RESEARCH ARTICLE

# Females facilitate male food patch discovery in a wild fish population

Lysanne Snijders[1,2] (iD)    |    Ralf H. J. M. Kurvers[1,3] (iD)    |    Stefan Krause[4]    |    Alan N. Tump[3]    |    Indar W. Ramnarine[5]    |    Jens Krause[1,6]

[1]Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany; [2]Department of Evolutionary Ecology, Leibniz-Institute of Zoo and Wildlife Research, Berlin, Germany; [3]Center for Adaptive Rationality, Max Planck Institute for Human Development, Berlin, Germany; [4]Department of Electrical Engineering and Computer Science, Lübeck University of Applied Sciences, Lübeck, Germany; [5]Department of Life Sciences, University of the West Indies, St Augustine, Trinidad and Tobago and [6]Faculty of Life Sciences, Humboldt-Universität zu Berlin, Berlin, Germany

**Correspondence**
Lysanne Snijders
Email: lysannesnijders@gmail.com

## Abstract

1. Responding to the information provided by others is an important foraging strategy in many species. Through social foraging, individuals can more efficiently find unpredictable resources and thereby increase their foraging success.
2. When individuals are more socially responsive to particular phenotypes than others, however, the advantage they obtain from foraging socially is likely to depend on the phenotype composition of the social environment. We tested this hypothesis by performing experimental manipulations of guppy, *Poecilia reticulata*, sex compositions in the wild.
3. Males found fewer novel food patches in the absence of females than in mixed-sex compositions, while female patch discovery did not differ regardless of the presence or absence of males.
4. We argue that these results were driven by sex-dependent mechanisms of social association: Markov chain-based fission–fusion modelling revealed that less social individuals found fewer patches and that males reduced sociality when females were absent. In contrast, females were similarly social with or without males.
5. Our findings highlight the relevance of considering how individual- and population-level traits interact in shaping the advantages of social foraging in the wild.

**KEYWORDS**

fission-fusion, foraging ecology, guppy, Markov chain analysis, *Poecilia reticulata*, sex ratio, social facilitation, social learning

## 1  |  INTRODUCTION

Social living is ubiquitous in nature and has important ecological consequences (Danchin, Giraldeau, Valone, & Wagner, 2004; Gil, Hein, Spiegel, Baskett, & Sih, 2018; Guttal & Couzin, 2010; Krause & Ruxton, 2002; Kurvers, Krause, Croft, Wilson, & Wolf, 2014). For example, when animals have incomplete information about resource distributions in their local environment, an essential foraging strategy can be to capitalize on the information of others (Dall, Giraldeau, Olsson, Mcnamara, & Stephens, 2005; Danchin et al., 2004; Galef &

Giraldeau, 2001; Giraldeau & Caraco, 2000; Hoppitt & Laland, 2013; Krause & Ruxton, 2002). Through social foraging, animals can obtain information from the cues and signals produced by the foraging behaviour of others and so increase their individual foraging success while reducing the need to sample the environment themselves. Furthermore, the mere presence of others, independent of the foraging information they provide, can result in increased foraging success (i.e. social facilitation (Zajonc, 1965)), for example by decreasing perceived predation risk (Blumstein, Fuong, & Palmer, 2017; Kelley, Morrell, Inskip, Krause, & Croft, 2011).

Many animals forage socially with conspecifics (Giraldeau & Caraco, 2000), yet individuals seldom respond to all conspecifics equally and there is ample evidence that animals preferentially associate with some conspecifics more than others (Croft et al., 2005; Formica et al., 2011; Kerth, Perony, & Schweitzer, 2011; Kurvers et al., 2014; Mourier, Vercelloni, & Planes, 2012; Shizuka et al., 2014). Such non-random social associations are expected to influence an individual's foraging success. Indeed, social associations have been shown to predict how individuals find new food patches in several species in the wild, including birds, mammals and fish (Aplin, Farine, Morand-Ferron, & Sheldon, 2012; Jones, Aplin, Devost, & Morand-Ferron, 2017; Schakner et al., 2017; Snijders, Kurvers, Krause, Ramnarine, & Krause, 2018).

Sex-biased social affinity is one of the most basic and widespread forms of preferential social association in nature and can have important fitness consequences (Cameron, Setsaas, & Linklater, 2009; Silk, Alberts, & Altmann, 2003). Next to sex-biased affinity, animals also show active sex-biased avoidance, for example, by specifically avoiding males to reduce male aggression or sexual harassment (Darden & Croft, 2008; Galezo, Krzyszczyk, & Mann, 2018; Galliard, Fitze, Ferrière, & Clobert, 2005). When individuals are indeed more socially attracted and/or responsive to one sex than the other, individual advantages of social foraging, such as increased food patch discovery, are likely to depend on the sex ratio in the local environment. Yet, studies that manipulate the sex ratio of foragers, while staying under the selective pressures of the wild, are extremely rare, especially in vertebrate systems. Due to the complexity of manipulating social composition under natural conditions, the few studies that link sex ratio to both male and female foraging dynamics in the wild are primarily correlational (e.g. Choudhury & Black, 1991; Madden, Drewe, Pearce, & Clutton-Brock, 2009; Tettamanti & Viblanc, 2014, but see Magurran & Seghers, 1994). Given that individuals in the wild self-select their social environment (e.g. Croft, Arrowsmith, et al., 2003b; Croft et al., 2005; Wilson & Dugatkin, 1997), drawing any causal inferences without experimental evidence is problematic, hampering our understanding of the social factors that shape individual foraging success in the wild.

