

Bioinspiration & Biomimetics



PAPER

OPEN ACCESS

RECEIVED

4 November 2022

REVISED

26 March 2023

ACCEPTED FOR PUBLICATION

4 April 2023

PUBLISHED

4 May 2023

Original Content from this work may be used under the terms of the [Creative Commons Attribution 4.0 licence](#).

Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.



Social competence improves the performance of biomimetic robots leading live fish

Moritz Maxeiner^{1,8}, Mathis Hocke^{1,8}, Hauke J Moenck^{1,8}, Gregor H W Gebhardt^{1,2}, Nils Weimar³, Lea Musiolek^{5,7}, Jens Krause^{4,6,7}, David Bierbach^{4,7,9}  and Tim Landgraf^{1,7,9,*} 

¹ Department of Mathematics and Computer Science, Freie Universität Berlin, Berlin, Germany

² Computational Systems Neuroscience, Institute of Zoology, University of Cologne, Cologne, Germany

³ Institute of Zoology, Rheinische Friedrich-Wilhelms-Universität Bonn, Bonn, Germany

⁴ Faculty of Life Sciences, Albrecht Daniel Thaer Institute of Agricultural and Horticultural Sciences, Humboldt Universität zu Berlin, Berlin, Germany

⁵ Department of Computer Science, Humboldt-Universität zu Berlin, Berlin, Germany

⁶ Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany

⁷ Cluster of Excellence 'Science of Intelligence', Technical University of Berlin, Marchstrasse 23, 10587 Berlin, Germany

⁸ Equal contribution.

⁹ Shared senior author.

* Author to whom any correspondence should be addressed.

E-mail: tim.landgraf@fu-berlin.de

Keywords: biomimetic robots, social competence, robot learning

Supplementary material for this article is available [online](#)

Abstract

Collective motion is commonly modeled with static interaction rules between agents. Substantial empirical evidence indicates, however, that animals may adapt their interaction rules depending on a variety of factors and social contexts. Here, we hypothesized that leadership performance is linked to the leader's responsiveness to the follower's actions and we predicted that a leader is followed longer if it adapts to the follower's avoidance movements. We tested this prediction with live guppies that interacted with a biomimetic robotic fish programmed to act as a 'socially competent' leader. Fish that were avoiding the robot were approached more carefully in future approaches. In two separate experiments we then asked how the leadership performance of the socially competent robot leader differed to that of a robot leader that either approached all fish in the same, non-responsive, way or one that did change its approach behavior randomly, irrespective of the fish's actions. We found that (1) behavioral variability itself appears attractive and that socially competent robots are better leaders which (2) require fewer approach attempts to (3) elicit longer average following behavior than non-competent agents. This work provides evidence that social responsiveness to avoidance reactions plays a role in the social dynamics of guppies. We showcase how social responsiveness can be modeled and tested directly embedded in a living animal model using adaptive, interactive robots.

1. Introduction

In complex social systems, the dynamics of individual interactions determine the emergent phenomena on the group level. To understand and reproduce the coordinated motion patterns of shoals and flocks, for example, simple inter-individual rules of attraction and repulsion have been shown to be a sufficient mathematical model of individual behavior [1].

Collectives in nature, however, often exhibit substantial phenotypical variation within and between

individuals and these variables often affect how animals interact. Differences in body size [2, 3], personality [4–8] or physiological states [9, 10], for example, have been shown to influence individual behavior and with that the structure and movement dynamics of groups. In sticklebacks (*Gasterosteus aculeatus*), individual differences have been shown to reinforce leader and follower roles [5, 7], indicating that individual rules can flexibly adapt to the group composition. Interaction rules may also change over time as a result of an increased familiarity between individuals [11–14].



Figure 1. The RoboFish system. The 3D printed fish replica is attached to a magnetic base plate (left panel). Its movements are controlled by a two-wheeled robot below the fish tank carrying a neodymium magnet (middle panel). The tank is a quadratic ($1\text{ m} \times 1\text{ m}$) with a triangular start box used as shelter for the live fish at the beginning of a test trial (right panel). The robot control software tracks the position and orientation of both the live fish and the robot in real-time (see section 2).

The ability to adapt interaction rules in response to the social environment allowed these animals, from an evolutionary perspective, to have higher reproductive success and survival rates. Such an ability has been termed ‘social competence’ or ‘social responsiveness’ [15, 16]. For a given fitness-relevant task, for example leadership [17], we hypothesize that a ‘socially competent’ leader should be more effective than a non-competent conspecific. It is not trivial to test this hypothesis because it is virtually impossible to reliably control the degree with which an animal adapts to social cues. Virtual interaction partners or robots that mimic conspecifics are increasingly used to disentangle the recursive social dynamics in groups [18, 19]. With artificial interaction partners we have full control over the existence and properties of social feedback loops. We can, for example, embody models of social competence in a robotic agent and compare its performance to that of a non-competent control behavior.

Interactive robotic systems with animal-in-the-loop control are still rare and mostly studied with various species of fish: zebrafish, *Danio rerio* [20–22]; guppies, *Poecilia reticulata* [23–26]; weakly electric fish, *Mormyrus rume probosciostris* [27, 28]; golden shiners, *Notemigonus crysoleucas* [29]; and mosquitofish, *Gambusia holbrooki* [30]. In fish, collective behavior is typically informed by the visual system [31] and in a previous work we have found that 3D-printed guppy replicas with glass eyes are well-accepted by live guppies [26].

Our interactive robotic guppy (‘RoboFish’) can observe and memorize the interaction partner’s past responses towards its own actions and adjust its interaction rules as a function of these observations (see figure 1 and section 2).

Motivated by the fact that most leadership interactions happen in close proximity (see *supplementary information, Interaction strength over inter-individual distance*), we have implemented two behavioral sub-routines, an ‘approach phase’ in which the robot closes in on a live fish, and a ‘lead phase’ in which it

swims ahead of the fish, along the tank walls as long as the fish stays close (cf figure 1).

In many examples of fission-fusion dynamics [32–34] in which animals switch between social and solitary periods (for guppies, see [35, 36]), animals may respond aversively to social proximity. Such avoidance behavior has been described in guppies and other members of the family Poeciliidae for various types of social contexts such as mating [37, 38], cannibalism [39], disease prevention [40, 41], or aggressive encounters [42]. An avoidance reaction may inform the approaching fish that the approached individual is unwilling to engage in social interactions and a perfect candidate for a behaviorally relevant observation. Here, we defined the socially competent leader as an individual, who detects avoidance reactions and appropriately adjusts its follow-up interaction by approaching more carefully.

The robot quantifies avoidance motions and continuously integrates these measurements into a scalar variable a_t (coined ‘carefulness’) that represents a short term memory of past observations. This variable then defines the angle and speed of the approach: fish that frequently avoid the competent robot produce carefulness values $a_t \approx 1$ resulting in subsequent approaches performed indirectly (at a $\approx 90^\circ$ angle) and slowly (at $8\text{ cm}^{-\text{s}}$). Observations of no or weak avoidance decrease the carefulness value over time. At the other end of the carefulness spectrum, fish are approached with high velocity and directness (maximum of $30\text{ cm}^{-\text{s}}$ and moving with 0° deviation from the fish’s direction for $a_t = 0$, see section 2 for details). Both minimal and maximal velocities have been determined empirically and correspond to approximately the 50th percentile and 99th percentile of the velocity distribution of live guppies (see [43] for data). Note that, in contrast to a fixed mapping, the behavioral observations define direction and magnitude of a change of the carefulness variable. This way, the robot can adapt to the optimal directness and speed a given individual allows.

