Guppies Leverage Sociality to Increase Foraging Efficiency

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Abstract

Social companions can aid animals in discovering novel resources, with socially connected individuals often locating food more quickly. However, increased sociality also heightens the risk of harassment and disease. Animals would thus benefit from flexibly switching between social and solitary states in response to resource fluctuations. Whether wild animals do this strategically and successfully remains unclear. We experimentally studied groups of wild guppies (*Poecilia reticulata*) in a resource-poor environment to test if they adjust their social state after recent experience with relatively unpredictable and short-lived novel food patches. Using individually marked fish, we found that groups exposed to ephemeral food patches significantly increased their time spent social—doubling it—compared to control conditions. Groups with stronger foraging motivation showed greater increases in sociality, and individuals in such groups were more successful in locating food patches thereby realizing greater food intake. In a second field experiment, we show that wild guppy groups similarly increased sociality in response to food odours, suggesting strategic adjustments of sociality rather than mere satiation-driven changes in activity budgets. Our findings thus provide causal evidence that animals can be active engineers, rather than passive recipients, of social foraging benefits, highlighting the adaptive nature of fission-fusion dynamics.

Keywords: animal social network, food provisioning, Markov chain analysis, resource predictability, social buffering, social facilitation, social flexibility, social learning, social plasticity, Trinidad & Tobago

1. Introduction

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

Sociality facilitates foraging success in many animals (Galef & Giraldeau, 2001). Specifically, social relationships can help locate novel resources (Firth et al., 2016; Heinen et al., 2022; Hasenjager et al., 2020), with more social or central individuals typically discovering resources more quickly and frequently (Aplin et al., 2012; Carter et al., 2016; Snijders et al., 2018, 2019) or experiencing less food intake variance (Jolles et al., 2017). Increased social connectivity can, however, also be costly, e.g., by increasing the risk of competition, harassment, and disease exposure (Godfrey et al., 2009; Darden 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 & Ma, 2021).

While previous studies indeed showed social behaviour to change with resource availability (Brown, 1988; Chapman et al., 1995; Dorning & Harris, 2019; Foster et al., 2012), it is challenging to disentangle whether such changes are part of a strategy to flexibly capitalise on social foraging benefits or a mere passive consequence of local aggregation near an ephemeral resource. To differentiate between such social foraging mechanisms and better understand the adaptive capacity of social systems, we need experimental resource manipulation (e.g., Heinen et al., 2022; Troisi et al., 2025; Bordes et al., 2025) and resource-independent sociality measurements. 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 better.

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 magnitude of social adjustment and testing if such adjustments are indeed beneficial in fitness-relevant contexts is crucial to assess if animals could mitigate resource fluctuations, or other forms of rapid environmental change, through social flexibility (i.e. 'social buffering').

Here, we investigated whether changes in resource availability induce adjustments in sociality and whether stronger social adjustment results in larger foraging benefits. Specifically, we experimentally studied the immediate and longer-term effects of ephemeral novel food patch availability on the social dynamics of 18 mixed-sex sets of wild Trinidadian guppies (*Poecilia reticulata*) in natural pools in the rainforest. For readability purposes, we refer to these sets as 'groups'. 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 socially changed in response to ephemeral novel food patch availability, predicting that groups would become more social to locate the spatially unpredictable and short-lived food patches. Third, we tested if these changes in the time groups spent socially translated into a higher foraging success for individuals in such groups. Lastly, in a follow-up field experiment, we replaced the food resources at the patches with food odour cues and tested if time spent socially also changed when fish merely 'perceived' food patch availability but did not consume any food. This latter experiment was crucial in ruling out satiation-related changes in activity budgets as the driver of any observed changes in sociality (e.g., Borgeaud et al., 2021; Gareta García et al., 2021).

