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Ephemeral Resource Availability Makes Wild Guppies More Social

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Abstract:

Resource availability and sociality are tightly coupled. Sociality facilitates resource access in a wide range of animal species. Simultaneously, resource availability may change sociality. However, experimental evidence for resource-driven social changes in the wild, beyond local aggregations at the resource, remains scarce. Moreover, it is largely unclear how potential changes in sociality relate to the social foraging benefits obtained by individual group members. Here, we recorded immediate and prolonged changes in social dynamics following ephemeral food availability in 18 mixed-sex Trinidadian guppies (*Poecilia reticulata*) groups in natural rainforest pools. Using a counter-balanced within-group design, the social associations within each group was observed before, between and after ephemeral patch availability for two consecutive days. We show that groups increased their time spent socially two-fold following ephemeral food patch, but not control (empty) patch, availability. Groups with stronger foraging motivation, measured as the average proportion of fish feeding, showed a stronger increase in sociality. This resource-induced increase in sociality was still detectable the next day. Increase in the time spent socially by a group also positively correlated with the more frequent arrival at detected food patches for individual members of motivated groups, which, in turn, correlated strongly with individual food consumption. Our study causally demonstrates that changes in ephemeral resource availability can induce rapid, substantial, and prolonged changes in the social dynamics of wild fish and that this change positively correlated with individual foraging success. Further research is needed to investigate whether this social change is a cause or consequence of individual foraging success and why some groups respond more strongly than others.

Keywords: dynamic social networks, foraging ecology, group personality, social facilitation, social foraging, social plasticity

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Introduction

The selective advantage of living in groups has 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, ranging from female savannah baboons (*Papio cynocephalus*) (Silk et al., 2003) and male wire-tailed manakin (*Pipra filicauda*) (Ryder et al., 2009) to male forked fungus beetles (*Bolitotherus cornutus*) (Formica et al., 2012). Fitness advantages of sociality can emerge via a variety of pathways (Krause & Ruxton, 2002), for example by facilitating predation avoidance (Karplus et al., 2006; Landeau & Terborgh, 1986; Shier & Owings, 2007), mating opportunities (Kaiser et al., 2018; Oh & Badyaev, 2010) or foraging success (Brown, 1988; Ellis et al., 2017; Herringe et al., 2022). An increase in foraging success can be especially impactful because it has the potential to positively affect both fitness components: survival, and reproduction (Abrahams, 1993; Blanckenhorn, 1991; Bradbury & Vehrencamp, 1977; Clark & Mangel, 1986; Clay et al., 2018; Ellis et al., 2017; Morse & Stephens, 1996).

Sociality facilitates foraging success in a wide range of animals, both in captivity (Grand & Dill, 1999; Harpaz & Schneidman, 2020; Krebs et al., 1972; Pitcher et al., 1982), and in the wild (Morand-Ferron & Quinn, 2011; Snijders et al., 2021). On an individual level, more social guppies (*Poecilia reticulata*) and great tits (*Parus major*) with more central network positions visited more novel food patches (Aplin et al., 2012; Snijders et al., 2018, 2019), while more social three-spined sticklebacks (*Gasterosteus aculeatus*) experienced less food intake variance (Jolles et al., 2017). Such individual variation in social tendency or position can be relatively consistent (Aplin et al., 2015; Bierbach et al., 2018; Harel et al., 2017; Jolles et al., 2017; Krause et al., 2017), indicating a target for natural selection to act on (Greenwood et al., 2013; Wright et al., 2006), e.g., through social foraging benefits.

Individuals that consistently differ in their social tendencies, may still adjust their social behaviour in response to a change in environmental context (Heathcote et al., 2017; Hoare et al., 2004; Ling et al., 2019; Rodriguez-Pinto et al., 2020; Schaerf et al., 2017; Snijders et al., 2017; Wolf et al., 2018). For example, social behaviour regularly changes with resource availability (Brown, 1988; Chapman et al., 1995; Dorning & Harris, 2019; Foster et al., 2012). Such social changes could be a consequence of independent aggregation near a resource but could also reflect a strategy to flexibly capitalise on social foraging benefits. These potential mechanisms are challenging to disentangle without experimental manipulation and resource-independent sociality measurements, yet these are key for better understanding of the mechanisms and functions of social systems. An experimental study in semi-captive ring-tailed lemurs (*Lemur catta*) showed that lemurs increased their social connections to individuals they had observed solving a newly introduced foraging task, and that 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 increasingly foraged in multispecies flocks (Grubb, 1987). These few experimental studies in the (semi) wild suggest the instrumental use of sociality by animals to gain foraging benefits.

