Wild guppies flexibly adjust sociality following experience with ephemeral resources

Lysanne Snijders[1,2], Stefan Krause[3], Alan Novaes Tump[4], Michael Breuker[3], Indar W. Ramnarine[5], Ralf H.J.M. Kurvers[4,6], Jens Krause[2,6,7]

*Corresponding author: lysanne.snijders@wur.nl

Author affiliations

1 Behavioural Ecology Group, Wageningen University, 6708 PB Wageningen, The Netherlands.

2 Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, 12587 Berlin, Germany.

3 Department of Electrical Engineering and Computer Science, Lübeck University of Applied Sciences, 23562 Lübeck, Germany.

4 Center for Adaptive Rationality, Max Planck Institute for Human Development, 14195 Berlin, Germany.

5 Department of Life Sciences, University of the West Indies, St Augustine, Trinidad and Tobago.

6 Cluster of Excellence "Science of Intelligence", Technical University of Berlin, Berlin, Germany, Marchstr. 23, 10587 Berlin, Germany

7 Faculty of Life Sciences, Humboldt-Universität zu Berlin, 10115 Berlin, Germany.

Abstract

Sociality can facilitate the discovery of novel resources, yet it can also entail costs, including increased competition, aggression, sexual harassment and disease transmission. Selection should therefore favour social flexibility as a response to changes in resource conditions, allowing individuals to optimally adjust their social associations. Quantifying these social adjustments and how they allow individuals to benefit in dynamically changing resource environments can provide insight into the adaptive capacity of wild animal populations. We experimentally studied social flexibility in wild guppies (*Poecilia reticulata*) by examining their fission-fusion dynamics. Using mixed-sex sets of individually marked fish, we manipulated recent foraging experience by presenting them with unpredictable, ephemeral food patches or control patches in the wild. Guppies exposed to ephemeral food patches significantly increased their sociality, doubling the proportion of time spent social compared to controls. This shift was driven by an increase in the probability of starting social contact and a decrease in the probability of ending social contact. Stronger increases in sociality were associated with individuals more often locating and feeding from ephemeral food patches, mediated by foraging motivation. Importantly, increased sociality was not merely the result of local aggregation, as exposure to ephemeral food patches increased, rather than reduced, spatial activity. And stronger spatial activity did not result in more time spent social. In a second experiment, fish were briefly presented with food patches they could see and smell but not actually consume. Again, fish increased their level of sociality compared to control, indicating that the observed social response was not merely driven by satiation-related changes in activity budgets. Together, our results highlight the adaptive and dynamic nature of fission-fusion social systems and support the view that wild animals adaptively shape their social environment in response to fluctuations in resource variability.

Keywords: environmental buffering, Markov chain analysis, resource predictability, social facilitation, social flexibility, social foraging, social learning

1. Introduction

The selective advantages of living in groups have shaped the evolution of sociality across numerous taxa (Garcia and De Monte, 2013; Rubenstein and Abbot, 2017). Indeed, social attributes positively predict fitness measures in a variety of species (Formica et al., 2012; Ryder et al., 2009; Silk et al., 2003). The fitness advantages of sociality can emerge through various pathways (Krause and Ruxton, 2002), such as facilitating predation avoidance, mating opportunities, or foraging success (Karplus et al., 2006; Oh and Badyaev, 2010; Shier and Owings, 2007; Snijders et al., 2021). Increase in foraging success can be especially impactful because it has the potential to positively affect both survival and reproduction (Abrahams, 1993; Blanckenhorn, 1991; Clark and Mangel, 1986; Clay et al., 2018; Ellis et al., 2017; Morse and Stephens, 1996).

Sociality facilitates resource discovery in many animals (Galef and Giraldeau, 2001; Oestreich et al., 2026). Specifically, social relationships can help locate novel resources (Firth et al., 2016; Hasenjager et al., 2020a, 2020b; Heinen et al., 2022), with individuals that spend more time socially or are more centrally positioned in the social network typically discovering resources more quickly and frequently (Aplin et al., 2012; Carter et al., 2016; Snijders et al., 2019, 2018) or experiencing less food intake variance (Jolles et al., 2017). Increased sociality can, however, also be costly, e.g., by increasing the risk of competition, (sexual) harassment, and disease exposure (Darden et al., 2009; Godfrey et al., 2009; Leu et al., 2016). Animals are, therefore, expected to flexibly adapt their social state to the prevailing resource conditions (Fisher et al., 2021; Komdeur and Ma, 2021).

When the prevailing resource conditions make social associations less costly or more beneficial, e.g., by reducing competition or facilitating resource localisation, sociality should increase. And various field studies found that social behaviour often varies or changes with natural resource variability (Brown, 1988; Chapman et al., 1995; Dorning and Harris, 2019; Egert-Berg et al., 2018; Foster et al., 2012). Furthermore, there is experimental evidence suggesting that individuals strategically adjust their social behaviour in response to changes in foraging opportunities. For example, an experimental study in semi-captive ring-tailed lemurs (*Lemur catta*) demonstrated that lemurs increased their social connections to individuals they had observed solving a newly introduced foraging task, and this adjustment persisted even after the task was removed (Kulahci et al., 2018). Another experimental field study showed that without easy access to supplemental food, wild blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) increasingly foraged in

multispecies flocks (Grubb, 1987), presumably to locate alternative feeding opportunities more effectively. These few experimental studies in the (semi) wild suggest that animals' instrumental use of sociality can yield potential foraging benefits, but these benefits have yet to be quantified. Quantifying the speed and magnitude of social adjustment and testing if such adjustments are indeed beneficial in fitness-relevant contexts is crucial to assess if animals can mitigate resource fluctuations, or other forms of rapid environmental change, through social flexibility (i.e.' social buffering'), allowing us to better understand the adaptive capacity of social systems.

Here, we investigated whether changes in resource availability induce adjustments in the sociality of wild Trinidadian guppies (*Poecilia reticulata*) and whether stronger social adjustment results in larger foraging benefits. Trinidadian guppies are an ideal study model for this question, since earlier field research showed that guppies exhibit fission-fusion dynamics, switching frequently between being alone and being in close proximity to conspecifics (Wilson et al., 2015, 2014). Individual guppies consistently vary in how much time they spend social (Krause et al., 2017), and this 'social time' positively correlates with their individual success in locating ephemeral food patches (Snijders et al., 2019, 2018). Moreover, a recent field study manipulated the number of guppies in a given pool, showing that an individual's food patch discovery and food consumption increased with the number of conspecifics (Snijders et al., 2021). Being more social thus has a clear positive effect on individual foraging success. Indeed, guppies have been a key model species for the study of social foraging and social learning of foraging information (Clément et al., 2017; Day et al., 2001; Franks and Marshall, 2013; Hasenjager and Dugatkin, 2017; Lachlan et al., 1998; Laland and Williams, 1997; Morrell et al., 2008; Reader et al., 2003; Swaney et al., 2001).

Building on these insights, we experimentally studied the effects of ephemeral food patch availability on the social dynamics and foraging success of 18 mixed-sex sets of wild guppies in natural rainforest pools. For readability purposes, we refer to these sets as 'groups' but emphasise that this terminology is not meant to indicate that these fish primarily move around as cohesive units. Using a counter-balanced within-group design, we exposed each group, *in situ*, to two series of food and control presentations, while observing their social dynamics before, in between and after. First, we tested whether groups consistently differed in the overall time their members spent in a social state (i.e., in proximity of at least one other group member) under control conditions. Second, we tested whether this time spent social changed following experience with ephemeral food patch availability, predicting that fish would become more social to better locate the patchy

and ephemeral food resources (Oestreich et al., 2026). To examine alternative explanations of changes in sociality, such as carry-over of local aggregation or increased spatial activity, we performed several supportive data analyses. Third, we tested if changes in the time groups spent social translated into a higher individual foraging success. Lastly, in a follow-up experiment, we replaced the food resources at the patches with food odour cues and tested if time spent social also changed when fish could detect ephemeral food patches but not consume them. This was done to investigate the potential role of satiation-related changes in activity budgets as the driver of observed changes in sociality (Abrahams, 1993; Borgeaud et al., 2021; Gareta García et al., 2021; Kolluru and Grether, 2005).

2. Materials and Methods

Study area and subjects

The study took place in the rainforest region of the Upper Turure River (10°41'8" N, 61°10'22" W) of Trinidad's Northern Range. This region is considered a low-predation and resource-poor site (Barbosa et al., 2018; Deacon et al., 2018; Grether et al., 2001). We conducted two experiments: Experiment (Exp) 1 (6 – 24 March 2019) studied how fish adjusted their sociality when experiencing a rapid influx of ephemeral food patches. Experiment 2 (8-15 April 2023) studied how fish adjusted their sociality when experiencing a similar set-up but without the possibility to become satiated by using food odour patches. We used four (Exp 1) or three (Exp 2) natural pools (approximate surface area range of the pools: 2–5 m^2; depth range: 5–30 cm), which were modified around the edges to allow a constant in- and outflow of water while minimising opportunities for fish migration. The use of natural pools allowed us to study the guppies in an ecologically relevant environment, including corresponding abiotic conditions, variations in water levels and substrates (rock, gravel and leaves) and low (but not absent) predation risk levels. Moreover, guppies could maintain their natural baseline foraging behaviour by allowing exploration and exploitation of low-quality food resources such as algae and detritus (Grether et al., 2001; Zandonà et al., 2011). Guppies originally occurring in these pools were removed. For our experimental groups, we collected guppies from a nearby stretch of the river. Upon capture, adult fish (Exp 1: N = 144; Exp 2: N = 160; 50/50 sex-ratio) were measured (Exp 1: females: (Mean ± SD) 24.3 ± 2.4 mm, males: 22.1 ± 1.6 mm; Exp 2: females: 24.5 ± 2.5 mm; males = 23.7 ± 1.6 mm) and individually marked using an established technique of Visible Implant Elastomer (VIE) tagging (©Northwest Marine Technology Inc.) (Croft et al., 2003; Jungwirth et al., 2019; Snijders et al., 2018, 2021). Colour marks were green, red, white or pink and placed either at the relative front or back of an individual. An earlier study with wild guppies showed that the use of red elastomers (which may most closely resemble orange, a relevant colour in guppy mate choice) did not affect the time a male (or a female) spent socially or how it distributed its contact moments (Snijders et al., 2019).