Here, we performed a unique manipulation of the social environment using individually colour-marked wild guppies, *Poecilia reticulata*, living in the rainforest streams of Trinidad. Guppies are a well-established model to study the mechanisms underlying social foraging (Reader & Laland 2000; Day, MacDonald, Brown, Laland, & Reader, 2001; Swaney, Kendal, Capon, Brown, & Laland,

2001; Morrell et al. 2008; Dyer, Croft, Morrell, & Krause, 2009; Hasenjager & Dugatkin, 2017). Wild guppies live in a fission–fusion society with adult sex ratios fluctuating heavily in time (i.e. season) and space (Arendt, Reznick, & López-Sepulcre, 2014; McKellar, Turcotte, & Hendry, 2009; Pettersson, Ramnarine, Becher, Mahabir, & Magurran, 2004). During the dry season, wild guppies naturally form ephemeral subpopulations in temporarily isolated pools (Magurran, 2005) that allowed us to manipulate subpopulation adult sex ratios in a natural context without the risk of individuals redistributing themselves. We formed single-sex (male and female) and mixed (50:50)-sex compositions (18 in total) and introduced them to local natural pools that were unfamiliar to them. In these pools, we studied the individuals' social behaviour, which we analysed with an individual-based dynamic modelling approach using first-order Markov chain (MC) models (Krause et al., 2017; Snijders et al., 2018; Wilson et al., 2014). Subsequently, we examined the individuals' success in locating (experimentally introduced) temporarily available food patches in a relatively resource-poor environment (i.e. upstream with low-light levels (Grether, Millie, Bryant, Reznick, & Mayea, 2001)). The temporary food patches also contained carotenoids, a valuable resource, especially for male guppies (Kodric-Brown, 1989).

With this study, we provide a direct experimental test of how two basic biological factors, individual sex and sex composition, interact to shape social dynamics and affect individual foraging success in the wild. First, we tested whether sex composition affected patch discovery success in individual males and females. Second, we tested whether sex composition affected the time an individual male or female spent socially, and third, we analysed whether this time spent socially was linked to patch discovery success. Given the positive relationship between sociality and patch discovery in several socially foraging species (e.g. Aplin et al., 2012; Snijders et al., 2018), the guppies' strong preference for female association partners in both sexes and the potentially disruptive social influence of male guppies on female associations (e.g. Darden & Croft, 2008; Darden, James, Ramnarine, & Croft, 2009), we predicted males to find more and females to find fewer food patches in mixed-sex compared with single-sex compositions. Moreover, we predicted that these patterns of foraging success could indeed be explained by both males and females spending more of their time socially when (more) females are present.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

Our study took place in the Upper Turure rainforest region (10°41'8"N, 61°10'22"W) of Trinidad (11–25 March 2017). The study area was located upstream and received little sunlight, likely making guppies relatively food-limited (Grether et al., 2001). Furthermore, the area has few guppy predators present (i.e. 'low-predation'). We conducted our study in three natural pools (approximate surface area range of the pools: 3–6 m$^2$). The in- and outflow of these pools

were slightly altered by rearranging rocks and pebbles to minimize the chance of fish migration. A continuous flow (e.g. through small crevices), however, was maintained. All adult guppies originally occurring in the pools were removed.

## 2.2 | Study subjects

Adult fish from nearby pools were used as experimental subjects. After capture, fish were sexed, sized and individually marked using an established method of elastomer colouring (VIE marks) (Croft, Albanese, et al., 2003a; Croft, Krause, & James, 2004). The use of red elastomer colouring did not affect the time a male (or a female) spent socially or how it distributed its contact moments (see Tables S1a-b and Data S1 for details). We used batches of eight fish, either all-male, all-female or mixed-sex (4 males and 4 females). Fish from each batch were caught from the same area, so fish were likely to be familiar with each other. Each sex composition was replicated twice in each pool, resulting in six batches for each of the three sex compositions. We balanced the sex composition (treatment) order across pools. In total, we used 18 batches of eight fish (N = 144). After marking, fish were released in the designated study pool and left overnight to settle prior to the social phenotype observations and the subsequent day of foraging trials. Because a few fish (<4%) migrated out of the observation pool before or after the social phenotype observations (through small crevices or due to overnight flooding), we ended up with slightly varying sample sizes for the social phenotyping and foraging trials (N social = 141, N foraging = 140, N combined = 139; see Tables S2a-d for details). The fish densities in our experiments were within the natural range of our study area, albeit on the lower end of general Trinidadian guppy population densities (Reznick & Endler, 1982).

We performed all research in accordance with the law and animal ethical standards of the country in which the study was performed, Trinidad and Tobago. Specifically, our study protocol adhered to 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 Committee on Research Ethics. All fish were released at the end of their trials.

## 2.3 | Social phenotypes

To quantify the social dynamics, we performed focal follow observations the day before, and thus independent of, the foraging trials. Between 09:00 and 15:00, each fish was followed for two min while recording its two nearest neighbours every 10 s. A fish was considered a neighbour if it was within four body lengths of the focal fish (Krause et al., 2017; Wilson et al., 2014), using a fixed distance based on the mean adult body length in this population (2016 = 21 mm; 2017 = 22 mm). After following each fish for two min, we waited for 5 min upon which we repeated this procedure five more times, resulting in a total of 12 min of focal follows per individual fish in each batch.