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 collectives adjusted their sociality when

experiencing a rapid influx of temporarily unpredictable food. Experiment 2 (8-15 April 2023) studied how groups adjusted their sociality when only experiencing the food odour. We used four (Exp 1) or three (Exp 2) natural pools (approximate surface area range of the pools: 2–5 m^2; depth range: 6–30 cm), which were modified around the edges to allow a constant in- and outflow of water while minimizing opportunities for fish migration. 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 given an individually-unique colour mark using Visible Implant Elastomer (VIE) tags (©Northwest Marine Technology Inc.) (Croft et al., 2003; Snijders et al., 2019).

The experimental groups consisted of eight fish (of equal sex ratio), and fish within the same group were caught in the same pool 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.

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. 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 short-lived novel food patches (F1 & F2) or control (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		

Novel food patch presentations

One session of presentations (food or control patch) consisted of 60 presentations, simulating an influx of spatially unpredictable, temporarily available food resources, e.g., fallen fruits or insects. Each presentation and each break between two presentations lasted 15 seconds (i.e. 30 minutes in total). Food or control patches were presented at five a-priori assigned locations spread out through the entire pool, and these locations were alternated randomly with the restriction that every five trials, each location received a presentation. As a food patch, we used small lead balls (8 mm diameter), which were covered with a mix of gelatine and crushed fish food flakes, including carotenoids (TetraPro©; Spectrum Brands Inc). Multiple individuals could feed from this food resource simultaneously. As a control, we used the same balls but without a food cover. During a presentation, we lowered the ball 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 took at least one bite from the food. The 60 presentations were followed by a two-minute break, after which we continued with the next social observation session. We conducted two series (F1 & F2 or C1 & C2, Table 1) of 60 presentations a day. During one series, the food patch was completely depleted before the final presentation and therefore ended 17 presentations early, leading to a total of 4,303 analysed presentations containing 33,481 individual presence/absence data points. Because feeding behaviour could not be reliably determined during

six of the presentations, we excluded these from the analysis of feeding events but retained them in the other analyses.

Social observations

To quantify potential changes in social dynamics following our treatments, we performed focal follow observation sessions of each group member before (S0), in between (S1), and after (S2) the food or control presentations (Table 1). Each individual was followed for three minutes during each session. To minimise selection bias, the identity of each focal fish was determined by a second person (who was not currently observing the fish). Every 10 seconds, we noted whether the focal fish was alone or social—and in the latter case, the identity of its nearest neighbour—and its location in the pool. We considered a guppy a neighbour when it was within four body lengths of the focal fish (Krause et al., 2017; Snijders et al., 2019; Wilson et al., 2014). To determine the location of the focal fish, we divided each pool into five zones covering the whole pool, corresponding to the nearest of the a-priori assigned food presentation locations. 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.

Experiment 2

Experimental design

Exp 2 followed a counter-balanced within-group design, similar to Exp 1, yet in Exp 2, groups received treatment and control on the same day (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 (at least 50% of the group for a maximum of 1 minute following the first bite) 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 cues and then control cues 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				Control odour				N = 9	N = 68
F1	S1	F2	S2	C1	S1	C2	S2		
Control odour				Food odour				N = 9	N = 69
C1	S1	C2	S2	F1	S1	F2	S2		

Food cue presentations

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 randomly alternated locations throughout the entire pool. We used the same crushed fish food flakes as in Exp 1 (TetraPro©; Spectrum Brands Inc; 0.4 grams) 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 feeding. 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/bite. 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 & 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 protocol as in Exp 1, except that there were no observations before the presentations (S1 and S2 only; Table 2), each individual was followed for two minutes during each session, and the pool was divided into nine zones.

