Mechanisms of Socially Facilitated Feeding in Zebrafish (*Danio rerio*)

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Abstract

The social facilitation of feeding, where individuals increase their feeding behavior in the presence of conspecifics, is widely documented, but the underlying mechanisms remain unclear, particularly regarding passive versus active facilitation and the role of individual differences, such as sex and personality. We investigated how visual exposure to non-feeding conspecifics influenced feeding behavior in zebrafish (*Danio rerio*), examining food consumption and other feeding related behaviors, while also assessing individual variation in boldness and sociability. Zebrafish consumed significantly more food pellets and manipulated food differently when conspecifics were present, indicating that passive social facilitation due to the mere presence of conspecifics was sufficient to increase feeding behavior. Males exhibited stronger socially facilitated feeding responses, consuming more pellets, spitting pellets more frequently, and orienting food spitting away from stimulus fish, suggesting competitive motivations. Females showed more cautious feeding behavior, holding pellets in their mouths for longer. Contrary to predictions, neither boldness nor sociability predicted individual differences in feeding behavior or responses to social context. Our findings demonstrate that social facilitation due to a passive audience and sex-specific competitive strategies influence the feeding behavior of zebrafish.

Introduction

Group living offers many animal species several advantages, including enhanced foraging efficiency and reduced predation risk (Barnard & Sibly, 1981; Pitcher et al., 1982; Webster & Hart, 2006). Foraging in groups can reduce the time and energy spent locating food through various mechanisms, such as social facilitation: a general increase in activity or the likelihood of some behaviors when in the presence of others, stimulus enhancement: being drawn to a specific object after seeing another interact with it, or local enhancement: being drawn to resource-rich locations by the activity of others (Giraldeau, 1997; Herman, 2015; Heyes et al., 2000; Whiten & Ham, 1992; Zajonc, 1965). Social facilitation, stimulus enhancement, and local enhancement can operate simultaneously, making their individual effects difficult to disentangle.

Social facilitation of feeding, where individuals eat more in the presence of others than when alone, has been documented in a wide range of species, including fish (Ojelade et al., 2022; Welty, 1934), rodents (Forkman, 1991; Harlow, 1932), birds (Rajecki et al., 1975; Tolman, 1964), bats (Wright et al., 2020), monkeys (Harlow & Yudin, 1933), and humans (de Castro & Brewer, 1992; Ruddock et al., 2019, 2021), and multiple mechanisms have been proposed to explain it. In social animals, group contexts may alleviate stress, a process known as social buffering, allowing foragers to shift their attention from vigilance to feeding (Higgs & Thomas, 2016; Kikusui et al., 2006). Alternatively, the presence of conspecifics may raise general arousal levels, stimulate appetite-related neuroendocrine systems, or elicit competitive motivations to consume food before it can be monopolized by others (Hirsch, 2007; Wee et al., 2022; Zajonc, 1965).

Socially facilitated feeding may also arise through active mechanisms, such as through information transfer via stimulus or local enhancement, where individuals learn about the quality of food or a food patch by observing others (Heyes et al., 2000; Templeton & Giraldeau, 1995), or through behavioral matching, in which individuals adjust their food intake to mirror those around them, potentially driven by competition, conformity, or social bonding motives (Ruddock et al., 2019). Active social facilitation has been observed in juvenile chum salmon, which increase their feeding when in the presence of other feeding conspecifics compared to when nearby conspecifics were not feeding (Ryer & Olla, 1991). The extent to which increased feeding in social contexts occurs through passive social facilitation (e.g., due to the mere presence of others) or active facilitation (e.g., due to information transfer through stimulus or local enhancement, or behavioral matching) remains an open question.

Despite the benefits associated with group foraging, it may also entail significant costs, particularly through increased competition for limited resources (Webster & Hart, 2006). As group size increases, competition often intensifies, leading to reduced individual food intake (Janson, 1988). Animals may adopt strategies to mitigate these competitive costs; for example, many fish species disperse more widely when food-deprived to reduce social interactions and direct competition (Hensor et al., 2003; Krause, 1993; Miller & Gerlai, 2007; Sekulovski & Miller, 2025). Competitive interactions can manifest as kleptoparasitism, stealing food discovered or captured by others – a foraging tactic observed in spiders (Higgins & Buskirk, 1998), marine invertebrates (Morissette & Himmelman, 2000; Zamora & Gómez, 1996), fish (Davis & Dill, 2012), birds (Brockmann & Barnard, 1979), and primates (di Bitetti & Janson, 2001). In archerfish (*Toxotes chatareus*), which typically capture prey by shooting jets of water at insects perched above the water surface, conspecific kleptoparasitism is common (Davis & Dill, 2012; der Weduwen et al., 2024). Archerfish counteract theft through strategic spitting and positioning, and may even jump out of the water to grab prey directly (Davis & Dill, 2012).

Zebrafish, which in the wild mainly consume small insects that fall onto the surface of the water (Spence et al., 2008; Suriyampola et al., 2016), may struggle to swallow the entire prey item at once. Zebrafish have been observed, in the lab, to repeatedly take into their mouths and then spit out single food pellets, apparently rasping off small particles of the food each time (personal observation), though this kind of behavior has only been formally studied in the context of accidental microplastic ingestion (Chen et al., 2022; Kim et al., 2019). Spitting and re-ingesting food items is, however, known to occur as part of normal feeding in other fish species, especially when the food items are hard to process (Sibbing, 1988). When a food item is spit out, there is a risk that a nearby conspecific will consume it before it can be re-ingested, a form of kleptoparasitism. There is thus potentially a cost to gradually breaking down large food items, spitting them out between bouts of eating. As a result, we might expect that fish will modify their spitting-out behavior under conditions of enhanced competition, for example by angling themselves away from nearby conspecifics when spitting out food, to minimize the risk of theft. Fish might also reduce the frequency of spitting out food when in a group of hungry conspecifics, though there may be limits to flexibility in this aspect of the behavior imposed by the physics of consuming large food items (Sibbing, 1988).