Here, we investigated whether changes in resource availability induce adjustments in sociality and whether individuals in groups that show stronger social adjustment accrue larger foraging benefits. We experimentally studied the immediate and longer-term effects of ephemeral resource availability on the social dynamics of 18 mixed-sex sets of wild Trinidadian guppies, in natural pools in the rainforest. Sets consisted of seven to eight fish caught from the same location. For readability purpose, we refer to these sets as 'groups'. Using a counter-balanced within-group design, we tested each group for two consecutive days using three social observation sessions per day. These observation sessions were

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alternated with two series of food (or control) presentations on the first day and vice versa on the second day. First, we tested if groups consistently differed in the overall time their members spent socially. Second, we tested if this time spent socially changed in response to ephemeral resource availability, predicting that groups would become more social to locate more of the spatially unpredictable ephemeral food resources. Third, we tested if these changes in the overall time groups spent socially translated into a higher foraging success for individuals in such groups.

Methods

Study area and subjects

The study took place in 2019 between March 6th and March 24th in the upper rainforest region of the Turure River (10°41'8"N, 61°10'22"W) of Trinidad's Northern Range. This region is considered a low predation site (Barbosa et al., 2018; Deacon et al., 2018) and is relatively resource-poor (Grether et al., 2001). We used four natural pools (approximate surface area range of the pools: 2.5–5 m^2; depth range: 10–30 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 our experimental pools were removed. We collected study subjects from a nearby stretch of the river. Upon capture, adult fish (N = 144, 50/50 sex-ratio) were measured (females: Mean ± SD = 24.3± 2.4 mm, males: Mean ± SD = 22.1 ± 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). We took care to compose the experimental groups (N = 18) with fish caught from the same pool to retain familiarity within groups. The subject groups were released in their respective experimental pools and left to settle overnight with experimental trials starting the next morning. Four fish left the experimental pool (one male, three females), resulting in a total of 14 groups of eight fish and four groups of seven fish. 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 Committee on Research Ethics. All subjects were released on the same day as their final trials.

Experimental design

We used a counter-balanced within-group design, meaning that all groups received both the food and control treatments, with half of the groups receiving the control treatments first and the other half the food treatments first. Each group was tested for two consecutive days, comprising one food treatment and one control day. Each day consisted of three social observation sessions alternated with two series of 60 food or control presentations following a 2 min break. Each day would thus start and end with a social observation session (Table 1).

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Table 1. Schematic overview of the experimental design. Groups of seven or eight individuals, distributed over four pools, received food on either day 1 and control on day 2 or vice versa. Within each day social behaviour was observed before (S0), in between (S1), and after (S2) food (F1 & F2) or control (C1 & C2) presentations.

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

Social observations

To quantify potential changes in social dynamics following ephemeral resource availability, we performed focal follow observations of each group member before (S0), in between (S1), and after (S2) the food or control presentations. Each individual was followed for three minutes while we noted the identity of its nearest neighbour and its location in the pool every 10 s. We considered a guppy a neighbour when it was within four body lengths of the focal subject (Krause et al., 2017; Snijders et al., 2019; Wilson et al., 2014). To determine the location of the focal subject, we divided each pool in five zones covering the whole pool, corresponding to the nearest of the five a-priori assigned resource presentation locations (see below). In addition, we scored aggression, display, and harassment events performed or received by the focal subject continuously during the three minute period.

Resource presentations

Following the first social observation session, we conducted the first series of food or control presentations. One series consisted of 60 presentations, simulating an influx of temporarily available resources, e.g., fallen fruits or insects. Each presentation and each break between two presentations lasted 15 seconds. 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 food resources, 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 resource simultaneously. As a control, we used the same balls but without 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. After the 60 presentations followed a two-minute break and we continued with the next social observation session. We thus conducted two series (F1 & F2 or C1 & C2, Table 1) of 60 presentations a day.

During one series the food resource 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 biting 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.