## 2.4 | Foraging trials

The day following the social phenotype scoring, we carried out foraging trials during which we presented novel food sources to the guppies. As a food source, we used small lead balls (8 mm diameter) covered in a mix of gelatine and fish food (TetraPro©; Spectrum Brands Inc), including carotenoids. Throughout the manuscript, we refer to this food source as a 'food patch', because multiple individuals could forage from it simultaneously. Within each pool, we introduced the food patches in five locations. Food introduction was standardized by entering the food through narrow opaque plastic cylinders floating at the water surface (but anchored to the bottom of the pool). The cylinders were open at the top and bottom. The five feeding locations within each pool were roughly evenly distributed over the pool, with approximately 80 cm (range: 60–100 cm) between the nearest locations. Upon the start of a trial, we gently lowered the food into the pool through the plastic cylinder using a monofilament fishing line attached to a wooden rod. Once in the water, the food was kept approximately two centimetres above the bottom. Once a fish discovered the food patch, we waited for one more minute after which we removed the food patch and ended the trial. The trial also ended if the food patch was not discovered within three minutes. After finishing a trial, we waited for five minutes before starting a new trial. We presented food at each of the five locations in a randomized order. Once we completed testing at all five locations, we repeated this procedure four more times, resulting in 25 food presentations per batch (and thus 18 × 25 = 450 food presentations in total). After we finished the food presentations for a given batch, all eight fish of that batch were caught and released further downstream.

## 2.5 | Video analyses

All foraging trials were recorded with Sony Handycams (SONY HDR-PJ530E), mounted on tripods. Tripods were positioned at favourable vantage points along the shoreline of each pool. A single observer used the open-source event-logging software BORIS (Friard & Gamba, 2016) (v 4.0) to score for each fish its presence (continuously) for one minute after the arrival of the first fish. An arrival (and subsequent presence) was defined as a fish being within two body lengths of the food patch. In addition, all harassment (aggressive and sexual), displacement (aggressive) and sexual display events were scored when within two body lengths of the food patch for one minute after the arrival of the first fish. In total, only three sexual displays were made near the food patch and this behaviour was therefore not further analysed. The event-logging data were reviewed by a second observer and cross-referenced with data on discovery time and fish identity collected in the field. If mismatches occurred, trials were double-checked and, if necessary, corrected by a third observer who had also been present in the field (L.S.). In 423 of the 450 trials (94%), at least one fish discovered the food patch. However, because of recording problems (e.g. water surface glare), only a subset of the

videos was of sufficient quality for reliable identification of all the individuals present (N = 391) and a further subset for reliable quantification of aggressive and sexual behaviours (N = 383). For the latter, we calculated the total number of aggressive and sexual harassment events initiated and received by an individual at a food patch. To control for differences in opportunity, we divided these numbers by the total number of patches an individual was present.

## 2.6 | Statistical analyses

### 2.6.1 | Generalized linear mixed models

We analysed the data using generalized linear mixed models (GLMM) with R (R Core Team, 2017) version 3.5.1 in R Studio version 1.0.453 (© 2009–2018 RStudio, Inc.), using the *glmer* function in the '*lme4*' package (Bates, Maechler, Bolker, & Walker, 2015) with 'bobyqa' as an optimizer. The main response variables for these models were patch discovery (binary), the proportion of patches reached first (fraction) and the proportion of total fish present (fraction). Control variables such as body length (fixed covariate, scaled and centred on sex), individual identity nested in batch identity (random factor) and pool identity (fixed factor with three levels) were kept in the model at all times. Individual identity was used as an observation-level random effect in proportional-binomial models to effectively manage overdispersion. Binary-binomial models additionally included the trial number (fixed covariate, scaled) and location nested in pool identity (random factor). To test the significance of fixed effects, we compared models with and without the fixed effect of interest, using log-likelihood ratio (LLR) tests. Post hoc pairwise comparisons (averaged over pools) were made using the R-package '*emmeans*' (Lenth, 2018). *P*-values were adjusted following the Tukey method for comparing a family of four estimates. We based conclusions for individual social traits on permutation models (see below).

### 2.6.2 | Markov chain social analyses

To quantify the social dynamics and their potential differences between sex compositions, we used the Markov chain-based fission–fusion model introduced by Wilson et al. (2014). The social behaviour of each individual fish is described as a sequence of behavioural (social) states, being either in the presence of a specific conspecific (within four body lengths) or alone. When an individual is with a specific conspecific, it can transition to being alone, but it can also stay with this specific 'nearest' neighbour or switch to another nearest neighbour [for more details, see the Supplementary material of Wilson et al. (2014)]. The data collected during the social phenotype observations were used to estimate the transition probabilities between each state for each individual fish. The overall social propensity (i.e. social time) of a particular fish is subsequently quantified as $P_{a \to s} / (P_{s \to a} + P_{a \to s})$, where $P_{a \to s}$ is the probability of ending being alone and $P_{s \to a}$ is the probability of ending being

a social contact. To examine whether individuals exhibited a sex bias in their time spent socially, we adapted the original model to distinguish between spending time socially with a male or female as a nearest neighbour (see Data S1 for details). Additionally, we calculated the $\Upsilon$-measure to quantify the degree to which individuals express preferences for particular social partners (see Data S1 for details). The $\Upsilon$-measure is the sum of squares of the normalized association strengths (relative number of contact moments) between one individual and all others (Boccaletti, Latora, Moreno, Chavez, & Hwang, 2006; Krause et al., 2017). It was previously shown that across changes in habitat and density, guppies differed consistently in both measures (Krause et al., 2017; Wilson et al., 2015).