The role of individual differences in these competitive and cooperative interactions further complicates the understanding of social facilitation phenomena. Personality, defined as consistent individual differences in behavior across time and contexts, including traits such as boldness and sociability, may partially predict foraging strategies and how individuals respond to stressors such as competition (Grunst & Grunst, 2024; Stamps & Groothuis, 2010). For example, bold individuals tend to forage more actively and take more risks, as observed in zebrafish (*Danio rerio*; Chen et al., 2022), lemon sharks (*Negaprion brevirostris*; Dhellemmes et al., 2021), and rainbow trout (*Onchorhyncus mykiss*; Frost et al., 2007). However, the relationship between personality and feeding behavior may not be seen in all species. For example, boldness is often expected to translate into dietary differences, because risky behaviors can increase access to different food resources (Luttbeg & Sih, 2010; Moran et al., 2021). Yet, although round gobies (*Neogobius melanostomus*) exhibit substantial individual variation in boldness and diet in the wild, personality traits are not predictive of dietary differences in this species (Moran & Behrens, 2024). The extent to which individual differences, such as personality and sex, interact in determining social foraging strategies remains unclear and understudied. It is also likely that personality will affect how fish eat, for example their spitting-out behavior. Bolder or more aggressive fish might be better at defending food, even when it is not in their mouths, which might make them more willing to spit food out to facilitate feeding. Dominant male zebrafish have been shown to defend feeding sites under some conditions (Hamilton & Dill, 2002), and the same dynamic might apply to partially-consumed food items.

Although social facilitation of feeding has been observed in group foraging across several taxa, the mechanisms underlying it, including social buffering, behavioral matching, or competition, as well as the possible role of individual differences, are poorly understood. To address these gaps, we investigated how visual exposure to non-feeding conspecifics influences feeding behavior in zebrafish. Specifically, we asked whether the mere presence of conspecifics increases feeding behavior, food consumption, and food-holding time, and alters body orientation during spitting-out, reflecting both passive social facilitation and potential competitive motivations. We predicted that receiving food in the presence of conspecifics would trigger a competitive response, which would lead to increased feeding and consumption, longer food-holding time, and orienting away from others while spitting to prevent kleptoparasitism. We also tested whether sex and individual variation in boldness and sociability correlated with baseline feeding behaviors or modulated responses to the social context. We had no specific predictions about the directions of these effects, but we expected personality to modulate feeding behavior and, based on past work, we expected to find differences in feeding behaviors between the sexes.

Methods

Subjects

Thirty adult wild-type zebrafish (*Danio rerio*; 16 males, 14 females) were used as experimental subjects, and an additional 10 males were used as stimulus fish. All fish were obtained from a breeding facility at Dalhousie University (Halifax, NS, Canada) and housed at Wilfrid Laurier University (Waterloo, ON, Canada). Fish were kept in 10-litre tanks within an automated high-density fish rack (Pentair Aquatic Habitats) in same-sex groups of five. Water temperature was maintained at 25 ± 2 °C, salinity between 500 and 700 ppm TDS, and pH between 6.8 and 7.2. For the purposes of individual identification, experimental subjects were tagged with different colored fluorescent visible implant elastomer (VIE; Northwest Marine Technology) injected subcutaneously, and given at least 4 days to recover before the start of testing. Stimulus fish were not tagged.

On non-experiment days, fish were fed twice daily *ad libitum* on a formulated diet (Skretting GEMMA Micro) supplemented with brine shrimp. On experiment days, fish were fed once daily, following the end of testing. To ensure sufficient appetite for the feeding assay, fish were food-deprived for 24 hours prior to the first feeding session. Any food consumed during the feeding trials was in addition to the daily ration. Both experimental and stimulus fish followed the same feeding schedule. All subjects were acclimated to housing conditions for a minimum of two weeks prior to the start of the experiment.

Apparatus

Boldness was measured using a rectangular Styrofoam tank (41 × 61 cm) containing a shelter along one short wall. The shelter (8 cm deep) contained artificial plants glued along the underside. Sociability was assessed in a glass tank (30.5 x 76 cm) lined with opaque white paper. This tank consisted of three chambers, separated by transparent partitions, with the center chamber measuring 47 cm in length to accommodate the focal fish, and the two outer chambers accommodating stimulus fish. Both tanks were filled to a height of 12 cm with system water (water taken from the home tanks). A webcam (Logitech C920) was mounted above the tanks to capture both arenas simultaneously for tracking purposes. LED lights lined the outside of the tanks to ensure consistent illumination. Fish movements were recorded and tracked in real-time using automated software developed in-house.

Feeding behavior was tested in a glass aquarium measuring 29.5 x 14.5 x 21 cm, filled with system water to a depth of 10 cm, lined with white opaque paper (Figure S1). The tank was divided into three sections by clear plastic barriers with a row of small holes along their bottoms, so that water and odors could transfer between the compartments. The central compartment, into which the test fish was placed, was 10 x 14.5 cm and the two side compartments, which contained the stimulus fish during social condition trials, were 9.5 x 14.5 cm each. A small tank size was selected to ensure that the camera could capture the detailed feeding behavior. A plastic tube was positioned along the side of the tank to deliver food pellets into the center chamber. An LED light was attached to the side of the tank to ensure consistent illumination. A webcam was mounted above the tank and zoomed in on the center chamber to allow accurate observation and recording of feeding behavior. Two identical tanks were placed beside each other, so that two fish could be tested concurrently.

Procedure

The goal of the personality assays was to classify each fish on two traits: boldness and sociability. Fish underwent three consecutive days of testing, completing one boldness trial and one sociability trial per day. Each trial lasted 15 minutes. Throughout all trials, fish movement and position were recorded for later analysis. To assess boldness, the subject was placed in the boldness tank, and movements and positions were tracked using automated software. Boldness was measured as the proportion of the session spent exploring the open area outside the shelter (dos Santos et al., 2023). To assess sociability, the subject was placed in the center chamber of the sociability tank, and five stimulus fish were placed in one of the outer chambers. The subject's movement and position were tracked throughout the trial. Sociability was measured as the proportion of the session spent in close proximity to the stimulus fish (within 10 cm of the social compartment wall; Cattelan et al., 2017).

