L., Anderson, R. C., Aureli, F., Brannon, E. M., Call, J., Drea, C. M., Emery, N. J., Haun, D. B. M., Herrmann, E., Jacobs, L. F., Platt, M. L., Rosati, A. G., Sandel, A. A., Schroepfer, K. K., Seed, A. M., Tan, J., van Schaik, C. P., & Wobber, V. (2012). How does cognition evolve? Phylogenetic comparative psychology. *Animal Cognition*, 15(2), 223–238. <https://doi.org/10.1007/s10071-011-0448-8>
- Marras, S., Killen, S. S., Lindström, J., McKenzie, D. J., Steffensen, J. F., & Domenici, P. (2015). Fish swimming in schools save energy regardless of their spatial position. *Behavioral Ecology and Sociobiology*, 69(2), 219–226. <https://doi.org/10.1007/s00265-014-1834-4>
- Massey, M. D., Fredericks, M. K., Malloy, D., Arif, S., & Hutchings, J. A. (2022). Differential reproductive plasticity under thermal variability in a freshwater fish (*Danio rerio*). *Proceedings of the Royal Society B: Biological Sciences*, 289(1982), 20220751. <https://doi.org/10.1098/rspb.2022.0751>
- Mathis, A., & Smith, R. J. F. (1993). Chemical alarm signals increase the survival time of fathead minnows (*Pimephales promelas*) during encounters with northern pike (*Esox lucius*). *Behavioral Ecology*, 4(3), 260–265. <https://doi.org/10.1093/beheco/4.3.260>
- Micheletta, J., Waller, B. M., Panggur, M. R., Neumann, C., Duboscq, J., Agil, M., & Engelhardt, A. (2012). Social bonds affect anti-predator behaviour in a tolerant species of macaque, *Macaca nigra*. *Proceedings of the Royal Society B: Biological Sciences*, 279(1744), 4042–4050. <https://doi.org/10.1098/rspb.2012.1470>
- Miller, N. Y., & Gerlai, R. (2011). Shoaling in zebrafish: What we don't know. *Reviews in the Neurosciences*, 22(1), 17–25. <https://doi.org/10.1515/RNS.2011.004>
- Miller, N., & Gerlai, R. (2012a). From schooling to shoaling: Patterns of collective motion in zebrafish (*Danio rerio*). *PLOS ONE*, 7(11), e48865. <https://doi.org/10.1371/journal.pone.0048865>
- Miller, N., & Gerlai, R. (2012b). Automated tracking of zebrafish shoals and the analysis of shoaling behavior. In A. Kalueff & A. Stewart (Eds.), *Zebrafish protocols for neurobehavioral research* (Neuromethods, Vol. 66, pp. 217–239). Humana Press. https://doi.org/10.1007/978-1-61779-597-8_16
- Nadler, L. E., McCormick, M. I., Johansen, J. L., & Domenici, P. (2021). Social familiarity improves fast-start escape performance in schooling fish. *Communications Biology*, 4, 897. <https://doi.org/10.1038/s42003-021-02407-4>
- Nevárez-Martínez, M. O., Lluch-Belda, D., Cisneros-Mata, M. A., Santos-Molina, J. P., Martínez-Zavala, M. de los A., & Lluch-Cota, S. E. (2001). Distribution and abundance of the Pacific sardine (*Sardinops sagax*) in the Gulf of California and their relation with the