Statistical analyses

Social dynamics

Social dynamics were analysed using the programming language Java (OpenJDK version "21.0.7"). 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 we refer to as 'social time' (Snijders et al., 2018, 2019; Wilson et al., 2014). Markov chain analyses allow inclusion and investigation of the more fine-grained social state change dynamics underlying broader social patterns. In our Markov chain analysis, we translated our focal observations to a sequence of behavioural social states for each individual, being either in the 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 $Pa \rightarrow s$, which is the probability of ending being alone, and $Ps \rightarrow a$, which is the probability of ending being social, using the formula: $Pa \rightarrow s / (Ps \rightarrow a + Pa \rightarrow s)$. 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). 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., $Ps \rightarrow a$ and $Pa \rightarrow s$) 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.

Aggregation carry-over and observation order effects

We 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 contacts in the zone of the last food presentation were higher after the food patch presentations (S1 or S2) than in that same zone before the food patch presentations (S0), using Matched-pairs Wilcoxon tests. To test if individual fish that were observed more quickly after the food presentations were more social, we measured the rank correlation (Kendall's coefficient) between 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.

General modelling approach

To analyse: i) group-level consistency in social time, ii) the effect of spatially unpredictable 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 food odour on group-level social time (Exp 2), we ran (generalized) linear mixed models (optimizer = bobyqa) from the *lme4* package (Bates et al., 2015) in R 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, certain fixed or random effects were included or excluded (but only those serving as control variables). 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, when including interactions). 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

We tested the consistency of group-level social time by constructing mixed models with group identity as a random factor, 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. 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*

To test if the time spent socially by groups 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 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 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.

(iii) Change in sociality as a predictor of individual foraging success

To test if a change in the time a group spends socially in response to ephemeral food patch availability predicted individual foraging success, we ran a generalised linear mixed model (family = binomial) with individual arrival at a detected food resource (two levels: yes, no) as the dependent variable (N = 9,663). Social change was calculated as the difference between group-level social time after the first food session (S1) and before (S0). The model included the interactions between social change and group-level foraging motivation, sex (two levels: male and female), and food presentation series (two levels: F1 and F2, Table 1). In addition, the model included day, size (length in mm, centred on sex, continuous), group size, and pool identity as the main effects. Group identity nested in pool identity (18 levels), individual identity nested in group identity (140 levels), presentation location nested in pool identity (20 levels), and presentation identity (1,237 levels) were included as random effects. Note that pool was not included as a random effect but as a fixed effect. We furthermore evaluated if social change as a significant predictor of foraging success (see Results) could be explained by a change in sexual behaviour frequency, i.e., if an increase in social time merely represents an increase in sexual behaviour following food intake. For this, the effect of sex-specific social change on food patch arrival was first tested using the final model for both sexes combined as the starting model. Subsequently, the change in sex-specific social time was replaced in the final model with change in sexual behaviours performed (males) or sexual behaviours received (females), and these models were compared based on AICc. We calculated AICc using the 'AICctab()' function of the *bbmle* package (Bolker & R Development Core Team, 2021). We report the difference in AICc, inferring a relevant model improvement if the AIC decreases by more than 2. To examine whether predicted effects of social change on individual foraging success could be explained by either social time before the first food resource availability (S0) or social time after the first food session (S1), we first tested for correlations between these variables using Spearman rank correlation tests. Next, we substituted social change in the final model for either of these social measures and calculated the AICc.

Lastly, to test if arrival at an ephemeral novel food patch also predicted food intake (Exp 1), we calculated the total number of feeding events per individual. We correlated these with the proportion of time an individual arrived at a novel food patch, using Spearman rank correlations. We ran these analyses for males and females separately.

(iv) Ephemeral food odour effects on sociality (Experiment 2)

To test if an increase in sociality was not merely driven by food consumption, we tested if the time spent socially by groups also increased following perceived ephemeral food patch availability (odour cue). We analysed the effect of treatment (two levels: food odour and control) on group-level social time (average of S1+S2) using a simplified linear mixed model (N = 36 values). As a control variable, we only added pool identity as a fixed effect. Group identity was included as a random effect. Including pool identity resulted in zero variance explained by group identity. However, including pool identity as a fixed or random effect or excluding pool identity from the model did not qualitatively change the conclusions. Note that we could not include a reliable measure of foraging motivation in this analysis due to the food not being accessible to the guppies.