Following the personality assays, fish underwent four consecutive days of feeding trials, alternating between a social condition (in the presence of stimulus fish) and an isolated condition (no stimulus fish) each day. The order of the conditions was counterbalanced across subjects. Each trial lasted a total of 20 minutes. The goal of these assays was to observe feeding behavior in zebrafish and to determine how this behavior changes depending on social context. In the social condition, two stimulus fish were placed in each of the two outer chambers. In the isolated condition, no stimulus fish were added. In both conditions, a single test fish was placed into the center chamber and given five minutes to habituate. Following habituation, a single 1 mm ∅ food pellet (Hikari Betta Bio Gold) was introduced into the center chamber through a tube (so that the fish could not see the experimenter). The subject was given five minutes to interact freely with the pellet (e.g., eat, swallow, ignore, spit out) before a second pellet was introduced. After another five minutes, a third and final pellet was added, and the subject was again allowed five minutes to interact. At the end of the session, test fish were gently returned to their home tanks.

Fish position and movement were tracked automatically using a custom tracking program. In the feeding assays, the food pellets were also tracked, manually. An eating event was defined as the pellet visibly entering the subject's mouth, and a spitting event was defined as the pellet being expelled from the mouth (see Video S1).

Analysis

Data from the tracking software were read into *Mathematica* (v.12.0; Wolfram Technologies) for analysis. Repeatability analyses were conducted in R (R Core Team, 2021) using the *rpt* function from the *RptR* package (Stoffel et al., 2017). We report the repeatability (R) along with a standard error (SE) and 95% confidence interval (CI) on R, and a P-value. We note that the GLM method used by the function to calculate repeatability does not allow the confidence interval to extend below 0 (Nakagawa & Schielzeth, 2010).

We compared personality traits, pellets consumed, eating/spitting out events, food holding times, or feeding latencies across sexes (between-subject factor) and conditions (isolated or social; within-subject factor) using 2-way mixed-factor ANOVAs. When the data were not normally distributed and could not be transformed to be normal, we used the aligned rank transformed (ART) ANOVA (Higgins et al., 1990) and employed two-way Anderson-Darling tests for post-hoc comparisons. For all ANOVAs we additionally report Mean Differences (MD) for all main effects, along with 95% confidence intervals (CI) on the MD. Pearson's correlation tests were used to correlate boldness or sociability with pellet consumption.

Pellet spitting direction was compared to a uniform distribution using a one-way Anderson-Darling test. Spitting angles were measured relative to the walls of the side compartments (see Figure S1) which, in the social condition, each contained two stimulus fish. We denote spitting while directly facing one of the side compartments as 0°, and facing directly away from it, toward the side wall, as 90° (which is the maximum angle a fish could turn before beginning to orient toward the opposite compartment). The same method – measuring the angle relative to the walls of the now empty side compartments – was applied to the isolated condition trials, allowing for comparisons across conditions.

To confirm that the order of testing did not affect behavior, we conducted all our analyses with Batch as an added between-subjects factor (indicating whether a subject had experienced the isolated or social condition on their first testing day). As this factor was not significant in any of the analyses and did not interact significantly with any other factor, we present the simpler results, collapsed across testing order conditions.

Results

Personality

We first analyzed the repeatability of the personality assays. We found that both boldness and sociability were quite robustly repeatable across the first two days of personality assays (boldness: R = 0.438, SE = 0.148, CI = [0.121, 0.694], P = 0.0058; sociability: R = 0.312, SE = 0.161, CI = [0, 0.609], P = 0.040). Neither trait was repeatable between the second and third days (boldness: R = 0, SE = 0.109, CI = [0, 0.355], P = 0.5; sociability: R = 0.252, SE = 0.160, CI = [0, 0.567], P = 0.081) nor across all three days (boldness: R = 0.158, SE = 0.112, CI = [0, 0.404], P = 0.083; sociability: R = 0.167, SE = 0.108, CI = [0, 0.398], P = 0.072). We therefore ran the remaining analyses using each subject's mean boldness or sociability from the first two days as scores.

We additionally assessed the raw scores from the personality assays. Table 1 gives the means and standard deviations of all personality scores by day and sex, for both boldness and sociability. Boldness scores changed across the two days of testing but did not differ between the sexes (Table 1; Mixed-factor ANOVA: main effect of Day, F(1,28) = 7.60, P = 0.01, MD = 0.14, CI = [0.04, 0.25]; main effect of Sex, F(1,28) = 0.025, P = 0.88, MD = 0.01, CI = [-0.18, 0.16]; Day*Sex interaction, F(1,28) = 0.02, P = 0.88). Sociability scores also differed across days but not sexes (Table 1), but there was also a significant interaction between day and sex, such that female fish decreased in sociability more across days than males (Day, F(1,28) = 30.45, P < 0.001, MD = 0.23, CI = [0.15, 0.32]; Sex, F(1,28) = 0.36, P = 0.55, MD = 0.04, CI = [-0.18, 0.10]; Day*Sex, F(1,28) = 8.54, P = 0.007; note: the main effects should be treated with caution given the significant interaction).

		Day 1	Day 2	Mean
Males	Boldness	0.43 ± 0.24	0.30 ± 0.24	0.34 ± 0.16
	Sociability	0.55 ± 0.22	0.44 ± 0.19	0.51 ± 0.14
Females	Boldness	0.45 ± 0.29	0.30 ± 0.28	0.39 ± 0.19
	Sociability	0.71 ± 0.19	0.36 ± 0.25	0.53 ± 0.17

Table 1. Mean scores ± SD for personality assays for each sex, day, and trait (boldness and sociability). The final column gives the mean scores across both days that were used to predict food consumption.