Statistical analyses

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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 we refer to as 'social time' (Snijders et al., 2018, 2019; Wilson et al., 2014). In the 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→s, which is the probability of ending being alone, and Ps→a, which is the probability of ending being social, using the formula: Pa→s/ (Ps→a + Pa→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 before, during, and after ephemeral resource availability, on the same day. However, this came at the cost of resolution at the individual level as we could only collect three minutes of data per individual per session. We, therefore, focussed our social analyses on the group and sex-level. To do this, we determined the overall transition probabilities (i.e., Ps→a and Pa→s) and social time per group (or per sex within each group) and social observation session. We estimated each overall transition probability based on the sum of the numbers 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 of each other, we did not apply a randomisation procedure for these data.

We evaluated potential carry-over effects of local aggregation from the food presentations by testing for effects of the location of the last food presentation and observation order. To test whether a higher social time is linked to the location of the last food presentation, we determined for each group the distribution of social contacts among the five spatial zones for each of the three social sessions on the food treatment day. We then compared the fractions of social contacts in the spatial zone of the last food presentation before (S0) and after food presentations (S1 or S2) using Matched-pairs Wilcoxon tests. To test for an effect of observation order, we performed within-group randomisation of the social times, to account for the dependency of within-group social data (10,000 randomisation steps), and measured the rank correlation (Kendall's coefficient) with the observation order.

General modelling approach

To analyse i) group-level consistency in social time, ii) the effects of ephemeral resource availability on group-level social time, and iii) the relation between group-level social change and individual foraging success, we ran (generalized) linear mixed models (optimizer = bobyqa) from the *lme4* package (Bates et al., 2015) in R (R Core Team, 2021) version 4.1.2 in R Studio version 1.4.1717 (© 2009–2021 RStudio, Inc.). 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 (but only those serving as control variables) were included or excluded. These changes did not qualitatively change our conclusions and are reported in the supplementary table captions. We evaluated the significance for 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

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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, respectively. We created the figures with the *ggplot2* package (Wickham, 2016). The data and R-script are available on the Open Science Framework: osf.io/75vtn (Snijders et al., 2022).

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 calculated the adjusted repeatability of group-level social time for the control and food treatment separately. 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 (overall proportion of present individuals feeding). A low group-level foraging motivation may be reflective of 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 treatment were tested using Levene's test for equal variances.

Ephemeral resource effects on sociality

To test if the time spent socially by groups increased following ephemeral resource 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 post-hoc 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, and pool identity and the interaction between treatment and foraging motivation. Group identity was included as random effect. Subsequently, we examined the effect of ephemeral resource availability on the group-level transition probabilities underlying social time (i.e., Ps→a and Pa→s). Similarly, we examined the effects of ephemeral resource availability on group-level social time for the sexes separately, using the final model for group-level social time as starting model. To test if ephemeral resource availability had a prolonged effect on group-level social time, 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 only including treatment. To test if ephemeral resource availability also affected the frequency of sexual behaviours, we calculated the sum of display and sexual harassment behaviours for each group per social session, distinguishing between behaviours performed by males and behaviours received by females. We applied generalized linear mixed models (family = Poisson) and used the model construction of the final model for sex-specific social time as the starting model. The frequency of aggression was low (5% of all social observations) and therefore not further explored.

Change in sociality and individual foraging success

To test if a change in the time a group spends social in response to ephemeral resource availability correlated with individual foraging success, we ran a generalized linear mixed model (family = binomial) with individual arrival at a detected food patch (two levels: yes, no) as 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

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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 a correlation between social change and 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, first, the effect of sex-specific social change on food patch arrival was tested using the final model for both sexes combined as starting model. Subsequently, 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 improvement of the model if the AIC decreases with > 2. To examine whether correlations between social change and individual foraging success could be explained by either social time before the first food patch 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 patch arrival predicted food intake, we calculated the total number of feeding events per individual and correlated these with the proportion of time an individual arrived at a food patch, using Spearman rank correlations. We ran these analyses for males and females separately.