3. Results

Ephemeral food patch effects on sociality

Wild guppy groups could be characterized by how much time their members spent social, with group-level sociality being repeatable (Control S0-S1-S2: R_{adj} = 0.48, SE = 0.17, P = 0.01, Fig. 1A & D) and relatively stable across the three control sessions (S0: **0.26**, 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 variances: $W_{2,51}$ = 0.49, P = 0.61, Fig. 1). Yet, when ephemeral and relatively unpredictable novel food patches became available in the environment, the average proportion of time spent socially significantly increased (Treatment*Session: $\chi2 = 55.65$, $P < 0.001$; Table S1 & S2, Fig. 1), rising twofold (S0: **0.22**, 95% CI = 0.18-0.26; S1: **0.46**, 95% CI= 0.39-0.53; S2: **0.48**, 95% CI = 0.40-0.57). In addition, the variance in sociality across groups increased ($W_{2,51}$ = 6.13, P = 0.004) and repeatability of group-level sociality disappeared (Food S0-S1-S2, R_{adj} = 0.15, SE = 0.14, P = 0.50, Fig. 1B & C). Interestingly, despite the substantial social changes following the initial presentations of novel food patches, sociality differences between groups quickly stabilised (Food S1-S2, R_{adj} = 0.66, SE = 0.15, P = 0.01, Fig. 1B & C).

This increased sociality following the short-lived novel food patches resulted from fish both decreasing their probability of ending a social contact (Treatment*Session: $\chi2 = 20.38$, $P < 0.001$, Table S3) and increasing the probability of starting a new social contact (Treatment*Session: $\chi2 = 28.72$, $P < 0.001$, Table S4). An increase in sociality was still detectable the next morning (Treatment: Estimate (Est) ± SE = 0.09 ± 0.04, N = 18, F = 6.42, P = 0.02, Fig. 1).

More motivated groups, changed their social behaviour more strongly in response to the short-lived novel food patches than less motivated groups (Treatment*Group-level foraging motivation: $\chi2 = 9.53$, $P = 0.002$, Table S1). Both females and males were more social following the food patches compared to control patches (Females: Treatment*Session: $\chi2 = 27.65$, $P < 0.001$, Table S5; Males: Treatment*Session: $\chi2 = 40.52$, $P < 0.001$, Table S6). Yet only males still showed an increase in sociality the next morning (Males: Treatment: Est ± SE = 0.11 ± 0.03, N = 18, F = 10.77, P = 0.005; Females: Treatment: Est ± SE = 0.07 ± 0.06, N = 18, F = 1.54, P = 0.23).