- environment. *Progress in Oceanography*, 49(1–4), 565–580. [https://doi.org/10.1016/S0079-6611\(01\)00041-6](https://doi.org/10.1016/S0079-6611(01)00041-6)
- Pérez-Escudero, A., & de Polavieja, G. G. (2011). Collective animal behavior from Bayesian estimation and probability matching. *PLOS Computational Biology*, 7(11), e1002282. <https://doi.org/10.1371/journal.pcbi.1002282>
- Pritchard, V. L., Lawrence, J., Butlin, R. K., & Krause, J. (2001). Shoal choice in zebrafish, *Danio rerio*: The influence of shoal size and activity. *Animal Behaviour*, 62(6), 1085–1088. <https://doi.org/10.1006/anbe.2001.1858>
- Riley, R. J., Gillie, E. R., Horswill, C., Johnstone, R. A., Boogert, N. J., & Manica, A. (2019). Coping with strangers: How familiarity and active interactions shape group coordination in *Corydoras aeneus*. *Royal Society Open Science*, 6(8), 190587. <https://doi.org/10.1098/rsos.190587>
- Riotte-Lambert, L., & Matthiopoulos, J. (2020). Environmental predictability as a cause and consequence of animal movement. *Trends in Ecology & Evolution*, 35(2), 163–174. <https://doi.org/10.1016/j.tree.2019.09.009>
- Robb, S. E., & Grant, J. W. A. (1998). Interactions between the spatial and temporal clumping of food affect the intensity of aggression in Japanese medaka. *Animal Behaviour*, 56(1), 29–34. <https://doi.org/10.1006/anbe.1998.0735>
- Rotenberry, J. T., & Wiens, J. A. (1980). Temporal variation in habitat structure and shrubsteppe bird dynamics. *Oecologia*, 47(1), 1–9. <https://doi.org/10.1007/BF00541768>
- Sekulovski, B., Soref, L., & Miller, N. (2025). Mechanisms of socially facilitated feeding in zebrafish (*Danio rerio*). *Learning & Behavior*. <https://doi.org/10.3758/s13420-025-00691-2>
- Sekulovski, B., & Miller, N. (2025). Mechanisms of social behaviour in the anti-social blind cavefish (*Astyanax mexicanus*). *Proceedings of the Royal Society B: Biological Sciences*, 292(2043), 20250052. <https://doi.org/10.1098/rspb.2025.0052>
- Schaefer, J., & Ryan, A. (2006). Developmental plasticity in the thermal tolerance of zebrafish *Danio rerio*. *Journal of Fish Biology*, 69(3), 722–734. <https://doi.org/10.1111/j.1095-8649.2006.01145.x>
- Scharf, I., & Farji-Brener, A. (2024). Wall-following behavior: Its ultimate and proximate explanations, prevalence, and implications. In M. Naguib (Ed.), *Advances in the Study of Behavior* (Vol. 56, pp. 1–49). Academic Press. <https://doi.org/10.1016/bs.asb.2024.02.003>
- Shams, S., Chatterjee, D., & Gerlai, R. (2015). Chronic social isolation affects thigmotaxis and whole-brain serotonin levels in adult zebrafish. *Behavioural Brain Research*, 292, 283–287. <https://doi.org/10.1016/j.bbr.2015.05.061>
- Shelton, D. S., Shelton, S. G., Daniel, D. K., Raja, M., Bhat, A., Tanguay, R. L., Higgs, D. M., & Martins, E. P. (2020). Collective behavior in wild zebrafish: Water flow predicts group size and fission–fusion dynamics. *Zebrafish*, 17(4), 243–252. <https://doi.org/10.1089/zeb.2019.1851>