The experimental groups consisted of eight fish (of equal sex ratio), and fish within the same group were caught from the same natural site to retain familiarity. We released the groups in their respective experimental pools and left them to settle overnight, with experimental trials starting the following morning. In Exp 1, four groups lost one fish overnight, resulting in 14 groups of eight

fish and four groups of seven (N = 18 groups, **Table 1**). In Exp 2, three groups lost one fish overnight, and two groups lost two fish, resulting in 13 groups of eight, three groups of seven, and two groups of six fish (N = 18 groups, **Table 2**). In addition, two groups in Exp 2 were completely replaced after losing three or more fish, likely due to overnight flooding. In Exp 1, the number of groups studied per unique pool ranged between three and six, while in Exp 2, there were six groups studied per unique pool.

Our research complied with the law and relevant ethical regulations at the time of and in the country of study (Trinidad and Tobago). Specifically, the study was performed in accordance with the 'Basic Principles Governing the Use of Live Animals and Endangered Species in Research' at the University of the West Indies as part of the 'Policy and Procedures on Research Ethics' of the University of the West Indies Campus Research Ethics Committee, St. Augustine (Ref: CREC-SA.270/03/2023). We released all subjects on the day of their final trials.

Experiment 1

Experimental design

We followed a counter-balanced within-group design, meaning that all groups received both the treatment and the control, with half of the groups receiving the control first and the other half receiving the treatment first. Control presentations were conducted to account for potential disturbance effects. Each group was tested for two consecutive days, comprising one treatment and one control day (**Table 1**). Each day consisted of three social observation sessions interspersed with two series of 60 food (or control) patch presentations following a 2-minute break. Each day would thus start and end with a social observation session.

Table 1. Schematic overview of the design for Experiment 1. Groups of seven or eight individuals, distributed across four pools, received the food patch treatment on day 1 and control on day 2, or vice versa. Within each day, we observed social dynamics before (S0), between (S1), and after (S2) two presentation series. The series included presentations of either ephemeral food patches (F1 & F2) or control patches (C1 & C2).

Day 1					**Day 2**					**Groups**	**Individuals**
Food patch					Control patch					N = 9	N = 71
S0	F1	S1	F2	S2	S0	C1	S1	C2	S2		
Control patch					Food patch					N = 9	N = 69
S0	C1	S1	C2	S2	S0	F1	S1	F2	S2		

171

172 *Ephemeral food patch presentations and behavioural observations*

173 One session of presentations (food or control patch) consisted of 60 presentations, simulating an
174 influx of patchy and ephemeral food resources, e.g., fallen fruits or insects in rainforest streams.
175 Each presentation and each break between two presentations lasted 15 seconds (i.e. 30 minutes in
176 total). Food or control patches were presented at five a-priori assigned locations, roughly evenly
177 distributed throughout the entire pool (with a minimum distance of 50 cm between nearest
178 locations). The order of presentation location was alternated randomly, with the restriction that
179 within every five trials, each location received a presentation. As a food patch, we used small lead
180 balls (8 mm diameter), which were covered with a mix of gelatine and crushed fish food flakes,
181 including carotenoids (TetraPro©; Spectrum Brands Inc). Food patches were shareable, as multiple
182 individuals could feed simultaneously. As a control, we used the same balls but without a food
183 cover. During a presentation, we lowered the ball into the water until approximately two cm above
184 the bottom. We scored the identity and the order of the individuals that arrived, and whether they
185 took at least one bite from the food (referred to as a 'feeding event' from here onwards). The 60
186 presentations were followed by a two-minute break, after which we continued with the next social
187 observation session. We conducted two series (F1 & F2 or C1 & C2, **Table 1**) of 60 presentations a
188 day. During one series, the food patch was completely depleted before the final presentation and
189 therefore ended 17 presentations early, leading to a total of 4,303 analysed presentations
190 containing 33,481 individual presence/absence data points. Because feeding behaviour could not
191 be reliably determined during six of the presentations, we excluded these from the analysis of
192 feeding events but retained them in the other analyses.

193 *Social observations*

194 To quantify potential changes in social dynamics following our treatments, we performed focal
195 follow observation sessions of each group member before (S0), in between (S1), and after (S2) the
196 food or control presentations (**Table 1**). Each individual was followed for three minutes during each
197 session. Every ten seconds, we noted whether the focal fish was alone or social. Fish primarily
198 swam just above the bottom of the pool, allowing us to also reliably note their spatial zone in the
199 pool (i.e. the nearest of five a priori assigned patch presentation locations) every ten seconds. Ten
200 seconds was considered an appropriate time interval, since earlier research (in a denser
201 population) showed that guppies encounter other individuals or shoals on average every fourteen

seconds (Croft et al., 2003). Staying consistent with previously used observation protocols, we considered a guppy social when it was within four body lengths of another guppy (Krause et al., 2017; Snijders et al., 2019; Wilson et al., 2014). In addition, we continuously scored events of sigmoidal display (an S-shaped body posture shown by males to display their body to females), sexual harassment (active chasing and attempts to physical contact performed by males towards females) and general harassment/aggression (active chasing and attempts to physical contact, excluding sexual harassment) performed or received by the focal fish during the focal observation. To minimise selection bias, the focal observation order was determined by a second person (who was not currently observing the fish). Due to the need for live observation, the social observations could not be conducted blindly. We acknowledge that this limitation could have introduced an observation bias but given the magnitude of the effect (see Results), we believe it is unlikely that this qualitatively influenced our results.

Experiment 2

Experimental design

Exp 2 followed a counter-balanced within-group design, similar to Exp 1. However, in Exp 2, groups received treatment and control on the same day, and there were no social observations before the first presentations (**Table 2**). A day consisted of two treatment and two control sessions, each including nine patch presentations, followed by a 2-minute break, after which the social observation session started. There was a break of at least 30 minutes between the control and treatment sessions. Note that we reduced the number of presentations during Exp 2 compared to Exp 1 to minimise potential habituation/learning effects (i.e., the guppies learning that the odour cue does not provide food access). During Exp 2, before the start of the experimental trials, guppies were allowed to take a few bites of the food item for a maximum of 1 minute to ensure they would associate the odour cue with a food resource during the experiments. We left at least 15 minutes between this brief food exposure and the experimental trials.

Table 2. Schematic overview of the design for Experiment 2. Groups of six to eight individuals, distributed across three pools, received food odour patches and then control odour patches on the same day, or vice versa. We observed social dynamics between (S1) and after (S2) the cue presentation series. The series included presentations of either ephemeral food cues (F1 & F2) or control cues (C1 & C2).

Within Day	Groups	Individuals

Food odour patch				Control odour patch				N = 9	N = 68
F1	S1	F2	S2	C1	S1	C2	S2		
Control odour patch				Food odour patch				N = 9	N = 69
C1	S1	C2	S2	F1	S1	F2	S2		

Ephemeral food cue presentations and behavioural observations

In Exp 2, one session of presentations (food odour or control) consisted of nine presentations. Each presentation lasted 30 seconds, and each break between two presentations lasted 20 seconds (i.e. 7.5 minutes in total). We presented food or control stimuli at nine a-priori assigned and roughly evenly spread locations throughout each pool (with a minimum distance of 25 cm between the nearest locations). The order of presentation location was randomly alternated throughout the entire pool. We used the same crushed fish food flakes as in Exp 1 as the food odour stimulus and small river pebbles as the control stimulus. Both stimulus types were wrapped in polyester plankton mesh (Sefar Petex®), creating items of approximately 15 by 15 mm. The mesh allowed the odour to diffuse but prevented the fish from accessing the crushed flakes. Multiple individuals could peck at a stimulus simultaneously. As in Exp 1, we lowered the stimulus into the water until approximately two cm above the bottom at the randomly assigned location. We scored the identity and the order of the individuals that arrived, and whether they made at least one peck. In contrast to Exp 1, we filmed the presentations in Exp 2 using camcorders (SONY HDR-PJ530E) on tripods and analysed the videos in BORIS v 8.20 (Friard and Gamba, 2016). Specifically, we quantified the number of pecks made at the stimulus and the social interaction events: sigmoidal display, inter- and intra-sexual harassment and displacement (departing at the moment another individual arrives) that took place within two body lengths of the stimulus.

Social observations

The social observations followed the same observation protocol as in Exp 1, but with no observations before the presentations (S1 and S2 only; **Table 2**) and each individual being followed for two (instead of three) minutes per session.