Food consumption and spitting

Males consumed more pellets than females and fish consumed more pellets when in a social context than when alone, but there was no interaction between the two effects (Figure 1 shows the frequency of consuming a certain number of pellets in a trial, from none to all 3, across all trials, by sex. Mixed-factor ANOVA, main effect of sex: F(1,28) = 7.79, P = 0.009, MD = 1.77, CI = [0.47, 3.07]; main effect of condition: F(1,28) = 11.16, P = 0.002, MD = 1.21, CI = [0.47, 1.95]; sex*condition interaction: F(1,28) = 0.95, P = 0.34. Mean number of pellets consumed ± SD: males, isolated = 2.07 ± 1.81; males, social: 3.63 ± 2.19; females, isolated: 0.64 ± 1.74; females, social: 1.50 ± 2.21). It was not possible to calculate the repeatabilities of pellet consumption across days or social contexts due to the high proportion of cases in which no pellets were consumed. We also found that males spat pellets out more often than females, as did fish in social conditions, and these effects interacted significantly (Figure 2 shows the mean number of spitting out events per trial, by sex and condition; note that the same pellet may be spat out and re-ingested several times. Mixed-factor ANOVA, main effect of sex: F(1,28) = 15.63, P < 0.001, MD = 23.80, CI = [11.47, 36.14]; main effect of condition: F(1,28) = 7.23, P = 0.012, MD = 12.33, CI = [2.94, 21.73]; sex*condition interaction: F(1,28) = 4.80, P = 0.037). Pellets consumed and spitting frequency did not correlate with either personality trait in either sex under either social context condition (Table S1).

Male fish in the social condition held pellets in their mouths for longer before spitting them out than isolated fish, and female fish in the social condition held pellets longer than males (Mixed-factor ART ANOVA, main effect of sex: F(1,852) = 0.52, P = 0.47, MD = 73.79, CI = [-34.21, 181.78]; main effect of condition: F(1,852) = 11.27, P < 0.001, MD = 88.04, CI = [-18.19, 194.27]; sex*condition interaction: F(1,852) = 4.50, P = 0.03. Post-hoc [2-way Anderson-Darling tests]: Male-social vs. Female-social, $A^2 = 7.67$, P = 0.0002; Male-isolated vs. Male-social: $A^2 = 7.67$, P = 0.0002; all other comparisons, $A^2 < 2.3$, P > 0.06; Table S2). Male fish in the social condition had a shorter latency to eat pellets (from when the pellet landed in the tank) than females (Mixed-factor ART ANOVA, main effect of sex: F(1,117) = 1.61, P = 0.21, MD =

14.37, CI = [-1.31, 30.04]; main effect of condition: F(1,117) = 1.86, P = 0.18, MD = 2.32, CI = [-13.36, 18.01]; sex*condition interaction: F(1,117) = 4.41, P = 0.04; post-hoc [2-way Anderson-Darling tests]: Male-social vs. Female-social, $A^2 = 2.56$, P = 0.046; all other comparisons, $A^2 < 2.45$, $P > 0.05$; Table S3).

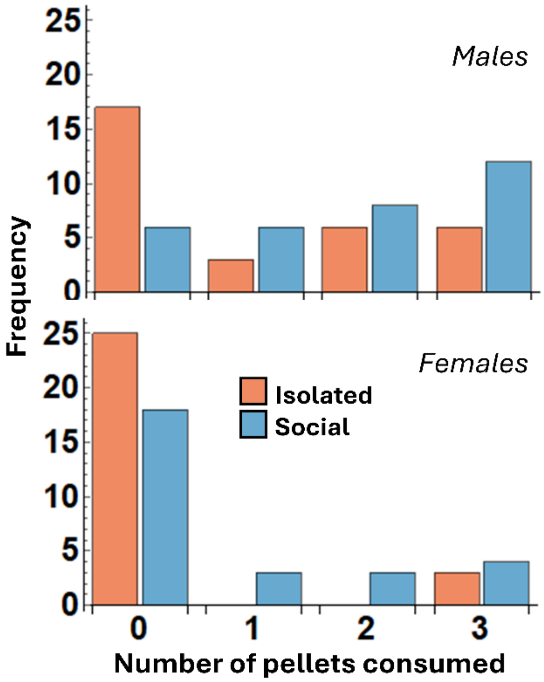

Figure 1. Number of pellets per trial consumed by male (top) and female (bottom) zebrafish when in a social (blue bars) or isolated (orange bars) context, across all feeding trials. The figures show how often fish consumed either none, 1, 2, or all 3 pellets in a trial. Pellets were delivered over a 20 min period. Fish consume more pellets in the social context, and males consume more than females.

Food spitting direction

Finally, we examined the direction fish were facing when they spat out pellets, to see if they were aiming them away from conspecifics in the social condition. The orientation of each fish at the time of each spitting out event was determined from its direction of movement between 5 frames before and after the event. This direction was normalized to indicate a range from facing directly towards one of the stimulus fish compartments (0 degrees) to facing 90 degrees away from the stimulus fish compartments (towards one of the side walls of the tank). A mean value was obtained for each individual on each trial (to avoid nonindependence). The distribution of spitting directions was compared to a uniform distribution (which would indicate that the fish do not orient in any specific way when spitting out the pellets). This analysis excluded female fish in the isolated condition, as insufficient spitting events occurred in this group (only 6 events in total, from just two subjects). We found that male fish in the social condition aimed their food-spitting away from the stimulus fish (Figure 3 shows distributions of the spitting angle relative to facing directly towards the stimulus fish compartments; $A^2 = 4.99$, P = 0.003, M = 60.44° ± 18.68) but a similar effect was not apparent in females ($A^2 = 0.42$, P = 0.82, M = 49.33° ± 28.09) nor in isolated males ($A^2 = 0.96$, P = 0.38, M = 53.39° ± 25.58).

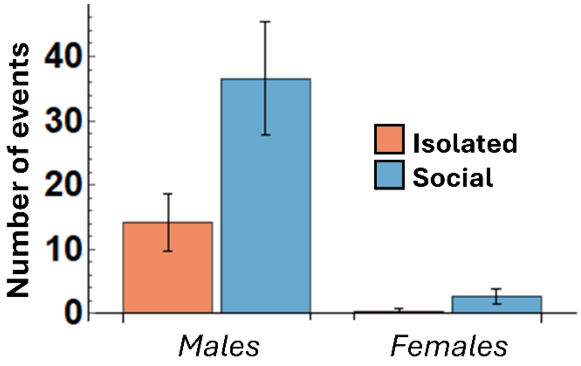

Figure 2. Mean number of spitting out events by sex and condition. The bars show the mean number of times that a fish spat out a previously eaten pellet (the same pellet can be spat out and re-ingested several times). Error bars show ± SEM. Males spit out pellets more than females, and fish spit out pellets more when in a social context.