If the fish accepts the robot's approach and stays in proximity (<12 cm distance) for 2 s, the robot switches to lead phase, swimming along the tank walls as long as the fish stays close (<28 cm distance with a 1 s tolerance). If the fish falls back, RoboFish switches back to approach phase.

We implemented two variants of a non-competent robot, one that either always uses the same choice of carefulness for its approaches (fixed mode, experiment 1) or one that uses a randomly chosen carefulness value (random mode, experiment 2). In pre-trials, we obtained the distribution of carefulness values for a competent robot. The mean carefulness was used in fixed mode ($\bar{a} = 0.528$, see section 2) resulting in approaches with moderate speed and directness ($v = 19 \text{ cm s}^{-1}$ and $\alpha = 47^\circ$). In random mode, the carefulness values were drawn from the reference distribution such that after each trial the distributions matched approximately the social competent reference. To quantify leadership performance, we determined the mean duration the fish followed the robot (total duration of all following episodes divided by their count), the number of approaches RoboFish performed for a given duration of following episodes (the fewer, the better) and the mean avoidance the fish showed throughout the trial. We predicted that a socially competent RoboFish produces less avoidance, is more efficient and elicits longer following episodes than the non-competent controls.

2. Methods

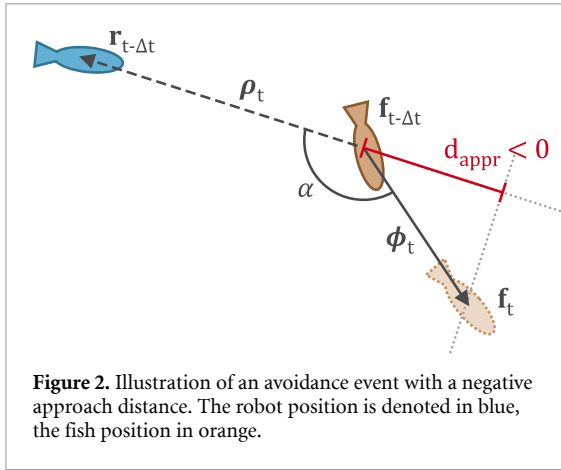
2.1. RoboFish setup

The RoboFish system consists of a glass tank ($120 \text{ cm} \times 120 \text{ cm}$) that is filled with 7 cm of aged tap water. Usually, guppies live in shallow rivers and streams. We expect to observe natural behavior in these low water levels. Four plastic walls separate an experimental area of $100 \text{ cm} \times 100 \text{ cm}$ in the center of the tank. The space between the inner and outer walls contains heating elements and a pump to maintain a constant temperature of 25°C and to aerate the water, respectively. The tank sits on an aluminum rack 1.40 m off the ground. Below the floor of the tank, we operate a two-wheeled differential drive robot on a transparent plastic pane (figure 1). This robot carries a neodymium magnet directed upwards toward the bottom side of the water tank. A 3D-printed fish replica (figure 1) is attached to a magnetic base inside the fish tank. This magnet aligns with the robot's coordinate system. Hence, the replica can be controlled directly by moving the robot. Three red-light LEDs are integrated in the bottom side of the robot, one pair on the right, and a single one on the left. The LEDs can be seen from below, through the transparent plastic pane, and are used

to estimate the robot's current position and orientation. A camera (Basler acA1300-200um, $1280 \text{ px} \times 1024 \text{ px}$) on the floor faces upwards to localize and track the robot. A second camera (Basler acA2040-90uc, $2040 \text{ px} \times 2040 \text{ px}$) is fixed 1.5 m above the tank to track both, live fish and replica. The entire system is enclosed in an opaque canvas to minimize exposure to external disturbances. The tank is illuminated from above with artificial LED lights reproducing the daylight spectrum. One personal computer (i7-6800K, 64GB RAM, GTX1060) is used for system operation. A custom robot controller software is used to track the robot in the bottom camera's feed and control the robot via a WiFi connection. A second program, BioTracker [44], records the video feed from the top camera, detects and tracks all agents in the tank and sends positional data to the robot control software. For each time step (@25 Hz), the robot control software updates positions and orientations of fish and robot in an internal data structure. Behavior modules can access this object and calculate target positions for the robot as a function of the state currently (or previously) observed. After receiving a new target position from the active behavior, the robot drives towards that target by first rotating and then moving forward with a maximum speed of 30 cm s^{-1} . All behaviors implemented for this study rely on positional feedback to recruit the fish. Following behavior rarely happens over large distances, hence we implemented variants of a two-staged behavior: the robot first approaches the fish, and then leads it to a target location. For more detailed information on RoboFish operation modes and construction, see [26]. A 3D printed triangular retainer ('start box', 19 cm side length) was used to house the fish before the start of the experiment (figure 1). The retainer contained a cylindrical region with a diameter of 10 cm from which the fish could enter the experimental area through a $3 \text{ cm} \times 2.5 \text{ cm}$ door. Besides the retainer, the environment was otherwise symmetric and monotone. A triangular plastic pane, not shown in figure 1, covered the start box.

2.2. Experimental procedures

We conducted two experiments to test the effects of social competence on leadership performance. In experiment 1, the socially competent robot was compared to a robot that always used the same carefulness value for its approaches (so-called fixed mode). In experiment 2, the non-competent baseline was implemented by a robot that used a randomly chosen carefulness value for each approach (random mode). In both experiments, trials were alternated between socially-competent and control. For each trial, we randomly caught a female guppy from its holding tank and carefully introduced her into the startbox (figure 1). Only female guppies were used to avoid



effects of sex-specific differences in responsiveness. After one minute of acclimatization, the front door of the startbox was opened. Until the fish left the refuge, RoboFish was set to execute a circular milling movement in front of the refuge's entrance with a diameter of 20 cm and a speed of 8 cm s^{-1} . This milling behavior was performed in all experiments to initially attract the live fish as it could see RoboFish from inside the box. Trials were started as soon as the fish left the startbox (full body length out of shelter). If the test fish did not leave after three minutes, we removed the lid covering the startbox and, after another three minutes the start box was removed entirely. Each live fish was tested only once. Body sizes were measured at the end of a trial to the nearest millimeter and test fish were put back into a holding tank.