Statistical analyses

Social dynamics

To quantify the social dynamics during the social observations, we used a Markov chain analysis to calculate the proportion of time an individual spends near other individuals, a measure referred to as 'social time' (Snijders et al., 2019, 2018; Wilson et al., 2014). Markov chain analyses allow an investigation of the more fine-grained social state change dynamics underlying broader social patterns (like time spent social). We translated our focal observations to a sequence of behavioural social states (i.e., one state every ten seconds): being either in the social proximity of another individual (i.e., within four body lengths) or alone. When in a social state, the focal individual can stay social or transition to being alone. The social time of each fish was quantified using the transition probabilities $P_{a\rightarrow s}$, which is the probability of starting social contact (i.e. transitioning from alone to social), and $P_{s\rightarrow a}$, which is the probability of ending social contact (i.e. transitioning from social to alone), using the formula: $P_{a\rightarrow s} / (P_{s\rightarrow a} + P_{a\rightarrow s})$. We estimated these probabilities based on the observed frequencies of state changes. If one of the state changes was not observed, we increased the frequencies of all state changes by 1 to avoid the unrealistic probability of 0. In earlier studies with Trinidadian guppies, social time and the transition probabilities underlying social time were shown to be consistent throughout water surface area manipulations and translocations (Krause et al., 2017; Wilson et al., 2015). Using this approach not only gives us insight into the overall social tendencies of the fish but also reveals if changes in social tendencies arise through more frequent social contact initiations, longer social contact durations or both. Our design allowed us to gather social data on the same day before (only Exp 1), in between, and after the food resource/odour presentations (Exp 1 and 2). However, this came at the cost of resolution at the individual level, as we could only collect three (Exp 1) or two (Exp 2) minutes of data per individual per session. We, therefore, focused our social analyses on the group-level (Exp 1 and 2) and sex-level (only Exp 1). To do this, we determined the overall transition probabilities (i.e., $P_{s\rightarrow a}$ and $P_{a\rightarrow s}$) and social time per group (or per sex within each group) and social observation session. We estimated each transition probability based on the sum of the number of state changes across all focal individuals in a group (or per sex of the focal individuals within a group). Because group-level social times are independent, we did not apply a randomisation procedure for these data. These social dynamics were analysed using Java (OpenJDK version "21.0.7").

General modelling approach

To analyse: i) group-level consistency in social time, ii) the effect of recent ephemeral food patch availability on group-level social time, iii) the relation between group-level social change and

individual foraging success (Exp 1), and: iv) the effect of recent ephemeral food odour patch availability on group-level social time (Exp 2), we ran (generalised) linear mixed models (optimiser = bobyqa) from the *lme4* package (Bates et al., 2015) in R (R Core Team, 2025) version 4.5.1 in R Studio version 2025.05.1 (© 2009–2025 Posit Software, PBC). Model assumptions were confirmed by checking normality, overdispersion, outliers, and quantile deviations using the 'simulateResiduals()' function of the *DHARMa* package (Hartig, 2021). Based on these model diagnostics and the presence of singularity issues, 'pool identity' was included as either a random or fixed effect. These changes did not qualitatively change our conclusions, and they are reported in the supplementary table captions. We evaluated the significance of variables by comparing the model with and without the fixed effect or interaction of interest, using analysis of deviance (Type III Wald Chi-square tests). REML was set to false for the evaluation of fixed effects. Non-significant interactions were removed ($P > 0.05$), while all main effects were kept irrespective of significance. All continuous variables were centred and scaled by subtracting the mean and dividing by the standard deviation. We created the figures with the *ggplot2* package (Wickham, 2016).

(i) Consistency of sociality (Experiment 1)

We tested the consistency of group-level social time by constructing mixed models with group identity as a random effect, using the 'rpt()' function (1000 bootstraps) of the *rptR* package (Stoffel et al., 2017). We separately calculated the adjusted repeatability of group-level social time for the control and food treatment. These models included social session (three levels: S0, S1, S2, **Table 1**), day (two levels: day 1, day 2, **Table 1**), and pool identity (four levels: Pool 1, 2, 3, and 4). In addition, we added the group-level variables group size (seven or eight fish) and group-level foraging motivation (the average proportion of fish feeding, calculated as the number of individuals feeding divided by the total number of fish that arrived at each discovered food patch, averaged across all discovered food patches). A low group-level foraging motivation may reflect a more fearful state, leading guppies to be more social for other reasons than foraging. Excluding these group-level variables did not qualitatively change our conclusions. Differences in variance between the social sessions within control and food patch treatment were tested using Levene's test for equal variances.

(ii) *Ephemeral food patch effects on sociality (Experiment 1)*

To test if the time spent socially increased following ephemeral food patch availability, we analysed the effect of the interaction between treatment (two levels: food and control) and social session on

group-level social time, using a linear mixed model (N = 108 sessions). In the case of a significant interaction, we performed posthoc contrasts using the *emmeans* package (method = sequential, simple = each, adjust = mvt) (Lenth, 2021). As control variables, we added the main effects of day, group size, pool identity and the interaction between treatment and group-level foraging motivation. Group identity was included as a random effect. Subsequently, we examined the effect of ephemeral food patches on the (group-level) social state transition probabilities underlying social time (i.e., Ps→a and Pa→s). Similarly, we examined the effects of ephemeral food patch availability on group-level social time for the sexes separately, using the final model for group-level social time as the starting model. To test whether ephemeral food patch availability affected group-level social time over a prolonged period, we tested whether treatment had a significant effect on the first social (baseline) session of the next morning. Due to the limited sample size for this final analysis (N = 18 groups/sessions), we used a simple linear model that included only treatment. To test if ephemeral food patches also affected the frequency of sexual behaviours, we calculated the sum of sexual display and harassment behaviours for each group per social session, distinguishing between behaviours performed by males and behaviours received by females. We applied generalised linear mixed models (family = Poisson) and used the final model construction for sex-specific social time as the starting model. The aggression frequency was low (5% of all social observations) and, therefore, not further explored.

Observation order, aggregation and spatial activity effects (Experiment 1)

To examine if there was any focal observation order effect on time spent social, we measured the rank correlation (Kendall's coefficient) between an individual's social time and observation order, while performing within-group randomisation of the social times (10,000 randomisation steps), to account for the dependency of within-group social data. Individuals were not more or less likely to be social if they were more quickly observed after the first session of temporary food patch presentations (S1: Kendall's correlation coefficient = 0.03, P = 0.37; **Fig. S1**), although they were slightly more likely to be social after the second session (S2: Kendall's correlation coefficient = 0.15, P = 0.01; **Fig. S2**). Overall, we conclude that observation order did not substantially affect the representativeness of the social behaviour.

We also evaluated potential carry-over of local aggregation during the last food presentation to the subsequent social observations, by testing whether a higher social time in Exp 1 is linked to the location of the last food patch presentation. Specifically, we tested whether the fractions of social

349 contacts in the zone of the last food presentation were higher after the food patch presentations
350 (S1 or S2) than in that same zone before the food patch presentations (S0), using Matched-pairs
351 Wilcoxon tests (see Results).

352 In addition, we calculated the spatial zone transition probabilities, quantifying how likely individuals
353 were to remain in the same spatial zone or to have moved to another spatial zone during the
354 subsequent observation point (i.e., ten seconds later). Similar to the social analysis, we focused
355 these analyses on the group level, meaning that we estimated each transition probability based on
356 the sum of the number of zone changes across all focal individuals in a group per observation
357 session. We evaluated whether the probability of changing zones increased following ephemeral
358 food patch exposure (see Results) using the same linear mixed modelling approach as described
359 above (see (ii) *Ephemeral food patch effects on sociality*). In addition, we tested whether social
360 time and the underlying social transition probabilities correlated with the probability of transitioning
361 between spatial zones (i.e. spatial activity) during the social sessions of the food treatment (i.e.
362 Sessions S0-S2, N = 54). For this we ran three linear mixed models with either social time,
363 probability to start social contact or probability to end social contact as dependent variable,
364 probability to change spatial zones as fixed covariate of interest and included social session (three
365 levels: S0-S2, **Table 1**), day (two levels: day 1, day 2, **Table 1**), group size (seven or eight fish)
366 and group-level foraging motivation as control variables. Group identity (18 levels) nested in pool
367 identity (four levels) was added as a random effect. In the models for both social transition
368 probabilities, pool identity was included as a fixed effect to account for model fit issues (see
369 '*General modelling approach*'). Again, including pool identity as either a fixed or random effect did
370 not qualitatively change our conclusions.

371 *(iii) Change in sociality as predictor of individual foraging success (Experiment 1)*

372 To test if a change in the time a group spends socially in response to ephemeral food patch
373 availability predicted individual foraging success, we ran a generalised linear mixed model (family
374 = binomial) with individual arrival at a detected food resource, 'detected' meaning that at least one
375 guppy in the pool arrived at the resource (two levels: yes, no) as the dependent variable (N =
376 9,663). Social change was calculated as the difference between group-level social time after the
377 first food session (S1) and before (S0). The model included the interactions between social change
378 and group-level foraging motivation, sex (two levels: male and female), and food presentation
379 series (two levels: F1 and F2, **Table 1**). In addition, the model included day, size (length in mm,

380 centred on sex, continuous), group size, and pool identity as the main effects. Group identity
381 nested in pool identity (18 levels), individual identity nested in group identity (140 levels),
382 presentation location nested in pool identity (20 levels), and presentation identity (1,237 levels)
383 were included as random effects. Note that pool was not included as a random effect but as a fixed
384 effect (see '*General Modelling Approach'*).

385 We furthermore evaluated if social change as a significant predictor of foraging success (see
386 Results) could be explained by a change in sexual behaviour frequency, i.e., if an increase in social
387 time merely represents an increase in sexual behaviour following food intake. For this, the effect of
388 sex-specific social change on food patch arrival was first tested using the final model for both sexes
389 combined as the starting model. Subsequently, the change in sex-specific social time was replaced
390 in the final model with change in sexual behaviours performed (males) or sexual behaviours
391 received (females), and these models were compared based on AICc. We calculated AICc using the
392 'AICctab()' function of the *bbmle* package (Bolker and R Development Core Team, 2021). We
393 report the difference in AICc, inferring a relevant model improvement if the AIC decreases by more
394 than 2. To examine whether predicted effects of social change on individual foraging success could
395 be explained by either social time before the first food resource availability (S0) or social time after
396 the first food session (S1), we first tested for correlations between these variables using
397 Spearman's rank correlation tests. Next, we substituted social change in the final model for either
398 of these social measures and calculated the AICc.