Discussion

We allowed individual zebrafish of both sexes to feed on sequentially delivered pellets either in the presence or absence of a small group of non-feeding male conspecifics. We tracked pellet consumption along with food-holding duration, latency to feed, and both the amount and direction of spitting behavior. We additionally assayed all the fish on their individual boldness and sociability.

We found that male fish consumed more pellets than females and also spat them out at greater rates, and that fish of both sexes consumed and spat pellets out more when in a social context than when isolated. Male fish, when in the social condition, oriented themselves so that they spat pellets out away from their conspecifics, but did not do so when isolated (there were insufficient data to draw conclusions about female orientations when spitting out food). When in a social context, females held food in their mouths for longer than males, and males held food longer when in a social context than when alone. In the social context, males also had a shorter latency to consume the food than females. Finally, none of our measures of food consumption or manipulation correlated with either of the two personality traits that were assayed.

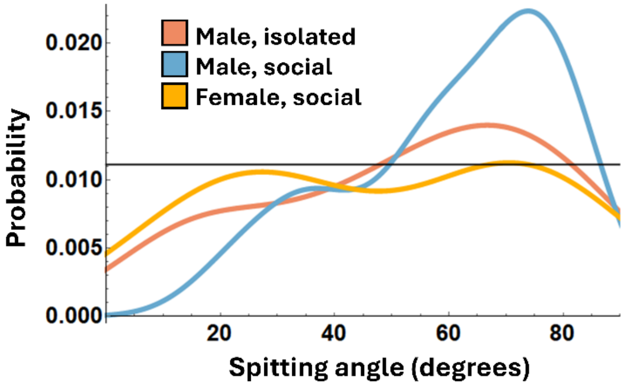

Figure 3. Density distributions of spitting out angle by condition and sex. Data are the angle that a fish was facing when it spat out a pellet, relative to facing directly towards the stimulus fish compartment (0°). The black horizontal line shows a uniform distribution. Female fish in the isolated context were excluded due to a lack of data.

Our results demonstrate that visual exposure to conspecifics significantly enhances feeding behavior in zebrafish, probably via a form of social facilitation (Herman, 2015; Zajonc, 1965). Specifically, zebrafish consumed more food, spat out pellets more frequently, and exhibited prolonged food-holding durations in the presence of non-feeding male conspecifics than when feeding in isolation. Although increased spitting behavior could be seen as prosocial, since expelled food might be available for others to consume, our findings suggest otherwise. Spitting appears to be a way to physically manipulate food, commonly observed when fish consume larger food items and likely serving to break them down or reposition them for easier swallowing (Sibbing, 1988). Spitting may increase the risk of partially-consumed items being stolen by nearby conspecifics. Thus, increased spitting may reflect a competitive motivation to consume the food faster. This interpretation is supported by our finding that male fish turned away from conspecifics while spitting, but had no preferred spitting direction when alone, and held pellets in their mouths for longer when others were present. These results are also consistent with our original rationale for measuring spitting, which could serve as a potential indicator of competition avoidance strategies expressed in food-handling behavior.

As the stimulus fish were visible but confined to separate compartments and not engaging in feeding, we were able to differentiate passive social facilitation – an increase in the consumption of food driven by the mere presence of others – from active mechanisms such as behavior matching, providing support for Zajonc's (1965) "mere presence" theory of social facilitation. These results contrast with some findings in humans, which suggest that the presence of a passive audience can decrease food consumption (Herman, 2015). Though the contribution of active social facilitation to feeding remains to be investigated in zebrafish, our findings make clear that a passive audience alone can increase their feeding behavior.

It is also likely that the stress of isolation contributed to reduced feeding behavior in the isolated condition. Zebrafish are highly social and are found in shoals of 5 to about 300 in the wild (Pritchard et al., 2001; Spence et al., 2008; Suriyampola et al., 2016). Isolation has been shown to induce stress in zebrafish (Daniel & Bhat, 2022), so the effects of social context that we observed may also reflect social buffering. The mere presence of conspecifics may reduce perceived risk and allow zebrafish to prioritize feeding over vigilance (e.g., as in birds; Barnard & Sibly, 1981). Stress may have more generally contributed to our test fish not consuming all the food. Fish were given 5 minutes to habituate to the arena before the delivery of the first food pellet, which may have been too little time for them to de-stress sufficiently to engage in feeding. We note, however, that all fish experienced the same schedule of feeding, so this explanation cannot account for the differences we observed between sexes and conditions.

In addition, our test fish received only three pellets, consecutively at 5 minute intervals. Fish might have fed differently, spat out food differently, and been affected by the presence of others differently, if a large number of pellets had been made available all at once, limiting their ability to monopolize the food supply (as in Hamilton & Dill, 2002).

We also observed large and consistent sex differences in feeding behavior. Males consumed more pellets, spat more frequently, and showed shorter latencies to feed in the social condition; females held pellets in their mouths for longer in both conditions, but especially when conspecifics were present. These sex differences may reflect divergent strategies under perceived competition. As all the stimulus fish were male, the presence of same-sex conspecifics may have triggered competitive motivations in focal males, leading to faster feeding and strategic spitting. Females, on the other hand, may have been more stressed by their inability to move away from the male stimulus fish (due to the small size of the test fish compartment), leading to a general reduction in feeding. However, male zebrafish are known to prefer the company of females (Ruhl & McRobert, 2005) and females have been shown to prefer to remain close to males (Delaney et al., 2002), though these results have been interpreted in the light of mating tendencies, not foraging. It is possible that our subjects would have reacted differently in the presence of female conspecifics, and this remains to be explored in future work.