2.3. Quantifying avoidance and determining robotic carefulness

In social competence mode the directness and the speed of the approach are controlled with the carefulness variable a_t , which represents the robot's memory of the fish's past avoidance responses. We quantify the avoidance response of the live fish by projecting the motion vector of the live fish onto the unit vector between fish and robot position. We call this quantity *approach distance*. Given the previous position of the robot $\vec{r}_{t-\Delta t}$ and the previous and current position of the fish $\vec{f}_{t-\Delta t}$ and \vec{f}_t , the approach distance can be computed as the inner product of the fish-movement vector $\vec{\phi}_t = \vec{f}_t - \vec{f}_{t-\Delta t}$ with the normalized fish-robot vector $\vec{\rho}_t = \vec{r}_{t-\Delta t} - \vec{f}_{t-\Delta t}$ as

$$d_t = \frac{\vec{\phi}_t^T \vec{\rho}_t}{|\vec{\rho}_t|}. \quad (1)$$

An illustration of the computation of the approach distance is given in figure 2. If the approach distance is negative, we consider the live fish to avoid RoboFish and integrate this value into the carefulness variable. The procedure is outlined in the following three steps.

1. Clip and normalize negative approach distances

$$e_t = \begin{cases} |-d_t|_{v_s}^{v_p} & \text{if } d_t < 0 \\ 0 & \text{otherwise} \end{cases}. \quad (2)$$

The notation $|\cdot|_a^b$ refers to clipping the value to the range $[a, b]$ and then normalizing to $[0, 1]$. For our experiments, the bounds were empirically determined: $v_s = 2.5$ and $v_p = 10$. Hence, slow or tangential movements are mapped to 0, fast movements away from the robot are mapped to 1.

2. Disregard when far away and exponential smoothing

Avoidance movements at the other end of the tank may not relate to the robot's behavior. We hence disregard fish motions outside an assumed interaction zone $d_1 = 56 \text{ cm}$. We compute the *avoidance score* \bar{e}_t as an exponential average of the normalized negative approach distances. We initialize $\bar{e}_0 = 0.5$ at the beginning of each trial and update as

$$\bar{e}_t = |(\beta I_s s_e e_t + (1 - \beta)\bar{e}_{t-1})|_{0.0}^{1.0}. \quad (3)$$

Here, $\beta = 0.0025$ is the smoothing factor, I_s is an indicator that is set to 1 if the fish is within the interaction zone and 0 otherwise, and $s_e = 8.0$ scales the incoming avoidance responses.

3. Calculation of carefulness

We incorporate the *avoidance score* relative to the baseline $b_e = 0.5$ into the *carefulness variable* again as an exponential average:

$$a_t = |(1 - \eta)a_{t-1} + \eta(\bar{e}_t - b_e)\Delta t|_{0.0}^{1.0}, \quad (4)$$

where Δt is the duration of a time step and $\eta = 0.075$ is another smoothing factor. The carefulness variable, hence, is increased if the avoidance score is above the baseline, and decreased otherwise.

The robot's next target location is a function of the carefulness variable. We first calculate the default target \vec{g}_t , 6 cm away from the fish, on the line connecting robot and fish. The robot then rotates g around its position proportional to its current carefulness a_t :

$$\vec{\tau}_t = \vec{R}(\delta_t)(\vec{g}_t - \vec{r}_t) + \vec{r}_t, \quad (5)$$

with rotation matrix $\vec{R}(\delta_t)$ and the deviation angle δ_t as a function of the approach parameter a_t as

$$\delta_t = a_t \frac{1}{2} \pi I_{\theta, \rho}. \quad (6)$$

Here, $I_{\theta, \rho}$ is an indicator which is positive if the robot is left of the fish (w.r.t. its movement direction $\vec{\theta}_t$), and negative otherwise. This makes

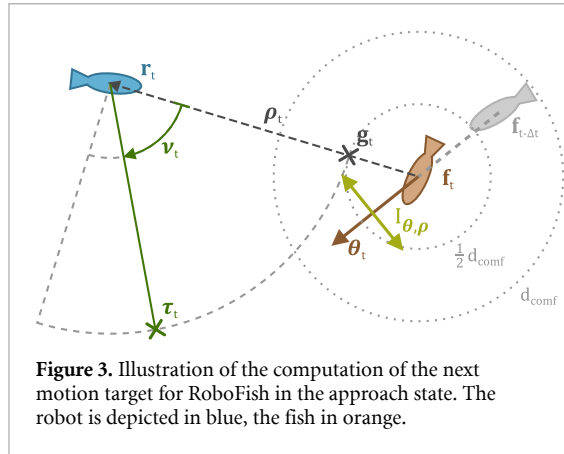


Figure 3. Illustration of the computation of the next motion target for RoboFish in the approach state. The robot is depicted in blue, the fish in orange.

careful approaches turn into the movement direction of the fish. The carefulness variable scales the approach angle up to 90° such that maximally careful robots move perpendicular to $\vec{\rho}_t$ at $a_t = 1$, circling around the fish (see figure 3).

The carefulness variable also affects the robot's movement speed through a scaling factor $s_t = 1 - a_t + s_c$ where $s_c = 0.2$ is its base speed. Hence, the maximum forward speeds are reached with $a_t = 0$ and $s_t = 1.2$. A set of low-level Proportional Integral Derivative (PID) controllers is used to calculate the motor speeds for turning towards and approaching the target. Linear ramps are used for smooth acceleration and stopping at target arrival. Note that due to the motion of the live fish and the high update rate, a new target point is computed before the robot reaches the previous one in virtually all cases.

Once the fish has been approached and it stays within a $d_{\text{comf}} = 12$ cm distance for more than 2 s, the behavior switches to *lead phase* unless the fish is too close $d < 6$ cm, in which case the behavior remains in the approach mode until the fish is back within the robot's comfort zone. This ensures that the robot switches to lead mode in always the same distance interval. The robot performs relatively fast movements in lead mode and preventing it from switching to lead mode in close proximity minimizes the risk of scaring the fish.

In *lead phase*, the robot tries to lead the fish along the walls of the tank. We define points close to the corners of the tank with a distance of 10 cm to the two adjacent walls as target points and cycle through these points clock-wise to select the next target. The robot does not drive to each target in one continuous pass but rather in short motion bursts using a sequence of target points. Each subsequent target location is calculated as a point 15 cm away on the line between robot and corner or the corner itself, if the robot is sufficiently close. Before the robot continues to its next target, it waits until the fish is within a distance of 28 cm. If fish and robot are farther apart for more than one second, the robot switches back to

approach phase. During lead phase, the robot moves with a speed factor $s_t = 0.8717$.

2.4. Non-competent behaviors

We compare the socially competent mode against two controls: the *fixed mode* and the *random mode*. In *fixed mode*, we used the mean carefulness ($\bar{a} = 0.528$) in every approach phase. This resulted in a constant approach angle of $\approx 47^\circ$ and constant approach speed of $19 \text{ cm}^{-\text{s}}$. In *random mode*, the robot randomly samples a carefulness value a_t at the start of each approach phase from a target distribution χ_a (initially set to the reference distribution) and uses this value throughout the approach phase. Before we sample a new a_t in the subsequent approach phase, we correct χ_a by subtracting the respective proportion of time the robot was in the last approach mode from the respective bin. This allows matching the reference distribution approximately.