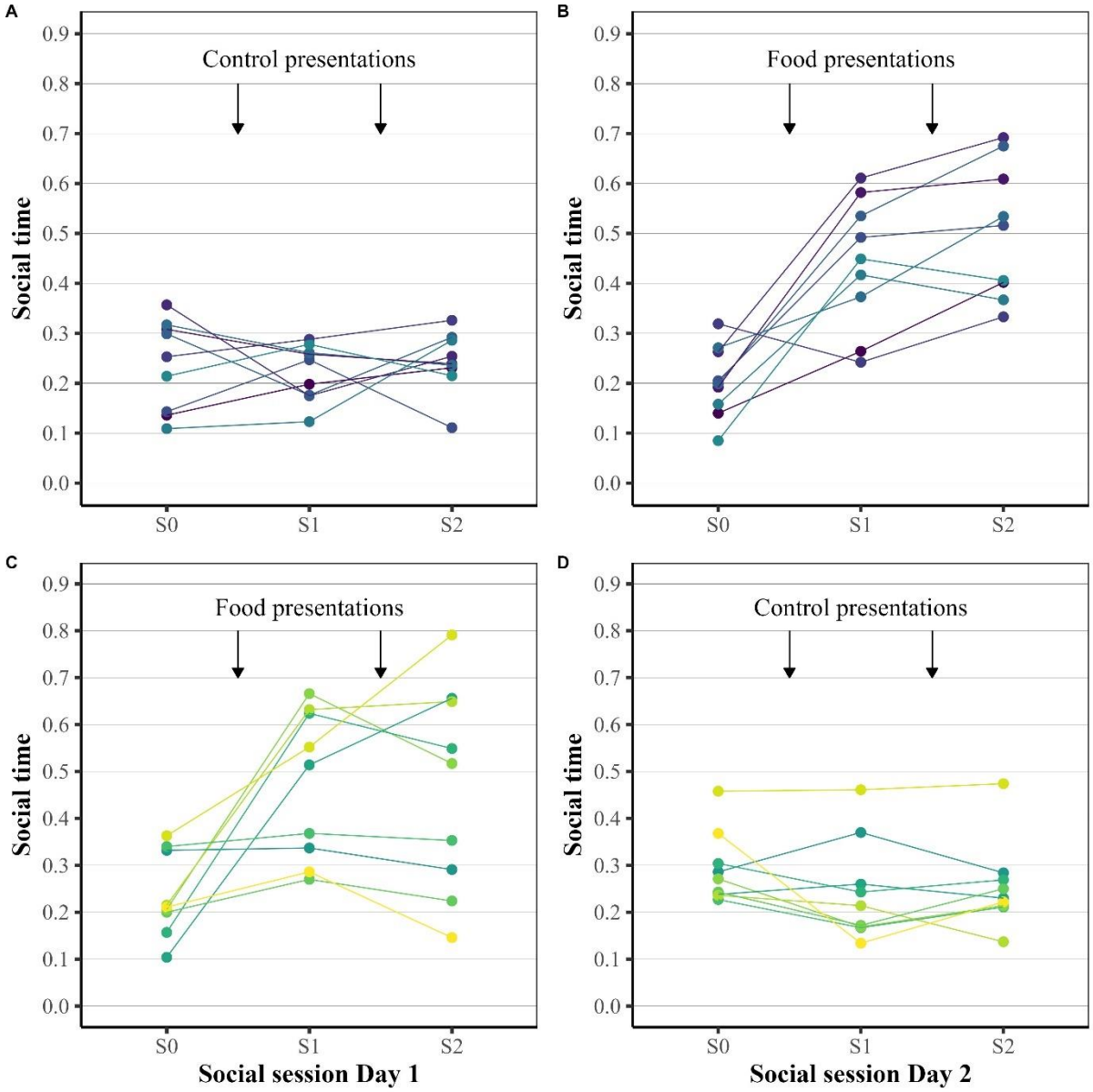

Figure 1. Time spent socially by 18 groups of wild guppies before, between, and after two series of repeated food patch or control patch presentations. Arrows indicate the timing of the presentations. A-B) Groups that received the control patches on the first day received the food patches on the second day. C-D) Groups that received the food patches on the first day 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.

Change in sociality as a predictor of individual foraging success

Change in group-level sociality positively correlated with arrival at novel food patches for individuals from highly motivated groups (Social change*Group-level foraging motivation: $\chi2 = 4.81$, $P = 0.03$; Table S7; 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 S7). Both females and males that reached more of the ephemeral food patches benefited from more feeding events (Females: $r_s = 0.94$, $N = 69$, $P < 0.001$; Males: $r_s = 0.90$, $N = 71$, $P < 0.001$).