### 2.6.3 | Model details

*Does sex composition influence the discovery of novel patches?*
To test our main prediction – that males find more and females find fewer food patches in mixed-sex batches compared with single-sex batches – we tested whether the interaction between sex and sex composition had a significant effect on individual patch discovery. We quantified individual patch discovery (dependent variable) as binary (yes/no; only including videos of sufficient quality for reliably identifying each individual as present or absent; N = 391). The binary-binomial model included the interaction between sex (male or female) and sex composition (mixed-sex or single-sex) as well as the above-mentioned control variables.

We constructed a proportional-binomial model to test whether males and females in mixed-sex batches differed in their likelihood of arriving first at a food patch. As the dependent variable, we quantified the number of patches an individual reached first, divided by the total number of patches reached by its batch (i.e. a fraction variable). The model included sex as a fixed factor and the above-mentioned control factors.

*Does sex composition influence social time?*
To test whether males and females differed in their time spent socially depending on sex composition, we used two approaches: a group comparison approach between compositions and a randomization approach within mixed-sex compositions. To test differences in time spent socially between males and females within mixed compositions, we permuted (10,000 repetitions) the (highly dependent) social times among males and females within each batch. As the test statistic, we used the absolute value of the difference in the mean social times between males and females. However, for the comparison of social times of male-only and female-only groups, it is problematic to randomize because it would involve permutations across groups, mixing up the values of dependent and independent variables. Therefore, we computed the overall social times per batch, which are independent, and used a Wilcoxon rank-sum test to compare the values for the female single-sex compositions with those for the male single-sex compositions. The same procedure was applied to the comparison of males/

females in mixed-sex compositions and males/females in single-sex compositions. Furthermore, we analysed the relationship between social time and body length, by permuting the individual social times within each batch and using Pearson's correlation coefficient between social time and body length as the test statistic (10,000 repetitions).

*Does social time predict novel patch discovery?*

To examine whether variation in individual patch discovery between the four combinations of sex (male, female) and sex composition (single-sex, mixed-sex) could be explained by the corresponding variation in social time, we replaced the factors sex and sex composition with the covariate social time in the binary-binomial model for patch discovery. Significance of social time was evaluated via a randomization procedure (see Data S1 for details). We repeated these randomizations 10,000 times and each time calculated the coefficient for social time. We then compared the original model coefficient for social time to the distribution of the coefficients of the permutated models (Farine & Whitehead, 2015). Social time and body size were significantly positively correlated in all sex compositions, that is larger fish were more social (female-only: *coefficient* = 0.48; *p* = .001, *N* = 47; male-only: *coefficient* = 0.24; *p* = .02, *N* = 48; mixed-sex: *coefficient* = 0.33; *p* = .03, *N* = 47), yet we found no collinearity issues (all generalized variance inflation factors < 2) and therefore left both social time and body size in the models for patch discovery. Conclusions did not change (effects only became stronger) when we omitted body size or replaced it by the residuals of body size over social time.

*Is there evidence for sex-specific attraction and aggression as potential mechanisms?*

To test whether males and females exhibited a sex preference in their social time, we calculated for each mixed-sex batch the percentages of time spent socially (based on our Markov model), distinguishing between sex of the focal individual and sex of the social partner. These observed percentages were then compared to percentages based on 10,000 permutations, swapping the identities of social partners. Furthermore, to test for sex-specific attraction during the foraging trials, we tested for mixed-sex compositions whether the sex of the first fish at a food patch predicted the proportion of batch members that would subsequently join. The proportional-binomial model included, for each of the detected trials, the number of fish present divided by the number of subjects in the batch as the (fraction-based) dependent variable and included sex of the first fish and the before-mentioned control variables as fixed effects. To investigate potential differences in responses between female and male 'followers', we ran the same model including only potential (i.e. available) male followers or only potential female followers.

To evaluate the potential role of competitive exclusion, we tested whether the number of aggressive events initiated or received by an individual per visited food patch was correlated to the total proportion of patches visited by this individual, using a Spearman correlation test.