2.5. Quantifying leadership performance: the 'Follow' metric

Similar to the avoidance response, we measure following behavior by projecting the motion vector of the live fish during the last time step onto the unit vector between fish and RoboFish. Given the position of RoboFish at the previous time step $\vec{r}_{t-\Delta t}$ and the fish's position at the previous time step $\vec{f}_{t-\Delta t}$ and at the current time step \vec{f}_t , this value can be computed by taking the inner product of the fish-movement vector $\phi_t = \vec{f}_t - \vec{f}_{t-\Delta t}$ with the normalized fish-robot vector $\rho_t = \vec{r}_{t-\Delta t} - \vec{f}_{t-\Delta t}$ as

$$d_t = \frac{\phi_t^T \rho_t}{|\rho_t|}. \tag{7}$$

If this value is positive, i.e. if the projected movement vector points towards the robot, we consider it as evidence for attraction which we compute as

$$o_t = \begin{cases} |d_t|^{v_p} & \text{if } d_t > 0 \\ 0 & \text{otherwise} \end{cases}, \tag{8}$$

where we use the notation $|\cdot|_a^b$ to denote that the value is clipped to the range $[a, b]$ and then normalized to $[0, 1]$. Here, the lower bound v_s and the upper bound v_p are hyper-parameters of the algorithm and were empirically determined, analogously to the computation of the avoidance score: $v_s = 2.5$ and $v_p = 10$. If the projected movement is negative, we consider it an avoidance. The follow score is computed similarly to the avoidance score (see main text). It is initialized to 0.5 at the beginning of each trial and then updated as exponential average at each time step with the follow events o_t as

$$\bar{o}_t = \left| (\beta_o I_s s_o c_o o_t + (1 - \beta_o) \bar{o}_{t-1}) \right|_{0,0}^{1,0}, \tag{9}$$

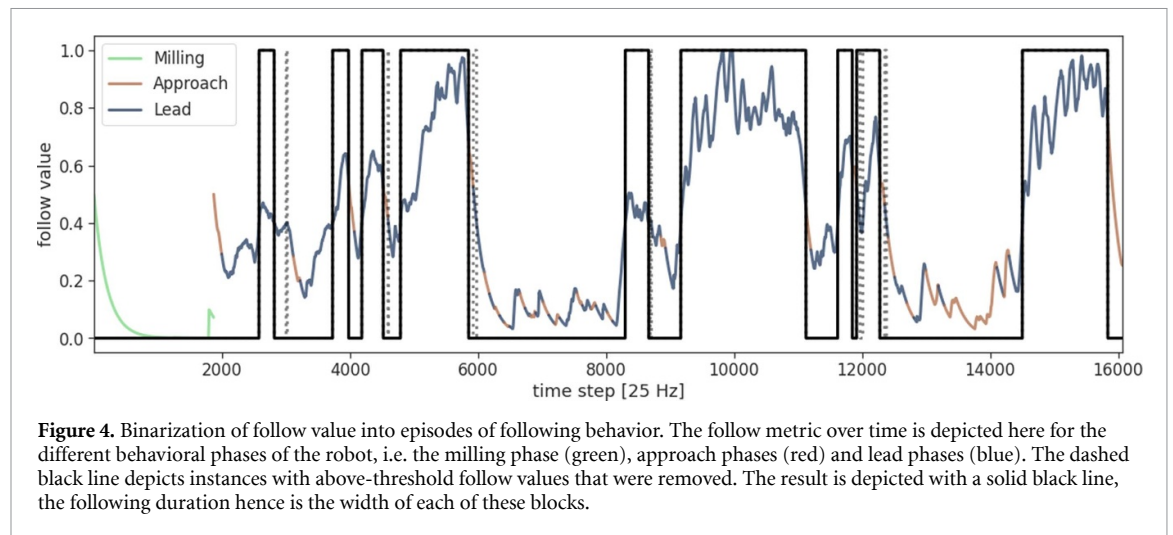


Figure 4. Binarization of follow value into episodes of following behavior. The follow metric over time is depicted here for the different behavioral phases of the robot, i.e. the milling phase (green), approach phases (red) and lead phases (blue). The dashed black line depicts instances with above-threshold follow values that were removed. The result is depicted with a solid black line, the following duration hence is the width of each of these blocks.

where c_o is a correction term defined as $c_o = 1 + \exp(-\frac{1}{3}o_t)$, $\beta_o = 0.005$ is the respective smoothing factor, and $s_o = 2.0$ scales incoming follow events. Both s_o and β_o are hyper-parameters of the algorithm and were empirically determined.

In contrast to the duration of the robot's lead phase, the follow metric more accurately reflects whether the fish was actually following. In fact, the robot much more often switches engages in a (short) lead phase than fish actually show noticeable follow episodes. We define that duration as an episode in which RoboFish is in its lead phase and the follow value \bar{o}_t is above a threshold of 0.4. We bridge small (less than 200 time steps wide) gaps between follow episodes and remove remaining short episodes of following behavior (less than 200 time steps) by applying erosion and dilation operations. An example visualizing this process is shown in figure 4.

2.6. Test fish and their maintenance

We used Trinidadian guppies (*P. reticulata*) that are descendants of wild-caught fish from the Arima-River system in Northern Trinidad. Test fish came from large, randomly outbred single-species stocks maintained at the animal care facilities at the Department of Life Sciences, Humboldt University of Berlin. To avoid inbreeding, stocks are regularly supplemented with wild-caught animals brought back from fieldwork in Trinidad and Tobago. We provided a natural 12:12 h light:dark regime and maintained water temperature at 25 °C in the rearing tanks, as well as in the experimental tank. Fish were fed twice daily ad libitum with commercially available flake food (TetraMin™). Experiments were done during normal office hours and always 1 h after the morning feeding. All fish were then fed a second time in the afternoon succeeding any experimental involvement. For the experiments, only female guppies were

used to avoid effects of sex-specific differences in responsiveness.

2.7. Statistical analysis

We used the conservative Mann–Whitney U tests to compare average behavioral measures between treatments and student-t tests to compare variables at different approaches. All analyses were performed using Python. All data and source code for the data analysis can be found online [45, 46]

3. Results

We ran a total of 82 trials (42 in experiment 1 and 40 in experiment 2). Over all trials, we observed sustained interest in the robot with a few exceptions of fish that showed pronounced avoidance reactions and no following behavior whatsoever. Pooling all treatments, we observed following behavior totaling to 3.9 h of theoretically possible 13.6 h (82 trials of 10 min duration). More than half of all following episodes occur within the first three minutes (104/197), accounting for 74% of the combined following durations (174 min/235 min).

3.1. Lower or similar avoidance in socially competent robots

Most fish were attracted by the robot at the beginning of the trial, hence, we consistently observed decreasing mean avoidance scores over the first minute into the trial (figure 5) for both competent and non-competent treatments. While the socially competent robot had a similar per-trial mean carefulness compared to fixed mode (median: 0.53/0.59, $N1/2 = 21/21$ $U = 210$, $P = .80$, $CLES = .52$), the per-trial mean avoidance scores were found to be significantly smaller (reporting median [min max]; fixed: 0.48 [0.027 0.95], competent: 0.17 [0.016 0.54], $N1/2 = 21$, $U = 329$ $P = .007$, $CLES = .75$, figure 5).