399 Lastly, to test if arrival at an ephemeral novel food patch also predicted food intake (Exp 1), and
400 thus was a relevant measure for foraging success, we calculated the total number of feeding events
401 per individual, i.e. the total number of times an individual took at least one bite from a visited food
402 patch. We correlated these with the proportion of time an individual arrived at a novel food patch,
403 using Spearman rank correlations. We ran these analyses for males and females separately.

404 *(iv) Ephemeral food odour patch effects on sociality (Experiment 2)*

405 To test if an increase in sociality may be merely driven by food consumption, we tested if the time
406 spent socially changed following the ephemeral availability of an inaccessible food patch (odour
407 cue). We analysed the effect of treatment (two levels: food odour and control) on group-level
408 social time (average of S1+S2) using a simplified linear mixed model (N = 36 values). As a control
409 variable, we only added pool identity (three levels) as a fixed effect. We included pool identity as a

410 fixed effect rather than a random effect following model diagnostics (see '*General modelling*

411 *approach*'). Group identity was included as a random effect.

412

413 # 3. Results

414 **Ephemeral food patch effects on sociality**

415 Wild guppy groups consistently differed in how much time their members spent social under
416 baseline conditions, with group-level sociality being repeatable (Control S0-S1-S2: R_{adj} = 0.48, SE
417 = 0.17, P = 0.01, **Fig. 1A & D**) and relatively stable across the three control sessions (S0: **0.26**,
418 95% CI = 0.22-0.31; S1: **0.23**, 95% CI= 0.19-0.27; S2: **0.25**, 95% CI = 0.21-0.29; Equality of
419 variances: $W_{2,51}$ = 0.49, P = 0.61, **Fig. 1**). After recent experience with patchy and ephemeral food
420 resources in the environment, the average proportion of time spent socially significantly increased
421 (Treatment*Session: $\chi2 = 55.65$, $P < 0.001$, **Table S1 & S2**), rising twofold (S0: **0.22**, 95% CI =
422 0.18-0.26; S1: **0.46**, 95% CI= 0.39-0.53; S2: **0.48**, 95% CI = 0.40-0.57, **Fig. 1**). In addition, the
423 variance in sociality across groups increased ($W_{2,51}$ = 6.13, P = 0.004) and repeatability of group-
424 level sociality disappeared (Food S0-S1-S2, R_{adj} = 0.15, SE = 0.14, P = 0.50, **Fig. 1B** & **C**).
425 Interestingly, despite the substantial social changes following the initial presentations of novel food
426 patches, sociality differences between groups quickly stabilised (Food S1-S2, R_{adj} = 0.66, SE =
427 0.15, P = 0.01, **Fig. 1B & C**). An increase in sociality was still detectable the next morning
428 (Treatment: Estimate (Est) ± SE = 0.09 ± 0.04, N = 18, F = 6.42, P = 0.02, S0 in **Fig. 1D** vs **B**).

429 More motivated groups changed their social behaviour more strongly in response to the ephemeral
430 food patches than less motivated groups (Treatment*Group-level foraging motivation: $\chi2 = 9.53$,
431 $P = 0.002$, **Table S1**). Both females and males were more social following ephemeral food patch
432 exposure compared to ephemeral control patch exposure (Females: Treatment*Session:
433 $\chi2 = 27.65$, $P < 0.001$, **Table S3**; Males: Treatment*Session: $\chi2 = 40.52$, $P < 0.001$, **Table S4**). Yet
434 only males still showed an increase in sociality during the first social observation session of the
435 next morning (Males: Treatment: Est ± SE = 0.11 ± 0.03, N = 18, F = 10.77, P = 0.005; Females:
436 Treatment: Est ± SE = 0.07 ± 0.06, N = 18, F = 1.54, P = 0.23).

437 The time a fish spends social is the result of both the probability of starting social contact and the
438 probability of ending social contact. Analysing these two components of sociality separately, we
439 observed that experience with ephemeral food patches increased the probability of fish starting
440 social contact (Treatment*Session: $\chi2 = 28.72$, $P < 0.001$, **Table S5**), as well as decreased the
441 probability of fish to end social contact (Treatment*Session: $\chi2 = 20.38$, $P < 0.001$, **Table S6**),
442 suggesting that fish initiated more as well as longer social associations.

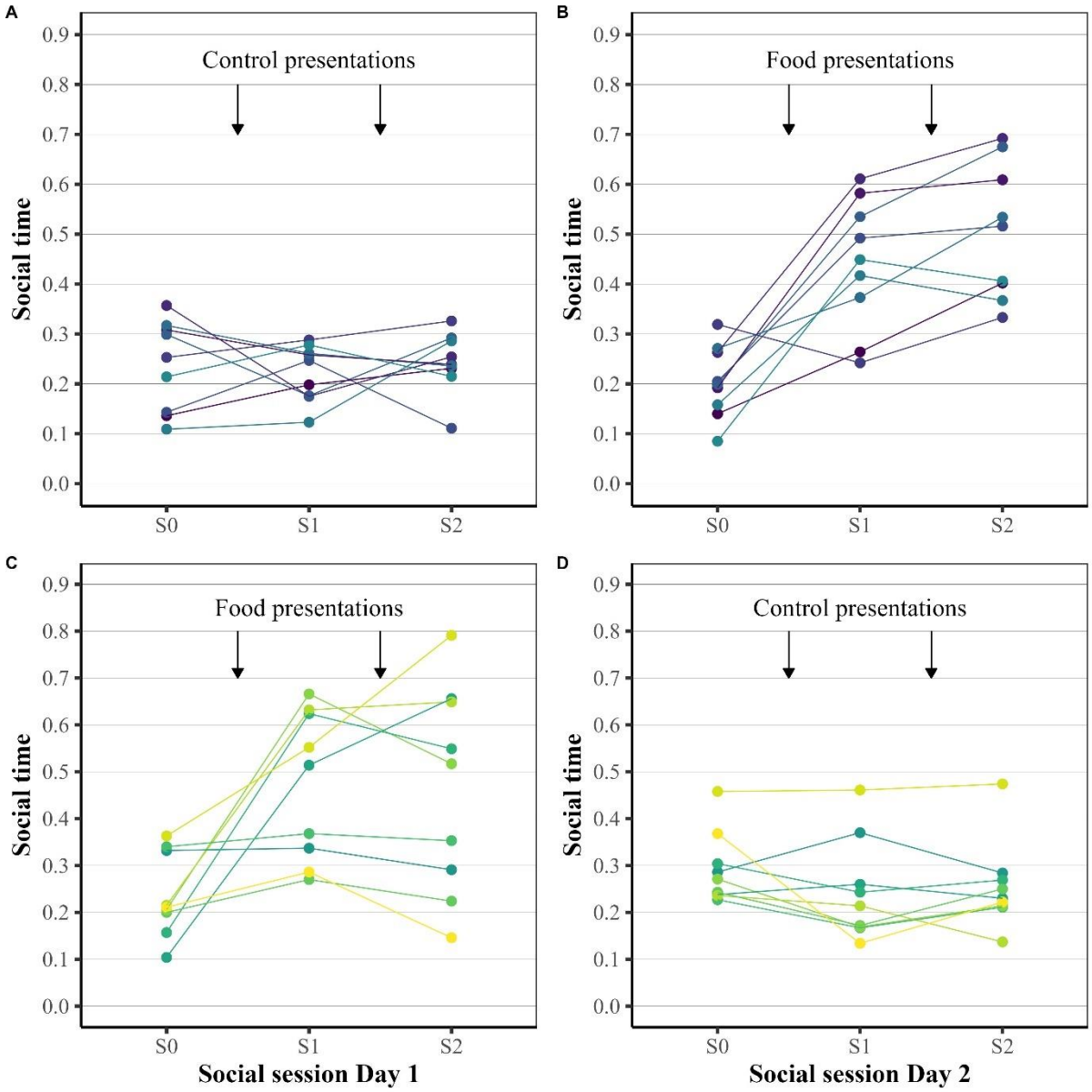

Figure 1. Time spent social by 18 groups of wild guppies before, between, and after two series of repeated food patch or control patch presentations. Arrows indicate the timing of the presentations. A) Groups that received the control patches on the first day, B) received the food patches on the second day. C) Groups that received the food patches on the first day, D) received the control patches on the second day. The values of the second day's first social observation session (S0) visualise the prolonged effects of exposure to ephemeral food patches on group-level social time. Colours depict group ID.

Local aggregation and spatial activity

Social contacts in the zones of the most recently visited food patch were just as likely to take place before as after the temporary food patch became available (**Table S7**), indicating that the increase in group-level sociality during the food patch treatment was not a carry-over effect of local aggregation at the last visited food resource. In fact, fish became more likely to transition between

spatial zones following ephemeral food patch exposure (Treatment*Session: $\chi2 = 7.92$, $P = 0.02$, **Table S8 & S9**), indicating increased spatial activity rather than spatial aggregation (S0: **0.17**, 95% CI = 0.14-0.20; S1: **0.23**, 95% CI= 0.19-0.27; S2: **0.22**, 95% CI = 0.19-0.26, **Fig. S3**), compared to control. However, increased spatial activity could, in turn, also lead to a passive increase in social time by increasing the chance of (random) social encounters. Nevertheless, more spatially active fish did not spend more of their time social (Est ± SE = 0.05 ± 0.26, N = 54, $\chi2 = 0.04$, $P = 0.84$, **Fig. S4A**). Even though a higher spatial activity, indeed, predicted a higher probability to start social contact (Est ± SE = 0.58 ± 0.13, N = 54, $\chi2 = 18.59$, $P < 0.001$, **Fig. S4B**), it also predicted a higher probability to end social contact (Est ± SE = 0.61 ± 0.28, N = 54, $\chi2 = 4.61$, $P = 0.03$, **Fig. S4C**), illustrating that increased movement activity, had a net zero effect on group-level sociality.