- Shier, D. M., & Randall, J. A. (2004). Spacing as a predictor of social organization in kangaroo rats (*Dipodomys heermanni arenae*). *Journal of Mammalogy*, *85*(5), 1002–1008. <https://doi.org/10.1644/107>
- Sih, A. (2024). Behavioural ecology for a changing world. In B. B. M. Wong & U. Candolin (Eds.), *Behavioural responses to a changing world* (pp. 329–345). Oxford University Press. <https://doi.org/10.1093/oso/9780192858979.003.0019>
- Smith, R. D., Ruxton, G. D., & Cresswell, W. (2001). Patch choice decisions of wild blackbirds: The role of preharvest public information. *Animal Behaviour*, *61*(6), 1113–1124. <https://doi.org/10.1006/anbe.2001.1704>
- Smolla, M., Alem, S., Chittka, L., & Shultz, S. (2016). Copy-when-uncertain: Bumblebees rely on social information when rewards are highly variable. *Biology Letters*, *12*(6), 20160188. <https://doi.org/10.1098/rsbl.2016.0188>
- Spence, R., Gerlach, G., Lawrence, C., & Smith, C. (2008). The behaviour and ecology of the zebrafish, *Danio rerio*. *Biological Reviews*, *83*(1), 13–34. <https://doi.org/10.1111/j.1469-185X.2007.00030.x>
- Taborsky, B. (2021). A positive feedback loop between sociality and social competence. *Ethology*, *127*(10), 774–789. <https://doi.org/10.1111/eth.13201>
- Templeton, J. J., & Giraldeau, L.-A. (1996). Vicarious sampling: The use of personal and public information by starlings foraging in a simple patchy environment. *Behavioral Ecology and Sociobiology*, *38*(2), 105–114. <https://doi.org/10.1007/s002650050223>
- Thompson, A. B., & Hare, J. F. (2010). Neighbourhood watch: Multiple alarm callers communicate directional predator movement in Richardson's ground squirrels, *Spermophilus richardsonii*. *Animal Behaviour*, *80*(2), 269–275. <https://doi.org/10.1016/j.anbehav.2010.04.028>
- Toni, M., Frabetti, F., Tedeschi, G., & Alleva, E. (2025). Effects of environmental temperature variation on the spatio-temporal shoaling behaviour of adult zebrafish (*Danio rerio*): A two- and three-dimensional analysis. *Animals*, *15*(14), 2006. <https://doi.org/10.3390/ani15142006>
- Utne-Palm, A. C., & Hart, P. J. B. (2000). The effects of familiarity on competitive interactions between three-spined sticklebacks. *Oikos*, *91*(2), 225–232. <https://doi.org/10.1034/j.1600-0706.2000.910203.x>
- Valone, T. J. (1989). Group foraging, public information, and patch estimation. *Oikos*, *56*(3), 357–363. <https://doi.org/10.2307/3565621>
- Valone, T. J., & Giraldeau, L.-A. (1993). Patch estimation by group foragers: What information is used? *Animal Behaviour*, *45*(4), 721–728. <https://doi.org/10.1006/anbe.1993.1086>
- Valone, T. J., & Templeton, J. J. (2002). Public information for the assessment of quality: A widespread social phenomenon. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1427), 1549–1557. <https://doi.org/10.1098/rstb.2002.1064>
- van Bergen, Y., Coolen, I., & Laland, K. N. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal*

- Society of London. Series B: Biological Sciences*, 271(1542), 957–962.
<https://doi.org/10.1098/rspb.2004.2684>
- Ward, A. J. W., Thomas, P., Hart, P. J. B., & Krause, J. (2004). Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, 55(6), 561–568. <https://doi.org/10.1007/s00265-003-0751-8>
- Ward, A. J. W., & Webster, M. M. (2016). *Sociality: The behaviour of group-living animals*. Springer. <https://doi.org/10.1007/978-3-319-28585-6>
- Webster, M. M., & Laland, K. N. (2011). Reproductive state affects reliance on public information in sticklebacks. *Proceedings of the Royal Society B: Biological Sciences*, 278(1702), 619–627. <https://doi.org/10.1098/rspb.2010.1562>
- Weih, D. (1973). Hydromechanics of fish schooling. *Nature*, 241(5387), 290–291. <https://doi.org/10.1038/241290a0>
- White, D. J., Gersick, A. S., Freed-Brown, G., & Snyder-Mackler, N. (2010). The ontogeny of social skills: Experimental increases in social complexity enhance reproductive success in adult cowbirds. *Animal Behaviour*, 79(2), 385–390. <https://doi.org/10.1016/j.anbehav.2009.11.014>
- Wiens, J. A. (1985). Habitat selection in variable environments: Shrub-steppe birds. In M. L. Cody (Ed.), *Habitat selection in birds* (pp. 227–251). Academic Press.
- Wingfield, J. C., & Kitaysky, A. S. (2002). Endocrine responses to unpredictable environmental events: Stress or anti-stress hormones? *Integrative and Comparative Biology*, 42(3), 600–609. <https://doi.org/10.1093/icb/42.3.600>
- Zhang, Y., & Lauder, G. V. (2024). Energy conservation by collective movement in schooling fish. *eLife*, 13, e90352. <https://doi.org/10.7554/eLife.90352>

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Data Accessibility: All the data reported here are available on our OSF repository (doi: 10.17605/OSF.IO/286MD).

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NM: study design, analysis, writing, editing, funding.