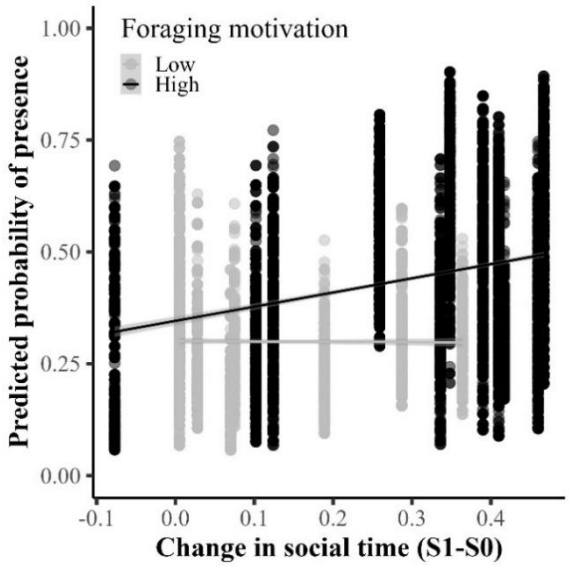

Figure 2. Predicted probability of an individual arriving at a detected food patch in relation to the change in time spent socially by an individual's group following the first series of ephemeral food patch presentations. Predictions were retrieved from the final model for individual presence or absence 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 S9) and, consequently, females received more

375 of such sexual behaviours (Treatment*Session: $\chi2 = 6.92$, $P = 0.03$; Table S10). Males also
376 displayed and harassed more frequently in the morning after food patch presentations than after
377 control (Treatment Males: Est ± SE = 1.02 ± 0.34, N = 18, $\chi2 = 9.00$, $P = 0.003$). Even though social
378 time and sexual behaviour frequency were correlated (Males: $r_s = 0.54$, N = 108, $P < 0.001$;
379 Females: $r_s = 0.57$, N = 108, $P < 0.001$), the increase in social time explained the increase in
380 individual arrivals at food patches better (Table S11-S12) than the increase in sexual behaviours
381 (Sexual behaviour Males: Delta AICc = -6.12; Females: Delta AICc = -3.59).

382 **Aggregation carry-over and observation order effects**

383 Social contacts in the zones of the most recently visited food patch were just as likely to take place
384 before as after the temporary food patch became available (Table S8), meaning that the increase
385 in group-level sociality during the food patch treatment was not a mere carry-over effect of local
386 aggregation at the last visited food resource. In addition, individuals were not more social if they
387 were more quickly observed after the first session of temporary food patch presentations (S1:
388 Kendall's correlation coefficient = 0.03, P = 0.37; Fig. S1), although they were after the second
389 (S2: Kendall's correlation coefficient = 0.15, P = 0.01; Fig. S2).

390 **Ephemeral food odour effects on sociality (Experiment 2)**

391 The average proportion of time spent socially during and after food odour presentations was
392 approximately 1.4 times higher (S1+S2 = **0.44**, 95% CI = 0.38-0.50) compared to control
393 exposure (S1+S2 = **0.31**, 95% CI = 0.26-0.36). Guppy groups thus also increased sociality when
394 they could perceive temporary novel food patches but not eat from them (Treatment: $\chi2 = 19.59$,
395 $P < 0.001$; Table S13, Fig. 3). The food odour stimulus received thirteen times as many pecks as
396 the control stimulus, confirming that the guppies recognised it as a relevant food source. Moreover,
397 the food odour and control presentations generated a comparable (minor) number of sexual and
398 agonistic social interactions at the stimulus (29 events each), suggesting the observed increase in
399 sociality was not a carry-over of increased social activity near the food odour stimulus.