Results

Consistency of sociality

Groups consistently differed in how much time their members spent socially across the three social sessions during control treatment, also when accounting for variation in group size and foraging motivation (R_{adj} = 0.48, SE = 0.16, P = 0.01, Fig. 1). In contrast to the control sessions, groups did not consistently differ in the time they spent socially across all three social sessions during food treatment (R_{adj} = 0.15, SE = 0.16, P = 1.00, Fig. 1), but they did differ when solely considering the second and third session, i.e., after the start of food patch presentations (R_{adj} = 0.62, SE = 0.15, P = 0.007, Fig. 1). This suggests that ephemeral food patch availability induced an apparent reranking among the groups in their level of sociality. Ephemeral food patch availability also significantly increased the variance among the groups in their time spent social (Food: $W_{2,51}$ = 6.13, P = 0.004; Control: $W_{2,51}$ = 0.49, P = 0.61, Fig. 1).

Ephemeral resource effects on sociality

Ephemeral food patch availability made the fish groups substantially more social (Treatment*Session: $\chi 2 = 55.65$, $P < 0.001$; Table S1 & S2, Fig. 1). The average proportion of time spent socially by fish groups rose twofold, from 0.22 (S0: 95% CI = 0.18-0.26) to 0.46 (S1: 95% CI= 0.39-0.53) and 0.48 (S2: 95% CI = 0.40-0.57). Across the three control sessions, the social time remained relatively constant, at 0.26 (S0: 95% CI = 0.22-0.31), 0.23 (S1: 95% CI= 0.19-0.27) and 0.25 (S2: 95% CI = 0.21-0.29), respectively. An increase in sociality following food patch availability 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

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motivated fish groups, i.e., groups in which a larger proportion of individuals fed when they were present at a food patch, showed a stronger social increase than less motivated groups (Treatment*Foraging motivation: $\chi2 = 9.53$, $P = 0.002$, Table S1). Increase in sociality following ephemeral food patch availability resulted from fish both decreasing their overall 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). Both females and males became more social in response to ephemeral food patch availability (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 morning after (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).