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Supplementary Materials

Supplementary methods

Open-Field Test (OFT)

Apparatus: Exploratory behaviour was measured in a Styrofoam tank (57 cm × 36 cm × 8 cm water depth; Figure S1), with a sheltered area (a strip of white corrugated plastic, along one short wall at the water surface; 36 cm × 8 cm) containing artificial plants glued along the underside. LED lights were placed next to the tank and a white shower curtain surrounded it. An overhead webcam (Logitech C920) recorded the OFT and the adjacent SPT simultaneously.

Procedure: The tank was filled with water matched to home tanks, refreshed daily. Each fish was net-transferred to the center of the tank and a 15-min trial began after the curtain was closed. The order of OFT and SPT was counterbalanced across fish. Each fish was tested once before housing condition assignment and once immediately after the 3-month exposure.

Tracking and Analysis: A custom Python script tracked fish in real time at 30 fps, extracting X-Y coordinates for every frame and calculating the total proportion of time fish spent outside of the shelter zone.

Social-Preference Test (SPT)

Apparatus: Social motivation was measured using a three-chamber glass tank (75 cm × 29.5 cm × 9 cm water depth; Figure S1), divided by clear plastic partitions into a 50.5 cm central test chamber and two 12 cm side stimulus chambers. The interior was lined with opaque white waterproof paper. See OFT for surroundings.

Procedure: The tank was filled with water taken from home tanks, refreshed daily. One stimulus chamber held five novel fish, while the other stimulus chamber remained empty. The side on which the stimulus shoal appeared was counterbalanced across subjects. Stimulus fish were placed in the tank at least 5 min before testing. Each fish was net-transferred to the center of the tank and a 15-min trial began after the curtain was closed. Each fish was tested once before housing condition assignment and once immediately after the 3-month exposure.

Tracking and Analysis: Real-time tracking was used to compute the total proportion of time fish spent in close proximity (within 10 cm) to the shoal chamber.

Novel-Tank Diving Test (NTDT)

Apparatus: Stress reactivity was evaluated using an established NTDT (Egan et al., 2009; Levin et al., 2007) in right trapezoid 5 L clear plastic tanks (32.5 cm top /26 cm bottom × 10.5 cm × 15 cm water depth; Figure S2). Two tanks were on a table and two were elevated on a riser

directly above, allowing four fish to be recorded simultaneously. Opaque white PVC walls behind the tanks enhanced contrast for side-view tracking and walls between adjacent tanks provided visual isolation. The front faces of the tanks were marked externally into equal-depth bottom, middle, and top thirds (5 cm per zone). LED bars on the sides illuminated the tanks, and a tripod-mounted webcam (Logitech C920; 30 fps) recorded the side-view of all four tanks.

Procedure: Tanks were filled with system water matched to home tanks, refreshed daily. Fish were individually net-transferred to one of the tanks and allowed ~10 s to settle and a 10 min trial began once the room door closed. Each fish completed the assay twice: Pre-exposure and Post-exposure. Pre-exposure NTDT trials were run across five days, directly after the OFT and SPT. Post-exposure trials were completed five days after the Post-exposure OFT and SPT.

Tracking & Analysis: A custom Python script generated X-Y coordinates per frame. Dependent variables were time spent in bottom and top thirds (middle excluded), freezing duration, and vertical zone switches. A greater proportion of time in the bottom third and increased freezing were interpreted as heightened stress.

Schooling Test

Apparatus: Group movement was measured in a white round rubber tub (60 cm diameter; 10 cm water depth; Figure S3). Overhead recording (Canon Vixia HF R700; 30 fps) captured behaviour.

Procedure: The tub was filled with system water matched to home tanks, refreshed after every third trial. Five fish from the same condition and (current) tank were net-transferred to the center of the tub and allowed to swim freely for 10 min. All fish completed this test within a week after completing the NTDT. Fish received this test and the follow Post-exposure only.

Tracking & Analysis: A custom Python script tracked fish positions and a custom R script calculated inter-individual distance (IID), nearest-neighbour distance (NND), polarization, speed, and thigmotaxis. The IID is the mean distance between each fish and every other fish, averaged over all focal fish; the NND is the mean distance between each fish and the closest fish to it; polarization is the degree to which all fish are swimming in the same direction (and varies from 0 to 1); and thigmotaxis is tendency to stay close to the wall (within the outer 10% of the tank radius). Metrics were averaged over the full session and within four consecutive 2.5 min epochs to examine changes across time.