Change in sociality as predictor of individual foraging success

Change in group-level sociality positively correlated with arrival at novel food patches for individuals from highly motivated groups, but not for individuals in lowly motivated groups (Social change*Group-level foraging motivation: $\chi2 = 4.81$, $P = 0.03$, **Table S10**; **Fig. 2**). This relationship between the arrival of individuals at detected novel food patches and group-level social change did not differ between the sexes (Social change*Sex: $\chi2 = 2.59$, $P = 0.11$, **Table S10**). In both females and males, the proportion of food patches reached positively predicted the number of feeding events (Females: $r_s = 0.94$, N = 69, $P < 0.001$; Males: $r_s = 0.90$, N = 71, $P < 0.001$), supporting that patch arrival is indeed a meaningful measure of foraging success in this study.

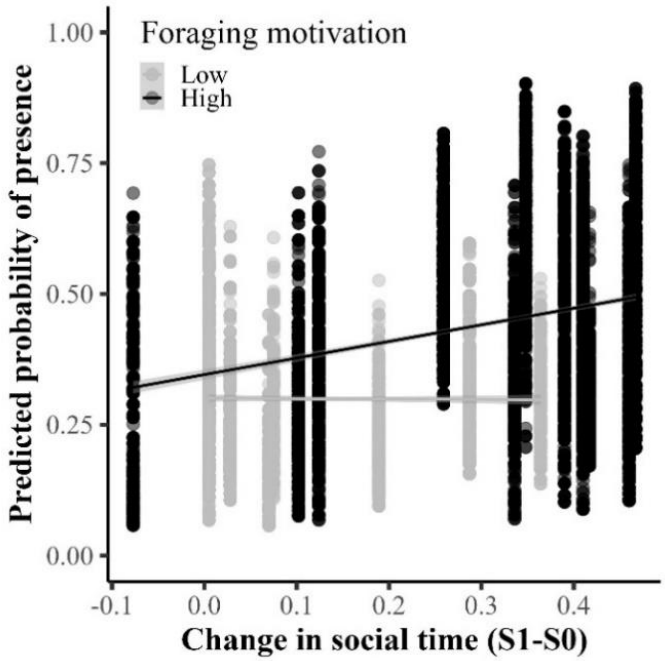

Figure 2. Predicted probability of an individual arriving at a detected food patch in relation to the change in time spent social by an individual's group following the first series of ephemeral food patch presentations. Predictions were retrieved from the final model for individual presence or absence at a discovered food patch. Group-level foraging motivation (proportion of arrived individuals feeding at a patch) is visualised as categorical for illustration purposes (Low: ≤ 0.5, High: > 0.5) but was analysed as a continuous variable. Trend lines and corresponding standard errors (grey area) were calculated using the function' geom_smooth()' from the package 'ggplot2'.

Ephemeral food patch effects on sexual behaviours

Corresponding with the increase in group-level sociality, males performed more display and harassment behaviours after the first session of novel food patch presentations (Treatment*Session: $\chi2 = 22.94$, $P < 0.001$, **Table S11**) and, consequently, females received more of such sexual behaviours (Treatment*Session: $\chi2 = 6.92$, $P = 0.03$, **Table S12**). Males also displayed and harassed more frequently in the first social session on the morning after food patch presentations than on the morning after control presentation (Treatment Males: Est ± SE = 1.02 ± 0.34, N = 18, $\chi2 = 9.00$, $P = 0.003$). Even though social time and sexual behaviour frequency were correlated (Males: $r_s = 0.54$, N = 108, $P < 0.001$; Females: $r_s = 0.57$, N = 108, $P < 0.001$), the increase in social time explained the increase in individual arrivals at food patches better (**Table S13-S14**) than the increase in sexual behaviours (Sexual behaviour Males: Delta AICc = -6.12; Females: Delta AICc = -3.59).

495 **Ephemeral food odour patch effects on sociality (Experiment 2)**

496 Guppy groups also increased sociality when they could see and smell ephemeral food patches (but
497 not eat from them (Treatment: $\chi 2 = 19.59$, $P < 0.001$, **Table S15**, **Fig. 3**). The average proportion
498 of time spent socially during and after food odour presentations was approximately 1.4 times
499 higher (S1+S2 = **0.44**, 95% CI = 0.38-0.50) compared to control exposure (S1+S2 = **0.31**, 95%
500 CI = 0.26-0.36).

501 The food odour stimulus received thirteen times as many pecks as the control stimulus, confirming
502 that the guppies recognised it as a relevant food source. Moreover, the food odour and control
503 presentations generated a comparable (minor) number of sexual and agonistic social interactions
504 at the stimulus (29 events each), suggesting the observed increase in sociality was not a carry-
505 over of increased social activity near the food odour stimulus.

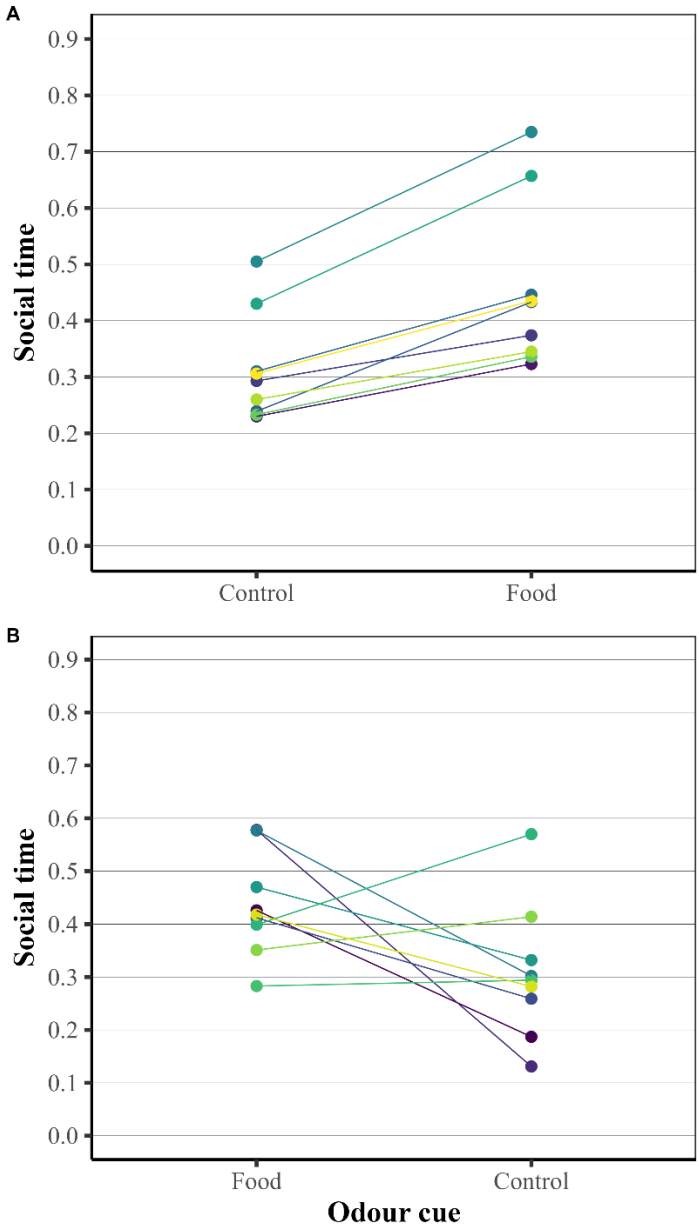

Figure 3. Time spent social by the 18 groups of wild guppies following exposure to two series of ephemeral food odour or control cue presentations. A) Nine groups first received two series of the control treatment, followed by two series of the food odour treatment. B) Nine groups first received two series of food odour treatment, followed by two series of control treatment. Social values from the two social observation sessions (S1 and S2) were combined into one value per group per treatment. Colours depict group ID.

513 # 4. Discussion

514 Social flexibility may make animals better prepared to cope with resource fluctuations. Our study
515 provides experimental support for the hypothesis that wild fish can flexibly alter fission-fusion
516 behaviour in response to patchy and ephemeral resource availability and so enhance resource
517 localisation. First, we show that experimentally providing experience with patchy and ephemeral food
518 resources leads to rapid and substantial changes in the time spent social by wild Trinidadian guppies
519 living in resource-poor environments. Our analyses of social and spatial transition probabilities do
520 not support increased spatial activity or local aggregation as the core mechanism underlying this
521 observed increase in sociality. Second, we demonstrate that group-level increase in the overall time
522 spent social positively predicts individual food patch discovery, mediated by group-level foraging
523 motivation. These findings are consistent with an earlier study showing that individual food patch
524 discovery and food consumption of wild guppies increased when the (manipulated) number of
525 guppies in the pool also increased (Snijders et al., 2021). Lastly, experience with patchy and
526 ephemeral food odour stimuli likewise resulted in substantially more time spent social, supporting
527 the hypothesis that the observed social state changes were not merely a consequence of satiation
528 effects. Together, our findings suggest that wild guppies may actively regulate sociality to better
529 locate ephemeral food patches and thus enhance their foraging efficiency in fluctuating
530 environments.