# 3 | RESULTS

## 3.1 | Males reach fewer novel patches in the absence of females

Male-, female- and mixed-sex compositions were very similar in food patch discovery success at a group level, that is the proportion of temporarily available patches discovered by at least one individual (Total% [Range]): all-male (*N* = 6): 93% (84–100), all-female (*N* = 6): 94% (72–100) and mixed (*N* = 6): 95% (88–100). On an individual level, however, fish differed in how likely they were to reach a novel food patch, depending on the combination of their own sex and the sex composition of their social environment (sex*sex composition: Estimate (Est) ± *SE* = −0.80 ± 0.24, $\chi^2$ = 10.95, *N* = 3,246, *N* individuals = 140, *p* = .0009). Males in mixed compositions were more likely than males in single-sex compositions to reach a new food patch (odds ratio ± *SE* = 1.72 ± 0.29, *z*-ratio = 3.24, *p* = .007, Figure 1), but females in mixed compositions did not differ from females in single-sex compositions (odds ratio ± *SE* = 0.78 ± 0.13, *z*-ratio = −1.52, *p* = .42, Figure 1). Males and females within mixed compositions were equally likely to reach a new food patch (odds ratio ± *SE* = 0.76 ± 0.14, *z*-ratio = 1.46, *p* = .46, Figure 1), while in
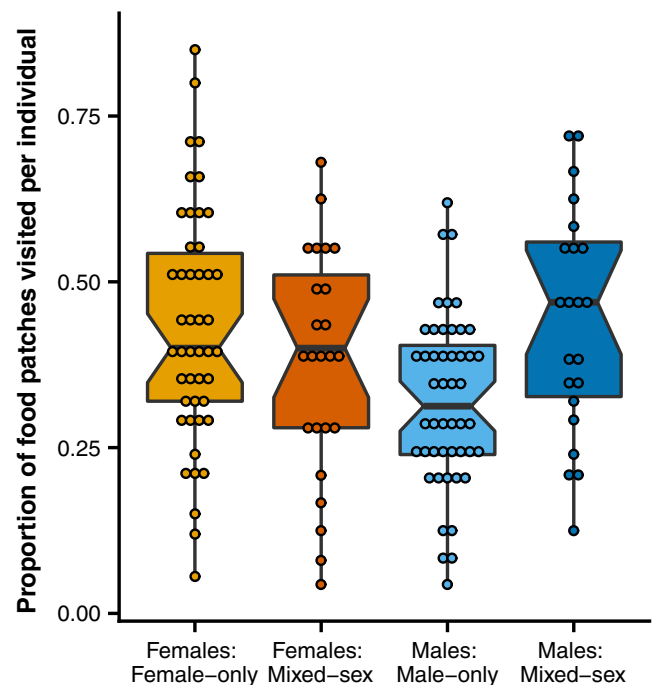


**FIGURE 1** The proportion of novel food patches visited by individual males and females in response to sex composition. Males in single-sex compositions reached fewer food patches than males in mixed-sex compositions, but females in single-sex compositions did not differ from females in mixed-sex compositions. Females in single-sex compositions reached more patches than males in single-sex compositions, yet males and females within mixed-sex compositions did not differ from each other. Box plots show median and 25th to 75th percentiles with whiskers of 1.5 interquartile distances. Non-overlapping notches suggest a significant difference in medians

single-sex compositions females reached more food patches than males (odds ratio ± SE = 1.68 ± 0.23, z-ratio = 3.75, p = .001, Figure 1). Individuals were more likely to reach a new food patch over time (i.e. trial number: Est ± SE = 0.15 ± 0.04, $\chi^2$ = 16.21, N = 3,246, N individuals = 140, p < .0001). Body size (centred on sex) did not predict the likelihood of reaching a patch (Est ± SE = 0.10 ± 0.06, $\chi^2$ = 2.83, N = 3,246, N individuals = 140, p = .09).

Importantly, individual males and females in mixed compositions did not differ in the proportion of detected patches at which they were the first to arrive (Est ± SE = −0.16 ± 0.24, $\chi^2$ = 0.43, N = 46, p = .51), suggesting that males and females did not differ in their skills to initially detect a food patch (i.e. without social information).

## 3.2 | Males are less social in the absence of females

The differences between sex and sex compositions in novel food patch discovery (Figure 1) closely mirrored differences in individual social time, that is the propensity of individuals to spend time near conspecifics before the foraging trials (Figure 2). Males in single-sex compositions spent substantially less time socially (mean = 14%, Table S3) than males in mixed-sex compositions
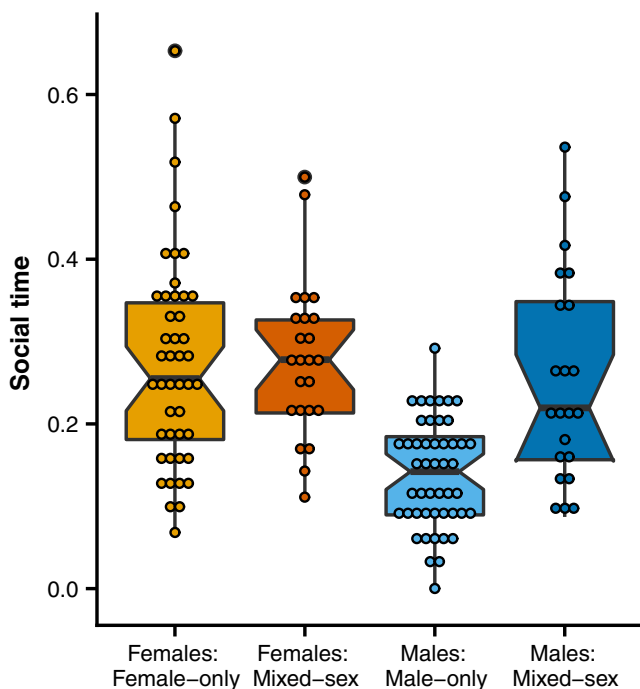


**FIGURE 2** Time spent socially by individual males and females in response to sex composition. A higher social time value indicates a stronger propensity to spend time in the proximity of conspecifics (before the foraging trials). Males in single-sex compositions spent less time socially than males in mixed-sex compositions or females in single-sex compositions. Within mixed-sex treatments, males and females did not differ. Females in mixed-sex compositions and females in single-sex compositions also did not differ in the time they spent socially. Box plots show median and 25th to 75th percentiles with whiskers of 1.5 interquartile distances. Non-overlapping notches suggest a significant difference in medians