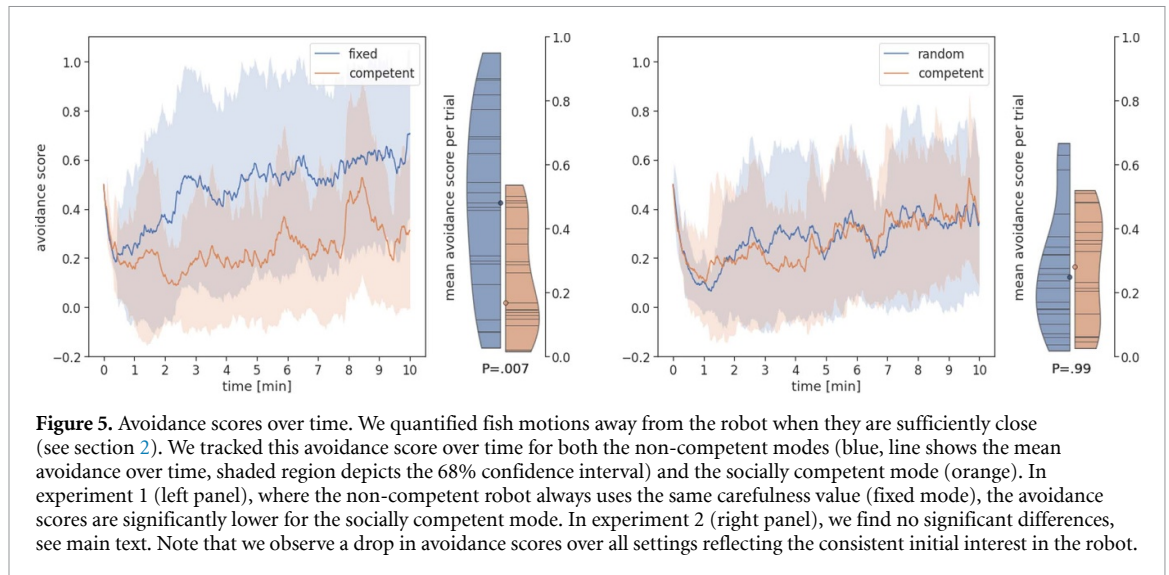


Figure 5. Avoidance scores over time. We quantified fish motions away from the robot when they are sufficiently close (see section 2). We tracked this avoidance score over time for both the non-competent modes (blue, line shows the mean avoidance over time, shaded region depicts the 68% confidence interval) and the socially competent mode (orange). In experiment 1 (left panel), where the non-competent robot always uses the same carefulness value (fixed mode), the avoidance scores are significantly lower for the socially competent mode. In experiment 2 (right panel), we find no significant differences, see main text. Note that we observe a drop in avoidance scores over all settings reflecting the consistent initial interest in the robot.

The random control behavior was designed to match the carefulness distribution of the socially competent robot. Yet, the randomly sampled carefulness values on average were slightly higher than for the socially competent robot (random: 0.69 [0.46 0.89], competent: 0.59 [0.15 0.89], $U = 253$, $P = .14$, $CLES = .64$), resulting in less direct approaches on average. Hence, the random control behavior tended to produce lower average avoidance scores than the socially competent robot (random: 0.33 [0.045 0.72], competent: 0.48 [0.17 0.71], $N1/2 = 22/18$, $U = 133$, $P = .08$, $CLES = .66$). Comparing the motion speeds of fish and robot, we find no significant differences in experiment 2 (random: 4.2 [2.01 7.68] $\text{cm}^{-\text{s}}$, competent: 4.74 [2.13 8.39] $\text{cm}^{-\text{s}}$, $U = 160$, $P = .31$, $CLES = .6$). See also *supplementary information, Comparison of motion speeds* for details.

3.2. Fish follow socially competent robots longer

In both experiments, the socially competent robot evoked, on average, longer follow episodes and longer total following durations.

In experiment 1 we observed a pronounced difference of the per-trial mean following duration (53.4 s [0 s 589 s] in competent mode and 3.1 s [0 s 138.6 s] in fixed mode, $U = 124$, $P = .016$, $CLES = .71$, see *supplementary information, Mean follow episode durations*). Summing up all episodes of following behavior within a trial yields total following durations of 82.6 s [0 s 554.3 s] for fixed mode and 458.4 s [0 s 589 s] for the socially competent robot ($U = 132$, $P = .027$, $CLES = .3$).

In experiment 2, although less pronounced, we observed both higher mean follow episode durations (random: 7.2 s [0 s 157.5 s], competent: 24.4 s [0 s 583.5 s], $U = 147$, $P = .17$, $CLES = .62$) and longer total following durations (random: 186.4 s

[0 s 557.52 s], competent: 341.78 s [0 s 583.45 s], $U = 151$, $P = .21$, $CLES = .38$).

In both experiments the majority of live fish followed at the beginning of a trial (see also *supplementary information, When and how frequently do fish follow?*). Consequently, the difference between the socially competent mode and the controls mainly pertained to the number of successful leadership episodes in response to the first few approaches (figure 6).