531 Wild guppy groups doubled their time spent social following the ephemeral presence of novel food
532 patches. This increase contrasts with previous environment and density manipulations, which did
533 not show such large effects on social time (Krause et al., 2017; Wilson et al., 2015), highlighting
534 the key role of the foraging context in social behaviour. Lab studies also observed group-level
535 social responses to changes in the foraging context, but in opposite directions (Hoare et al., 2004;
536 Jolles et al., 2018; Schaerf et al., 2017). For example, x-ray tetras (*Pristella maxillaris*) and
537 banded killifish (*Fundulus diaphanus*) reduced encounter frequency and group size, respectively,
538 when exposed to a more uniformly presented food cue (Hoare et al., 2004; Schaerf et al., 2017).
539 These varying responses suggest that sociality's benefits may depend on factors like baseline
540 sociality and intraspecific competition costs. Highly social groups should do better by initially
541 reducing sociality or becoming more disordered (MacGregor et al., 2020), allowing for the
542 gathering of more independent private information, while guppies in low-predation populations,
543 with low baseline sociality and minimal aggression, may benefit from increased sociality when

social food cues are present (e.g., odour and movement cues), enhancing opportunities for acquiring social information. Moreover, the perceived spatial distribution of food resources is predicted to strongly affect the expected individual resource gain of social information use (Oestreich et al., 2026), with social information being more valuable for detecting patchy rather than uniformly distributed resources, and may thus additionally explain the contrasting results of the studies.

Recent evidence highlights consistent yet responsive sociality in animal groups (Jolles et al., 2018; MacGregor and Ioannou, 2022; Schaerf et al., 2017). Our guppy groups showed consistent variation in sociality during control presentations, similar to a recent lab study with the same species (Clark et al., 2025), yet between-group variances increased following exposure to ephemeral food patches. We can rule out time or familiarity effects (MacGregor and Ioannou, 2022), as no similar pattern occurred in control treatments. Some groups changed more strongly than others, contrasting with Jolles et al., (2018), who found consistent group structure in sticklebacks (*Gasterosteus aculeatus*) before and after resource depletion. Individual heterogeneity within groups likely played a role, as it can influence group functioning (Farine et al., 2015; Jolles et al., 2020a) and foraging success (Dyer et al., 2009; Hasenjager et al., 2020a). Differences in locomotion and personality types can drive group cohesion, alignment, and leadership (Jolles et al., 2020b, 2017). However, little is known about how group composition affects responsiveness to environmental changes and challenges in the wild (but see Cerritelli et al., 2025). Specific phenotypes may enhance group adaptability, influencing the natural selection of these phenotypes.

Wild animals often need to spend a substantial amount of time on locating food resources, constraining the time available for other behaviours, such as sexual pursuits (Borgeaud et al., 2021; Gareta García et al., 2021; Kolluru and Grether, 2005). The increase in sexual behaviour of male guppies following food patch localisation indeed illustrates how increased access to food can influence behavioural time budgets and shows how male guppies, living in resource-limited environments, may enjoy additional reproductive benefits from finding more high-quality food resources (Abrahams, 1993; Kolluru and Grether, 2005). However, to rule out that the observed change in sociality was merely a consequence of satiation-related time-budget changes, rather than an active social strategy, we repeated our experiment using food cues (Hoare et al., 2004; Schaerf et al., 2017), and again observed a substantial increase in time spent socially. Alternatively, a reduction in perceived competition costs following an increase in the temporary

575 (perceived) availability of food could have altered the guppies' social behaviour. However, the
576 comparable low frequency of aggressive interactions we observed near food and control odour cues
577 suggests relatively high levels of social tolerance (De la Fuente et al., 2022; DeTroy et al., 2021), a
578 population-level characteristic that was also documented in earlier studies (e.g., Snijders et al.,
579 2021). We therefore consider changes in perceived or real competition following our treatments as
580 an unlikely explanation of the substantial changes in sociality we observed.

581 Group-level responses are not necessarily the sum of individual responses (Bengston and Jandt,
582 2014), and groups may outperform individuals (Harpaz and Schneidman, 2020; Pitcher et al.,
583 1982; Sasaki et al., 2013). Our experimental design limited our ability to gather robust individual-
584 level data, preventing exploration of whether group-level changes were emergent properties.
585 Future research, with advancements in automated video-tracking, could examine whether changes
586 in group-level sociality predict individual foraging success better than individual-level changes. This
587 may reveal that individuals differ in how much their foraging success improves through social
588 associations versus foraging alone, which could explain individual differences in sociability and its
589 maintenance through selective forces in dynamic resource environments. For example, more social
590 foragers will be more vulnerable to large fluctuations in population density (Harel et al., 2017),
591 while more solitary foragers will generally experience greater variance in foraging, making them
592 more at risk during large fluctuations in available resources (Brown, 1988; Jolles et al., 2017;
593 Oestreich et al., 2026).

594 In conclusion, through multiple lines of evidence, our study provides new insight into the adaptability
595 of fission-fusion systems under rapidly changing resource conditions in the wild. Specifically, we
596 showed that ephemeral food patch availability generates substantial and profitable changes in an
597 otherwise consistent group-level social trait. By considering and testing alternative explanations for
598 social change following exposure to temporary food patches, such as carry-over of spatial
599 aggregations, increased spatial activity following food anticipation, sexually motivated behaviours,
600 satiation effects and changes in perceived competition costs, we built a strong case for instrumental
601 use of sociality as a likely explanation. Overall, our findings are consistent with earlier studies in the
602 same population linking increased sociality to increased food patch localisation (Snijders et al., 2021,
603 2019, 2018). Further experimentation is required to reveal the precise social mechanism underlying
604 increased food patch localisation efficiency (e.g., social facilitation or social information use).
605 Furthermore, revealing the individual and group-level factors driving variation in (adaptive) social

responsiveness, the potential mediating effects of individual learning and the relative effects of resource variability on social responsiveness would provide relevant avenues for future research.

Data availability statement

Supplemental tables and figures can be accessed through the Supplemental Information file. The data and code are available on the Open Science Framework:
https://osf.io/75vtn/overview?view_only=7fb9124575ad447e80ccbb8b6264aa35

Acknowledgements

We are grateful to Bertrand Jayles for help with the data collection and Eline Weenink for the video analysis. L.S. was funded by a Humboldt Research Fellowship for Postdoctoral Researchers awarded by the Alexander von Humboldt-Stiftung (2019; Ref 3.3 – NLD – 1192631 - HFST-P), supported by the Klaus Tschira Boost Fund (2019; KT09) and a Veni Fellowship awarded by the Netherlands Organisation for Scientific Research (NWO) (2020–2023; VI.Veni.192.018).

Author contributions

L.S., R.H.J.M., S.K., J.K. and I.W.R. conceived the ideas and designed the methodology. L.S., R.H.J.M., S.K., A.N.T, M.B., and J.K. collected the data; L.S. and S.K. analysed the data; L.S., I.W.R., R.H.J.M.K., and J.K. contributed materials and infrastructure to the study; L.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of Interest

All authors declare no conflict of interest.

References

Abrahams, M.V., 1993. The trade-off between foraging and courting in male guppies. Anim. Behav. 45, 673–681. https://doi.org/10.1006/anbe.1993.1082

Aplin, L.M., Farine, D.R., Morand-Ferron, J., Sheldon, B.C., 2012. Social networks predict patch discovery in a wild population of songbirds. Proc. R. Soc. B Biol. Sci. 279, 4199–4205. https://doi.org/10.1098/rspb.2012.1591

Barbosa, M., Deacon, A.E., Janeiro, M.J., Ramnarine, I., Morrissey, M.B., Magurran, A.E., 2018. Individual variation in reproductive behaviour is linked to temporal heterogeneity in predation risk. Proc. R. Soc. B Biol. Sci. 285, 20171499. https://doi.org/10.1098/rspb.2017.1499

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Bengston, S.E., Jandt, J.M., 2014. The development of collective personality: the ontogenetic drivers of behavioral variation across groups. Front. Ecol. Evol. 2, 81. https://doi.org/10.3389/fevo.2014.00081

Blanckenhorn, W.V., 1991. Fitness consequences of foraging success in water striders (*Gerris remigis*; Heteroptera: Gerridae). Behav. Ecol. 2, 46–55. https://doi.org/10.1093/beheco/2.1.46

Bolker, B., R Development Core Team, 2021. bbmle: Tools for General Maximum Likelihood Estimation. R package.