Male fish avoided spitting pellets out towards conspecifics in the social context, an effect that likely represents a competition-avoidance strategy intended to prevent attracting competitors or food theft. Males also held food in their mouths longer in the social condition compared to in isolation, potentially attempting to delay consumption until the competitive pressure subsided. Dominant male zebrafish are known to attempt to monopolize consistent food-delivery sites and directing food spitting away from conspecifics may be another aspect of this behavior (Hamilton & Dill, 2002). This result suggests that competitive motivations can partially underlie socially facilitated feeding. Even in the absence of direct threat (as the stimulus fish were behind a barrier), the perception of competition may be enough to alter feeding behavior, suggesting that the adaptive functions of some forms of social facilitation relate to intra-species competition and resource defense.

Consistent with previous literature, we found that males and females did not differ in boldness (Mustafa et al., 2019), and we also observed no sex differences in sociability. However, our measures of both traits were not robustly repeatable, and neither trait correlated with pellet consumption, spitting frequency, latency, or food-holding duration, nor the magnitude of social facilitation of feeding. These results contrast with a recent study linking boldness to increased feeding activity in zebrafish (Chen et al., 2022), probably due to test-specific differences.

Conclusion

Our results highlight the complexity of the factors shaping feeding behavior. Social context and sex differences significantly influenced food consumption and related feeding behaviors. Additionally, social facilitation, a phenomenon observed across species, including in humans (de Castro & Brewer, 1992; Ruddock et al., 2019, 2021), may operate through passive mechanisms, such as heightened arousal, shifts in attentional focus, or perceived competition. Though group foraging introduces potential costs, such as increased competition, it also offers adaptive benefits that can outweigh those risks, particularly for prey species like zebrafish.

References

Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour, 29*(2), 543–550. https://doi.org/10.1016/S0003-3472(81)80117-0

Brockmann, H. J., & Barnard, C. J. (1979). Kleptoparasitism in birds. *Animal Behaviour, 27*(2), 487–514. https://doi.org/10.1016/0003-3472(79)90185-4

Cattelan, S., Lucon-Xiccato, T., Pilastro, A., & Griggio, M. (2017). Is the mirror test a valid measure of fish sociability? *Animal Behaviour, 127*, 109–116. https://doi.org/10.1016/j.anbehav.2017.03.009

Chen, Y., Li, W., Xiang, L., Mi, X., Duan, M., & Wu, C. (2022). Fish personality affects their exposure to microplastics. *Ecotoxicology and Environmental Safety, 233*, 113301. https://doi.org/10.1016/j.ecoenv.2022.113301

Daniel, D. K., & Bhat, A. (2022). Alone but not always lonely: Social cues alleviate isolation-induced behavioural stress in wild zebrafish. *Applied Animal Behaviour Science, 251*, 105623. https://doi.org/10.1016/j.applanim.2022.105623

Davis, B. D., & Dill, L. M. (2012). Intraspecific kleptoparasitism and counter-tactics in the archerfish (*Toxotes chatareus*). *Behaviour, 149*(11–12), 1367–1394. https://doi.org/10.1163/1568539X-00003026

de Castro, J. M., & Brewer, E. M. (1992). The amount eaten in meals by humans is a power function of the number of people present. *Physiology & Behavior, 51*(1), 121–125. https://doi.org/10.1016/0031-9384(92)90212-K

der Weduwen, D., Jones, N. A. R., Dubosque, A., Schuster, S., Sillar, K. T., Webster, M., & Rendell, L. (2024). Archerfish foraging success varies with immediate competition level but not group size. *Behavioral Ecology, 35*(4), arae040. https://doi.org/10.1093/beheco/arae040

di Bitetti, M. S., & Janson, C. H. (2001). Social foraging and the finder's share in capuchin monkeys (*Cebus apella*). *Animal Behaviour, 62*(1), 47–56. https://doi.org/10.1006/anbe.2000.1730

dos Santos, C. P., de Oliveira, M. N., Silva, P. F., & Luchiari, A. C. (2023). Relationship between boldness and exploratory behavior in adult zebrafish. *Behavioural Processes, 209*, 104885. https://doi.org/10.1016/j.beproc.2023.104885

Delaney, M., Follet, C., Ryan, N., Hanney, N., Lusk-Yablick, J., & Gerlach, G. (2002). Social interaction and distribution of female zebrafish (*Danio rerio*) in a large aquarium. *Biological Bulletin, 203*(2), 240–241. https://doi.org/10.2307/1543418

Dhellemmes, F., Finger, J., Smukall, M. J., Gruber, S. H., Guttridge, T. L., Laskowski, K. L., & Krause, J. (2021). Personality-driven life history trade-offs differ in two subpopulations of free-ranging predators. *Journal of Animal Ecology, 90*(1), 260–272. https://doi.org/10.1111/1365-2656.13283

Forkman, B. A. (1991). Social facilitation is shown by gerbils when presented with novel but not with familiar food. *Animal Behaviour, 42*(5), 860–861. https://doi.org/10.1016/S0003-3472(05)80132-0

Frost, A. J., Winrow-Giffen, A., Ashley, P. J., & Sneddon, L. U. (2007). Plasticity in animal personality traits: Does prior experience alter the degree of boldness? *Proceedings of the Royal Society B: Biological Sciences, 274*(1608), 333–339. https://doi.org/10.1098/rspb.2006.3751

Giraldeau, L. A. (1997). The ecology of information use. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (4th ed., pp. 42–68). Blackwell Science.