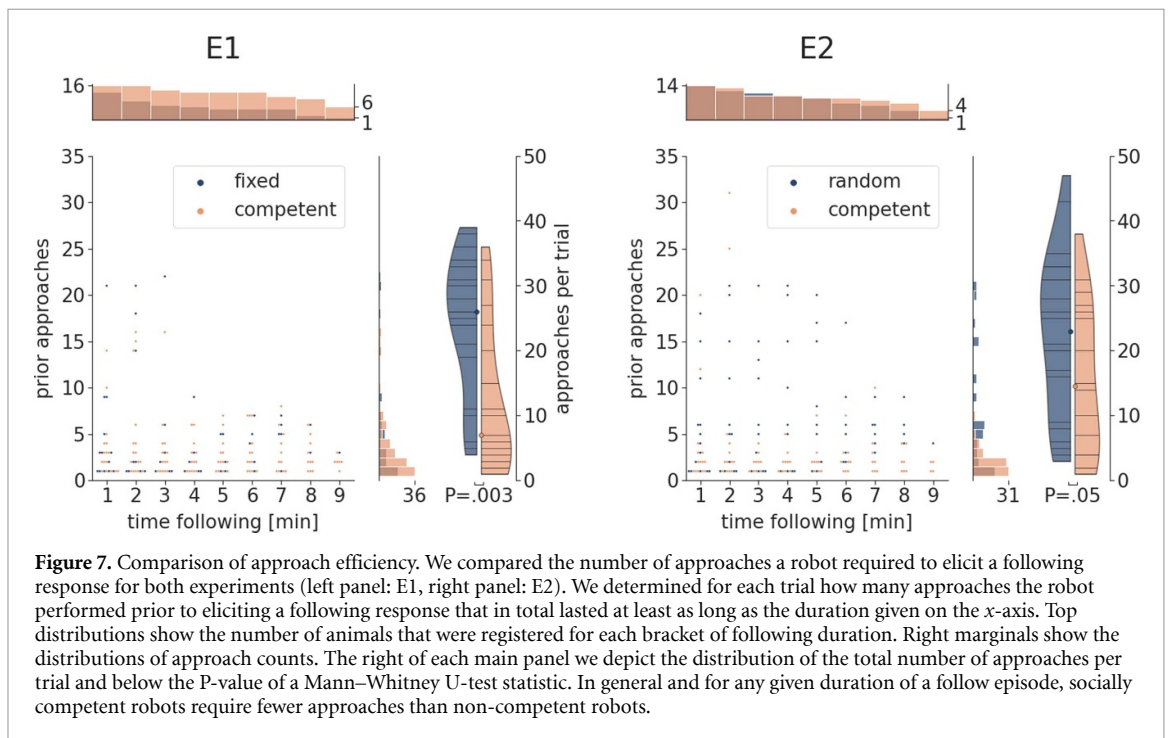
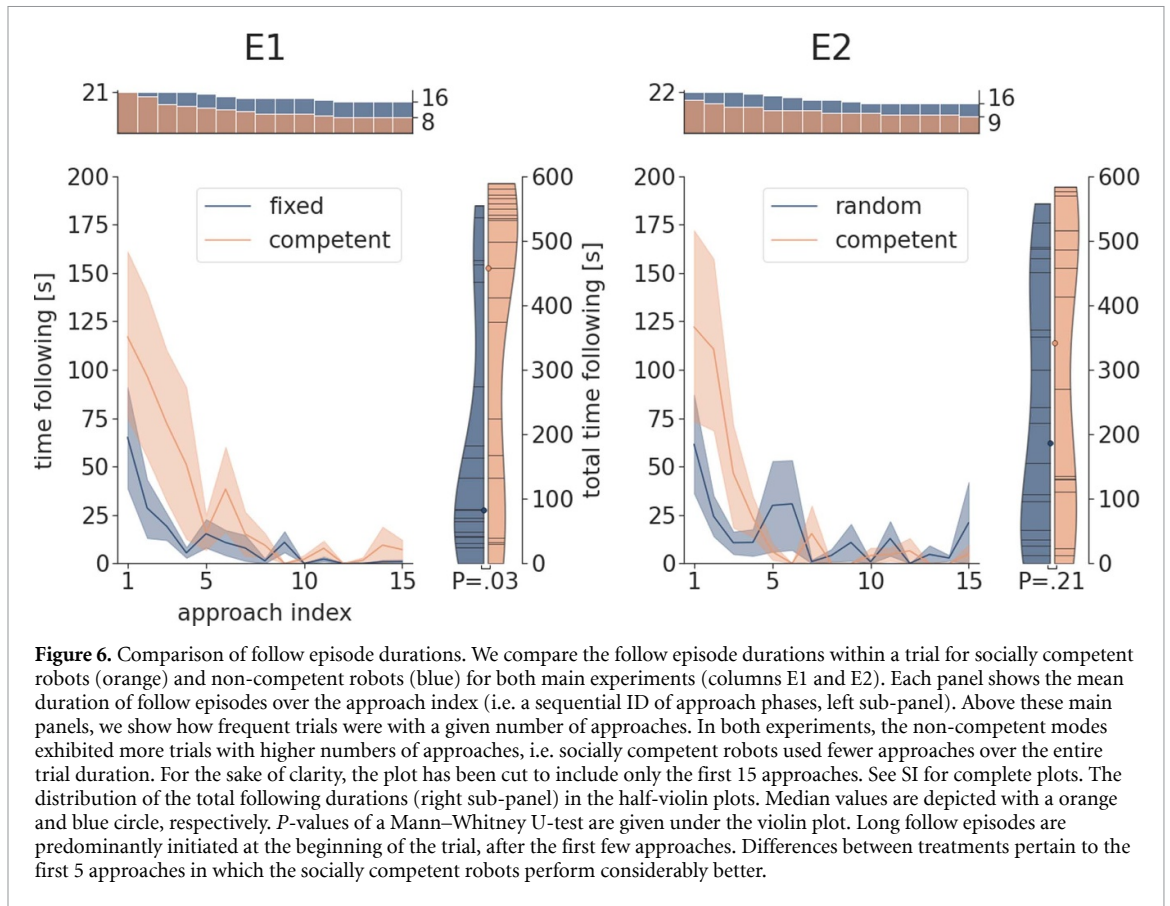
3.3. Socially competent robots are more efficient

The number of approaches the robot initiated in a trial was significantly lower for the competent compared to the non-competent agents in experiment 1 (fixed: 26 [4 39], competent: 7 [1 36], $U = 339.5$, $P = .0028$, $CLES = .76$) and experiment 2 (random: 23 [3 47], competent: 14.5 [1 38], $U = 270$, $P = .052$, $CLES = .67$).

We analyzed how many approaches the robot required for a given total duration of the subsequent follow episodes. In both experiments, the non-competent robot performed more approaches for any given duration of follow episodes (for details see figure 7).

The difference between socially competent and random modes appears more pronounced for longer follow episodes. Fewer approaches could indicate longer approach durations; however, we found that our data does not support that view for both, experiment 1 (fixed: 9, 5 s [3.1 s 27.1 s], competent: 7.1 s [3.4 s 34.5 s], $U = 256$, $P = .38$, $CLES = .58$) and experiment 2 (random: 9.3 s [6.4 s 30.6 s], competent: 7.8 s [3.6 s 26.1 s], $U = 244$, $P = .22$, $CLES = .62$).

Naturally, short follow episodes were frequent in both experiments and both respective treatments. Trials with long total follow episode durations (>6 min) consistently appear more frequently in the socially competent mode.



4. Discussion

We implemented a socially responsive robot which was found to be more effective and efficient in a leadership task with live guppies than non-competent robots.

We tested against two non-competent controls, one that always used the same carefulness (fixed mode) and one that sampled its carefulness value from a given reference distribution (random mode) irrespective of the avoidance behavior observed previously.

We found that the socially competent mode performed better than the fixed mode in all metrics. It produced less avoidance behaviors, on average longer follow episodes and it required fewer approaches to elicit following behavior. The lower avoidance levels, however, could have been caused by lower motion speeds. The fixed mode was designed to reproduce the mean carefulness of the socially competent mode as measured in pre-trials and it succeeded in doing so. The velocities of the socially competent mode depend, however, on the avoidance behavior of the fish, and the way we selected experimental fish from our holding tank may have introduced a size bias (smaller and therefore younger fish in later trials) which may explain higher carefulness and lower speeds in the socially competent mode.

In contrast to this finding, the motion speeds of both robot and fish did not differ between treatments in experiment 2. The carefulness values of the socially competent robot were slightly lower, and the fish's avoidance levels even slightly higher than in the random control. We, hence, could not confirm our initial hypothesis of social competence reducing avoidance reactions. Still, the socially competent robot elicited longer mean follow episode durations using fewer approaches. The differences we observed are less pronounced compared to experiment 1, due to both the socially competent robot being slightly less effective and the random mode being more effective as the fixed mode. A possible explanation for the latter is that the random mode exhibited higher behavioral variability than the fixed mode which may have had an attractive effect. At high carefulness values the robot barely approached the fish. Subsequent follow episodes, hence, are likely caused by the fish coming sufficiently close to the robot on its own.

We reexamined the data of the random treatment in which the robot may still have accidentally changed its carefulness in coherence with our definition of social competence. We found that fish which show increasing avoidance in a given approach phase predominantly follow in the next lead phase if the robot accidentally increased its carefulness (see *supplementary information, Analysis of accidental social competence in random mode*). Due to the randomness of its carefulness choice, the robot, however, is much less predictable from the fish's perspective. It remains to be studied how attractive both high predictability and behavioral variation are in a similar experimental setup.