Borgeaud, C., Jankowiak, B., Aellen, M., Dunbar, R.I.M., Bshary, R., 2021. Vervet monkeys socialise more when time budget constraints are experimentally reduced. Ethology 127, 682–696. https://doi.org/10.1111/eth.13205

Brown, C.R., 1988. Social foraging in cliff swallows: local enhancement, risk sensitivity, competition and the avoidance of predators. Anim. Behav. 36, 780–792. https://doi.org/10.1016/S0003-3472(88)80161-1

Carter, A.J., Torrents Ticó, M., Cowlishaw, G., 2016. Sequential phenotypic constraints on social information use in wild baboons. eLife 5, e13125. https://doi.org/10.7554/eLife.13125

Cerritelli, G., Giunchi, D., Musters, R., Vertua, I., Vanni, L., Rubolini, D., Gagliardo, A., Carere, C., 2025. Personality composition affects group cohesion of homing pigeons in response to novelty and predation threat. Anim. Behav. 223, 123122. https://doi.org/10.1016/j.anbehav.2025.123122

Chapman, C.A., Chapman, L.J., Wrangham, R.W., 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav. Ecol. Sociobiol. 36, 59–70. https://doi.org/10.1007/BF00175729

Clark, C.W., Mangel, M., 1986. The evolutionary advantages of group foraging. Theor. Popul. Biol. 30, 45–75. https://doi.org/10.1016/0040-5809(86)90024-9

Clark, M.A., Waples, E., Radford, A.N., Simpson, S.D., Ioannou, C.C., 2025. Group personality, rather than acoustic noise, causes variation in group decision-making in guppy shoals. Sci. Rep. 15, 18801. https://doi.org/10.1038/s41598-025-03225-y

Clay, T.A., Pearmain, E.J., McGill, R.A.R., Manica, A., Phillips, R.A., 2018. Age-related variation in non-breeding foraging behaviour and carry-over effects on fitness in an extremely long-lived bird. Funct. Ecol. 32, 1832–1846. https://doi.org/10.1111/1365-2435.13120

Clément, R.J.G., Vicente-Page, J., Mann, R.P., Ward, A.J.W., Kurvers, R.H.J.M., Ramnarine, I.W., de Polavieja, G.G., Krause, J., 2017. Collective decision making in guppies: a cross-population comparison study in the wild. Behav. Ecol. 28, 919–924. https://doi.org/10.1093/beheco/arx056

Croft, D. P., Albanese, B., Arrowsmith, B.J., Botham, M., Webster, M., Krause, J., 2003. Sex-biased movement in the guppy (*Poecilia reticulata*). Oecologia 137, 62–68. https://doi.org/10.1007/s00442-003-1268-6

Croft, D. P., Arrowsmith, B.J., Bielby, J., Skinner, K., White, E., Couzin, I.D., Magurran, A.E., Ramnarine, I., Krause, J., 2003. Mechanisms underlying shoal composition in the Trinidadian guppy, *Poecilia reticulata*. Oikos 100, 429–438. https://doi.org/10.1034/j.1600-0706.2003.12023.x

Darden, S.K., James, R., Ramnarine, I.W., Croft, D.P., 2009. Social implications of the battle of the sexes: sexual harassment disrupts female sociality and social recognition. Proc. R. Soc. B Biol. Sci. 276, 2651–2656. https://doi.org/10.1098/rspb.2009.0087

Day, R.L., MacDonald, T., Brown, C., Laland, K.N., Reader, S.M., 2001. Interactions between shoal size and conformity in guppy social foraging. Anim. Behav. 62, 917–925. https://doi.org/10.1006/anbe.2001.1820

De la Fuente, M.F., Sueur, C., Garber, P.A., Bicca-Marques, J.C., Souto, A., Schiel, N., 2022. Foraging networks and social tolerance in a cooperatively breeding primate (*Callithrix jacchus*). J. Anim. Ecol. 91, 138–153. https://doi.org/10.1111/1365-2656.13609

Deacon, A.E., Jones, F.A.M., Magurran, A.E., 2018. Gradients in predation risk in a tropical river system. Curr. Zool. 64, 213–221. https://doi.org/10.1093/cz/zoy004

DeTroy, S.E., Ross, C.T., Cronin, K.A., Leeuwen, E.J.C. van, Haun, D.B.M., 2021. Cofeeding tolerance in chimpanzees depends on group composition: A longitudinal study across four communities. iScience 24, 102175. https://doi.org/10.1016/j.isci.2021.102175

Dorning, J., Harris, S., 2019. Individual and seasonal variation in contact rate, connectivity and centrality in red fox (*Vulpes vulpes*) social groups. Sci. Rep. 9, 1–11. https://doi.org/10.1038/s41598-019-56713-3

Dyer, J.R.G., Croft, D.P., Morrell, L.J., Krause, J., 2009. Shoal composition determines foraging success in the guppy. Behav. Ecol. 20, 165–171. https://doi.org/10.1093/beheco/arn129

Egert-Berg, K., Hurme, E.R., Greif, S., Goldstein, A., Harten, L., Herrera M., L.G., Flores-Martínez, J.J., Valdés, A.T., Johnston, D.S., Eitan, O., Borissov, I., Shipley, J.R., Medellin, R.A., Wilkinson, G.S., Goerlitz, H.R., Yovel, Y., 2018. Resource Ephemerality Drives Social Foraging in Bats. Curr. Biol. 28, 3667-3673.e5. https://doi.org/10.1016/j.cub.2018.09.064

Ellis, S., Franks, D.W., Nattrass, S., Cant, M.A., Weiss, M.N., Giles, D., Balcomb, K.C., Croft, D.P., 2017. Mortality risk and social network position in resident killer whales: Sex differences and the importance of resource abundance. Proc. R. Soc. B Biol. Sci. 284, 20171313. https://doi.org/10.1098/rspb.2017.1313

Farine, D.R., Montiglio, P.-O., Spiegel, O., 2015. From Individuals to Groups and Back: The Evolutionary Implications of Group Phenotypic Composition. Trends Ecol. Evol. 30, 609–621. https://doi.org/10.1016/j.tree.2015.07.005

Firth, J.A., Sheldon, B.C., Farine, D.R., 2016. Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. Biol. Lett. 12, 20160144. https://doi.org/10.1098/rsbl.2016.0144

Fisher, D.N., Kilgour, R.J., Siracusa, E.R., Foote, J.R., Hobson, E.A., Montiglio, P.-O., Saltz, J.B., Wey, T.W., Wice, E.W., 2021. Anticipated effects of abiotic environmental change on intraspecific social interactions. Biol. Rev. 96, 2661–2693. https://doi.org/10.1111/brv.12772

Formica, V.A., Wood, C., Larsen, W., Butterfield, R., Augat, M., Hougen, H., Brodie, E., 2012. Fitness consequences of social network position in a wild population of forked fungus beetles (*Bolitotherus cornutus*). J. Evol. Biol. 25, 130–137. https://doi.org/10.1111/j.1420-9101.2011.02411.x

Foster, E.A., Franks, D.W., Morrell, L.J., Balcomb, K.C., Parsons, K.M., van Ginneken, A., Croft, D.P., 2012. Social network correlates of food availability in an endangered population of killer whales, *Orcinus orca*. Anim. Behav. 83, 731–736. https://doi.org/10.1016/j.anbehav.2011.12.021

Franks, V.R., Marshall, R.C., 2013. Mechanisms and extent of information transfer in socially foraging guppies, *Poecilia reticulata*. Anim. Behav. 85, 103–108. https://doi.org/10.1016/j.anbehav.2012.10.013

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods Ecol. Evol. 7, 1325–1330. https://doi.org/10.1111/2041-210X.12584

Galef, B.G., Giraldeau, L.-A., 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim. Behav. 61, 3–15. https://doi.org/10.1006/anbe.2000.1557

Garcia, T., De Monte, S., 2013. Group Formation and the Evolution of Sociality. Evolution 67, 131–141. https://doi.org/10.1111/j.1558-5646.2012.01739.x

Gareta García, M., Farine, D.R., Brachotte, C., Borgeaud, C., Bshary, R., 2021. Wild female vervet monkeys change grooming patterns and partners when freed from feeding constraints. Anim. Behav. 181, 117–136. https://doi.org/10.1016/j.anbehav.2021.08.027

Godfrey, S.S., Bull, C.M., James, R., Murray, K., 2009. Network structure and parasite transmission in a group living lizard, the gidgee skink, *Egernia stokesii*. Behav. Ecol. Sociobiol. 63, 1045–1056. https://doi.org/10.1007/s00265-009-0730-9

Grether, G.F., Millie, D.F., Bryant, M.J., Reznick, D.N., Mayea, W., 2001. Rain forest canopy cover, resource availability, and life history evolution in guppies. Ecology 82, 1546–1559. https://doi.org/10.2307/2679799

Grubb, T.C., 1987. Changes in the flocking behaviour of wintering English titmice with time, weather and supplementary food. Anim. Behav. 35, 794–806. https://doi.org/10.1016/S0003-3472(87)80116-1

Harel, R., Spiegel, O., Getz, W.M., Nathan, R., 2017. Social foraging and individual consistency in following behaviour: testing the information centre hypothesis in free-ranging vultures. Proc. R. Soc. B Biol. Sci. 284, 20162654. https://doi.org/10.1098/rspb.2016.2654

Harpaz, R., Schneidman, E., 2020. Social interactions drive efficient foraging and income equality in groups of fish. eLife 9, e56196. https://doi.org/10.7554/eLife.56196

Hartig, F., 2021. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package.