(mean = 26%, W = 34, p = .009, N = 12 groups, Figure 2, Table S3) and females in single-sex compositions (mean = 27%, Wilcoxon rank-sum test, W = 35, p = .004, N = 12 groups, Figure 2, Table S3). The social times of individual females in single-sex compositions and in mixed-sex compositions did not differ (Mean = 28%, W = 19, p = .94, N = 12 groups, Figure 2, Table S3). Within mixed compositions, there was no difference between males and females in the time they spent socially (10,000 randomization steps, score = 0.022; p = .47, N = 47 individuals, Figure 2) nor in how they distributed their social contact moments over social partners, that is the $\Upsilon$-measure (10,000 randomization steps, score = 0.004; p = .62, N = 47 individuals). When comparing the underlying social dynamics (i.e. transition probabilities) between the different sex and sex compositions, we found that males in single-sex compositions had a higher likelihood of leaving their nearest neighbour, a higher probability of transitioning from a social state to being alone and a lower probability of transitioning from being alone to being social, compared with individuals in the other sex compositions (Figure 3, Table S3).

## 3.3 | Individuals that are more social reach more novel patches

Differences in individual social time between sex compositions are highly relevant because social time positively predicted the proportion of novel food patches an individual would reach (10,000 randomization steps, coefficient = 0.22, N = 3,344, N individuals = 144, p = .0009, Figure 4; Table S4, Figure S1). There was also an overall tendency for individuals to reach more novel food patches when they spread their contact moments more evenly over social partners (i.e. smaller $\Upsilon$-measure; Table S5).

## 3.4 | Partial evidence for sex-biased attraction

Surprisingly, neither males nor females in mixed-sex compositions were more likely than chance to have a female as a social partner (Table S6). This suggests that males increase social contact with both sexes when females are present (Figure 2). Male–male associations showed a higher probability of ending (leaving the nearest neighbour) compared with female–female associations (Table S7). However, male–female (or female–female) association probabilities overlapped with both male–male and female–female probabilities (Table S7). A similar trend was visible for the probability of individuals to transition from a social state to being alone, but not vice versa (Table S7). Finally, the observed number of contact moments between males and females in mixed-sex compositions did not differ from what would be expected in the absence of a sex bias.

During the foraging trials, sex biases in social attraction were more apparent. In mixed compositions, a larger proportion of fish joined at a novel food patch if the first individual to arrive was a female compared with a male (Est ± SE = 0.60 ± 0.27, $\chi^2$ = 4.95, N = 138, N individuals = 42, p = .03). Specifically, a larger proportion
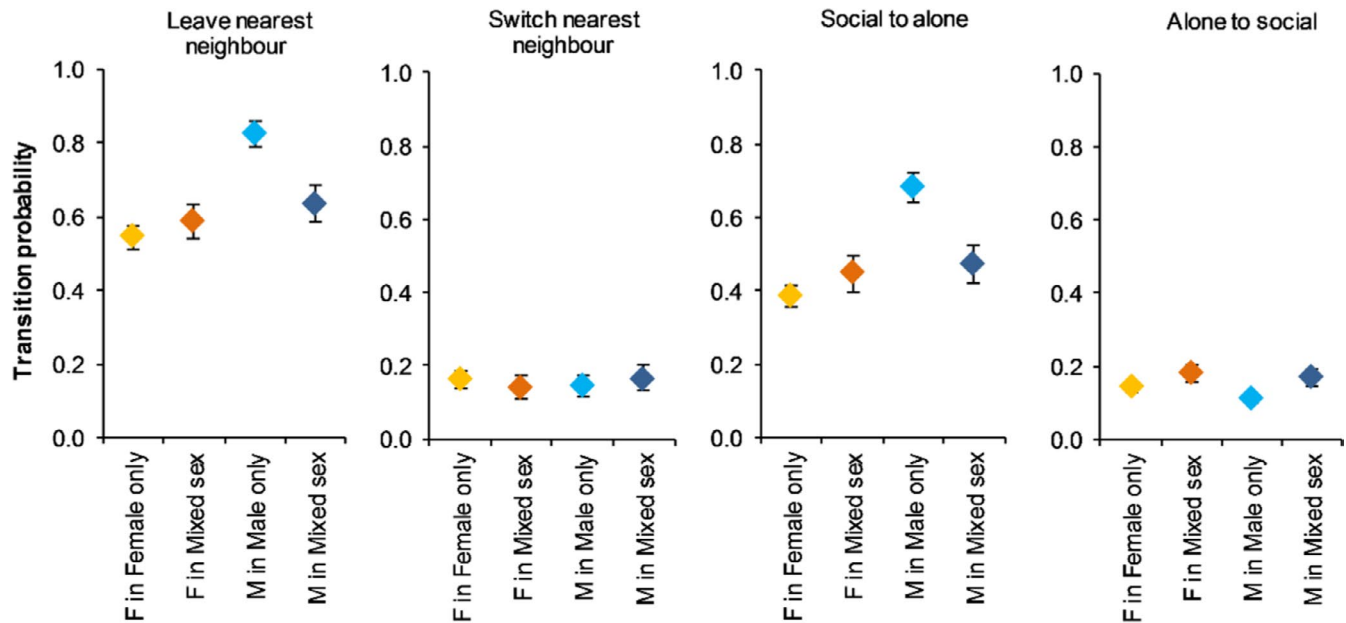
**FIGURE 3** Markov Chain transition probabilities between social and solitary states of individuals in relation to sex composition. Males in male-only compositions (light blue) were more likely to leave their nearest neighbour, more likely to switch from a social state to being alone and less likely to transition from being alone to a social state, than fish in other compositions. There were no differences between sex compositions in the transition probability to switch the nearest neighbour. Error bars represent 95% confidence intervals