In both experiments, we observe long follow episodes with both very careful and very bold approaches. It remains unclear why both strategies worked to a similar extent. Live fish may accept leaders with either strategy similarly, or each leader's strategy could be effective with only a certain subset of the tested population. Sticklebacks prefer to follow individuals whose personality matches their own [47] and our

previous research found guppies to differ consistently in their following tendencies towards both a robotic leader and another live fish [48]. Thus possible future research might repeatedly test the same individuals for their responses towards different adaptive robotic behaviors.

Live fish across experiments and treatments showed low avoidance reactions towards RoboFish and every cohort included fish that followed the robot closely for several minutes even in the non-competent settings. Biomimetic robots have been increasingly used to study social behavior in species of small freshwater fish [49] and our current results support the feasibility of this approach.

In an earlier work we proposed that the social acceptance of biomimetic robots might be achieved not only through a realistic reproduction of static and dynamic cues (e.g. visual appearance and motion patterns), but also through implementing probable social conventions, e.g. by matching the robot's response to behaviors that may be expected by interaction partners [26]. Although the exact mechanism remains unknown, our study may also indicate that adaptive, short-term responses may play a crucial role in the ability of interactive biomimetic robots to be sustainably accepted by the group.

Here, we used avoidance motions as behavioral feedback. Much more complex adaptive rules are conceivable that may use avoidance or other behavioral metrics. Most biomimetic robots, however, have been used in open loop, executing behaviors without feedback from the environment. Incorporating the animals in the control loop of interactive robots allows more complex investigations of the social group dynamics. Almost all interactive robots for the study of animal behavior still use a fixed behavioral policy, i.e. a behavior that always performs the same action when given the same input. Here, we propose the first example of adaptive interactive robots that may be used in studies specifically investigating social responsiveness (see [50] for definitions).

The ubiquitous presence of fission-fusion societies [32–34] in the animal kingdom highlights that subjects are often approached by familiar or unfamiliar conspecifics. Our behavioral model represents a first example of how observations of the social environment can inform behavioral changes of an adaptive robotic agent. The short-term memory variable used to control the socially-competent agent was designed to mimic the response of a live leader. Our results help demonstrate the importance of social competence and responding to an interaction partner's behavior appropriately to enhance social interactions [15, 16]. This work furthermore provides evidence for the feasibility of more complex interaction models of biomimetic robots which have matured into powerful tools for the study of social interactions in animal groups.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: <https://zenodo.org/record/7635910#.Y-pC6-zMJm>.

Acknowledgments

We acknowledge financial support from the German Research Foundation (BI 1828/2-1, LA 3534/1-1) and Germany's Excellence Strategy (EXC 2002/1 'Science of Intelligence', Project Number 390523135). Furthermore, H M has been financially supported by the Andrea von Braun foundation and the German Research Foundation.

Ethics note


Experiments reported in this study were carried out in accordance with the recommendations of 'Guidelines for the treatment of animals in behavioural research and teaching' (published in *Animal Behavior* 1997) and comply with current German law approved by LaGeSo Berlin (G0117/16 to D B).

Conflict of interest

The authors have no competing interests to declare.

ORCID iDs

David Bierbach  <https://orcid.org/0000-0001-7049-2299>

Tim Landgraf  <https://orcid.org/0000-0003-4951-5235>

References

- [1] Couzin I D, Krause J, James R, Ruxton G D and Franks N R 2002 Collective memory and spatial sorting in animal groups *J. Theor. Biol.* **218** 1–11
- [2] Romenskyy M, Herbert-Read J E, Ward A J W and Sumpter D J T 2017 Body size affects the strength of social interactions and spatial organization of a schooling fish (*Pseudomugil signifer*) *R. Soc. Open Sci.* **4** 161056
- [3] Hemelrijk C K and Kunz H 2004 Density distribution and size sorting in fish schools: an individual-based model *Behav. Ecol.* **16** 178–87
- [4] Jolles J W, Ostojić L and Clayton N S 2013 Dominance, pair bonds and boldness determine social-foraging tactics in rooks, *Corvus frugilegus* *Animal Behav.* **85** 1261–9
- [5] Nakayama S, Stumpe M C, Manica A and Johnstone R A 2013 Experience overrides personality differences in the tendency to follow but not in the tendency to lead *Proc. R. Soc. B* **280** 20131724
- [6] Kurvers R H J M, Eijkelenkamp B, van Oers K, van Lith B, van Wieren S E, Ydenberg R C and Prins H H T 2009 Personality differences explain leadership in barnacle geese *Animal Behav.* **78** 447–53
- [7] Harcourt J L, Sweetman G, Johnstone R A and Manica A 2009 Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks *Animal Behav.* **77** 1501–5
- [8] Jolles J W, Boogert N J, Sridhar V H, Couzin I D and Manica A 2017 Consistent individual differences drive collective behavior and group functioning of schooling fish *Curr. Biol.* **27** 2862–8.e7
- [9] Bumann D and Krause J 1993 Front individuals lead in shoals of three-spined sticklebacks (*Gasterosteus aculeatus*) and juvenile roach (*Rutilus rutilus*) *Behaviour* **125** 189–98
- [10] Killen S S, Marras S, Nadler L and Domenici P 2017 The role of physiological traits in assortment among and within fish shoals *Phil. Trans. R. Soc. B* **372** 20160233
- [11] Dugatkin L A and Godin J-G J 1993 Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects *Behav. Ecol.* **4** 289–92
- [12] Lachlan R F, Crooks L and Laland K N 1998 Who follows whom? Shoaling preferences and social learning of foraging information in guppies *Animal Behav.* **56** 181–90
- [13] Swaney W, Kendal J, Capon H, Brown C and Laland K N 2001 Familiarity facilitates social learning of foraging behaviour in the guppy *Animal Behav.* **62** 591–8
- [14] Bierbach D et al 2011 Male fish use prior knowledge about rivals to adjust their mate choice *Biol. Lett.* **7** 349–51
- [15] Taborsky B and Oliveira R F 2012 Social competence: an evolutionary approach *Trends Ecol. Evol.* **27** 679–88
- [16] Wolf M and McNamara J M 2013 Adaptive between-individual differences in social competence *Trends Ecol. Evol.* **28** 253–4
- [17] Strandburg-Peshkin A, Papageorgiou D, Crofoot M C and Farine D R 2018 Inferring influence and leadership in moving animal groups *Phil. Trans. R. Soc. B* **373** 20170006
- [18] Krause J, Winfield A F T and Deneubourg J-L 2011 Interactive robots in experimental biology *Trends Ecol. Evol.* **26** 369–75
- [19] Chouinard-Thuly L et al 2017 Technical and conceptual considerations for using animated stimuli in studies of animal behavior *Curr. Zool.* **63** 5–19
- [20] Kopman V, Laut J, Polverino G and Porfiri M 2013 Closed-loop control of zebrafish response using a bioinspired robotic-fish in a preference test *J. R. Soc. Interface* **10** 20120540
- [21] Cazenille L, Chemtob Y, Bonnet F, Gribovskiy A, Mondada F, Bredeche N and Halloy J 2018 How to blend a robot within a group of zebrafish: achieving social acceptance through real-time calibration of a multi-level behavioural model *Biomimetic and Biohybrid Systems (Lecture Notes in Computer Science)* ed V Vouloutsis, J Halloy, A Mura, M Mangan, N Lepora, T J Prescott and P F Verschure (Cham: Springer) pp 73–84
- [22] Chemtob Y, Cazenille L, Bonnet F, Gribovskiy A, Mondada F and Halloy J 2020 Strategies to modulate zebrafish collective dynamics with a closed-loop biomimetic robotic system *Bioinspir. Biomim.* **15** 046004
- [23] Jolles J W, Weimar N, Landgraf T, Romanczuk P, Krause J and Bierbach D 2020 Group-level patterns emerge from individual speed as revealed by an extremely social robotic fish *Biol. Lett.* **16** 20200436
- [24] Landgraf T, Nguyen H, Forgo S, Schneider J, Schröer J, Krüger C, Matzke H, Clément R O, Krause J and Rojas R 2013 Interactive robotic fish for the analysis of swarm behavior *Advances in Swarm Intelligence (Lecture Notes in Computer Science)* ed Y Tan, Y Shi and H Mo (Berlin: Springer)
- [25] Landgraf T, Nguyen H, Schröer J, Szengel A, Clément R J, Bierbach D and Krause J 2014 Blending in with the shoal: robotic fish swarms for investigating strategies of group formation in guppies *Conf. on Biomimetic and Biohybrid Systems (Cham: Springer)* pp 178–89
- [26] Landgraf T, Bierbach D, Nguyen H, Muggelberg N, Romanczuk P and Krause J 2016 RoboFish: increased acceptance of interactive robotic fish with realistic eyes and natural motion patterns by live Trinidadian guppies *Bioinspir. Biomim.* **11** 015001
- [27] Worm M, Landgraf T, Prume J, Nguyen H, Kirschbaum F and Emde G v d 2018 Evidence for mutual allocation of