Hasenjager, M.J.; Dugatkin, L.A., 2017. Fear of predation shapes social network structure and the acquisition of foraging information in guppy shoals. Proc. Biol. Sci. 284, 20172020-NA. https://doi.org/10.1098/rspb.2017.2020

Hasenjager, M.J., Hoppitt, W., Dugatkin, L.A., 2020a. Personality composition determines social learning pathways within shoaling fish. Proc. R. Soc. B Biol. Sci. 287, 20201871. https://doi.org/10.1098/rspb.2020.1871

Hasenjager, M.J., Hoppitt, W., Leadbeater, E., 2020b. Network-based diffusion analysis reveals context-specific dominance of dance communication in foraging honeybees. Nat. Commun. 11, 1–9. https://doi.org/10.1038/s41467-020-14410-0

Heinen, V.K., Benedict, L.M., Sonnenberg, B.R., Bridge, E.S., Farine, D.R., Pravosudov, V.V., 2022. Experimental manipulation of food distribution alters social networks and information transmission across environments in a food-caching bird. Anim. Behav. 193, 1–12. https://doi.org/10.1016/j.anbehav.2022.08.007

Hoare, D.J., Couzin, I.D., Godin, J.-G.J., Krause, J., 2004. Context-dependent group size choice in fish. Anim. Behav. 67, 155–164. https://doi.org/10.1016/j.anbehav.2003.04.004

Jolles, J.W., Boogert, N.J., Sridhar, V.H., Couzin, I.D., Manica, A., 2017. Consistent individual differences drive collective behavior and group functioning of schooling fish. Curr. Biol. 27, 2862-2868.e7. https://doi.org/10.1016/j.cub.2017.08.004

Jolles, J.W., King, A.J., Killen, S.S., 2020a. The Role of Individual Heterogeneity in Collective Animal Behaviour. Trends Ecol. Evol. 35, 278–291. https://doi.org/10.1016/j.tree.2019.11.001

Jolles, J.W., Laskowski, K.L., Boogert, N.J., Manica, A., 2018. Repeatable group differences in the collective behaviour of stickleback shoals across ecological contexts. Proc R Soc B 285, 20172629. https://doi.org/10.1098/rspb.2017.2629

Jolles, J.W., Weimar, N., Landgraf, T., Romanczuk, P., Krause, J., Bierbach, D., 2020b. Group-level patterns emerge from individual speed as revealed by an extremely social robotic fish. Biol. Lett. 16, 20200436. https://doi.org/10.1098/rsbl.2020.0436

Jungwirth, A., Balzarini, V., Zöttl, M., Salzmann, A., Taborsky, M., Frommen, J.G., 2019. Long-term individual marking of small freshwater fish: the utility of Visual Implant Elastomer tags. Behav. Ecol. Sociobiol. 73, 49. https://doi.org/10.1007/s00265-019-2659-y

Karplus, I., Katzenstein, R., Goren, M., 2006. Predator recognition and social facilitation of predator avoidance in coral reef fish Dascyllus marginatus juveniles. Mar. Ecol. Prog. Ser. 319, 215–223. https://doi.org/10.3354/meps319215

Kolluru, G.R., Grether, G.F., 2005. The effects of resource availability on alternative mating tactics in guppies (*Poecilia reticulata*). Behav. Ecol. 16, 294–300. https://doi.org/10.1093/beheco/arh161

Komdeur, J., Ma, L., 2021. Keeping up with environmental change: The importance of sociality. Ethology 127, 790–807. https://doi.org/10.1111/eth.13200

Krause, J., Ruxton, G.D., 2002. Living in groups. Oxford University Press, Oxford, UK.

Krause, S., Wilson, A.D.M., Ramnarine, I.W., Herbert-Read, J.E., Clément, R.J.G., Krause, J., 2017. Guppies occupy consistent positions in social networks: mechanisms and consequences. Behav. Ecol. 28, 429–438. https://doi.org/10.1093/beheco/arw177

Kulahci, I.G., Ghazanfar, A.A., Rubenstein, D.I., 2018. Knowledgeable Lemurs Become More Central in Social Networks. Curr. Biol. 28, 1306–1310. https://doi.org/10.1016/j.cub.2018.02.079

Lachlan, R.F., Crooks, L., Laland, K.N., 1998. Who follows whom? Shoaling preferences and social learning of foraging information in guppies. Anim. Behav. 56, 181–190. https://doi.org/10.1006/anbe.1998.0760

Laland, K.N., Williams, K., 1997. Shoaling generates social learning of foraging information in guppies. Anim. Behav. 53, 1161–1169. https://doi.org/10.1006/anbe.1996.0318

Lenth, R.V., 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package.

Leu, S.T., Farine, D.R., Wey, T.W., Andrew, S., Michael Bull, C., 2016. Environment modulates population social structure: experimental evidence from replicated social networks of wild lizards. Anim Behav 111, 23–31. https://doi.org/10.1016/j.anbehav.2015.10.001

MacGregor, H.E.A., Herbert-Read, J.E., Ioannou, C.C., 2020. Information can explain the dynamics of group order in animal collective behaviour. Nat. Commun. 11, 2737. https://doi.org/10.1038/s41467-020-16578-x

MacGregor, H.E.A., Ioannou, C.C., 2022. Collective motion diminishes, but variation between groups emerges, through time in fish shoals. R. Soc. Open Sci. 8, 210655. https://doi.org/10.1098/rsos.210655

Morrell, L.J., Croft, D.P., Dyer, J.R.G., Chapman, B.B., Kelley, J.L., Laland, K.N., Krause, J., 2008. Association patterns and foraging behaviour in natural and artificial guppy shoals. Anim. Behav. 76, 855–864. https://doi.org/10.1016/j.anbehav.2008.02.015

Morse, D.H., Stephens, E.G., 1996. The consequences of adult foraging success on the components of lifetime fitness in a semelparous, sit and wait predator. Evol. Ecol. 10, 361–373. https://doi.org/10.1007/BF01237723

Oestreich, W.K., Kohles, J.E., Abrahms, B., Benoit-Bird, K.J., Berdahl, A.M., Ryan, J.P., Dechmann, D.K.N., 2026. Resource variability shapes the ecology of social information and collective sensing. Trends Ecol. Evol. *In Press*. https://doi.org/10.1016/j.tree.2026.01.010

Oh, K.P., Badyaev, A.V., 2010. Structure of social networks in a passerine bird: Consequences for sexual selection and the evolution of mating strategies. Am. Nat. 176, E80–E89. https://doi.org/10.1086/655216

Pitcher, T.J., Magurran, A.E., Winfield, I.J., 1982. Fish in larger shoals find food faster. Behav. Ecol. Sociobiol. 10, 149–151. https://doi.org/10.1007/BF00300175

R Core Team, 2025. R: A Language and environment for statistical computing.

Reader, S.M., Kendal, J.R., Laland, K.N., 2003. Social learning of foraging sites and escape routes in wild Trinidadian guppies. Anim. Behav. 66, 729–739. https://doi.org/10.1006/anbe.2003.2252

Rubenstein, D.R., Abbot, P., 2017. Comparative Social Evolution. Cambridge University Press, Cambridge, UK.

Ryder, T.B., Parker, P.G., Blake, J.G., Loiselle, B.A., 2009. It takes two to tango: reproductive skew and social correlates of male mating success in a lek-breeding bird. Proc. R. Soc. B Biol. Sci. 276, 2377–2384. https://doi.org/10.1098/rspb.2009.0208

Sasaki, T., Granovskiy, B., Mann, R.P., Sumpter, D.J.T., Pratt, S.C., 2013. Ant colonies outperform individuals when a sensory discrimination task is difficult but not when it is easy. Proc. Natl. Acad. Sci. 110, 13769–13773. https://doi.org/10.1073/pnas.1304917110

Schaerf, T.M., Dillingham, P.W., Ward, A.J.W., 2017. The effects of external cues on individual and collective behavior of shoaling fish. Sci. Adv. 3, e1603201. https://doi.org/10.1126/sciadv.1603201

Shier, D.M., Owings, D.H., 2007. Effects of social learning on predator training and postrelease survival in juvenile black-tailed prairie dogs, *Cynomys ludovicianus*. Anim. Behav. 73, 567–577. https://doi.org/10.1016/j.anbehav.2006.09.009

Silk, J.B., Alberts, S.C., Altmann, J., 2003. Social bonds of female baboons enhance infant survival. Science 302, 1231–1234. https://doi.org/10.1126/science.1088580

Snijders, L., Krause, S., Tump, A.N., Breuker, M., Ortiz, C., Rizzi, S., Ramnarine, I.W., Krause, J., Kurvers, R.H.J.M., 2021. Causal evidence for the adaptive benefits of social foraging in the wild. Commun. Biol. 4, 1–8. https://doi.org/10.1038/s42003-020-01597-7

Snijders, L., Kurvers, R.H.J.M., Krause, S., Ramnarine, I.W., Krause, J., 2018. Individual- and population-level drivers of consistent foraging success across environments. Nat. Ecol. Evol. 2, 1610–1618. https://doi.org/10.1101/260604

Snijders, L., Kurvers, R.H.J.M., Krause, S., Tump, A.N., Ramnarine, I.W., Krause, J., 2019. Females facilitate male food patch discovery in a wild fish population. J. Anim. Ecol. 88, 1950–1960. https://doi.org/10.1111/1365-2656.13086

Stoffel, M.A., Nakagawa, S., Schielzeth, H., 2017. rptR: Repeatability estimation and variance decomposition by generalised linear mixed-effects models. Methods Ecol. Evol. 8, 1639–1644. https://doi.org/10.1111/2041-210X.12797

Swaney, W., Kendal, J., Capon, H., Brown, C., Laland, K.N., 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. Anim. Behav. 62, 591–598. https://doi.org/10.1006/anbe.2001.1788

Wickham, H., 2016. ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York.

Wilson, A.D.M., Krause, S., James, R., Croft, D.P., Ramnarine, I.W., Borner, K.K., Clément, R.J.G., Krause, J., 2014. Dynamic social networks in guppies (*Poecilia reticulata*). Behav. Ecol. Sociobiol. 68, 915–925. https://doi.org/10.1007/s00265-014-1704-0

Wilson, A.D.M., Krause, S., Ramnarine, I.W., Borner, K.K., Clément, R.J.G., Kurvers, R.H.J.M., Krause, J., 2015. Social networks in changing environments. Behav. Ecol. Sociobiol. 69, 1617–1629. https://doi.org/10.1007/s00265-015-1973-2

Zandonà, E., Auer, S.K., Kilham, S.S., Howard, J.L., López-Sepulcre, A., O'Connor, M.P., Bassar, R.D., Osorio, A., Pringle, C.M., Reznick, D.N., 2011. Diet quality and prey selectivity correlate with life histories and predation regime in Trinidadian guppies. Funct. Ecol. 25, 964–973. https://doi.org/10.1111/j.1365-2435.2011.01865.x