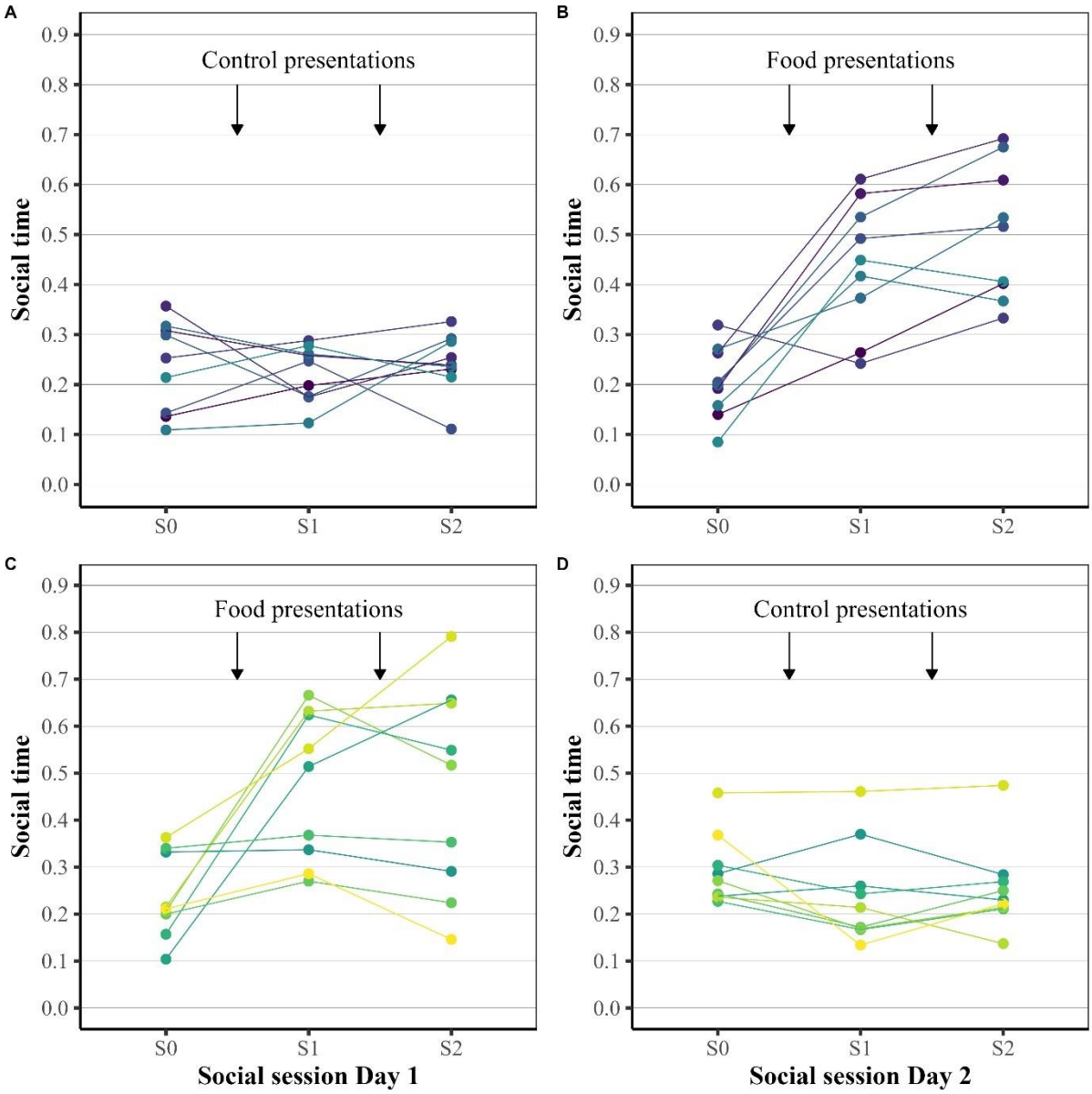

Figure 1. Time spent socially by 18 groups of wild guppies before, between, and after two series of repeated food patch or control patch presentations at five fixed locations per pool. The timing of the presentations is indicated by arrows. A) Groups that received the control treatment on the first day received B) the food treatment on the second day. C) Groups that received the food treatment on the first day received D) the control treatment on the second day. The social time values at the first social observation session (S0) of the

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second day visualizes the prolonged effects of exposure to ephemeral food availability on group-level social time. Different colours depict group ID's.

Change in sociality and individual foraging success

Change in group-level sociality positively correlated with food patch arrival for individuals from motivated groups (Social change*Foraging motivation: $\chi2 = 4.81$, $P = 0.03$; Table S7; Fig. 2). This relationship between the arrival of individuals at detected 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 benefitted from more feeding events (Females: $r_s = 0.94$, N = 69, $P < 0.001$; Males: $r_s = 0.90$, N = 71, $P < 0.001$). The degree to which groups changed in sociality related negatively to the social time before the first food patches were available (S0: $r_s = -0.54$, N = 18, P = 0.02) and positively to the social time after the first availability (S1: $r_s = 0.88$, N = 18, $P < 0.001$). Social time at S0 and S1 could independently explain the arrival of fish at food patches as good as social change (Delta AICc < 2).

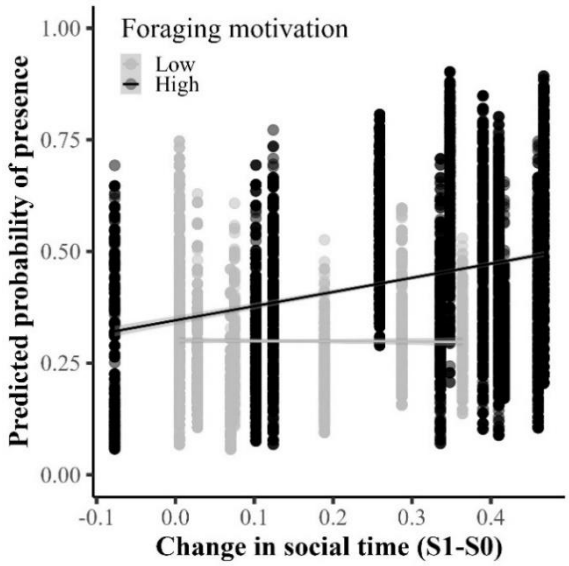

Figure 2. Predicted probability of an individual arriving at a detected food patch in relation to the change in time spent socially by an individual's group following the first series of ephemeral food patch presentations. Predictions were retrieved from the final model for individual presence or absence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

No carry-over effects

The increase in group-level sociality during the food treatment was not a simple consequence of food-induced local aggregation. Social contacts after food presentations were not more likely to take place in the spatial zone of the most recent food patch presentation compared to the same zone before any food patch became available (Table S8). Individuals were also not more social if they were more quickly observed after the first food presentations (S1: Kendall's correlation coefficient = 0.03, P = 0.37; Fig. S1), although they were after the second (S2: Kendall's correlation coefficient = 0.15, P = 0.01; Fig. S2).