Social Information Test (SIT)

Apparatus: Social information use was tested using a modified demonstrator-observer paradigm (Coolen et al., 2003; van Bergen et al., 2004; Webster & Laland, 2011), in a white PVC arena (99.5 cm × 59 cm, 12 cm water depth; Figure S4), with a triangular divider partially

split the tank (43×37 cm), creating two feeding chambers (28 top \times 49 bottom \times 37 cm) and a long front neutral zone (99.5×22 cm). Each feeding chamber contained a floating red plastic ring feeder (diameter: 6 cm) positioned beneath an externally mounted acrylic tube for pellet delivery. A transparent half-cylinder start box ($6.5 \times 4.5 \times 28.5$ cm), with a nylon pull line, was placed midway along a long wall. Removable barriers (one transparent barrier 98×25 cm; two shorter opaque black barriers 47×20.5 cm) were used to alternately enclose or reveal the feeding chambers. The white shower curtains covered the sides of the arena, and an overhead webcam (Logitech C920) recorded probe trials.

Procedure: The arena was filled with system water matched to home tanks and refilled every third day, with heaters and airstones run overnight to maintain temperature and oxygenation.

To simplify the typical SIT, demonstrators were presented with a fed vs. unfed feeder, rather than a rich vs. poor feeder (i.e., more food vs. less food; Coolen et al., 2003; van Bergen et al., 2004; Webster & Laland, 2011). Approximately 30 demonstrator fish were pre-selected for the SIT and CIT based on whether they would feed in a novel environment to ensure more consistent demonstrator performance. Demonstrators were fed exclusively on test food pellets used during testing (Hikari Betta Bio Gold; 1 mm diameter) for at least 7 days prior to training (and continued after the SIT until the CIT). Over two consecutive days before testing, demonstrators were placed in the arena for 20 min with food delivered to both feeders and only fed in the arena.

Test fish were fasted for 24 h before testing and were habituated to the arena for 20 min in their tank groups, with all barriers removed the day before testing. For the SIT, with all barriers closed, three demonstrators were net-transferred to each feeding chamber. Demonstrators swapped chambers between trials and only participated in one or two (never consecutively) feeding demonstrations per day to maintain consistent feeding motivation. Test fish were individually poured into the start box with a beaker, acclimating for 2 min before opaque barriers were removed, leaving the transparent barrier. After 30 s, ten food pellets were delivered to one ring feeder (sides counterbalanced across subjects) via the attached tubes (ensuring that the experimenter was not visible to the fish). Demonstrators were allowed to feed for 8 min while the test fish observed. Following the demonstration, opaque barriers were reinserted, and demonstrators and pellets, if any, were removed. Uneaten pellets were counted and reported. Water was briefly cross-mixed between feeding chambers using a beaker to control for residual olfactory cues. All barriers were then removed and, after a 30 s delay, the test fish was released into the arena for 5 min.

Tracking & Analysis: Videos were manually tracked using a custom Python script, extracting the frame number each time the fish entered a zone. ROIs included the neural zone, each feeding chamber, and around each ring feeder. The variables of interest were the proportion

of time the fish spent on each side of the arena, initial choice, and the number of pellets left uneaten by the demonstrators.

Conflicting Information Test (CIT)

Apparatus: The CIT used the same arena as the SIT (Figure S4).

Procedure: Fish completed the CIT within approximately two months after the SIT. Test fish were exclusively fed the test pellets for at least seven days before training (~3 pellets per fish per feeding), using ring feeders placed in the home tanks and fasted for 24 h before the first day of personal information. The arena was filled with system water matched to home tanks and refilled every third day, with heaters and airstones run overnight to maintain temperature and oxygenation.

Fish were trained in groups (current tankmates) for seven consecutive days to associate one side of the arena with food. With only the transparent barrier in place, each tank was split randomly between the two feeding chambers, and after 30 s, 20 pellets were delivered to the ring feeder on one designated side (counterbalanced across tanks and conditions) and never the other (i.e., only half the fish were fed). Fish fed for 15 min before being net-transferred to the opposite chamber for the next trial. Each tank received four training trials per day (two per side) and only fed during training on these seven days. On the final day of personal information training, all barriers were removed and test fish were placed in the arena overnight in their home tank groups for habituation to decrease exploratory behaviour during testing. Over two consecutive days before testing, demonstrators were placed in the arena for 20 min with food delivered to both feeders, always after test fish completed their training.