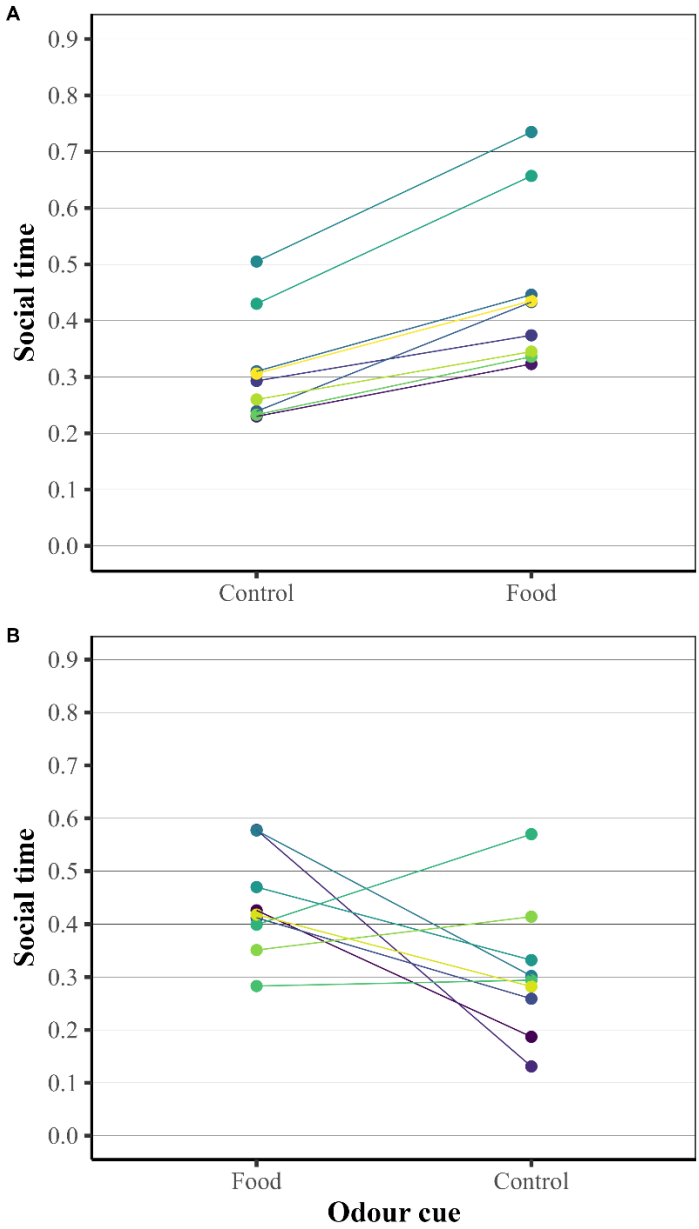

Figure 3. Time spent socially by the 18 groups of wild guppies following exposure to two series of ephemeral food odour or control cue presentations. A) Nine groups first received two series of the control treatment, followed by two series of the food odour treatment. B) Nine groups first received two 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.

4. Discussion

Social flexibility may make animals better prepared to cope with resource fluctuations. However, it remains unclear whether individuals actively alter their social state to fit the prevailing resource conditions. Our study provides experimental evidence that wild fish strategically use fission-fusion

behaviour to enhance resource localisation in response to short-lived and spatially unpredictable availability of high-quality food patches. First, we show that experimentally providing temporary food patches at various locations in random order leads to rapid, substantial, and sustained spatially independent changes in the time spent socially by wild Trinidadian guppies living in resource-poor environments. Second, we demonstrate that group-level social state changes predict individual foraging success when controlling for group-level foraging motivation. Lastly, when we manipulated the perception of ephemeral food patch availability by providing temporary food odours at random locations in the environment, time spent socially likewise increased, eliminating the possibility that the observed social state changes were merely a consequence of relaxed feeding constraints. Together, our findings suggest that wild guppies can strategically leverage sociality to quickly locate temporarily available food patches and thus enhance their foraging efficiency in fluctuating environments.