of the males joined (Est ± $SE$ = 0.64 ± 0.26, $\chi^2$ = 5.85, $N$ = 138, $p$ = .04), whereas females did not discriminate based on the sex of the first fish at a novel patch (Est ± $SE$ = 0.29 ± 0.24, $\chi^2$ = 1.48, $N$ = 138, $p$ = .22). Individual males made, on average, 0.23 ($SD$ = 0.24) female-directed harassment attempts per visited food patch. Body size of the first fish did not influence the proportion of batch members joining at a food patch (Est ± $SE$ = 0.07 ± 0.09, $\chi^2$ = 0.51, $N$ = 138, $N$ individuals = 42, $p$ = .47).

## 3.5 | Limited evidence for competitive exclusion

Merely 50% or less of the males in either sex composition ever initiated or received aggression near the food patch (single-sex: initiated = 31%, received = 44%; mixed-sex: initiated = 36%, received = 50%). Females initiated aggression only in four events (and exclusively to males) and never received aggression from other females. Individual males in single-sex compositions initiated and received more aggression per visited patch (mean ± $SD$ = 0.34 ± 0.66 and 0.45 ± 0.55, respectively) compared with males in mixed-sex compositions (mean ± $SD$ = 0.05 ± 0.08 and 0.07 ± 0.09, respectively). However, males in single-sex compositions that received more aggression per visited patch did not reach fewer food patches ($r_s$ = −0.04, $N$ = 48, $p$ = .80), suggesting that aggression did not substantially hamper patch discovery. In contrast, the initiation of aggressive events per patch was positively correlated with the proportion of patches reached ($r_s$ = 0.37, $N$ = 48, $p$ = .01). There was no relationship between the number of aggressive events initiated and received ($r_s$ = −0.11, $N$ = 48, $p$ = .45).

## 4 | DISCUSSION

Despite great research interest into the mechanisms underlying social foraging, few studies to date have directly manipulated the social environment of foragers in the wild. By experimentally manipulating the sex composition, we show that sex composition can be a relevant determinant of individual foraging success in a wild fish population. Male guppies reached more novel food patches when foraging with females, while female guppies, against our expectations, experienced similar foraging success with or without males. Our study provides unique experimental evidence from the wild on how individual-level traits can interact with population-level traits to shape social foraging success for individuals.

Finding novel resources is key for animals foraging in dynamic environments, such as tropical rainforests. Individuals can improve the detection of new resources via specialized behaviours, such as increased sensitivity to specific environmental cues (Dahmani et al., 2018) or specific movement or search strategies (Humphries, Weimerskirch, Queiroz, Southall, & Sims, 2012). Such strategies might vary among individuals and between sexes (Croft, Albanese, et al., 2003a). Correspondingly, within several species, individuals were shown to differ in their likelihood of being a producer (e.g. initial detector of a resource) versus scrounger (Aplin & Morand-Ferron, 2017; Barnard & Sibly, 1981; Harten et al., 2018; Kurvers et al., 2010). Sex differences in producer–scrounger strategies, however, are unlikely to explain our findings since males and females were equally successful in initially detecting the food patches (i.e. being the first), both at the group and at the individual level. Also, in a previous study comprising of only mixed-sex compositions, we
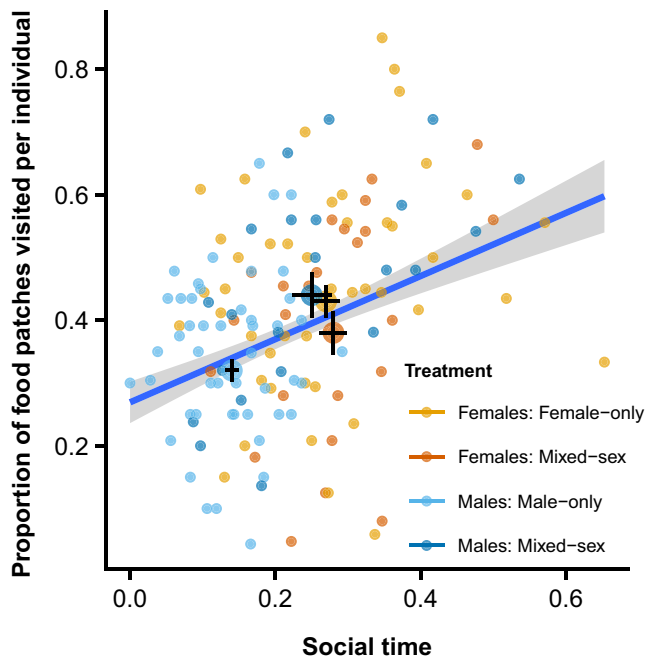
**FIGURE 4** The proportion of novel food patches visited by individuals in response to the time they spent socially. A higher social time value indicates a stronger propensity to spend time in the proximity of conspecifics (before the foraging trials). Fish that spend more of their time socially find more novel food patches. Larger dots with horizontal and vertical bars indicate observed treatment group means ± 1 *SE*. Regression line and *95% CI* (shaded area) are based on fitted model values

found no evidence for consistent individual differences in guppy producer–scrounger ratios (Snijders et al., 2018). Instead, we here provide multiple lines of evidence that suggest that the effects of sex composition on individual patch discovery were modulated by composition-dependent changes in social dynamics.