Each fish was tested individually on their learned side preference (Probe 1) the day after the last day of training. All barriers were removed from the arena, and the test fish was poured into the start box. After 1 min of acclimation, the fish was released, and then removed immediately following their first choice (crossing fully into one chamber). If a fish did not make a choice within 3 min, it was removed and excluded from analysis. All fish then proceeded directly to the public demonstration, regardless of choice. The public demonstration and Probe 2 were identical to the SIT, except demonstrators fed on the opposite side from the one associated with food during personal training, creating conflict between privately learned and publicly observed information about the location of the food.

Tracking & Analysis: As in SIT, manual Python tracking extracted time spent in each zone. The same variables of interest from the SIT, as well as the latency to make an initial choice during both Probe 1 and 2, the number of switches, and whether fish shifted their preference toward the demonstrated location (indicating conformity; van Bergen et al., 2004) were examined.

Table S1.

Day	Temp (°C)	Feeding	Group N	Plants
1	20	10, 14	10, 10, 10, 10	2
2	22	11, 13		
3	26	10, 16		
4	27	12, 15	5, 5, 15, 15	7
5	24	10, 15		
6	19	12, 16		
7	18	10, 12	9, 9, 11, 11	5
8	21	10, 16		
9	25	11, 14		
10	28	11, 16	8, 8, 12, 12	1
11	26	10, 14		
12	22	12, 14		
13	27	10, 16	6, 6, 14, 14	3
14	25	13, 16		
15	20	10, 15		
16	19	11, 15	7, 7, 13, 13	6
17	21	14, 16		
18	24	12, 14		

Dynamic condition environmental variation. In Dynamic condition tanks, the environment was varied following this table, on a repeating 18-day cycle. Water temperature (**Temp**) varied each day, with no more than a 5 °C change per day. All values were within ranges that zebrafish can easily tolerate (Lawrence, 2007), and the mean value across the cycle matched the temperature maintained in the Stable condition tanks. Feeding times (**Feeding**) also varied daily, pseudo-randomly between 10:00 and 16:00 h, with a minimum of 2 h between feedings. Mean feeding times matched those in the Stable tanks. Group size & composition (**Group N**) was varied every third day (on Switching days). On these days, all 40 Dynamic condition fish were net-transferred into one bucket and then randomly redistributed across the four tanks in pseudorandom group sizes (5-15 fish per tank). Mean group size across the cycle was 10 fish per tank, matching the Stable tanks. Finally, habitat complexity (**Plants**) was varied by changing the number of artificial plants in the tank on Switching days. The mean across the cycle was 4 plants, as in the Stable tanks.

Figure S1: Open-Field Test and Social-Preference Test. Diagram (left) and photo (right) of the open-field test arena (on the left of each pair) and the social-preference test arena (on the right). The black area indicates a shelter; dotted lines indicate transparent walls. In the photos, which are screenshots from the automated tracking program, green lines show the tracking ROI and the test fish are outlined in red.