Grunst, A. S., & Grunst, M. L. (2024). Animal personality in multiple stressor environments: The evolutionary ecology of among-individual differences in responses to stressor suites. *Proceedings of the Royal Society B: Biological Sciences, 291*, 20241620. https://doi.org/10.1098/rspb.2024.1620

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

Harlow, H. F. (1932). Social facilitation of feeding in the albino rat. *The Pedagogical Seminary and Journal of Genetic Psychology, 41*(1), 211–221. https://doi.org/10.1080/08856559.1932.9944151

Harlow, H. F., & Yudin, H. C. (1933). Social behavior of primates: I. Social facilitation of feeding in the monkey and its relation to attitudes of ascendance and submission. *Journal of Comparative Psychology, 16*(2), 171–185. https://doi.org/10.1037/h0071690

Hensor, E. M. A., Godin, J.-G. J., Hoare, D. J., & Krause, J. (2003). Effects of nutritional state on the shoaling tendency of banded killifish, *Fundulus diaphanus*, in the field. *Animal Behaviour, 65*(4), 663–669. https://doi.org/10.1006/anbe.2003.2075

Herman, C. P. (2015). The social facilitation of eating: A review. *Appetite, 86*, 61–73. https://doi.org/10.1016/j.appet.2014.09.016

Heyes, C. M., Ray, E. D., Mitchell, C. J., & Nokes, T. (2000). Stimulus enhancement: Controls for social facilitation and local enhancement. *Learning and Motivation, 31*(2), 83–98. https://doi.org/10.1006/lmot.1999.1041

Higgins, J. J., Blair, R. C., & Tashtoush, S. (1990). The aligned rank transform procedure. Conference on Applied Statistics in Agriculture. https://doi.org/10.4148/2475-7772.1443

Higgins, L. E., & Buskirk, R. E. (1998). Spider-web kleptoparasites as a model for studying producer-consumer interactions. *Behavioral Ecology, 9*(4), 384–387. https://doi.org/10.1093/beheco/9.4.384

Higgs, S., & Thomas, J. (2016). Social influences on eating. *Current Opinion in Behavioral Sciences, 9*, 1–6. https://doi.org/10.1016/j.cobeha.2015.10.005

Hirsch, B. T. (2007). Costs and benefits of within-group spatial position: A feeding competition model. *The Quarterly Review of Biology, 82*(1), 9–27. https://doi.org/10.1086/511657

Janson, C. H. (1988). Food competition in brown capuchin monkeys (*Cebus apella*): Quantitative effects of group size and tree productivity. *Behaviour, 105*(1–2), 53–76. https://doi.org/10.1163/156853988X00449

Kikusui, T., Winslow, J. T., & Mori, Y. (2006). Social buffering: Relief from stress and anxiety. *Philosophical Transactions of the Royal Society B: Biological Sciences, 361*(1476), 2215–2228. https://doi.org/10.1098/rstb.2006.1941

Kim, S. W., Chae, Y., Kim, D., & An, Y-J. (2019). Zebrafish can recognize microplastics as inedible materials: Quantitative evidence of ingestion behavior. *The Science of the Total Environment, 649*, 156–162. https://doi.org/10.1016/j.scitotenv.2018.08.310

Krause, J. (1993). The influence of hunger on shoal size choice by three-spined sticklebacks (*Gasterosteus aculeatus*). *Journal of Fish Biology, 43*(5), 775–780. https://doi.org/10.1111/j.1095-8649.1993.tb01154.x

Luttbeg, B., & Sih, A. (2010). Risk, resources and state-dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society B: Biological Sciences, 365*(1560), 3977–3990. https://doi.org/10.1098/rstb.2010.0207

Miller, N., & Gerlai, R. (2007). Quantification of shoaling behaviour in zebrafish (Danio rerio). *Behavioural Brain Research, 184*(2), 157–166. https://doi.org/10.1016/j.bbr.2007.07.007

Moran, N. P., & Behrens, J. W. (2024). Behavioural and trophic variation within a well-established invasive round goby population. *Animal Behaviour, 215*, 263–280. https://doi.org/10.1016/j.anbehav.2024.07.006

Moran, N. P., Sánchez-Tójar, A., Schielzeth, H., & Reinhold, K. (2021). Poor nutritional condition promotes high-risk behaviours: A systematic review and meta-analysis. *Biological Reviews, 96*(1), 269–288. https://doi.org/10.1111/brv.12655

Morissette, S., & Himmelman, J. H. (2000). Subtidal food thieves: Interactions of four invertebrate kleptoparasites with the sea star *Leptasterias polaris*. *Animal Behaviour, 60*(4), 531–543. https://doi.org/10.1006/anbe.2000.1500

Mustafa, A., Roman, E., & Winberg, S. (2019). Boldness in male and female zebrafish (*Danio rerio*) is dependent on strain and test. *Frontiers in Behavioral Neuroscience, 13*, Article 248. https://doi.org/10.3389/fnbeh.2019.00248

Nakagawa, S., & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews, 85*(4), 935–956. https://doi.org/10.1111/j.1469-185X.2010.00141.x

Ojelade, O., Iyasere, O., Durosaro, S., Abdulraheem, I., & Akinde, A. (2022). Social isolation impairs feed intake, growth and behavioural patterns of catfish under culture conditions. *Animal, 16*, 100521. https://doi.org/10.1016/j.animal.2022.100521

Pitcher, T. J., Magurran, A. E., & Winfield, I. J. (1982). Fish in larger shoals find food faster. *Behavioral Ecology and Sociobiology, 10*(2), 149–151. https://doi.org/10.1007/BF00300175

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

R Core Team (2021). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*. URL https://www.R-project.org/.

Rajecki, D. W., Kidd, R. F., Wilder, D. A., & Jaeger, J. (1975). Social factors in the facilitation of feeding in chickens: Effects of imitation, arousal, or disinhibition? *Journal of Personality and Social Psychology, 32*(3), 510–518. https://doi.org/10.1037/h0077065

Ruddock, H. K., Brunstrom, J. M., & Higgs, S. (2021). The social facilitation of eating: Why does the mere presence of others cause an increase in energy intake? *Physiology & Behavior, 240*, 113539. https://doi.org/10.1016/j.physbeh.2021.113539

Ruddock, H. K., Brunstrom, J. M., Vartanian, L. R., & Higgs, S. (2019). A systematic review and meta-analysis of the social facilitation of eating. *The American Journal of Clinical Nutrition, 110*(4), 842–861. https://doi.org/10.1093/ajcn/nqz155

Ruhl, N., & McRobert, S. P. (2005). The effect of sex and shoal size on shoaling behaviour in *Danio rerio*. *Journal of Fish Biology, 67*, 1318–1326. https://doi.org/10.1111/j.0022-1112.2005.00826.x