Ephemeral resource effects on sexual behaviours

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Corresponding with the increase in group-level sociality, males performed more display and harassment behaviours after the first availability of ephemeral food patches (Treatment*Session: $\chi2 = 22.94$, $P < 0.001$; Table S9) and, consequently, females received more of such sexual behaviours (Treatment*Session: $\chi2 = 6.92$, $P = 0.03$; Table S10). Males also displayed and harassed more frequently in the morning after food patch availability, compared to after control (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 patch arrival better (Table S11-S12) than the increase in sexual behaviours (Sexual behaviour Males: Delta AICc = 6.12; Females: Delta Delta AICc = 3.59).

Discussion

With our experimental field study, we showed that groups of wild guppies consistently differed in sociality under baseline conditions, yet rapidly, substantially, and prolongedly responded to ephemeral resource availability with an increase in sociality. In motivated groups, this increase in sociality positively correlated to individual foraging success for both sexes.

Ephemeral resource availability doubled the social time of wild guppy groups. This increase was not a simple reflection of resource-induced local aggregation. Rather the increase in social time was present independent of the location of the last detected resource and after the resources were no longer available. Interestingly, previous manipulations of environment and density in the same population did not similarly alter social time with this magnitude (Wilson et al., 2015; Krause et al., 2017), emphasizing the importance of foraging context for sociality. Experimental lab studies similarly showed group-level social responses towards a change in the foraging context, albeit in a different direction than ours (Hoare et al., 2004; Jolles et al., 2018; Schaerf et al., 2017). For example, x-ray tetra's (*Pristella maxillaris*) and banded killifish (*Fundulus diaphanus*) reduced encounter frequency and group size, respectively, during exposure to food cues (Hoare et al., 2004; Schaerf et al., 2017). Given that the benefit of sociality varies between populations and species, and likely depends on factors such as the baseline level of sociality and the cost of aggressive food competition, this is not surprising. 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. However, guppies in our wild low-predation population are much less social, spending the majority of their time alone, and show very little aggression. Individuals in such systems, i.e., non-aggressive fission-fusion or shoaling rather than schooling populations, may thus do better by increasing sociality, rather than reducing, and so increase exposure to social information on resources gathered by conspecifics. A population comparison would be an interesting next step.

Evidence for consistent, yet responsive, sociality has grown in recent years (Jolles et al., 2018; MacGregor & Ioannou, 2022; Planas-Sitjà et al., 2015; Schaerf et al., 2017). Our guppy groups consistently varied in sociality across control (i.e., empty) patch availability, but not across resource availability. Additionally, variation in group-level sociality remained comparable across control but increased across resource availability. We can exclude a mere effect of time or familiarity on increasing group differences in sociality (MacGregor & Ioannou, 2022), as we did not see a similar pattern during control treatments. Interestingly, groups did vary consistently across resource availability when excluding the social observations before the first series of food patch availability, i.e., the social baseline,

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suggesting a resource-induced change in which groups are generally most social. Some groups thus responded more strongly, and arguably more appropriately, than others. This appears in contrast to Jolles *et al.* (2018), who found that differences in group-structure between groups of three-spined sticklebacks remained consistent before and after resource depletion. Variation in the foraging motivation of our groups is an unlikely explanation since repeatability estimates were adjusted for motivation. Possibly, individual heterogeneity in within-group composition played a role. Individual heterogeneity can impact group functioning (Farine et al., 2015; Jolles et al., 2019) and individual foraging success (Dyer et al., 2009). Between-group differences in group composition, such as variation in the locomotion and personality types of group members can generate consistent between-group differences in cohesion, alignment, and leadership (Jolles et al., 2017, 2020). There is, however, little evidence on how group composition affects group-level responsiveness to ecologically relevant changes in the environment. And even less so in the wild. Particular compositions of (social) phenotypes may generate more adaptively responsive groups and so shape the natural selection of these phenotypes.