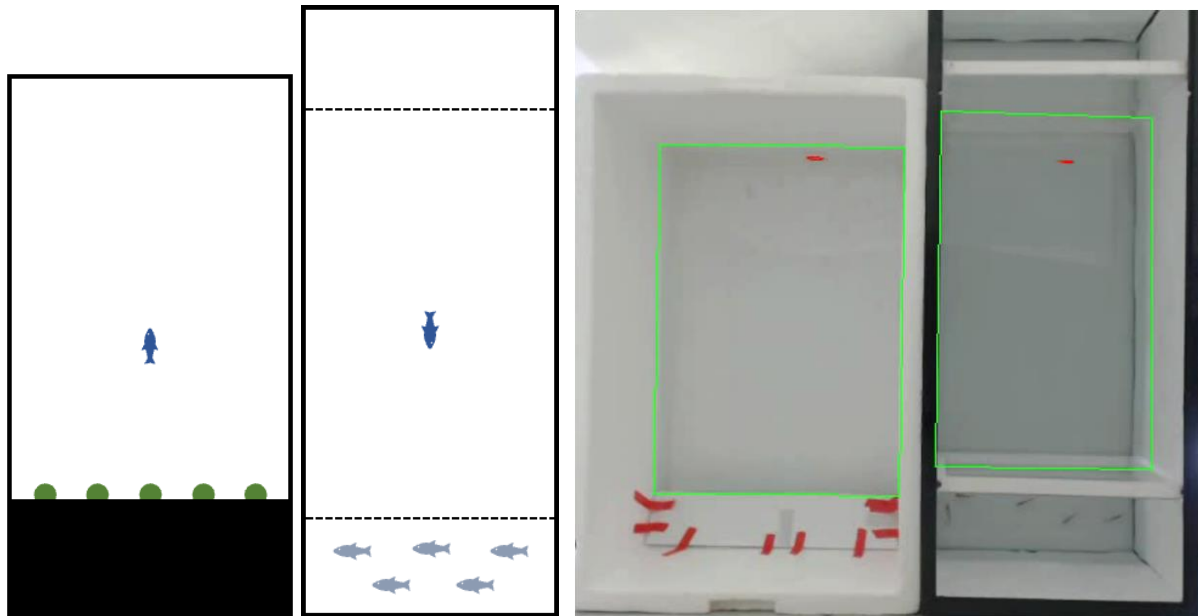


Figure S2: Novel-Tank Diving Test. Diagram (left) and photo (right) of the novel-tank diving test arena. Dashed lines show the limits of the three vertical zones, used for analysis. In the photo, which is a screenshot from the automated tracking program, green lines show the tracking ROIs for each tank, and the test fish are outlined in red.

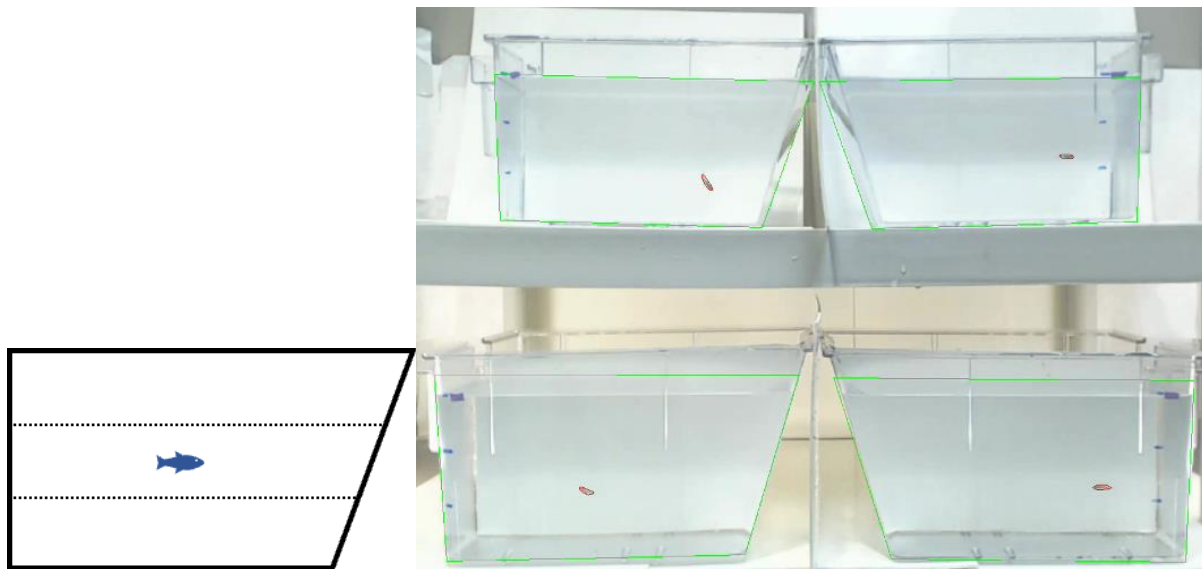


Figure S3: Schooling Test. Diagram (left) and photo (right) of the schooling test arena. In the photo, which is a screenshot from the automated tracking program, fish are indicated by colored and labeled dots.