Ryer, C. H., & Olla, B. L. (1991). Information transfer and the facilitation and inhibition of feeding in a schooling fish. *Environmental Biology of Fishes, 30*(4), 317–323. https://doi.org/10.1007/BF02028847

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*, 20250052. https://doi.org/10.1098/rspb.2025.0052

Sibbing, F. A. (1988). Specializations and limitations in the utilization of food resources by the carp, *Cyprinus carpio*: a study of oral food processing. *Environmental Biology of Fishes, 22*, 161–178. https://doi.org/10.1007/BF00005379

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

Stamps, J., & Groothuis, T. G. G. (2010). The development of animal personality: Relevance, concepts and perspectives. *Biological Reviews, 85*(2), 301–325. https://doi.org/10.1111/j.1469-185X.2009.00103.x

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution, 8*, 1639-1644. https://doi.org/10.1111/2041-210X.12797

Suriyampola, P. S., Shelton, D. S., Shukla, R., Roy, T., Bhat, A., & Martins, E. P. (2016). Zebrafish social behavior in the wild. *Zebrafish, 13*(1), 1–8. https://doi.org/10.1089/zeb.2015.1159

Templeton, J. J., & Giraldeau, L.-A. (1995). Public information cues affect the scrounging decisions of starlings. *Animal Behaviour, 49*(6), 1617–1626. https://doi.org/10.1016/0003-3472(95)90084-5

Tolman, C. W., & Wilson, G. F. (1965). Social feeding in domestic chicks. *Animal Behaviour, 13*(1), 134–142. https://doi.org/10.1016/0003-3472(65)90083-7

Webster, M. M., & Hart, P. J. B. (2006). Kleptoparasitic prey competition in shoaling fish: Effects of familiarity and prey distribution. *Behavioral Ecology, 17*(6), 959–964. https://doi.org/10.1093/beheco/arl037

Wee, C. L., Song, E., Nikitchenko, M., Herrera, K. J., Wong, S., Engert, F., & Kunes, S. (2022). Social isolation modulates appetite and avoidance behavior via a common oxytocinergic circuit in larval zebrafish. *Nature Communications, 13*, Article 2573. https://doi.org/10.1038/s41467-022-29765-9

Welty, J. C. (1934). Experiments in group behavior of fishes. *Physiological Zoology, 7*(1), 85–128. https://doi.org/10.1086/physzool.7.1.30151215

Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. *Advances in the Study of Behavior, 21*, 239–283. https://doi.org/10.1016/S0065-3454(08)60146-1

Wright, G. S., Wilkinson, G. S., & Moss, C. F. (2020). Social facilitation in short-tailed fruit bats, *Carollia perspicillata* (Linnaeus). *Behaviour, 157*(12), 1193–1210. https://doi.org/10.1163/1568539X-bja10047

Zajonc, R. B. (1965). Social facilitation: A solution is suggested for an old unresolved social psychological problem. *Science, 149*(3681), 269–274. https://doi.org/10.1126/science.149.3681.269

Zamora, R., & Gómez, J. M. (1996). Carnivorous plant-slug interaction: A trip from herbivory to kleptoparasitism. *Journal of Animal Ecology, 65*(2), 154–160. https://doi.org/10.2307/5718

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Availability of Data: All the data reported here are available on our OSF repository (https://osf.io/wk8ec/?view_only=1b0e72ce79294fada90247dd1ed3863b).

Supplementary Material

Table S1. Correlations of personality traits (Boldness and Sociability) with number of pellets consumed in each social context (Isolated or Social), for all fish combined (top row) or broken down by sex. Each cell of the table gives the correlation coefficient (r) and a P-value.

	Boldness		Sociability	
	Isolated	Social	Isolated	Social
All fish	r = -0.13 P = 0.50	r = -0.03 P = 0.87	r = -0.13 P = 0.51	r = -0.33 P = 0.08
Males	r = -0.07 P = 0.80	r = 0.32 P = 0.23	r = -0.34 P = 0.21	r = -0.28 P = 0.30
Females	r = -0.20 P = 0.50	r = -0.39 P = 0.17	r = 0.12 P = 0.69	r = -0.34 P = 0.24

Table S2. Pairwise comparisons of time pellets were held in the mouth across conditions. Each cell gives the Anderson-Darling test statistic (A^2) for a comparison between the groups, along with a P-value. The rightmost column gives group mean time (in seconds) ± SD.

Group	Male isolated	Male social	Female isolated	Means ± SD
Male, isolated				63.87 ± 233.50
Male, social	$A^2 = 7.67$ P = 0.0002			65.93 ± 219.35
Female, isolated	$A^2 = 2.28$ P = 0.06	$A^2 = 1.90$ P = 0.10		77.17 ± 70.61
Female, social	$A^2 = 1.56$ P = 0.16	$A^2 = 5.13$ P = 0.002	$A^2 = 0.85$ P = 0.44	87.92 ± 167.72

Table S3. Pairwise comparisons of latency to consume a pellet across conditions. Each cell gives the Anderson-Darling test statistic (A^2) for a comparison between the groups on latency, along with a P-value. The rightmost column gives group mean latencies (in seconds) ± SD.

Group	Male isolated	Male social	Female isolated	Means ± SD
Male, isolated				47.56 ± 54.65
Male, social	$A^2 = 0.58$ P = 0.66			42.43 ± 43.25
Female, isolated	$A^2 = 1.85$ P = 0.11	$A^2 = 1.11$ P = 0.31		23.08 ± 21.72
Female, social	$A^2 = 1.71$ P = 0.13	$A^2 = 2.56$ P = 0.046	$A^2 = 2.44$ P = 0.05	72.64 ± 74.14

Figure S1. The testing apparatus. *Left*: photograph of the feeding test tank; food pellets were delivered through the funnel and tube into the central compartment manually by the experimenter, who could not be seen by the fish. *Right*: frame from a video of a trial, showing the test fish in the central compartment and one stimulus fish in each side compartment (there are two stimulus fish in each side compartment; the second one is out of frame).