Social time after the first series of food patch presentations could explain patch arrival equally well as the change in social time. Given that patch discovery and food intake were highly correlated, it is therefore difficult to disentangle whether the observed increase in sociality is the result of a strategy to increase patch discovery, for example, by increasing exposure to social information on food patch locations, or the result of an increase in sexual or anti-predator behaviour following patch discovery (and thus food intake). However, change in social time better explained individual arrival at detected food patches than the change in sexual behaviours, indicating that an increase in sexual behaviours following feeding is not sufficient to explain our findings. The increase in sexual behaviour is nevertheless interesting as it illustrates how males may enjoy both survival and reproductive benefits from finding more food patches (Abrahams, 1993). Increased investment in anti-predator behaviour after feeding also seems an unlikely explanation for the increase in sociality in this low-predation population. The lack of interaction between social change and the two series of food presentations suggests that individuals were still motivated to forage during the second series of food presentations, and thus that a potential change to a more risk-averse state after the first series of presentations is improbable. To get a better insight into whether the observed change in sociality could be (partly) a strategic response to locate more ephemeral resources, future studies would ideally repeat our experiment using food cues (Hoare et al., 2004; Schaerf et al., 2017), rather than actual food. This is, however, a challenging endeavour to accomplish with fish in the wild.

Group-level responses are not necessarily the sum of individual responses (Bengston & Jandt, 2014) and groups may outperform individuals (Sasaki et al., 2013). Our experimental design to test for changes in sociality in the wild restricted our ability to additionally gather robust estimates on the individual level and thus to explore to what degree the group-level sociality change may have been an emergent property. In future research, when advancements in automated video-tracking allow the collection of robust social data on both individual and group-level for fish in the wild, it would be interesting to test whether the change in group-level sociality is a better predictor of individual foraging success than the change in individual-level sociality. And if so, whether this holds for all individuals. Individuals may differ in how much they improve in foraging success when foraging socially compared to solitary, which may drive individual differences in sociability, which in turn may be maintained through alternating selective forces in dynamic environments. Social foragers will be more vulnerable to large fluctuations in population density (Harel et al., 2017), while solitary foragers will generally experience greater variance

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in foraging success and thus be more at risk during fluctuations in resource availability (Brown, 1988; Jolles et al., 2017).

Our finding that ephemeral resource availability substantially affects the social dynamics of a wild fish population has implications for our understanding of the social impacts of purposeful or unintended supplemental feeding of wild animals in the context of eco-tourism (e.g. shark chumming), garden bird feeding and garbage and waste management. Several studies have quantified changes in the social behaviour of wildlife at provisioning sites (Hundt et al., 2022; Jacoby et al., 2021; Smulders et al., 2021), but few have studied whether social behaviour is also affect away from the resource sites (e.g., Grubb, 1987). A recent study of green turtles (*Chelonia mydas*) revealed that during touristic feeding events, turtles showed atypical aggressive behaviour (Smulders et al., 2021), while another study found partial evidence for reduced connectivity in the preference networks of tiger sharks (*Galeocerdo cuvier*) at ecotourist provisioning sites (Jacoby et al., 2021). It would be relevant to investigate whether substantial local impacts of provisioning on wildlife sociality carry over to the overall social structure and whether such carry-overs may be acceptable from a (disease) management perspective or whether changes to the provisioning protocols are desired (Snijders, Blumstein, et al., 2017; van Overveld et al., 2020). Similarly, in situations in which wildlife, such as crows, coyotes (*Canis latrans*), gulls, and rats, take advantage of unintended food provisioning (e.g., garbage), it would be fascinating to experimentally examine whether these animal populations become more social to take advantage of these ephemeral anthropogenic resources.

In summary, we show that ephemeral resource availability generates substantial changes in an otherwise consistent group-level trait. Individuals from groups that changed more, obtained fitness-relevant benefits in the form of increased foraging success. If all, or certain classes of, individuals from facultatively social populations indeed profit from being in more socially responsive and motivated groups, we may expect natural selection to favour individual traits that induce or find such groups.

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Author contributions

L.S., R.H.J.M., S.K., and J.K. designed the study. L.S., R.H.J.M., S.K., A.N.T, M.B., and J.K. collected 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. wrote the first draft of the manuscript, and all authors provided feedback.