- social attention through interactive signaling in a mormyrid weakly electric fish *Proc. Natl Acad. Sci.* **115** 6852–7
- [28] Worm M, Landgraf T and von der Emde G 2021 Electric signal synchronization as a behavioural strategy to generate social attention in small groups of mormyrid weakly electric fish and a mobile fish robot *Biol. Cybern.* **115** 599–613
- [29] Swain D T, Couzin I D and Ehrlich Leonard N 2012 Real-time feedback-controlled robotic fish for behavioral experiments with fish schools *Proc. IEEE* **100** 150–63
- [30] Polverino G, Soman V R, Karakaya M, Gasparini C, Evans J P and Porfiri M 2022 Ecology of fear in highly invasive fish revealed by robots *iScience* **25** 103529
- [31] Strandburg-Peshkin A et al 2013 Visual sensory networks and effective information transfer in animal groups *Curr. Biol.* **23** R709–11
- [32] Aureli F et al 2008 Fission-fusion dynamics: new research frameworks *Curr. Anthropol.* **49** 627–54
- [33] Couzin I D 2006 Behavioral ecology: social organization in fission-fusion societies *Curr. Biol.* **16** R169–71
- [34] Krause J and Ruxton G D 2002 *Living in Groups* (Oxford: Oxford University Press)
- [35] Wilson A D M, Krause S, Dingemanse N J and Krause J 2013 Network position: a key component in the characterization of social personality types *Behav. Ecol. Sociobiol.* **67** 163–73
- [36] Wilson A D M, Krause S, James R, Croft D P, Ramnarine I W, Borner K K, Clement R J G and Krause J 2014 Dynamic social networks in guppies (*Poecilia reticulata*) *Behav. Ecol. Sociobiol.* **68** 915–25
- [37] Plath M 2008 Male mating behavior and costs of sexual harassment for females in cavernicolous and extremophile populations of atlantic mollies (*Poecilia mexicana*) *Behaviour* **145** 73–98
- [38] Magurran A 2011 Sexual coercion *Ecology and Evolution of Poeciliid Fishes* ed J Evans, A Pilastro and I Schlupp (Chicago, IL: University of Chicago Press) pp 209–17
- [39] Chapman B B, Morrell L J, Benton T G and Krause J 2008 Early interactions with adults mediate the development of predator defenses in guppies *Behav. Ecol.* **19** 87–93
- [40] Stephenson J F, Perkins S E, Cable J and Dingemanse N 2018 Transmission risk predicts avoidance of infected conspecifics in Trinidadian guppies *J. Animal Ecol.* **87** 1525–33
- [41] Croft D P, Edenbrow M, Darden S K, Ramnarine I W, van Oosterhout C and Cable J 2011 Effect of gyrodactylid ectoparasites on host behaviour and social network structure in guppies *Poecilia reticulata* *Behav. Ecol. Sociobiol.* **65** 2219–27
- [42] Bierbach D, Makowicz A M, Schlupp I, Geupel H, Streit B and Plath M 2013 Casanovas are liars: behavioral syndromes, sperm competition risk and the evolution of deceptive male mating behavior in live-bearing fishes *F1000Research* **2** 75
- [43] Klamser P P, Gómez-Nava L, Landgraf T, Jolles J W, Bierbach D and Romanczuk P 2021 Impact of variable speed on collective movement of animal groups *Front. Phys.* **9** 715996
- [44] Mönck H J, Jörg A, von Falkenhausen T, Tanke J, Wild B, Dormagen D, Piotrowski J, Winklmayr C, Bierbach D and Landgraf T 2018 BioTracker: an open-source computer vision framework for visual animal tracking (arXiv:1803.07985 [cs])
- [45] Maxeiner M, Hocke M, Moenck H J, Bierbach D and Landgraf T 2022 Source code for the publication ‘Socially competent robots’ (Berlin: Freie Universität) Accepted 2022-11-14T12:39:19Z
- [46] Moenck H J, Maxeiner M, Hocke M, Bierbach D, and Landgraf T 2022 Data for the publication “Socially competent robots” (Zenodo) (available at: <https://zenodo.org/record/7635910>)
- [47] Nakayama S, Harcourt J L, Johnstone R A and Manica A 2016 Who directs group movement? Leader effort versus follower preference in stickleback fish of different personality *Biol. Lett.* **12** 20160207
- [48] Bierbach D, Landgraf T, Romanczuk P, Lukas J, Nguyen H, Wolf M and Krause J 2018 Using a robotic fish to investigate individual differences in social responsiveness in the guppy *R. Soc. Open Sci.* **5** 181026
- [49] Romano D, Donati E, Benelli G and Stefanini C 2019 A review on animal-robot interaction: from bio-hybrid organisms to mixed societies *Biol. Cybern.* **113** 201–25
- [50] Landgraf T, Gebhardt G H W, Bierbach D, Romanczuk P, Musiolek L, Hafner V V and Krause J 2021 Animal-in-the-loop: using interactive robotic conspecifics to study social behaviour in animal groups *Annu. Rev. Control Robot. Auton. Syst.* **4** 487–507