Wild guppy groups doubled their time spent socialising following the temporary presence of novel food patches, independent of patch location and after food patches were gone. This increase contrasts with previous environment and density manipulations, which did not show such large effects on social time (Wilson et al., 2015; Krause et al., 2017), highlighting the key role of the foraging context in social behaviour. Lab studies also observed group-level social responses to changes in the foraging context, but in opposite directions (Hoare et al., 2004; Jolles et al., 2018; Schaerf et al., 2017). For example, x-ray tetras (*Pristella maxillaris*) and banded killifish (*Fundulus diaphanus*) reduced encounter frequency and group size, respectively, when exposed to food cues (Hoare et al., 2004; Schaerf et al., 2017). These varying responses suggest that sociality's benefits depend on factors like baseline sociality and intraspecific competition costs. Highly social groups may do better by initially reducing sociality or becoming more disordered (MacGregor et al., 2020), allowing for the gathering of more independent private information, while guppies in low-predation populations, with low baseline sociality and minimal aggression, may benefit from increased sociality when food cues are present, enhancing social information on novel food patch locations. Comparing highly social and less social guppy populations in Trinidad would, therefore, be a valuable next step.

Recent evidence highlights consistent yet responsive sociality in animal groups (Jolles et al., 2018; MacGregor & Ioannou, 2022; Schaerf et al., 2017). Our guppy groups showed consistent variation in sociality during control presentations, while food patch availability induced additional variation.

We can rule out time or familiarity effects (MacGregor & Ioannou, 2022), as no similar pattern occurred in control treatments. Some groups responded 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., 2019) and foraging success (Dyer et al., 2009). Differences in locomotion and personality types can drive group cohesion, alignment, and leadership (Jolles et al., 2017, 2020). 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 need to spend substantial amounts of valuable time on locating food resources, constraining the time available for other behaviours (Borgeaud et al., 2021; Gareta García et al., 2021), such as sexual pursuits. 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 both survival and reproductive benefits from finding more food resources (Abrahams, 1993). However, to rule out that the observed change in sociality is 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 (perceived) availability of food could have altered the guppies' social behaviour. However, the comparable low frequency of aggressive interactions we observed near food and control odour cues suggests relatively high levels of social tolerance (De la Fuente et al., 2022; DeTroy et al., 2021), a population-level characteristic we also documented in earlier studies with the same population (e.g., Snijders et al., 2019). We therefore consider changes in perceived or real competition following our treatments as an unlikely explanation of the substantial changes in sociality we observed.

Group-level responses are not necessarily the sum of individual responses (Bengston & Jandt, 2014), and groups may outperform individuals (Harpaz & Schneidman, 2020; Pitcher et al., 1982; Sasaki et al., 2013). Our experimental design limited our ability to gather robust individual-level data, preventing exploration of whether group-level changes were emergent properties. Future

research, with advancements in automated video-tracking, could examine whether changes in group-level sociality predict individual foraging success better than individual-level changes. This may reveal that individuals differ in how much their foraging success improves when socialising versus foraging alone, which could explain individual differences in sociability and its maintenance through selective forces in dynamic resource environments. For example, more social foragers will be more vulnerable to large fluctuations in population density (Harel et al., 2017), while more solitary foragers will generally experience greater variance in foraging, making them more at risk during large fluctuations in available resources (Brown, 1988; Jolles et al., 2017).

In conclusion, through multiple lines of evidence, our study provides new insights into the adaptability of fission-fusion systems under rapidly changing resource conditions in the wild. Specifically, we showed that ephemeral food patch availability generates substantial and profitable changes in an otherwise consistent group-level social trait. By considering, testing and rejecting alternative explanations for social change following exposure to temporary food patches, such as carry-over of spatial aggregations, changes in time-budget constraints and changes in perceived competition costs, we built a strong case for instrumental use of sociality as the most likely explanation. Further experimentation is required to reveal the precise social mechanism underlying increased food patch localisation efficiency (e.g., social information use, social facilitation; see also Snijders et al., 2021). Furthermore, revealing the individual and group-level factors variation in (adaptive) social responsiveness, the potential mediating effects of individual learning and the relative effects of temporal and spatial resource predictability on social responsiveness, in addition to other resource characteristics, would provide relevant avenues for future research.

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Conflict of Interest

All authors declare no conflict of interest.

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.

Data availability statement

The data and R-script are available on the Open Science Framework: osf.io/75vtn.

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