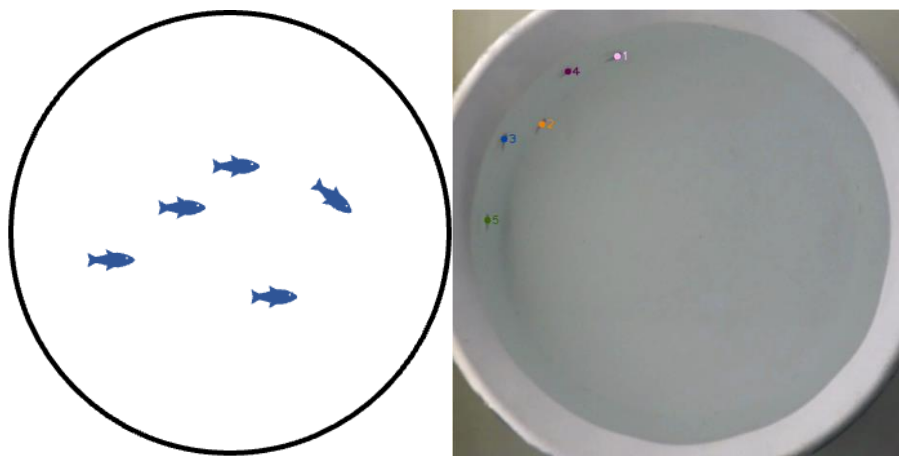


Figure S4: Social Information Test and Conflicting Information Test (during public demonstration). Diagram (top) and photo (bottom) of the arena used for both the public information test and the conflicting information test. Dashed black lines indicate a transparent wall. Red dashed lines indicate the tracking zones. Blue circles are feeders.

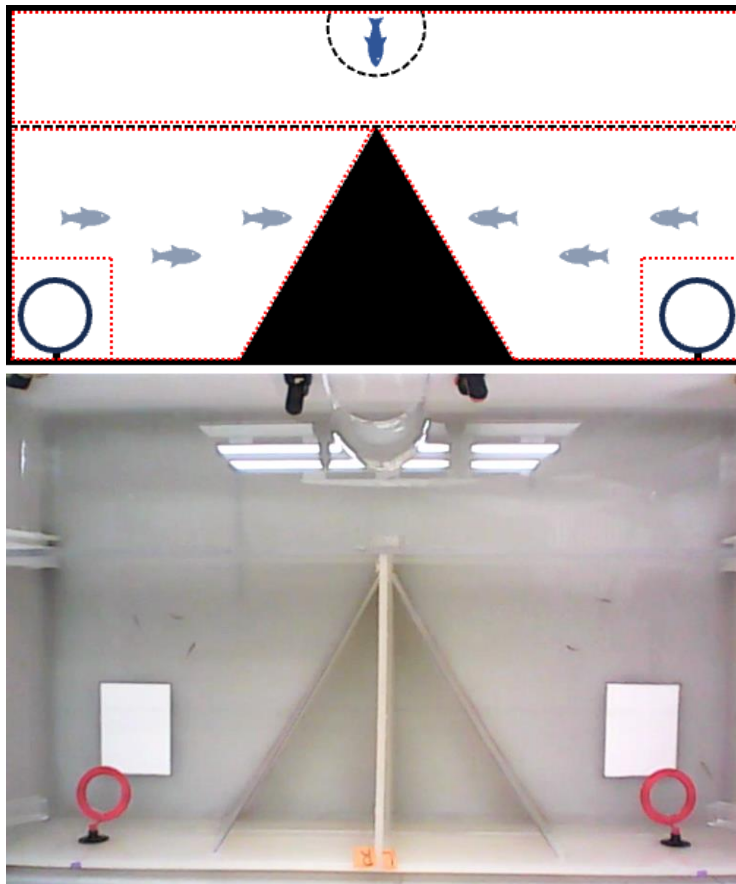


Figure S5. Effects of housing condition on stress reactivity. Violin plots of measures from the Novel Tank Diving Test (NTDT) for the Stable (“St”, blue shades) and Dynamic (“Dy”, purple shades) conditions both before (“Pre-exp”, light shades) and after (“Post-exp”, dark shades) a 3-month exposure to varying housing conditions. A: proportion of time spent in the bottom third of the tank during the entire 10-min session; B: proportion of time in the bottom third during the first half of the session; C: proportion of time spent freezing; D: number of vertical zone crossings. Short horizontal black lines show group means. Colours are as in Figure 1 in the main paper.