We demonstrated that sex composition affects how much time individuals spent near conspecifics, but this effect was, in turn, sex-specific, with males, but not females, varying in their time spent socially, depending on the presence or absence of the other sex. There are several, non-mutually exclusive mechanisms to explain these findings. Males might have become more social in the presence of females in an effort to solicit mating opportunities, as suggested by the sexual harassment attempts made by males at the food patches when in mixed-sex compositions. Consequently, males might have ended up at food patches primarily motivated by the mere presence of female conspecifics (i.e. local enhancement (Reader, Kendal, & Laland, 2003; Webster & Laland, 2013)). Additionally, males in single-sex compositions experienced higher levels of aggression (Magurran & Seghers, 1991), which may have caused them to spent less time socially (i.e. avoidance of dominant males) and reach fewer patches (i.e. competitive exclusion), compared with mixed-sex compositions. Although initiating aggression was positively correlated with the number of patches reached, we did not find evidence that receiving aggression hampered males in

reaching food patches. Aggressive events, however, were quantified when individuals had already reached a patch. To further elucidate the role of competitive exclusion as a potential mechanism for patch discovery, future studies should also quantify aggressive events further away from the food patch. Regardless of the exact mechanism, our study shows that sex composition can impact foraging success of males in the wild, complementing the very few studies that manipulated sex composition in the field, but that primarily focussed on consequences for females (e.g. Magurran & Seghers, 1994).

There are several sex-independent mechanisms through which spending more time socially can increase an individual's chances of finding food, ranging from social facilitation to information sharing (Giraldeau & Caraco, 2000). For example, spending time near conspecifics likely results in greater exposure to social information (Danchin et al., 2004; Duboscq, Romano, MacIntosh, & Sueur, 2016). Interestingly, our data suggest that male guppies increased time spent with conspecifics of both sexes when in mixed compositions. This change in social connectivity could have led to greater access to social information since animals can be flexible in the sources of social information they use (Firth, Sheldon, & Farine, 2016). There is a wide variety of species, including tit species (Family: *Paridae*), humpback whales (*Megaptera novaeangliae*) and California sea lions (*Zalophus californianus*), in which social connections predict how novel (foraging) information 'flows' through a population (Allen, Weinrich, Hoppitt, & Rendell, 2013; Aplin et al., 2012; Schakner et al., 2017). Though it is important to note that such correlations do not necessarily reflect active information transfer, as they could result from individuals regularly being at the same place at the same time (Atton, Hoppitt, Webster, Galef, & Laland, 2012; Hasenjager & Dugatkin, 2016) or individuals being socially assorted by traits that are linked to the probability of asocial learning, for example personality (Croft et al., 2009). Alternatively, being more social might be linked to increased social responsiveness (Kurvers et al., 2014; Wolf & Krause, 2014), including responsiveness to social foraging cues (Webster & Laland, 2011). Future experimental studies manipulating social foraging cues and monitoring the responses of individuals with various levels of 'social time' will be necessary to reveal whether social responsiveness (or social 'awareness') is an underlying mechanism of increased foraging success.

Against our expectations, females did not show a reduction in patch discovery in the company of males. This was surprising because we expected females to be less social in the presence of males (see Wilson et al., 2015) to reduce sexual harassment (Croft et al., 2006; Darden et al., 2009), consequently finding fewer patches. Yet, females in a mixed composition were not less social compared with females in a single-sex composition. In a previous study, female guppies actively preferred areas with lower male presence even if these areas were associated with higher predation risk (Darden & Croft, 2008). Yet, in our study females did not show a distinct preference for socializing with other females over males nor were they more likely to follow a first female over a first male at a food patch. Possibly, foraging

females in resource-limited habitats, like our study site, are more tolerant towards males, also because males, in such habitats, may spend relatively more time foraging and less time harassing females. Indeed, male guppies are known to prioritize foraging over courting when they are hungry (Abrahams, 1993) and were shown to spend relatively more time foraging and less time courting when they originated from resource-poor environments (Kolluru & Grether, 2005). The relatively low rate of sexual harassment exhibited by males near food patches (0.44 harassment events per discovered patch in mixed-sex compositions) supports this hypothesis. Resource-limited habitats may thus both enhance the need for social foraging as well as its effectiveness by increasing social tolerance between the sexes. A cross-population (cross-habitat) experiment would be an exciting next step to test this prediction.

In conclusion, we experimentally demonstrated how the interaction between sex and sex composition can influence social foraging success in the wild. Emphasis of future research should be on quantifying the varying trade-offs in social foraging for males and females under different environmental scenarios in the wild, for example by varying the levels of resource abundance, resource predictability and predation risk. Indeed, the Trinidadian guppy study system would allow ecologists to manipulate such key environmental factors and thus to more thoroughly understand the driving forces of foraging success in the wild.

## AUTHORS' CONTRIBUTIONS

L.S., R.H.J.M., SK, A.N.T and JK designed the study and collected the data; L.S. and S.K. analysed the data; 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 contributed substantially to revisions.

## DATA AVAILABILITY STATEMENT

The data supporting the results are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.rf951h1 (Snijders et al., 2019).

## CONFLICT OF INTERESTS

The authors declare no competing interests.

## ORCID

*Lysanne Snijders* https://orcid.org/0000-0003-0911-3418
*Ralf H. J. M. Kurvers* https://orcid.org/0000-0002-3460-0392

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## SUPPORTING INFORMATION

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